Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 115, No. 6

REVISION OF THE AFRICAN TORTOISES AND TURTLES OF THE SUBORDER CRYPTODIRA

By Arthur Loveridge and Ernest E. Williams

With Eighteen Plates

CAMBRIDGE, MASS., U.S.A.
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No. 6 — *Revision of the African Tortoises and Turtles of the Suborder Cryptodira*

By Arthur Loveridge and Ernest E. Williams[1]

CONTENTS

INTRODUCTION

The last comprehensive treatises to embrace all African testudinates were the "Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum," by G. A. Boulenger (1889a), and "Synopsis der rezenten Schildkröten mit Berücksichtigung der in historischer Zeit ausgestorbenen Arten," by F. Siebenrock (1909a).[2] The present contribution is an attempt to bring our knowledge up to date by summarizing all the available information of importance regarding African Cryptodira. This completes the coverage of African Testudinata, as the Pleurodira have already been dealt with by one of us.[3]

Material. We have collaborated in completely rewriting detailed descriptions of the external characteristics of each of the

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[1] These names are listed alphabetically, or according to the authors' respective antiquity, without further significance. The entire osteological and paleontological accounts, all major discussions, and the selection of illustrations are the work of my industrious colleague, Dr. E. E. Williams, whose unrivalled knowledge of the Testudinata is well known. Without his erudition and drive, it is safe to say that this monograph would never have been completed in so comprehensive a form. A.L.

[2] Though published on October 31, 1955, the checklist of the turtles of the world by Drs. Mertens and Wermuth, unfortunately did not reach us until the manuscript of this paper had been submitted for publication. It was thus too late for citation under genera and species and should be consulted for the numerous differences.

[3] Loveridge, A., 1941, Bull. Mus. Comp. Zool., **88:** 465-524. One of a series of revisionary studies of various families of African reptiles published between 1939 and 1947.

32 species or forms here recognized. In doing so we have been fortunate in having available in the Museum of Comparative Zoology African material of all 32 forms with the exception of one marine species, together with many paratypical or topotypical examples of them or their synonyms.

In order to examine other types, and in search of additional information, one of us (E. E. W.), as a Guggenheim Fellow, spent many months studying testudinates in most of the principal museums of Europe (Leiden; London; Munich; Paris; Frankfurt-am-Main) and eastern North America (Chicago; New York; Philadelphia; Washington). Upon his return, the curators of all these and many other institutions generously loaned for further comparative study much critical material — often of a bulky or fragile nature necessitating careful packing.

When such loaned material is referred to, we have indicated the institution by one of the following abbreviations:

A.M.N.H., American Museum of Natural History, New York.
B.M., British Museum (Natural History), London.
C.M., Carnegie Museum, Pittsburgh.
C.N.H.M., Chicago Natural History Museum, Chicago.
G.M., Museum d'Histoire naturelle, Geneva.
H. M., Zoologisches Museum, Hamburg.
I.F.A.N., Institut Français d'Afrique Noire, Dakar.
L.M., Rijksmuseum van Natuurlijke Historie, Leiden.
M.M., Zoologische Sammlung des Bayerischen Staates, Munich.
P.M., Museum National d'Histoire naturelle, Paris.
N.R., Naturhistoriska Riksmuseum, Stockholm.
S.M., Senckenbergische Naturforschende Gesellschaft, Frankfurt a. M.
T.M., Transvaal Museum, Pretoria.
U.S.N.M., United States National Museum, Washington.
V.M., Naturhistorisches Museum, Vienna.
W.M., Naturwissenschaftliche Sammlung, Neues Museum, Wiesbaden.
Y.P.M., Yale Peabody Museum, New Haven, Connecticut.
Z.M.U., Zoologisches Museum der Universität, Berlin.

Acknowledgements. We herewith welcome this opportunity to express our appreciation for the coöperation of colleagues both here and abroad, especially of those who, with unfailing courtesy, have answered endless questions of a seemingly trivial nature that involved careful examinations of specimens in their charge. We have made exceptionally heavy demands on the

British and Transvaal Museums, whose collections of African Cryptodira are particularly rich.

For lending specimens and/or answering queries we desire to express our grateful thanks to:

V. Aellen (Geneva Museum)
J. C. Battersby (British Museum)
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D. M. Cochran (United States National Museum)
J. Eiselt (Vienna Museum)
V. F. FitzSimons (Transvaal Museum)
J. T. Gregory (Peabody Museum, Yale)
J. Guibé (Paris Museum)
F. Heineck (Wiesbaden Museum)
W. Hellmich (Munich Museum)
A. C. Hoffman (Bloemfontein Museum)
R. F. Inger (Chicago Museum)
W. Lanz (Geneva Museum)
R. F. Lawrence (Natal Museum)
M. E. Malan (Stellenbosch University)
R. Mertens (Senckenberg Museum)
B. L. Mitchell (Nyasaland Tsetse Control)
E. Mohr (Hamburg Museum)
C. F. Moysey (Devonshire, England)
F. Neubar (Wiesbaden Museum)
H. W. Parker (British Museum)
J. A. Peters (Brown University)
N. B. Richmond (Carnegie Museum, Pittsburgh)
H. Rendahl (Swedish Museum)
C. A. du Toit (Stellenbosch University)
A. Villiers (I.F.A.N. Museum, Dakar)
H. Wermuth (Zoologische Museum, Berlin)
J. G. Williams (Coryndon Museum, Nairobi)
G. F. de Witte (I.R.S.N. de Belgique)

We also wish to express our appreciation to Mr. Thomas Andersen of Kidugallo, Tanganyika Territory, for endeavoring to obtain for us certain specimens of *Malacochersus;* to W. H. Archer of East London, South Africa, for writing us about *Geochelone;* to G. S. Cansdale of London, England, for answering questions regarding Gold Coast *Kinixys;* to C. Jacot-Guillarmod of Basutoland, respecting the occurrence in that country of *Psammobates;* to our colleague Dr. Ernst Mayr for advice on various taxonomic enigmas; to T. S. Jones, Esq., of Sierra Leone, for securing specimens that established the presence of *Kinixys b. nogueyi* in that country, and not least to J. M. Savage of University of Southern California for his kindness in reading over, and commenting on, this manuscript.

We welcome this opportunity to acknowledge our indebtedness to the following artists whose numerous drawings add much to the usefulness of this revision: Mr. S. B. McDowell of New York, Miss E. R. Turlington of London, Miss P. M. Washer of the Museum of Comparative Zoology. We are also grateful to Messrs. Peter Green of London, England, and Frank White of Cambridge, Massachusetts, for their photographic achievements, and to the Trustees of the British Museum (Natural History) for permission to reproduce various photographs of specimens in that institution.

Taxonomy. Though, as a result of collaboration, the scope of this revision is greater than that of its predecessors, changes in nomenclature are remarkably few, for we have endeavored to maintain a conservative attitude throughout. The only fresh names proposed are: *Aldabrachelys,* new subgenus for the giant tortoises of Aldabra, etc., *Pseudotestudo,* new subgenus for the dwarf tortoise of Egypt and Libya. No new species or races have been erected, though in certain instances (*Malacochersus, Cycloderma*) the possibility of their existence has been noted.

At the specific and infraspecific level emphasis has been rather on the suppression of names, never lightly or on theoretical grounds, but only after a careful examination of the available material failed to support their claims to specific or racial distinction. In some cases (such as *Kinixys belliana*) the accumulation of additional tortoises may produce valid reasons for the revival of forms we have not recognized. But to sustain these names will require more comprehensive and careful studies than those on the basis of which they were proposed. It cannot be too strongly emphasized that testudinates should never be described on single characters and but rarely on a single specimen. Conclusions based on series that are limited to less than ten individuals should be viewed with suspicion, for it is highly probable that the apparently constant characters displayed by so small a sample will prove to be unstable when a larger series is available.

The status of one species, *Cyclanorbis elegans* Gray, founded on a juvenile, has been clarified by synonymizing with it *oligotylus* Siebenrock, founded upon an adult.

At the generic level the changes recommended,[1] though not minor, are infrequent. Thus, after a careful survey which included consideration of extra-limital forms, we have concurred with present South African usage in recognizing the large tortoises of Africa as generically separable from *Testudo, sensu stricto,* as are also the members of the *geometricus* group and *angulata* (for details cf. pp. 218ff). Another change in the concept of a genus has necessitated our removing the North American pond-turtle species *blandingii* to the genus *Emydoidea,* retaining in *Emys* only the species *orbicularis* of Europe and Africa.

At every point in our taxonomic study we have been faced with the fact that in *all* characters the amount of variation exhibited by members of this order is frequently astonishing and always disconcerting. In our descriptions of external characters we have endeavored to record every major variation encountered. The number of such observed variations, it should be noted, is apt to bear a direct ratio to the number of specimens studied. Thus, where relatively large series were available to us, as in the case of *Geochelone p. babcocki, Malacochersus tornieri* or *Kinixys b. belliana,* our earlier crude observations were constantly subjected to qualifying comment. If we have used such words as ''always'' or ''never'' anywhere in the descriptions, it has been in a moment of unguarded enthusiasm.

This high degree of variability extends to osteology also. There are no grounds for assuming that internal characters are more constant than external ones. The only certain test of stability for both is the empirical one of examining a large series. Here a practical difficulty arises, as series of skeletons are rarely available. Since, with good reason, generic definitions are largely

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[1] See also footnote on p. 220.

based on osteological characters, the lack of skeletal series has been a real handicap.

In this predicament our method has been to rely upon determination of the range of variation in a test species, *Geochelone pardalis babcocki,* for which numbers of skulls and skeletons were available. Whatever species, judged by even a few specimens, lay wholly outside the variation of this form in several major skeletal characters (e.g. maxillary ridging, pygal number, neural shape, etc.) could, we felt, be safely regarded as only remotely related and hence possibly generically distinct. However, we have not been content with this estimate of morphological distance only, but wherever possible have endeavored to trace lineages in the fossil record. We have accepted paleontological evidence as constituting additional osteological material, and where the separation of lineages proved to be of great antiquity — as, for example, going back to the Eocene — accepted it also as modest warranty of generic distinction.

While availing ourselves of published descriptions and illustrations, our first assessment of the degree of osteological variation in any given species or genus has been based on specimens we ourselves have examined. Thus of the 27 African terrestrial or freshwater species dealt with in this study, we have seen skeletal material of all except three, viz. *Psammobates geometricus, Homopus signatus* and *H. femoralis.* Of certain other species relatively little material (less than three skulls or skeletons) has been available: only single skulls of *Geochelone sulcata, Psammobates oculifer, Homopus boulengeri* and *Cycloderma aubryi.* On the other hand, our understanding of the African species and our ideas as to the variational range within their subfamilies and families have benefited by the examination of much extralimital material including, for example, both skulls and skeletons of most of the species and every species-group of the Testudininae.

Categories at every taxonomic level need to be studied against a background of the next higher category if they are to be fully understood. Thus no subspecies can be properly evaluated without a reasonably adequate knowledge of the entire species of which it forms a part. No species can be appreciated without a substantial acquaintance with the whole genus in which it is included. No genus can be satisfactorily defined except in terms of full information of at least the section of the subfamily to which it is assigned. Consequently we have not hesitated to explore — for their background value — extralimital forms and problems whenever these seemed likely to shed significant light on their African counterparts. It is on this account that family or subfamily phylogenics have been included, together with discussions of non-African genera or species, and even definitions of certain extralimital forms.

Despite all our care, our definitions, whether specific, generic or familial, are weakened, at least in appearance, by the fantastic variability on which we have commented above. Our key to the external characters of families mentions lack of horny scutes in a solitary sea turtle. On another occasion one of us (Williams, 1954, Breviora, No. 29) has called attention to variation in a ''family character'' of an African pleurodire species. Such radical variations cannot in honesty be omitted from the record, but it is important to recognize that *they do not actually diminish the value as phyletic units of the categories whose ''definitions'' they disturb.* However, they do show how necessary it is to use the greatest care and the most broadly based knowledge in dealing with the vexing problem of the recognition of natural groups. Some aspects of these matters have been discussed in very percipient fashion by Zangerl and Turnbull (1955, Fieldiana: Zoology, **37**:366 ff.)

At the outset, the idea occurred to us to include under each species a synopsis of any *Problems remaining,* or gaps in the life-history requiring to be filled. However, we soon realized that such synopses would be unavoidably repetitious and much too long. Perhaps the most fully documented form is the Eastern Leopard Tortoise (*Geochelone pardalis babcocki*), but no African cryptodiran can be said to be well known. One has only to refer to the various headings given under each species or race to realize how very sketchy is our knowledge of their respective ecologies, dietetic preferences, reproductive habits, geographic variation and range.

In the case of *Anatomy* the information was in general so scanty that this heading was also omitted throughout, though references to anatomical papers are retained in the citations for each species. Only once has the anatomy of an African species been studied adequately, and this was done on non-African material. We refer to the very old but classic work of Bojanus (1819-1821) on *Emys orbicularis*. Less meritorious, but possibly based on African specimens, at least in part, is that of Thomson (1932) on "the Tortoise" (i.e. "*Testudo graeca*" = *hermanni*, and "*Testudo ibera*" = *graeca*). Other anatomical discussions involving African turtles either mention African forms incidentally or in a more general context (e.g. sundry papers by Siebenrock), or else record anatomical observations of no great scope.

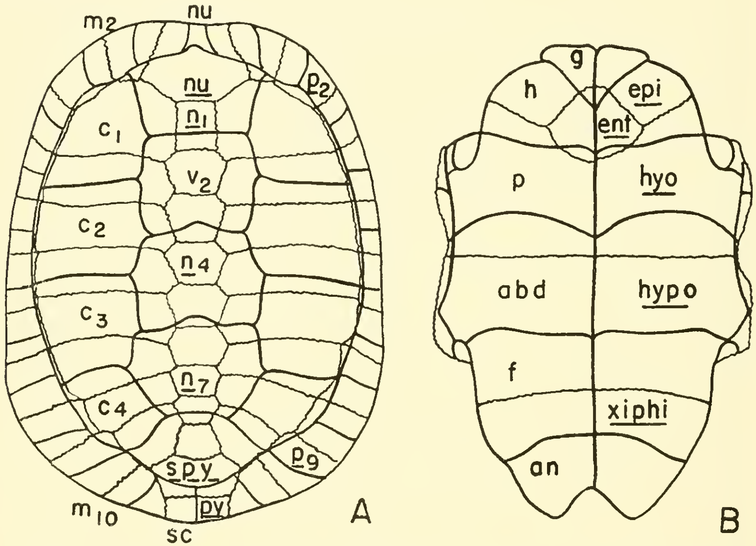

Fig. 1. *Clemmys caspica leprosa:* diagram of shell to show nomenclature of horny scutes and bony plates, the latter's abbreviations underlined in the figure and italicized below. *A,* Carapace: c 1-4 = costals; m 2, 10 = second and tenth marginals; *n* 1-7 = neurals; nu = nuchal scute; *nu* = nuchal bone; *p* 2, 9 = second and ninth peripherals; *py* = pygal; spy = suprapygal; v 2 = second vertebral. *B,* Plastron; abd = abdominal; an = anal; *ent* = entoplastron; *epi* = epiplastron; f = femoral; g = gular; h = humeral; *hyo* = hyoplastron; *hypo* = hypoplastron; p = pectoral; *xiphi* = xiphiplastron.

(P. Washer del.)

Terminology. We have introduced no new terms or new usages to the nomenclature of either bones or horny shields. For the dorsal shell our usage is that of George Baur in his several papers, differing from that of Boulenger only by distinguishing the rib-containing bony plates as "pleurals," and the bones surrounding the shell as "peripherals." Our nomenclature for the dorsal shell is contrasted with that of other authors in Table I (see also Fig. 1).

Fortunately there has never been any confusion with regard to the names of either the bones or horny shields of the ventral shell. To express length-relationship between the various plastral shields we have introduced a new "plastral formula" in which the shields are listed in order from longest to shortest. This formulation is not a substitute for precise studies of the length ratios between plastral shields, but, despite variability, it tends to be characteristic of species, genera, and occasionally of even

TABLE 1

Nomenclature of the parts of a turtle shell

HORNY SHIELDS

Our usage	Boulenger 1889	Hay 1908	Carr 1952
nuchal	nuchal	nuchal	precentral
vertebral	vertebral	vertebral	central
supracaudal	supracaudal	supracaudal	postcentral
costal	costal	costal	lateral
marginal	marginal	marginal	marginal

BONES

Our usage	Boulenger 1889	Hay 1908	Carr 1952
nuchal	nuchal	nuchal	proneural[1]
neural	neural	neural	neural
suprapygal	pygal	suprapygal	epipygal
pygal	pygal	pygal	pygal
pleural	costal	costal	pleural
peripheral	marginal	peripheral	peripheral

[1] Though, by the invention of this and other novelties, Carr intended his terminology to reduce confusion, here it is definitely at fault. The very similar term "preneural" has long been in use for an element that is immediately posterior to the nuchal of authors in certain Asiatic and fossil trionychids and some other fossils.

higher units. Thus a plastral formula[1] with Abd>h> (all other elements), or with Abd> (all other elements) turns out to be very characteristic of testudinines.

As for head shields in the testudinines, we have adopted the terms used by Miss Procter for *Malacochersus tornieri.* In this species, as also in the members of the genus *Testudo*, the dorsal aspect of the head possesses the most elaborate regular scutellation to be found in tortoises. The terms employed are "supranasals," "prefrontals" and "frontals." With regard to the still more elaborate head scutellation of the marine turtles, we follow Deraniyagala (1939:192:fig. 76) except in employing the term "supratemporals" for what he calls "temporals," as being more appropriate.

Folklore. Probably few reptiles figure so frequently in African folk tales as do tortoises. All manner of superstitions are entertained concerning them, and references to such beliefs constantly crop up in books of travel by the earlier explorers. As we came across relatively few examples in our search of zoological papers we have omitted the subject altogether, rather than treat it inadequately. The matter merits the attention of some anthropologist who, preferably in collaboration with a zoologist, would scan the literature and publish a classified synopsis of these tales and beliefs.

Citations. Following the name of each species, when used as a heading, citations to it or its synonyms are given in an abbreviated form which can be amplified by reference to the Bibliography on p. 503. Almost 550 papers (1758-1955) in which we have found references to African Cryptodira are listed. Omitted from the bibliography are papers involving some single generic or specific description for which an adequate citation has already been given in the synonymy. Also omitted are citations to non-African species or races mentioned in the text; these are given in parentheses or as footnotes.

Attention is directed to the Synopsis Methodica (a folding chart or table in which binomials are employed) at the end of the first volume of Lacépède, 1788 "Histoire naturelle des Quadrupèdes ovipares et des Serpens," a work frequently rejected by systematists since only popular names are employed in the text.

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[1] See Fig. 1 for significance of abbreviations.

An extraordinary volume that cannot be taken seriously, is that of Rochebrune, 1884a, "Faune de la Sénégambie. Reptiles." In it the author lists as occurring in Senegal such impossibilities as *Testudo marginata, T. geometrica, Homopus signatus, H. areolatus* and *Cycloderma frenatum.* Despite the fact that definite Senegambian localities are furnished for them, only four, or at most five, of the eighteen land and freshwater turtles listed by Rochebrune actually occur in Senegal.

A question arises with regard to the priority of J. E. Gray's contributions cited as 1831b and 1831c. The latter — Synopsis Reptilium — contains many original descriptions and was clearly intended to be published first. Unfortunately, the evidence suggests that 1831b — Synopsis of the Species of the Class Reptilia — which appears as an appendix to Edward Griffith's translation of Cuvier's Animal Kingdom, came out first. In Gray's own bibliography the date is given as 1830; this is possibly the date of its completion, an advance copy, or an earlier edition than the usually accepted one of 1831. This synopsis in Griffith makes only passing reference to, or gives the scantiest descriptions of, species more fully dealt with in 1831c. For this reason, whenever a new species is involved, we have cited 1831c in advance of 1831b. In no case does it affect priority of nomenclature.

In listing a reference to some form, we do not intend to infer that the *entire synonymy* of the author cited necessarily applies to the species or race to which it is assigned.

Localities. It will be noted that localities are listed alphabetically under their respective countries. The latter, beginning with Morocco, are arranged clockwise around the continent. The only exception to this is in the case of trionychids from north of the equator, whose ranges are given from the Nile west to Senegal. Generally speaking, we have adopted the orthography of the government administering the area, though a few exceptions such as Algiers (instead of Alger), and Tangiers (in lieu of Tanger), have been allowed to stand. Where the current spelling of a place name differs from that used in the original record given in the literature, the rejected spelling is given in parenthesis after the preferred one.

A locality preceded by an asterisk implies that a specimen from the place in question has been studied by us; usually it is in the Museum of Comparative Zoology. If it is in some other institution, however, the key letters of the museum where it is preserved follow the locality in parenthesis. In many instances such asterisk-bearing localities constitute fresh records of occurrence for the species and will not be found in the literature.

A locality that appears in quotation marks is one that has been taken from the literature but which we have failed to find on any map. In some instances, at least, the name may have been misspelled or misprinted.

Unfortunately, all localities appearing in the literature cannot be accepted. The handsome and ornate shells of tortoises have attracted the attention of mankind from earliest times. This is especially true in South Africa where primitive tribes were accustomed to wear the shells of the smaller species as ornaments, or used them as scoops or receptacles, especially for *buchu* ointment (cf. *Psammobates geometricus* under the heading *Enemies*). Doubtless they were used in barter and, passing from one itinerant African to another, were transported far from their place of origin. In due course some were seen and purchased by European travellers, especially those bent on acquiring objects of anthropological interest. Naturally the shells were labeled as coming from the place where purchased.

In recent times car drivers are likely to stop and pick up any small tortoises encountered wandering on the road. After being transported great distances the reptiles may escape, be liberated, or handed over to whoever happens to put the driver up for the night. All localities that appear questionable are either mentioned in footnotes or at the end of the section dealing with the *Range* of the species in question.

For the convenience of those who wish to see at a glance what species are currently known to occur in a particular country, a chart is provided (p. 179). In general the name of the country only is given, but the Union of South Africa covers so vast an area that its component divisions (e.g. Transvaal, Natal, etc.) have been cited. Similarly, though not invariably, French Equatorial and West Africa have been listed under their major territories (e.g. Gabon, Senegal, etc.) when this appeared advisable.

List of the CRYPTODIRA in Africa[1]

Page

Order TESTUDINATA

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[1] Names in square brackets are those of non-African groups which had to be defined or discussed for taxonomic reasons.

LIST OF KEYS AND TABLES

Recorded distribution of African Cryptodira around that continent	Clemmys c. leprosa	Emys orbicularis	Geochelone sulcata	Geochelone p. babcocki	Geochelone p. pardalis	Testudo g. graeca	Testudo kleinmanni	Malacochersus tornieri	Psammobates oculifer	Psammobates geometricus	Psammobates t. verroxii	Psammobates t. trimeni	Psammobates t. tentorius	Chersina angulata	Homopus signatus	Homopus boulengeri	Homopus femoralis	Homopus areolatus	Kinixys b. belliana	Kinixys b. nogueyi	Kinixys homeana	Kinixys erosa	Trionyx triunguis	Cyclanorbis elegans	Cyclanorbis senegalensis	Cycloderma aubryi	Cycloderma frenatum	Chelonia mydas	Eretmochelys imbricata	Lepidochelys o. olivacea	Caretta caretta	Dermochelys coriacea
Rio de Oro																															•	
Spanish Morocco	•					•																										
French Morocco	•	•				•																									•	
Algeria	•	•				•																									•	•
Tunisia	•	•				•																									•	•
Libya (Tripoli etc.)	•					•	•																									
Egypt							•																•					•	•	?	•	•
Sudan			•	•															•				•	•	•							
Eritrea			•																•				•						•	•		
Ethiopia			•	•															•				•									
•French Somaliland																																
British Somaliland				•															•													
Somalia				•															•				•					•				
Sokotra Island																												•	•	•	•	
Uganda Protectorate				•															•			•	•									
Kenya Colony				•				•											•				•					•	•		•	?
Tanganyika Territory				•				•											•								•	•	•	•	•	
•Pemba Island																																
Zanzibar Island																			•									•	•			
Mafia Island																			•													
Mozambique				•															•								•	•	•		•	
Nyasaland				•															•								•					
Northern Rhodesia				•															•								?					
Southern Rhodesia				•															•													
Bechuanaland Protectorate				•					•										•													
Union of South Africa																																
(Transvaal)				•					•										•													
(Natal)				•															•													
(Orange Free State)									•		•						•															
•Basutoland																																
(Cape Province)				•	?				•	•	•	•	•	•	•	•	•	•										•	•	•	•	•
South-West Africa				•	•				•		•	•		?	•	?															•	•
•St. Helena Island																																
Ascension Island																												•	•		•	
Angola				•															•				•					•				
Cabinda																						•	•			•		•				
Belgian Congo																			•		•	•	•			•		•		•	•	
•Belgian Ruanda-Urundi																																
French Equatorial Africa																					•	•	•		•	•		•	•	•	•	•
Rio Muni																					•	•										
•Annobom Island																																
São Thomé Island																												•	•			
Principe Island																												•	•			
•Fernando Po Island																																
French Cameroon																			•	•	•	•	•		•				•			
British Cameroon																					•	•	•							•		
Nigeria			•																	•	•			•	•							
Dahomey																				•												
Togo																				•			•	•	•							•
Gold Coast																				•	•	•	•					•	•	•		•
Ivory Coast																					•	•									•	
Liberia																					•	•	•					•	•	•		•
Sierra Leone																				•		•	•						•			
French Guinea																				•												?
Portuguese Guinea																				•			•					•				
Gambia	•																			•		•	•		•							
Senegal			•																	•			•		•			•	•	•	•	•
French West Africa	•		•																	•			•									
Cape Verde Islands																												•	•		•	
Canary Islands																												•			•	
Madeira Islands																															•	

• No records known to us

TABLE 2

SYSTEMATIC DISCUSSION

Suborder CRYPTODIRA

1870. *Cryptodira* Cope (part), Proc. Amer. Assoc. Adv. Sci., 19:235.

Definition. Skull with temporal region frequently emarginate behind; parietal usually not in contact with squamosal; nasals rarely, and lacrimals never, present; prefrontals almost always joining vomer; epipterygoids usually present; pterygoids without lateral rolled-up expansions, always excluding basisphenoid from quadrate; quadrate never enclosing eustachian tube; articular region of mandible concave; splenial rudimentary or absent; dentaries always united.

Head withdrawn by a vertical flexure of the neck; atlas rarely fused to odontoid; cervical vertebrae with rudimentary transverse processes situated anteriorly; posterior cervical spines low; cervical postzygapophyses widely separated; central cervical articulations well developed, posteriorly broad and (usually) double; sacral ribs well developed; pelvis never ankylosed to carapace or plastron; caudal vertebrae usually procoelous.

Shell primitively complete (except for the always absent mesoplastra), variably reduced or its elements lost in specialized forms; horny shields present or absent; if absent, an epithecal component of the bony shell greatly developed.

Key to the Families of Cryptodira in Africa

(Based on external characters)

1. Limbs not modified as flippers, each with 3, 4 or 5 claws 2
   Limbs modified as flippers, with 0, 1 or 2 claws 3
2. Carapace with horny shields; feet with 4 or 5 claws..TESTUDINIDAE (p. 181)
   Carapace without horny shields; feet wtih 3 claws ..TRIONYCHIDAE (p. 412)
3. Carapace with large horny shields;[1] flippers with 1 or 2 claws .... CHELONIIDAE (p. 472)
   Carapace without large horny shields; flippers clawless DERMOCHELYIDAE (p. 498)

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[1] Shields were absent on a single aberrant adult *Chelonia mydas* captured at Karaduva Island (13.xi.1928) where it was examined, while still alive, by Deraniyagala (1939: 227).

Family TESTUDINIDAE

1825. *Testudinidae* Gray, Ann. Philos. (2), 10:210.

Definition. Cryptodirous testudinates, semi- or fully aquatic or terrestrial in habit. Horny shields always present; costal scutes almost always 4 pairs; marginals exclusive of the nuchal and supracaudal, usually 11 pairs; inframarginals complete or reduced to axillary and inguinal scutes; plastron with 6 pairs of scutes; normally no intergulars.

Skull without nasal bones; prefrontals always in contact dorsally, with descending processes that may be scarcely or widely separated inferiorly; parietal never meeting squamosal; either postorbital or quadratojugal sometimes absent; temporal region posteriorly emarginate or not; quadrate enclosing or not enclosing stapes; post-otic antrum well developed; upper jaw frequently with one or more ridges on its triturating surfaces; vomer always present, separating palatines; mandible with well-developed coronoid bone.

Neck vertebrae usually with 2 biconvex centra, typically the eighth centrum doubly convex in front; coracoids with median borders narrow or markedly widened; tuberosities of humerus widely separated to closely approximated; trochanteric fossa of femur tending to be reduced; phalanges with condyles; claws normally 4 or 5.

Carapace without epithecal component, united to plastron by suture or ligament; sometimes either carapace or plastron with more or less of a hinge; nuchal without well-developed costiform processes; typically peripheral and pleural bones solidly united; neural bones variably shaped; pygals usually 3; plastron never cruciform, usually without fontanelles in adults (except in *Malacochersus*); entoplastron always present; buttresses very strong to absent.

Range. World-wide except for the Australian region.

Remarks. The conception of the TESTUDINIDAE to which we have adhered is that of Williams (1950), in which the family includes the Platysterninae together with the Emydinae and Testudininae. Though only two of these subfamilies occur in Africa, the family definition has been phrased so as to embrace the genus *Platysternon* and the definitions of Emydinae and Testudininae drafted so as to afford contrasts with that Asiatic genus. In order to clarify the statement of some of the characters cited, it has seemed advisable to present, in addition to the diagnoses of the African subfamilies, one of the Platysterninae also.

Subfamily PLATYSTERNINAE

1950. *Platysterninae* Williams, Bull. Amer. Mus. Nat. Hist., **94**:513, 556.

Definition. Aquatic terrapins. Skin of head undivided; scales on forelimb neither spurlike nor with dermal ossifications; small spurlike tubercles on hinder side of thigh; scent glands present; bursae anales present.

Skull with prefrontals whose descending processes are closely approximated inferiorly; frontal excluded from orbit; postorbital enormously developed, largely covering temporal region; temporal region posteriorly but very slightly emarginate; temporal arcade very solidly constructed; quadratojugal large, in contact with the maxilla; jugal not entering orbit, surrounded by other bones; quadrate not enclosing stapes; surangular largely covered by dentary, only narrowly exposed laterally.

Coracoids with narrow medial borders; tuberosities of humerus widely separated; trochanteric fossa of femur widely open; epipodials moderate; second and third digits always have 3 phalanges.

Carapace very low; rib heads stout, well developed; neural bones rather quadrate; inframarginal series of scutes complete.

Range. Southeastern Asia.

Key to the Subfamilies of Testudinidae in Africa

Skin of head smooth and undivided; digits fully webbed, the second and third with 3 phalanges. Range: ponds and streams of northwest Africa .... EMYDINAE (p. 183)

Skin of head divided into larger or smaller shields; digits not webbed, the second and third with only 2 phalanges. Range: all of Africa in suitable areas .. TESTUDININAE (p. 209)

Subfamily EMYDINAE

1909. *Emydinae* Siebenrock, Zool. Jahrb. Syst., Suppl., 10:451.

Definition. Testudinid terrapins of aquatic to fully terrestrial habits. Skin of head entirely smooth or posteriorly divided into small shields; scales on forelimb sometimes bandlike, never spurlike or with osteoderms; spurlike tubercles on hinder side of thigh absent or very small; scent glands present; bursae anales present, occasionally rudimentary.[1]

Skull with prefrontals whose descending processes are typically very closely approximated inferiorly, at most only moderately separated; frontal often entering orbit, sometimes entering temporal fenestra; postorbital typically well developed, never absent; temporal region posteriorly always emarginate; temporal arcade sometimes interrupted by reduction or absence of the quadratojugal; quadratojugal tending to be reduced or absent; quadratojugal and maxilla rarely in contact; quadrate usually not enclosing stapes; surangular largely covered by dentary, only narrowly exposed laterally.

Coracoids with narrow medial borders; tuberosities of humerus usually widely separated; trochanteric fossa of femur usually widely open, except in the more terrestrial forms where it tends to be narrowed or reduced; epipodials moderately elongate; second and third digits always with 3 phalanges, except on the forefeet of the American genus *Terrapene*, where there are only 2, as in tortoises.

Carapace usually low arched; rib heads typically well developed, sometimes much elongated; neural bones primitively hexagonal, short-sided anteriorly, sometimes short-sided posteriorly, rarely octagonal, never vestigial; of the inframarginal series only the axillaries and inguinals normally present.

Range. North and South America; Europe; Asia; North Africa. Absent from tropical and South Africa and the Australian region.

Fossil record. Throughout Cenozoic of North America, Europe and Asia; first reported in the Pliocene of Africa; not known fossil in South America.

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[1] Bursae anales were not found in *Cyclemys* (= *Pyxidea*) *mouhoti* by J. Anderson, 1876, Jour. Linn. Soc., 12: 434-444.

Remarks. Only two emydine genera occur in Africa. A study of the African testudinid fauna is, therefore, not an appropriate place for a revision of emydine genera. Nevertheless we have become involved in the problem of their definition and grouping since the distribution of one of the African genera (*Emys*), as currently understood, includes a species (*orbicularis*) from North Africa, Europe, and neighbouring portions of Asia, and a second (*blandingii*) in eastern North America. An investigation of the evidence for this peculiar distribution has convinced one of us (E.E.W.) that the two species are not congeneric.

The basic reasons for this decision were in fact stated by Baur in 1889 (Amer. Nat. **23:** 1099-1100), and will become evident to anyone who studies *skeletons* of *Deirochelys reticularia, "Emys" blandingii* and *Emys orbicularis.*

A decision of this sort involves a sorting out of convergent and phylogenetically meaningful characters. It is best done in a frame of reference that includes a conception of the relationships of all emydine genera. Figure 2 is an attempt to provide this appropriate background. The scheme given there is tentative; it is not a phylogeny since it neglects the temporal dimension and omits all fossil forms (disregarded for this subfamily, as they are poorly known and worse analysed). However, the diagram, wherever it indicates the direct derivation of one genus from another does predict that the actual ancestral fossil will "key" out very near the living genus which has been given the more central and thus "primitive" position.

In Figure 2 we have postulated an unknown (presumably Asiatic) ancestral emydine, inferring as the characters of this hypothetical animal those which would most closely approach the characters found in related and primitive families (estimating primitiveness from the characters held in common by the older fossil families). On this basis we consider that the ancestral emydine had:

1. a carapace with surface sculpture;
2. a skull with a strong temporal arcade;
3. moderate axillary and inguinal buttresses;
4. maxillae with rather wide triturating surfaces but no secondary palate;
5. quadrate not enclosing the stapes;

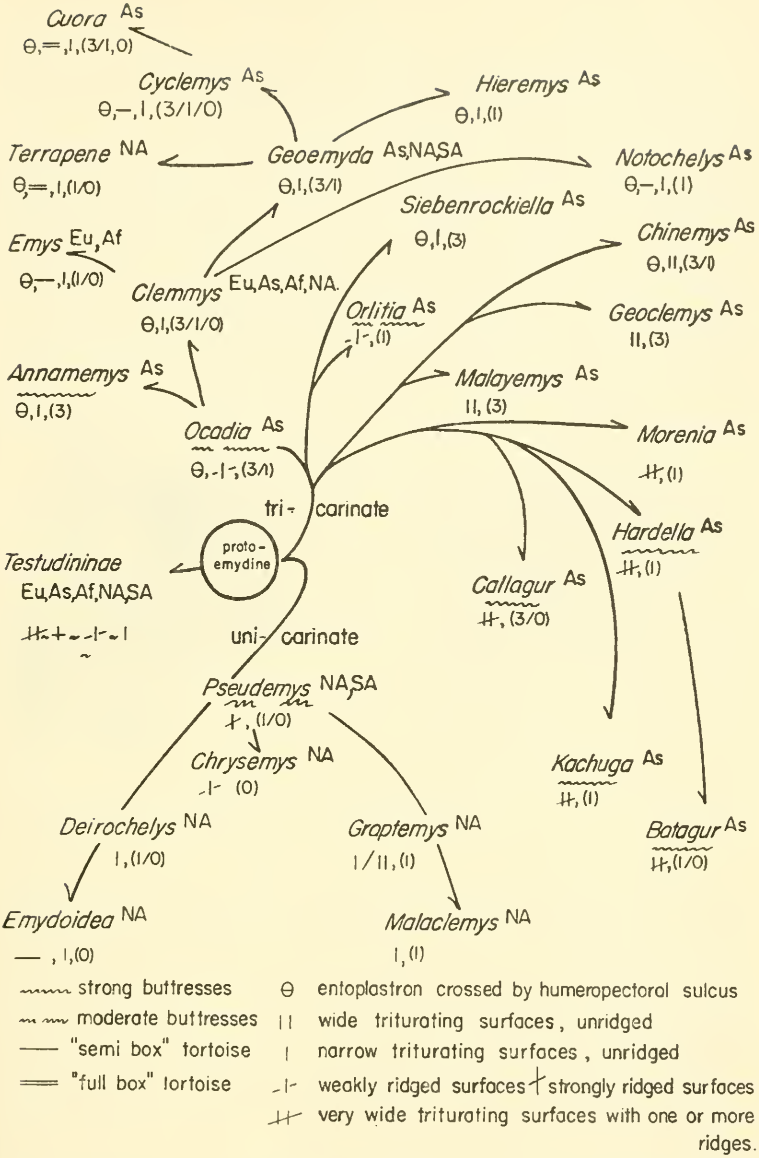

Fig. 2. Dendrogram of emydine relationships. With the exception of *Emydoidea,* the names are those of currently accepted genera. Numerals in parentheses refer to the number of keels on the carapace. NA, SA, Eu, Af, As = abbreviations for the continents on which these genera occur.

(P. Washer del.)

6. the entoplastron anterior to the humeropectoral sulcus;
7. moderate maxillary triturating ridges;
8. three keels on the rather flat shell.

The listing of these characters is somewhat in the order of our confidence in them. *Pseudemys* in the Western Hemisphere, and *Ocadia* in the Eastern, are living forms possessing most of these characters and so in our estimation closest to the postulated ancestral emydine. From the vicinity of these two central types there radiate, according to this view, three major phyletic lines, each with certain characteristic trends, and each with their subsidiary radiations.

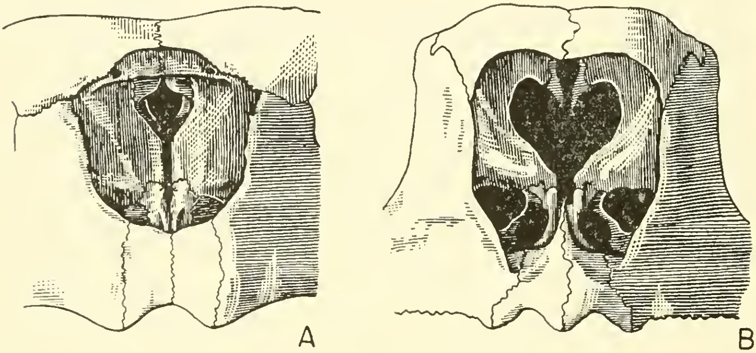

Fig. 3. Condition of the prefrontal descending process. *A*. typical emydine (*Clemmys insculpta*); *B*, typical testudinine (*Gopherus agassizii*). (S. McDowell del.)

The land tortoises, we believe, form a unified series diverging at a very early date from the emydine stock. They appear to be united by certain parallel trends in the scalation of the head, thighs, and lower limbs; by the universal extreme weakness or absence of vertebral keeling; by the downgrowths of the frontals underarching the olfactory tract; and by a wide separation of the ventral processes of the prefrontals (in contrast to the usual median approximation of these processes in emydines, see Fig. 3). Further discussion of this lineage is given below (pp. 211-219).

Within the emydines, after the separation of the tortoise line, one major group appears to be primarily North American. This group — *Pseudemys* and its relatives — never has a *tricarinate* carapace. One subgroup (*Chrysemys*) loses the surface sculpture of the shell and weakens the ridging of the maxillary triturating surfaces; another subgroup *Malaclemys* and *Graptemys* acquires a tuberculate condition of the median keel and a greater or lesser development of a secondary palate, while the subgroup *Deirochelys-Emydoidea* narrows the triturating surfaces, loses the maxillary ridging, elongates the head and neck, strengthens the extensor muscles of the neck with a corresponding bowing out of the carapace ribs at their point of attachment to the column and, finally, in *Emydoidea* itself achieves a plastral hinge.

The second major division of the emydines is primarily Asiatic and primitively tricarinate. This series subdivides immediately into several lines.

One lineage is that of the "river turtles" or "diving turtles" of Asia. In all, the skulls have a very characteristic habitus with a rather angular, somewhat elongate, shape and a tendency to an upturned snout; all have an extraordinarily developed secondary palate with strong maxillary ridging. Typical members of the group have extreme development of the shell buttresses, with a resulting internal partitioning of the shell far more extreme than in any other emydines — with the possible exception of *Annamemys*. Of the entire group only *Callagur* shows any trace of lateral keels on the carapace. In skull structure and general habitus *Morenia* is an obvious member of this lineage, but it has diverged radically in having the buttresses very poorly developed.

A second lineage within the major group is that of *Orlitia* and *Siebenrockiella*, a small and relatively primitive group, lacking the evident specializations of the other lines and sharing minor habitus features.

A third lineage comprises the group of Asiatic genera (united by Boulenger as "*Damonia*") which are strongly tricarinate with reduced buttresses and wide unridged triturating surfaces.

The most successful of the primarily Asiatic lineages is that to which *Ocadia* and *Clemmys* belong. This series has invaded Europe, North Africa, North America and (as *Geoemyda*) even South America.

This lineage has as its conspicuous specialization the combination of narrowing of the triturating surfaces of the skull with a bringing forward of the humeropectoral sulcus of the plastron so that it lies across the entoplastron well in front of the latter's posterior border. This series begins with *Ocadia,* a form with moderate buttressing, and proceeds in *Annamemys* to a secondary extreme development of buttresses. However, on four separate occasions (*Emys, Terrapene, Notochelys* and *Cyclemys-Cuora*) the same series has given rise to forms with hinged plastra and consequent loss of buttresses.

According to this interpretation *Emys orbicularis* is a close relative and, in fact, derivative of the genus *Clemmys,* while the species *blandingii,* here referred to the genus *Emydoidea* Gray, is considered very remote from *orbicularis* and *Clemmys,* being, instead, a close relative and derivative of the genus *Deirochelys.*

There are undoubted resemblances between *blandingii* and *orbicularis* and equally undoubted resemblances between *blandingii* and *Deirochelys reticularia.* One or the other of these sets of resemblances must be convergent.

The resemblances between *orbicularis* and *blandingii* are four in number:

1. coloration of the carapace;
2. the plastral hinge;
3. narrow maxillary triturating surfaces;
4. quadrate tending to enclose the stapes.

The last two are resemblances also to *Deirochelys.* In the face of any contradictory evidence the color character would not be regarded seriously by anyone, especially as the plastral coloration is quite different in the two species. The plastral hinge and the enclosure of the stapes are phenomena which have repeatedly occurred; the hinge has an evident adaptive value and the enclosed stapes may similarly convey some selective advantage.

The resemblance between *blandingii* and *reticularia* are generally less easy to verbalize consisting of characters in the general habitus of shell and skeleton. However, certain of these lend themselves to ready statement:

1. Both have an elongate head and neck, this elongation being more extreme than in any cryptodirous turtles except the trionychids.

2. Both have extremely narrow maxillary triturating surfaces with a very similar, gently arching, external contour.
3. Both have the orbits wholly exposed dorsally with correspondingly narrow interorbital space.
4. Both have the dorsal rib heads very slender and greatly arched, thus accommodating very powerful extensor muscles of the neck.

Dealing with these characters in the same order we offer the following comments:

1. Apparently no other emydines exhibit any tendency to elongation of head and neck, i.e., unlike plastral hinging, this is not a repeated trend.
2. This character exemplifies one of the many striking similarities in skull shape that are greater and more detailed than any to be expected except in cases of direct relationship.
3. In this orbital character it might be noted that *blandingii* and *orbicularis* are poles apart. This character also serves to separate broad groups within the Emydinae, the *Clemmys* series tending to have the orbits covered, the *Pseudemys* group tending to have them exposed dorsally.
4. The slender arched ribs are undoubtedly correlated functionally with the elongate neck, but the similarity in detail between *blandingii* and *reticularia* is far greater than between these and such a form as *Chelydra* in which powerful cervical extensors also occur.

In order to further clarify some of the modifications in our definition of *Emys*, made necessary by our new restricted concept of the genus, we append a definition of *Emydoidea.*

Genus EMYDOIDEA Gray

1870e. *Emydoidea* Gray, Suppl. Cat. Shield Rept. Brit. Mus., part 1, p. 19. Type: *Cistuda blandingii* Holbrook (by monotypy).

1929. *Neoemys* Lindholm, Zool. Anz., 81:282 nom. nov. for *Emydoidea* Gray, considered unavailable on nomenclatorial grounds.

Definition. Beak never hooked, mesially notched; skin on hinder part of head smooth, undivided; back of thighs without tubercles; digits fully webbed.

Skull with orbits fully exposed in dorsal view; triturating surface of maxilla narrow, without ridges; anterior palatine foramina small; posterior palatine foramina large; temporal arcade complete; quadrate enclosing stapes.

Carapace smooth, never with vermiculate sculpture; neurals hexagonal, short-sided in front, broader than long; buttresses absent; rib heads slender and strongly arched to accommodate the strongly developed extensors of the long neck.

Plastron united to the carapace by ligament, a more or less distinctly developed hinge between hyo- and hypoplastra: entoplastron posteriorly touching, though usually not crossed by, the humeropectoral sulcus.

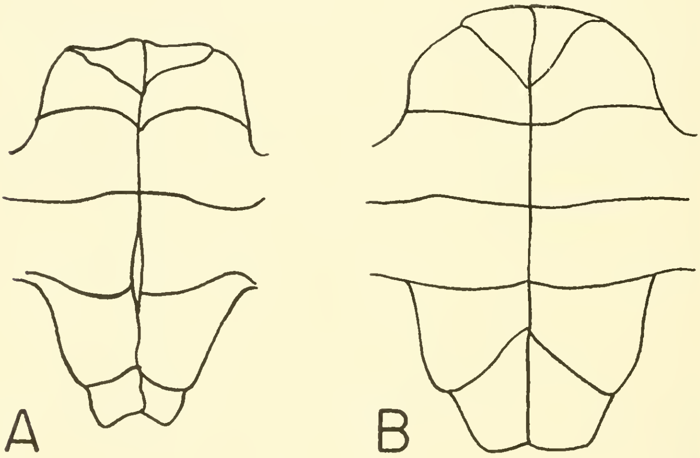

Fig. 4. Plastral shapes of juvenile African Emydinae. *A, Clemmys caspica leprosa* (M.C.Z. 53798), *B, Emys orbicularis* (M.C.Z. 1896).

(P. Washer del.)

Range. A limited area in eastern North America.

Fossil record. Known only from the Pleistocene of North America a little west of its present range.

Key to the Emydinae in Africa

Plastron never hinged; anals pointed, their median suture always shorter than the interabdominal suture (cf. Fig. 4a) . . *Clemmys caspica leprosa* (Schweigger) (p. 192)

Plastron hinged in adults; anals rounded, their median suture always longer than the interabdominal suture (cf. Fig. 4b) .... *Emys orbicularis* (Linnaeus) (p. 202)

Genus CLEMMYS Ritgen

1828. *Clemmys* Ritgen, Nova Acta Acad. Leopold.-Carol., 14:272. Type: *Testudo punctata* Schoepff = *T. guttata* Schneider (designation by Stejneger 1907, Herpetology of Japan, p. 492).

1832. *Chelopus* Rafinesque, Atlantic Jour., 1:64. Type: *Testudo guttata* Schneider (designation by Stejneger).

1857. *Nanemys* Agassiz, Contr. Nat. Hist. U.S.,1:442. Type: *Testudo guttata* Schneider (by monotypy).

1857. *Calemys* Agassiz, Contr. Nat. Hist. U.S., 1:443. Type: *Testudo muhlenbergii* Schoepff (by monotypy).

1857. *Glyptemys* Agassiz, Contr. Nat. Hist. U.S., 1:443. Type: *Testudo insculpta* Leconte (by monotypy).

1869d. *Mauremys* Gray, Proc. Zool. Soc. London; 500. Type: *Emys fuliginosa* Gray (by original designation).

1870e. *Geoclemmys* Gray (*not Geoclemmys* Gray: 1855), Suppl. Cat. Shield Rept., part 1, p. 26. Type: *Testudo guttata* Schneider (designation by Stejneger.)

1870e. *Sacalia* Gray, Suppl. Cat. Shield Rept., part 1, p. 35. Type: *Cistuda bealei* Gray (by monotypy).

1870e. *Emmenia* Gray, Suppl. Cat. Shield Rept., part 1, p. 38. Type: *Emys grayi* Günther = *Testudo caspica* Schweigger (by monotypy).

1870e. *Eryma* Gray, Suppl. Cat. Shield Rept., part 1, p. 44. Type: *Emys laticeps* Gray = *Emys leprosa* Schweigger (by monotypy).

1919. *Melanemys* Shufeldt, Aquatic Life (Philadelphia), p. 155. Type: *Testudo guttata* Schneider (designation by Dunn, 1920. Copeia, p. 8).

Definition. Beak never hooked, not or mesially notched; skin on hinder part of head smooth, undivided; back of thighs without tubercles; digits fully webbed.

Skull with orbits largely concealed in dorsal view; triturating surface of maxilla narrow, without ridges; anterior palatine foramina small; posterior palatine foramina large; temporal arcade complete; quadrate not enclosing stapes.

Carapace smooth or with concentric grooves, never with vermiculate sculpture; neurals hexagonal, short-sided in front, as long as, or longer than, broad; buttresses short, extending only to the outer margins of the pleurals (costal bones); rib heads short, not slender or strongly arched.

Plastron united to the carapace by suture, without a hinge; entoplastron crossed by the humeropectoral sulcus well in advance of its posterior border.

Range. North America, North Africa, Europe and Asia.

Fossil record. Cenozoic of North America, Europe, Asia. The earliest occurrence in Africa is in the Pliocene of Algeria.

Key to the Forms of CLEMMYS CASPICA[1]

Plastral pattern of both young and adults predominantly dark brown or black, the bridge always dark with at most some small yellow spots or streaks. Range: South Dalmatia; Greece; Ionian Islands; Crete[1]; Cyprus; Asia Minor (only in west and south); Syria........*c. rivulata*

Plastral pattern of both young and adults consisting of a dark brown or black blotch covering most of each shield but leaving a yellow margin, at least laterally; bridge predominantly yellow with only the sutures between the shields dark. Range: Asiatic Russia; Asia Minor (middle and east); Iraq and Iran ....*c. caspica*

Plastral pattern *in young* consisting of a dark brown or black blotch occupying the entire medial area but leaving a wide yellow margin laterally; bridge yellow with two large dark brown blotches usually coalescing; *in adults* all markings become obsolescent. Range: Iberian Peninsula and northwest Africa (Morocco to Tunisia) south to the central Sahara, west to the Gambia (i.e. about 13°N) .... *c. leprosa*

CLEMMYS CASPICA LEPROSA (Schweigger)

1812. *Emys leprosa* Schweigger, Königsberger Arch. Naturw. Math., **1**:298, 339; No locality.
1814. Schweigger, 29 (reprint of 1812).
1862b. Strauch, 18.
1894. Oliver, 101.
1896b. Oliver, 118.
1899. Doumergue, 247, pl. i.
1903. Mayet, 10.
1904. Chaignon, 2.
1907. Barbier, 73.
1919. Leblanc, 177.
1824. *Emys marmorea* Spix, Animalia nova Species testud. ranarum Brasil . . ., p. 13, pl. x; No locality.
1831c. Gray, 25.

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[1] We are without material of *C. c. cretica* Mertens (1946, Senckenbergiana, **27**: 115) of Crete, which appears to differ but slightly from *c. rivulata*.

1835. Duméril and Bibron, 248.
1829. *Clemmys Sigriz* Michahelles, Isis von Oken, col. 1295; Spain.
1831. *Terrapene sigriz* Bonaparte, 87 (translation of last).
1831c. *Emys vulgaris* Gray, Synopsis Reptilium, p. 24, pl. iv: Southern Europe.
1831b. Gray, 9 (Spain).
1841. Schlegel, 108.
1860. Tristram, 405 (Sahara).
1833. *Les Emydes* Rozet, 231.
1835. *Emys sigriz* Duméril and Bibron, 240.
1850. Guichenot, 2.
1854. Eichwald, 415.
1887. Lortet, 19, pl. vii.
1897. Bateman, 54.
1836. *Emys lutaria* Bell (part: not of Lacépéde), text and col. pls.
1844. *Emys caspica* Gray (part: not of Gmelin), 19.
1855. Gray, 22.
1867a. Steindachner, 5.
1854. *Emys laticeps* Gray, Proc. Zool. Soc. London, 1852, p. 134: Gambia River, West Africa (M. Castang coll.).
1855. Gray, 23, pl. ix.
1857. *Tortue aquatique* Labouysse, 83.
1860c. *Emys fuliginosus* Gray, Proc. Zool. Soc. London, p. 232, pl. xxx: North Africa?
1862a. *Clemmys laticeps* Strauch, 32.
1865. Strauch, 75.
1884a. Rochebrune, 18.
1862a. *Clemmys marmorea* Strauch, 32.
1865. Strauch, 75.
1862a. *Clemmys leprosa* Strauch, 122.
1865. Strauch, 74.
1880c. Vaillant, 33, 88.
1889a. Boulenger, 105.
1889b. Boulenger, 306.
1890. Strauch, 69.
1891c. Boulenger, 96, 106.
1892. Anderson, 11.
1892. König, 15.
1894. Werner, 76.
1895. König, 404.
1896. Escherich, 278.
1898. Jeude, 7. (*Clemnys*)
1900. Boettger and Tornier, 64.
1901. Gadow, 357, fig. 80 (skull).

1908. Kerville, 96.
1908. Zulueta, 451.
1909. Siebenrock, 481.
1911. Lampe, 144.
1912. Kollman, 101, figs. 1, 3, 4. (*Clemnys*)
1912b. Pellegrin, 262.
1912b. Werner, 408.
1913. Pellegrin (1912), 420.
1914. Pellegrin, 347.
1914b. Werner, 334.
1916e. Chabanaud, 233.
1917c. Chabanaud, 105.
1918. Seurat, 23.
1920. Mourgue, 233.
1925. Flower, 922.
1926a. Pellegrin (1925), 315.
1926e. Pellegrin, 121.
1927. Fejérváry, 517.
1927a. Pellegrin, 261.
1929. Dollfus, 112.
1929. Flower, 17.
1929b. Werner, 12, 15, 21.
1930. Seurat, 182.
1931c. Werner, 275.
1932. Ghigi, 208.
1934. Mosauer, 51.
1935. Laurent, P., 345.
1935. Hediger, 3.
1937. Hediger, 187, 191.
1938. Angel and Lhote, 376.
1938. Gorham and Ivy, 181.
1947. Braestrup, 5.
1950c. Villiers, 343.
1950. Williams, 550.
1951. Aellen, 168, 195.
1952. Stemmler-Morath, 217, photos 1-2.
1953c. Girons, 76, 79.
1954. Noël-Hume, 90, 112.
1865. *Clemmys fuliginosa* Strauch, 76.
1869d. *Mauremys laniaria* Gray, Proc. Zool. Soc. London, p. 499, pl. **xxxvii**: No locality (ex Zool. Gardens from a dealer).
1869d. *Mauremys fuliginosa* Gray, 500.
1870e. Gray, 35.
1872. Sclater, P. L., 603 (synonymizes with *leprosa*).

1873b. Gray, 35.
1869e. *Emys flavipes* Gray, Proc. Zool. Soc. London, p. 643; No locality.
1869e. *Emys fraseri* Gray, Proc. Zool. Soc. London, p. 643: North Africa (ex Mr. Fraser).
1870e. Gray, 36.
1873b. Gray, 35.
1873d. Gray, 146.
1870e. *Emys laniaria* Gray, 37.
1870e. *Eryma laticeps* Gray, 45.
1873b. Gray, 36.
1873b. *Emys lamaria* (*sic*) Gray, 36.
1874. *Emys caspia* var. *leprosa* Boettger, 126.
1882. *Clemmys caspica sigriz* Bedriaga (1881), 340.
1883a. *Clemmys caspia* var. *leprosa* Boettger, 131.
1886. *Clemmys Caspica* Parenti and Picaglia (not of Gmelin), 86.
1927. *Clemmyde lépreuse* Seurat, 81.

Synonymy. Schweigger (1812) cites Schoepff as the author, having taken the name from an unpublished manuscript of the latter. He had seen the type in the Paris Museum.

Common Names. Leprous Terrapin (preferred); Marbled Terrapin (Gray: 1831c); Mud Tortoise (Tristram: 1860); Iberian Water-Tortoise (Gadow: 1901); Spanish Terrapin (Flower: 1929); *Fakroun-el-ma* (Arabic: Doumergue: 1899).

Illustrations. This terrapin is well represented in the fine colored plate of Lortet (1887: pl. vii).

Description. Beak distinctly notched; edge of jaws not or but finely denticulated; mandibular width at symphysis less than (young) or almost equal to (adults) the horizontal diameter of the orbit; skin on upper surface of head undivided; forelimb anteriorly covered with smooth, flattened shields of very diverse size of which about 5 (3 along outer margin and usually 2 internal to them) greatly enlarged; digits webbed to the 5 claws; hind foot strongly webbed, claws 4; tail long.

Carapace rather strongly depressed, anterior and posterior margins not expanded, not or but feebly reverted, not serrated, not notched — at most but slightly incurved — in nuchal region; nuchal moderate, *broader than long,*[1] wider posteriorly; vertebral keel distinct in young[2] but scarcely distinguishable in some

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[1] Longitudinally divided in an Algerian terrapin (Strauch: 1890).

[2] Up to individuals of about 120 or 130 mm. according to Doumergue (1899: 51) who has additional notes on growth changes.

adults; vertebrals 5, rarely 6,[1] broader than long, broader than the costals (young) or variable (adults); costals 4, costal (lateral) keels present but interrupted and indistinct; marginals (exclusive of nuchal and supracaudals) 11; supracaudal divided.

Front lobe of plastron anteriorly truncate, not or but slightly produced, not notched, slightly concave in ♂♂, flat or convex in ♀♀; gulars paired; pectorals wide; axillary 1, moderate; inguinal 1, moderate, not in contact with femoral; hind lobe broadly or deeply notched, anals pointed (cf. Fig. 4 for contrast with *Emys*).

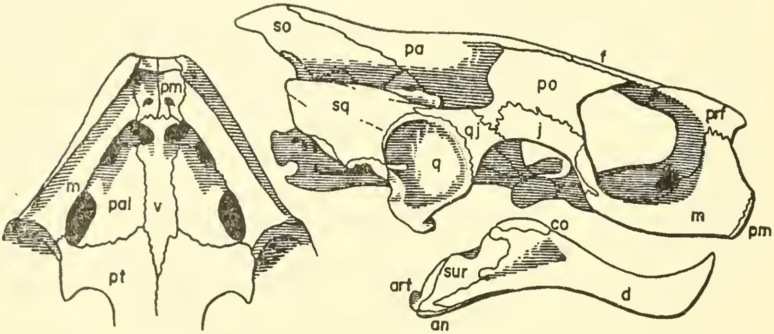

Fig. 5. Skull of *Clemmys caspica leprosa* (M.C.Z. 2210). Condylobasal length 39 mm. *an* = angular; *art* = articular; *co* = coronoid; *d* = dentary; *f* = frontal; *j* = jugal; *m* = maxillary; *pa* = parietal; *pal* = palatine; *pm* = premaxillary; *po* = postorbital; *prf* = prefrontal; *pt* = pterygoid; *q* = quadrate; *qj* = quadratojugal; *so* = supraoccipital; *sq* = squamosal; *sur* =surangular; *v* = vomer.

(S. McDowell del.)

Plastral formula: Abd > or = (p > or = or < f) > (an > or = or < g) > h.

Color. Carapace of young pale or dark olive to olive brown, uniform, or each costal shield with a black-bordered yellowish spot or streak; the vertebrals with a narrow or broad median streak; marginals uniform or each marbled with yellow to a variable degree, frequently edged with yellow laterally. When any pattern is present each shield is apt to be narrowly edged with black, becoming more or less uniform in adults.

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[1] Six in a specimen from Ain Sefra (M.C.Z. 27345).

Plastron of young yellow with the central area dark brown (with or without a median light line), and dark brown blotches usually coalescing on the bridge; marginals ventrally exhibit dark brown blotches at the sutures. Both plastron and marginals more or less uniform without definite pattern in adults.

Head olive to olive gray, its sides streaked or vermiculated with yellow (reddish orange), between eye and tympanum a small round yellow (orange) spot usually present, around the tympanum a more or less well-defined ring of yellow (orange); sides of neck olive gray with 4 or 5 longitudinal yellow (orange) streaks; throat streaked or vermiculated with yellow (orange); limbs olive streaked or vermiculated with yellow (orange).

In life, judging by the detailed description given by Bedriaga (1882), the coloration would appear to be even more striking than suggested by our description. However, according to Mosauer (1934), considerable color variation occurs between juveniles from different localities such as Gabes and Gafsa. In old individuals all bright markings tend to disappear. For further color changes due to age, see Doumergue (1899: 52).

Breeding. Mating takes place either on land or in water, usually on the surface though sometimes a mated pair will descend to the bottom where they may remain immobile for several hours (Lortet: 1887). The artificial conditions of captivity that render hibernation unnecessary, upset the breeding behavior so that eventually mating may take place at any time of the year. In his eagerness to secure a mate the ♂ is apt to bite at the collarlike folds of skin within which the ♀ withdraws her head. His repeated attentions result in sores and swellings that in due course prevent the ♀ from wiping her eyes with the back of a forefoot — a practice common to many species. Ultimately the eyes fester and the terrapin becomes almost blind, gives up feeding, and leaves the water in a condition that is very difficult to cure (Gadow: 1901).

Early May, according to Lortet (1887) is the usual month for laying. Doumergue (1899), however, records that between the evening of September 2 and the following morning a large Algerian ♀ laid 9 white eggs ranging in size from 21 x 34.5 to 21 x 38 mm. Usually 6 to 8 are deposited in shallow excavations in mud, sand, or between the roots of a tree. Twenty-five days after the eggs have been laid, hatching takes place (Lortet: 1887). In Tunisian oases, towards the end of May, hatched-out eggshells were encountered in small holes, chiefly between the roots of trees, bordering the waterholes. No hatchlings were seen, however (Mosauer: 1934).

Upon hatching, the young immediately hasten to the water where few remain near the surface or venture to bask on the rocks; instead they dive to the bottom where they hide in the mud. There, by means of a net, large numbers can be captured with comparative ease (Lortet: 1887). The carapaces of many young measured on April 13, 1898, were 30 mm.; by mid-August they had increased to 45 mm. (Doumergue: 1899).

Longevity. Despite their dispensing with seasonal rest as a result of congenial climatic conditions, most of Gadow's many captives lived "with undiminished appetites for more than twelve years" (Gadow: 1901). A terrapin in the Giza Zoological Gardens lived for 5 years, 1 month, and 10 days; another in the London Zoo only survived 4 years, 6 months, twelve days (Flower: 1925b).

Diet. Hatchling terrapins are eaten by old ones (Doumergue), though the principal food of this species consists of frogs, toads, tadpoles, fishworms, aquatic insects and their larvae (Lortet). Twenty terrapins were observed feeding on the corpses of horses that had fallen into the water (Rozet: 1833). In the absence of animal food these essentially carnivorous reptiles will eat algae and aquatic plants (Labouysse: 1857), lettuce, legumes and scraps of bread (Doumergue). By seizing bait and getting hooked they constitute a nuisance to fishermen (Labouysse).

Clearly Lortet errs when he says that the prey is always devoured under water, for Stemmler-Morath (1952) often found some feeding on Arab excrement on the far side of an earthen wall at least a yard from the nearest water. Another half-dozen were found in a dry ditch used by natives as a toilet. They were in good health and were said to have lived there as long as a local farmer could remember.

Parasites. The name *leprosa* refers to the leprous appearance of the carapace resulting from attacks by freshwater algae, to which this terrapin is especially prone owing to its manner of life. When the mud-encrusted reptile emerges from its slimy pool to bask in the hot sun, its horny shields tend to become brittle and flake off. Entering through the cracks, the algae flourish in the Malpighian layer and even in the underlying bone, which becomes gangrenous in places. Terrapin inhabiting permanent lakes or watercourses are not subject to attack and remain as clean as other species (Gadow: 1901). Stemmler-Morath (1952) remarks that these green and brown algae may attain a length of as much as 50 mm., and were present on all the specimens caught by him. Seurat (1918) has recorded three species of nematodes (*Camallanus microcephalus; Falcaustra lambdiensis,* and *Spiroxys contortus*) from Algerian terrapin.

Enemies. Hundreds were on sale in the fish market at Algiers (Strauch: 1865). As previously mentioned, small terrapin are eaten by the adults (Doumergue: 1899). At Rabat one terrapin was recovered from the stomach of a heron (Pellegrin: 1926a).

Defense. Apart from seeking safety by burying themselves in the muddy bottom of their habitat, the chief defense of these terrapin would seem to be their odoriferousness. This derives from a large pair of inguinal glands that open just behind the plastral bridge. Freshly caught *leprosa* emit a powerful stench, but captive specimens cease to do so after becoming accustomed to being handled (Gadow: 1901).

Apparently the odor may be influenced by diet, for at times it reeks of fish and an excess of animal food increases its intensity (Werner: 1912b). Doumergue (1899) claims that the smell is scarcely noticeable in winter and early spring, but we reject his deduction that the odoriferousness of these terrapins derives from the mud in which they live, and tends to disappear when they are kept in clear water.

Temperament. Excessively wary, scrambling into the water when anyone approaches to within ten or five meters. Such behavior makes their capture difficult. Why they should be so nervous is not readily explained, for Moroccans do not molest them and no other potential enemy is in evidence (Stemmler-Morath: 1952). This opinion is certainly inapplicable to Algerian Arabs if Strauch's statement (1865) holds good today (cf. *Enemies*).

Aestivation and Hibernation. During the hot summer months (August-September), as ponds and watercourses shrink in the torrid heat, these terrapin crowd into the remaining pools. There their numbers contribute to the daily increasing foulness of the stagnant water until everything edible is consumed. Then the reptiles leave the pool to seek shelter among the rocks where they bury themselves until aroused by the return of rainy weather.

During the winter months (November-March) hibernation occurs but is intermittent (Lortet: Doumergue: Aellen). These terrapin neither aestivate nor hibernate in captivity when temperature conditions are congenial and a current of warm water is kept circulating through their tanks. However, Gadow's terrapins showed a fondness for the hot-water pipes against which dozens of them would huddle until their shields, and even the plastral bones, suffered from the excessive heat. To prevent recurrence of such injuries it was found necessary to keep the reptiles away from the pipes by screening. Some *leprosa* in an English garden successfully passed the winter under a heap of moss and rubbish; others remained in the mud beneath the ice in a deep concrete pond where they survived several very severe winters to emerge each spring in perfect health (Gadow: 1901).

Habitat. Many early travellers — from Rozet (1833) onwards — record the astonishing abundance of *leprosa* in Algeria, where scarcely a pool, stream or river is without some terrapins. Werner (1894), however, considered it less common in east Algeria than in the west. In Morocco they are present in almost incredible numbers in all bodies of water except the most temporary of desert streams (Stemmler-Morath: 1952). The latter writer found terrapins living in the swift streams of the High Atlas, an observation that appears to qualify Werner's statement that *leprosa* prefers level country. He also found half-a-dozen individuals living in a ditch some distance from water, as is recorded under *Diet.*

Localities. Spanish Morocco: *Larache (U.S.N.M.); Tangier (Tanger). *French Morocco:* Aïn el Auda; Behalil near Sefrou; Berguent; Bin el Ouidan (Ouidane); Casablanca; Daïet el Roumi; Fes (Fez); Mogador; *Oudjda; Oued Akrech (Akreuch), south of Rabat; Oued Berkine; Oued Fes; Oued Ifrane, middle Atlas; Oued Imoughoud (Tmoughout), south of Taza; Oued Ksib near Mogador; Oued Liboud; Oued Sebou; Oued Sous; Oued Tensift; Oued Tiflet; Oued Yguem (Yquem); Oued Za; Ouezzane; Rabat;

Sehoul; *Sidi Yahia; Sous; Taourirt; Tetouan (Tetuan). *Algeria:* Aïn el Bahir; Aïn el Hadjar; Aïn Sefra; Aïn Temouchent; *Algiers (Alger); Arba; Arlal; Aumale; Batna; Bedeau; *Biskra (U.S.N.M.); Biskra to Constantine; *Bone; Bordja Saada; Boudsareah; *Bou Saada; Cheliff (Chelif); Constantine; Der Kaid Embarek (Embareek M'Toughi); El Khreider; Geryville; Hamman Salahine near Biskra; Lake Fetzara (Tetzara; Tetzura); Macta; Medea; Oran; Ouargla; Oued Andalouses at Bredeah; Oued Asseila (? Asselar); Oued Baccaura; Oued el Biodh; Oued el Harrach; Oued Safsaf at Tlemcen; Oued Saida at Aïn el Hadjar; Oued Sebaou near Tizi Ouzou; Oued Sig (Zig); Oued Tafna at Sebdou; Oued Tlelat; Perregaux; Rhadames; Sahara; Touggourt; Ziban Oases. *Tunisia:* Aïn Draham; Aïn Hameraia; Bir Meherga to Zaghouan; Djerba Id.; Douirat (Duirat); El Hamma (Hamman) near Tozeur; Gabes; Gafsa; Ischkeul; Kairouan (Kairwan); Maxula Rades; Oued Bagra; Oued Debbane; Oued el Amor; Oued el Mahdi; Oued Guedouiaris; Oued Leben; Oued Miliani (Milane); Oued Oum Mela; Oued Rzella; Oued Siliana; Soliman; Tabarca; Tozeur (Touzla; Tozzer); Zaghouan. *Libya:* Murzuch (Murzouk) in Fezzan; Tripolitania. *French West Africa:* Adrar des Iforas; Agades (Agadez), Aïr region; Fort Gouraud or Idjil (probably Koudja d'Idjil), Mauretania. *Gambia:* Gambia River (Gray: 1853).

Range. Iberian Peninsula and north Africa (Morocco to Libya) south to the central Sahara, west to the Gambia (i.e. about 13°N.). We reject the record of Porto Novo, Dahomey (Chabanaud: 1917c).[1]

Genus EMYS Duméril

1806. *Emys* Duméril (part), Zool. analytique, p. 76. Type: *Testudo lutaria* Linnaeus = *T. orbicularis* Linnaeus (designation by Fitzinger, 1843, Syst. Rept., Part 1, p. 29).

1814. *Hydrone* Rafinesque, Specchio Sci. (Palermo), 2, p. 66. Type: *T. orbicularis* Linnaeus (by present designation).[2]

1844. *Lutremys* Gray, Cat. Tortoises, Crocodiles, Amphisbaenians in Brit. Mus., p. 31. Type: *Testudo europaea* Schneider (by monotypy).

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[1] This record should be discarded. Dr. Chabanaud (1917c:105) who identified the two specimens, informs us (22.xii.55) that they were subsequently destroyed with other material identified at that time. Furthermore nothing concerning the itinerary of the donor (Waterlot) can be found in the Museum records at Paris.

[2] The included species were *T. orbicularis*, *lutaria* and *geometrica*.

Definition. Beak never hooked, mesially notched; skin on hinder part of head smooth, undivided; back of thighs without tubercles; digits fully webbed.

Skull with orbits wholly concealed in dorsal view; triturating surface of maxilla narrow, without ridges; anterior palatine foramina small; posterior palatine foramina large; temporal arcade complete; quadrate barely enclosing stapes.

Carapace smooth or with concentric grooves, never with vermiculate sculpture; neurals hexagonal, short-sided in front, as long or longer than broad; buttresses absent; rib heads stout, not slender or strongly arched.

Plastron united to the carapace by ligament, a more or less distinctly developed hinge between hyo- and hypoplastra; entoplastron crossed by the humeropectoral sulcus well in advance of its posterior border.

Range. North Africa, Europe and contiguous parts of Asia.

Fossil record. Most fossil species assigned to this genus do not really belong to it. Perhaps the only certain records are those from the Pleistocene of Europe.

EMYS ORBICULARIS (Linnaeus)[1]

1758. *Testudo orbicularis* Linnaeus, Syst. Nat., ed. 10, **1**, p. 198: Southern Europe.

1766. Linnaeus, 351.

1758. *Testudo lutaria* Linnaeus (part), Syst. Nat., ed. 10, **1**, p. 198: "Italia, Oriente."

1783. *Testudo Europaea* Schneider, Naturg. Schildkröten, p. 323: most countries in Europe.

1819. Bojanus, 1-178, figs. 1-201 (anatomy).

1788. *La Jaune* Lacépède, Hist. Nat. Quad. Ovip. Serpens, **1**, p. 135, and *Testudo flava* at end of same volume in Synopsis methodica, a table in which binomials are employed: Europe (other localities in error).

1790. *Testudo meleagris* Shaw, Nat. Misc., **4**, pl. cxliv: "America" (in error).

1792. *Testudo pulchella* Schoepff, Naturg. Schildkröten, p. 134, pl. xxvi (ed. 2, 1801, p. 113, col. pl. xxvi): No locality.

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[1] In conformity with our practice we have included all known synonyms; in this instance, however, our *orbicularis* material is too inadequate for us to express an opinion as to whether any of them are possibly recognizable geographical races. We have omitted "*Emys antiquorum* Valenciennes," listed as a synonym by Gray (1855:41) as no such name was found in the reference he gives.

1802. *Testudo rotunda* Sonnini and Latreille, Hist. Nat. Rept., 1., p. 107; 2, p. 282: No locality (Sometimes attributed to Lacépède (1788) who, however, uses only the French equivalent in conjunction with *orbicularis*).

1833. *Cistuda hellenica* Bibron and Bory de Saint Vincent, Reptiles et Poissons, *in* Bory de Saint Vincent Exped. Sci. Morée, **3**: Zool. 1, p. 61: Nisi Plain, Pamisus Basin, Messina, Greece.

1833. *Emys hellenica* Valenciennes (for plate only) *in* Bory, *op. cit.*, Atlas, pl. viii, figs. 2-2a.

1833. *Emys iberica* Valenciennes (for plate only) *in* Bory, p. 61, *op. cit.*, Atlas, pl. ix, fig. 1.

1836. *Emys Hofmanni* Fitzinger, Ann. Wiener Mus., 1, p. 123: *n.n.* to combine *hellenica* with *orbicularis*.

1850. *Cistudo Europaea* Guichenot, 2.
1860. Tristram, 405 (''Sahara'' applied erroneously).
1899. Doumergue, 252.
1904. Chaignon, 3.
1925a. Seurat, 150.

1851. *Emys lutaria* Bianconi, 71.
1862a. Strauch (part), 101.
1865. Strauch, 49.
1897. Bateman, 50, fig. 34 (habits in captivity).

1854. *Emys europaea* Eichwald, 416.
1877. Bruhl, pl. xxxiii, figs. 8, 14; pl. xxxiv, figs. 4, 9.
1880. Bruhl, pl. lxix, figs. 3-4.
1915. Rawitz, 671, pl. xlix, figs. 76-78.

1855. *Lutremys europaea* Gray, 1, 40 (*Lutremys* was proposed in 1844).
1887. Lortet, 15, pl. vi (did not encounter any when in Africa).

1862b. *Cistudo lutaria* Strauch, 17.
1867. Lallement (not seen).
1894. Oliver, 101.

1889a. *Emys orbicularis* Boulenger, 112.
1891c. Boulenger, 96, 105.
1896. Doumergue, 477.
1897. Siebenrock, 247, pl. iii, fig. 14.
1901. Gadow, 351, fig. 79.
1907. Johnson, 13, 69, photo.
1908. Kerville, 96.
1909a. Siebenrock, 486.
1912b. Werner, 412, fig. (not used).
1913. Pellegrin (1912), 420.
1920. Mourgue, 233.

1925b. Flower, 922.
1927a. Pellegrin, 261.
1929. Dollfus, 112.
1930. Seurat, 179.
1937a. Flower, 4.
1938. Gorham and Ivy, 181.
1951. Aellen, 169, 195.
1954. Noël-Hume, 94, 112.
1903. *Emys orbicularis hellenica* Kovatscheff, Verh. Zool.-Bot. Ges. Wien, **53**, 171 (revives name as subsp.).
1916. *Emys orbicularis aralensis* Nikolsky, Faune Russie, Rept., **1**, p. 24: Lake Aral (presumably Aral Sor, just north of the Caspian Sea, Astrakhan, U.S.S.R.).
1934a. *Emys orbicularis orbicularis* Mertens and Müller *in* Rust, 7.

Another citation of *Emys lutaria* will be found under *Clemmys caspica leprosa*. An extensive bibliography of *orbicularis* is furnished by Boulenger (1889a), and another by Siebenrock (1909). After careful checking we have omitted most of them from the above list as they deal exclusively with European or Asiatic material; a selected few have been included on account of their taxonomic importance or because of the observations that they contain.

Names. European Terrapin (preferred); European Pond Tortoise (Flower: 1929); Speckled Terrapin (Shaw: 1790); Mud Tortoise (Bateman: 1897).

Illustrations. This terrapin has often been well figured, though usually from European specimens as in the colored plate of Lortet (1887:pl. vi).

Description. Beak distinctly notched; edge of jaws smooth; mandibular width at symphysis less than (young) or subequal to (adults) the horizontal diameter of the orbit; skin on upper surface of head undivided; forelimb anteriorly covered with smooth, flattened shields of very diverse size, of which none is conspicuously enlarged; digits webbed to the 5 claws; hind foot strongly webbed, claws 4; tail long.[1]

Carapace moderately depressed, anterior and posterior margins not expanded, not reverted, not serrated, not notched in nuchal region; nuchal moderate to small, longer than broad; dorsal shields concentrically striated except in aged specimens; verte-

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[1] Alleged age and sexual distinctions displayed by tail length that are mentioned by Boulenger (1889a:113) are not discernible even in our limited material.

bral keel distinct in young but scarcely distinguishable in adults; vertebrals 5, broader than long, broader than the costals (young) or narrower than the costals (adults); costals 4, with indistinct, interrupted keels (young) or without trace of keels (adults); marginals (exclusive of nuchal and supracaudals) 11; supracaudal divided.

Front lobe of plastron anteriorly truncate, not produced, not notched, possibly slightly concave in ♂♂, flat or convex in ♀♀, hinged at humeropectoral suture; gulars paired, rarely two pairs;[1] pectorals wide; axillary 1,[2] moderate; inguinals variable, often indistinct, not in contact with femoral; hind lobe very broadly or not notched; anals truncate or rounded, not pointed (cf. Fig. 4, for contrast with *Clemmys*).

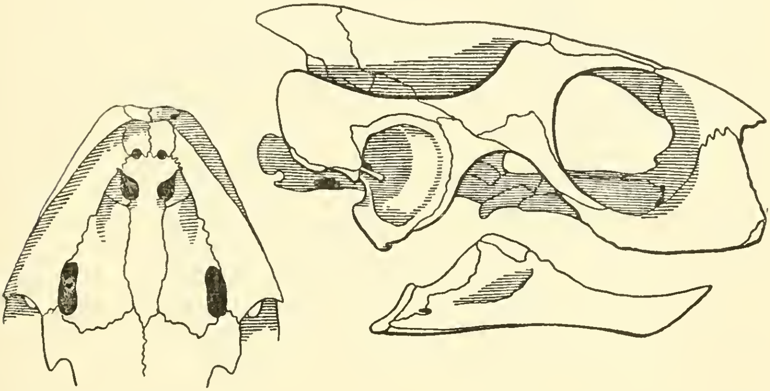

Fig. 6. Skull of *Emys orbicularis* (A.M.N.H. 73604). Halfgrown. Condylobasal length 28 mm. Certain features of this specimen are due to its comparative youth. (S. McDowell del.)

Plastral formula: An > (g, p, abd subequal) > f > h.

Color. Carapace of young, dark brown or black, uniform, or with more or less numerous yellowish dots or radiating lines. Adults similar.

Plastron of young, dark brown or black, the outer side of each plastral shield and underside of each marginal with a large

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[1] Two pairs in an Algerian specimen (U.S.N.M. 10986).

[2] Occasionally 2, as on right side of a Tiflis terrapin (M.C.Z. 5309).

yellow spot. Plastron of adult nearly entirely blackish brown, brown and yellow, or yellow, each shield more or less narrowly edged with black. Adults similar.

Head above, dark brown or black, uniform, or spotted or vermiculated with yellow; sides of head and throat spotted or vermiculated with yellow, the latter sometimes predominating on the throat; limbs and tail dark brown or blackish, more or less sparsely spotted with yellow, the tail streaked with yellow.

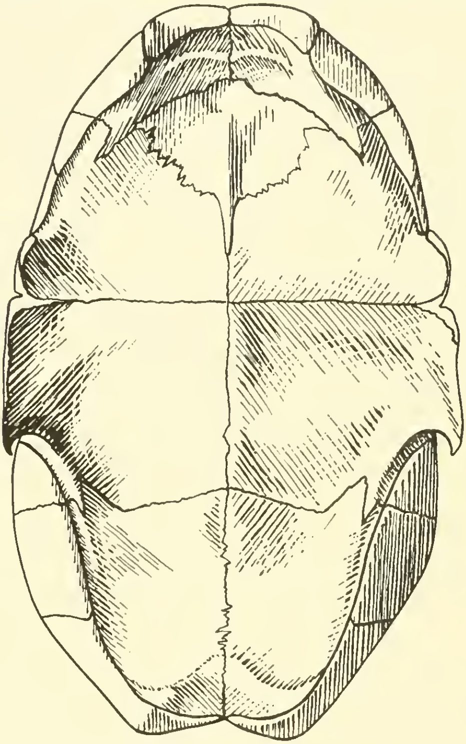

Fig. 7. *Emys orbicularis* (M.C.Z. 31976) Internal view of plastron. x 2/3. (P. Washer del.)

We are unable to confirm Boulenger's statement (1889a) that the color of the spots has a sexual significance, i.e. yellow in ♀, pale brown in ♂. Gadow (1901) states that both the color and shape of the carapace alter with age.

Size. Carapace length of largest ♂ (M.C.Z. 5187) from Algiers, 128 mm., breadth 94 mm., height 48 mm.; carapace length of largest ♀ (M.C.Z. 5189) from Algiers, 138 mm., breadth 96 mm., height 62 mm. Both far surpassed by an unsexed European record of 190 mm. (Boulenger: 1889a). A juvenile (M.C.Z. 3482) from southern Europe has a carapace length of 30 mm., breadth 24 mm., height 14 mm.

Sexual dimorphism. Both tail length and spotting were believed by Boulenger (1889a) to be indications of sex, but we have been unable to confirm his findings with the limited material at our disposal.

Breeding. On warm spring nights during the pairing season these terrapins emit short piping calls until they find a mate, after which the couple swim about together.

When gravid, the ♀, having selected a suitable spot free of vegetation, where the soil is firm, prepares the site by ejaculations of fluid from the bladder and anal water-sacs. Then, holding her body rigid while stiffening the tail, she uses the latter as a borer, pushing it into the ground. Following this preparatory loosening of the soil, it is scooped out and heaped around the periphery of a hole that may be as much as five inches in depth, i.e. as far down as her hind feet can reach. The feet are also employed to separate and spread the eggs which are deposited in a single layer on the bottom of the pit.

After about 10 eggs have been laid, the loose soil is returned to the hole and tamped down by allowing the plastron to fall upon it as, time and again, the terrapin raises herself to her full height and then drops on the site. After some additional stamping over the area, the terrapin roughens the surface with her claws before leaving the place for good.

The incubation period varies in relation to locality and temperature, embryos sometimes hibernating within the egg. In a garden at Kiev, U.S.S.R., some eggs did not hatch until 11 months after they were laid. For some obscure reason, hatchlings of *orbicularis* are more difficult to rear than are those of other terrapin. (The foregoing remarks probably refer to European specimens and are taken from Gadow: 1901.)

Growth. One hatchling, reared in captivity, which wintered beneath moss in an unheated room in England, took 4 years to attain a carapace length of 50 mm. A 25 mm. terrapin grew to 134 mm. in carapace length during 11 years, at the end of which time it weighed 491 grams (about 1 lb.). Another, over a period of 8 years, increased in carapace length from 110 to 132 mm., and from 83 to 106 mm. in breadth. This particular terrapin, however, did not hibernate as it was kept in a greenhouse (Gadow: 1901).

Longevity. Perhaps the best authenticated record is 27 years, 11 months, 17 days, in the Jardin des Plantes (Vaillant:1892:223[1]) cited by Flower (1925b) who, however, (1937a) refers also to a ♀, already adult in 1868, which bred regularly for 60 years in a French garden until her death on February 27, 1928. This, and a record of 120 years, are taken from Rollinat (1934:110[2]). Probably all these instances of longevity are based on French, rather than African, terrapins.

Diet. In captivity young European Terrapins will readily take flies, tiny worms or tadpoles; larger individuals eat insects, frogs, fish and even raw meat. Though normally feeding in water, tame terrapins will come out on land to be fed if sufficiently hungry. Usually, however, the prey must be seen in motion before a terrapin will attack it.

Frogs are stalked as they sit on a floating leaf. Rising slowly from below, the terrapin thrusts its nostrils and eyes above the surface close to the frog and waits motionless. After a while it may sink to rise again with its snout actually touching the unsuspecting frog's toes which, after smelling at them, it seizes with a sudden sidewise biting motion. While maintaining its hold the terrapin employs its sharp foreclaws to tear the living prey to pieces. This occupies considerable time for only the intestines and scraped-off flesh are devoured.

Fish too are stalked, the terrapin moving slowly along the bottom as it cautiously approaches its prey. Then, with a few gentle movements of its fully-extended webbed feet, the reptile rises almost imperceptibly and, gaping widely, grabs at the fish's belly. The bones are picked clean as the skeleton sinks to the bottom, but the air-bladder floats away on the surface to serve as an indication of the presence of a terrapin in the pond (Gadow:1901).

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[1] Vaillant, L., 1892, Arch. Mus. Paris (3), 4, pp. 221-253.

[2] Rollinat, R., 1934, La Vie des Reptiles de la France Central (Paris).

Defense. The European Terrapin lacks a defensive odor like that which is so characteristic of *Clemmys* (Gadow:1901).

Hibernation. In Europe this terrapin buries itself in mud and does not reappear until spring is well advanced (Gadow:1901).

Migration. At times, extended migrations take place, either under the stimulus of a food shortage or because the occupied pool is in process of drying up (Gadow:1901).

Habits. European Terrapins should not be kept in an aquarium unless there is growing vegetation and facilities to land, stones to bask on and bark or moss under which they can retire when so inclined (Bateman: 1897; Gadow:1901).

Habitat. The statement as to the abundance of this terrapin in Algeria, made by Guichenot (1850), is due to confusion with *Clemmys,* according to Boulenger (1891c). The same author points out that its reported occurrence in the "Sahara" by Tristram (1860) is due to a misapplication of this term to the high plateau of southern Algeria. The frequency with which *Emys* occurs in Tunisian streams in the absence of *Clemmys,* or *vice versa,* is remarked upon by Chaignon (1904); however, both apparently coexist in a dozen localities.

Localities. French Morocco: Oued Ifrane; Oued Nkhol. *Algeria:* *Algiers; Bone; La Calle; Lake Fetzara; Oued Harrach; Oued Sebaou (as Wed Sebaon); "Sahara" (in error). *Tunisia:* Aïn Draham; Cap Bon streams; Krombalea to Soliman; Oued Belli; Oued Bezirk; Oued el Amor; Oued el Kebir; Oued Melah (as Mala); Oued Sidi Saad, 3 km. south of Cebala; Tabarca (as Taborca).

Range. Northwest Africa (Morocco to Tunisia); central and south Europe; southwestern Asia.

Formerly the range was much more extensive. Post-glacial remains have been found in Sweden, Denmark, the Netherlands and in the peat of England (Norfolk and Cambridgeshire). According to Bateman (1897) specimens that have escaped from captivity survive English winters, having been recaptured in a healthy condition years later.

Subfamily TESTUDININAE

1909. *Testudininae* Siebenrock, Zool. Jahrb. Syst., Suppl., **10**, p. 508.

Definition. Testudinid tortoises of strictly terrestrial habit. Skin of head divided into larger or smaller shields; scales on forelimb more or less enlarged, often with dermal ossifications; hinder side of thigh often with large spurlike tubercles; scent glands absent; bursae anales absent.

Skull with prefrontals whose descending processes are more or less widely separated inferiorly; frontal entering or excluded from orbit; postorbital tending to be reduced, rarely absent; temporal region always emarginate posteriorly; temporal arcade rarely interrupted by absence of the postorbital; quadratojugal typically well developed, never absent, never in contact with

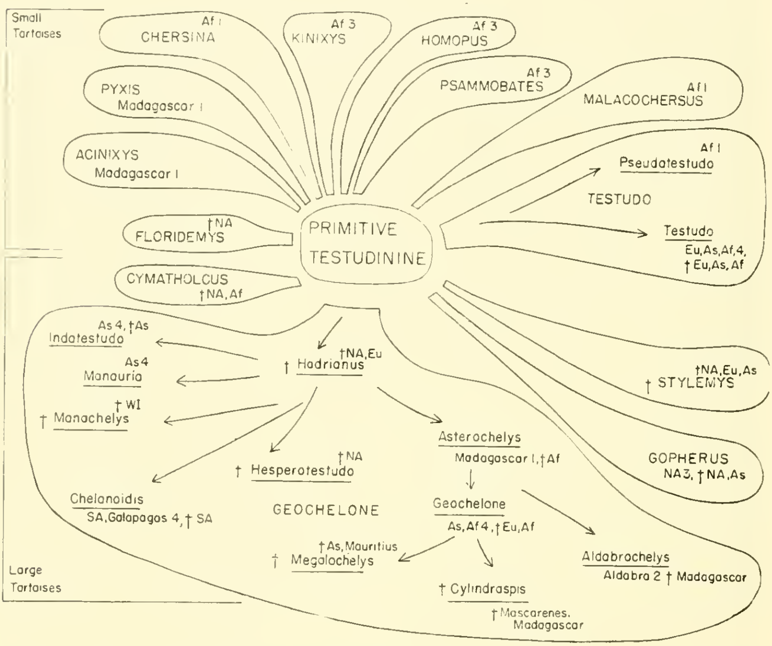

Fig. 8. A dendrogram of testudinine relationships. Names in capitals are those of full genera. Names underlined are those of subgenera as recognized in this revision. With each subgenus or genus is given its range and the number of Recent species, if any. The symbol † indicates an extinct form.

(P. Washer del.)

maxilla; jugal entering orbit; quadrate usually enclosing stapes; surangular not covered by dentary, often extensively exposed laterally.

Coracoids with median borders markedly widened; tuberosities of humerus tending to be approximated; trochanteric fossa of femur restricted by union of trochanters; epipodials very short; no digit with more than 2 phalanges, except in an extinct genus.

Carapace usually arched, high; rib heads often vestigial; neural bones primitively hexagonal, tending to become alternately quadrangular and octagonal, sometimes vestigial; of the inframarginal series only the axillaries and inguinals normally present.

Range. World-wide except for Australian region.

Remarks. The separation of the land tortoises into generic groups is not easy. Like the emydines they are a closely knit assemblage in which there has been much parallel evolution. Even more than in the emydines, it is difficult to distinguish between those characters that are merely convergent and those that may indicate natural divisions.

In a revision of African forms, however, the problem is a pressing and immediate one since nowhere else in the world do the tortoises achieve the diversity or the numbers of species that they have in Africa.

We have made a beginning by assembling the recognizable forms into species groups. Estimation of relationships at this level rests upon relatively secure foundations. With almost equal confidence we may proceed to the level of groups that may be termed subgenera, but above this uncertainties increase. In Figure 8 we have attempted a diagram of relationships between species-assemblages that are at least subgenera, and to which the available Latin names have been attached. We have included the evidence of fossil forms where these have been sufficiently well analyzed to be usable. Fortunately, in the testudinines, in contrast to the emydines, the fossil record approaches adequacy, at least in some periods and places.

In preparing Figure 8 we have considered the following as the characters which the primitive testudinine must have had.

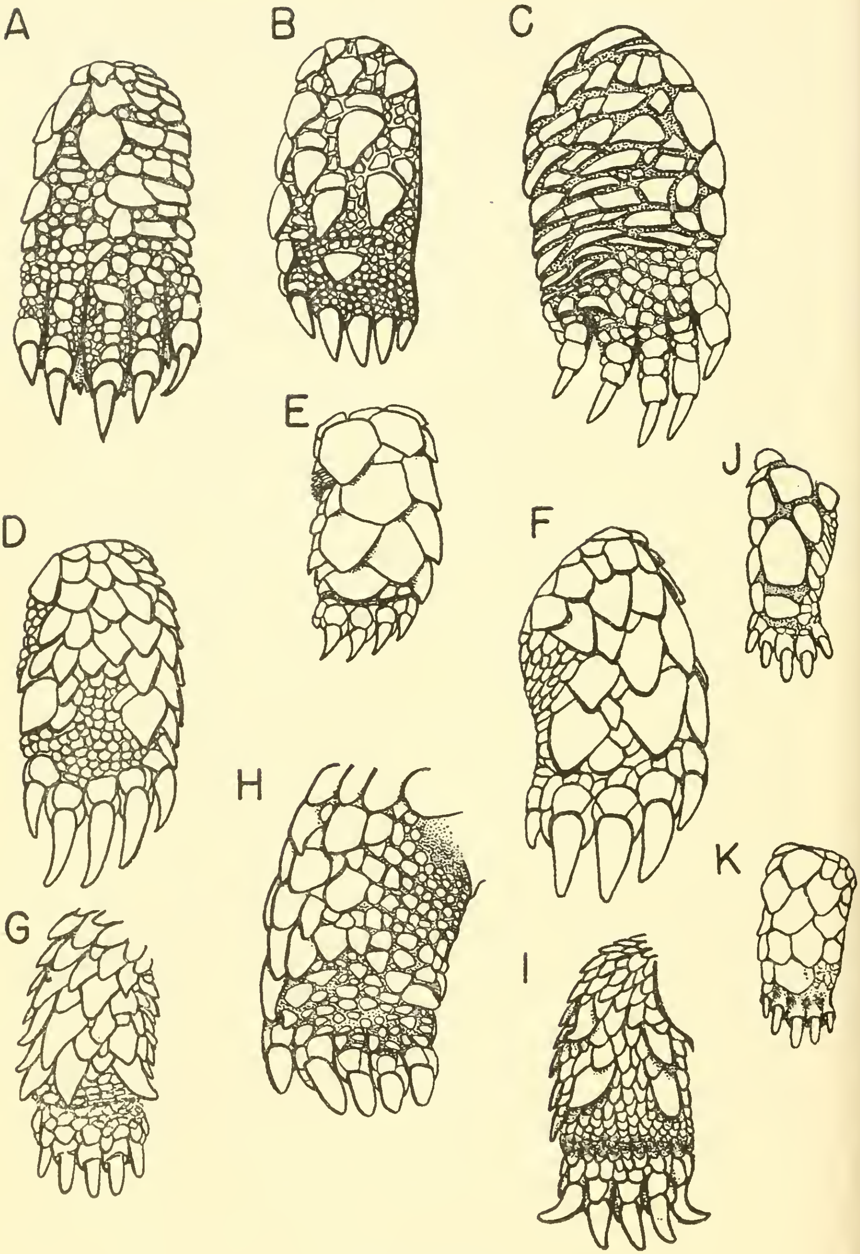

FIGURE 9

Osteological characters

1. Interval between ventral processes of the prefrontals only moderately widened.
2. Maxilla with triturating surface ridged, but premaxilla unridged.
3. Anterior palatine foramina small, concealed.
4. Temporal arcade strong.
5. Prootic well exposed dorsally.
6. Quadrate not enclosing stapes.
7. Surangular subequal in height to prearticular.
8. Fourth cervical centrum biconvex.
9. Anterior neurals hexagonal.
10. Suprapygal *one,* anterior to the vertebral-supracaudal sulcus.
11. Entoplastron anterior to humeropectoral sulcus.
12. Digital phalangeal formula 2, 3, 3, 3, 3.

External characters

1. At least prefrontal and frontal head scutes present.
2. Scales on forelimb numerous, not greatly enlarged.
3. Large femoral tubercles present.
4. Claws on forelimb 5, on hind limb 4.
5. Tail claw absent.
6. Carapace moderately convex.
7. Neither carapace nor plastron hinged.
8. Nuchal present.
9. Vertebrals not conical.
10. Vertebral keel very weak, lateral keels absent.
11. Supracaudal divided.

Fig. 9. Forelimb scalation in certain testudinids. *A, Clemmys caspica leprosa* (M.C.Z. 1894) (x 2); *B, Geochelone pardalis babcocki* (M.C.Z. 50304) (x 1); *C, Emys orbicularis* (M.C.Z. 5189) (x 1⅓); *D, Testudo hermanni* (M.C.Z. 3063) (x 1⅓); *E, Testudo kleinmanni* (M.C.Z. 5081) (x 2); *F, Testudo graeca graeca* (M.C.Z. 1497) (x 1⅓); *G, Malacochersus tornieri* (N.R. Stockholm), Njoro, (x 1); *H, Chersina angulata* (M.C.Z. 3998) (x 1); *I, Malacochersus tornieri* (M.C.Z. 30003), Mangasini, (x 1); *J, Psammobates t. trimeni* (M.C.Z. 42227) (x 1); *K, Psammobates t. tentorius* (M.C.Z. 21332) (x 1).

(P. Washer del.)

12. Submarginal scute absent.
13. Gular area but slightly produced or thickened.
14. Gulars paired.
15. Anal notch moderate.

Most of these characters are primitive emydine and are inferred to be also primitive testudinine on the well-grounded theory that the Emydinae are ancestral to the Testudininae. In several instances where there is a good fossil record for a tortoise lineage, it is possible to observe a shift in these characters from

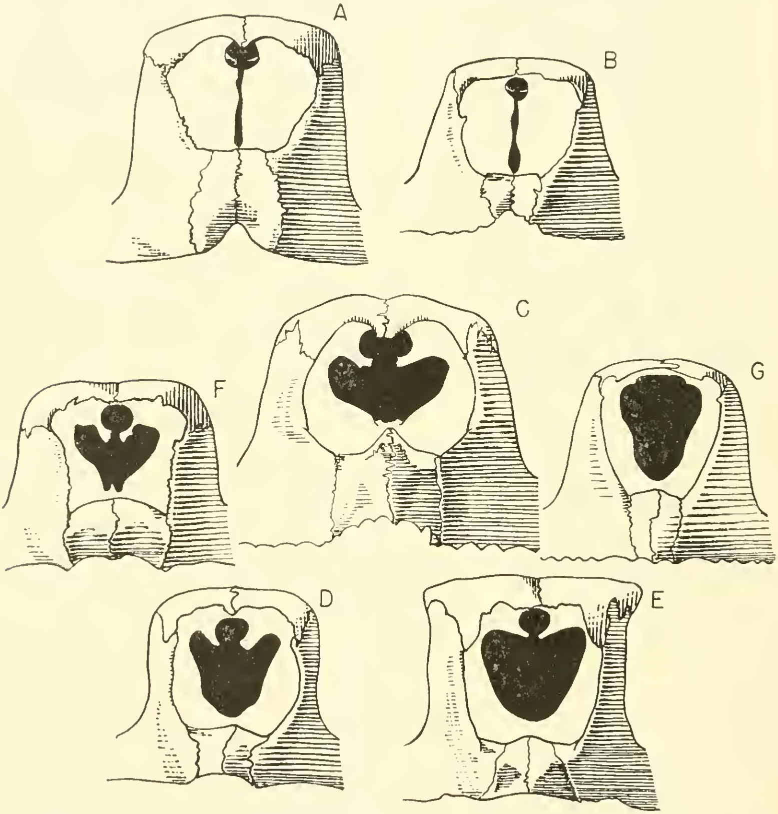

Fig. 10. Interprefrontal space in African testudinids I. *A, Clemmys caspica leprosa* (M.C.Z. 2210); *B, Emys orbicularis* (A.M.N.H. 74604); *C, Geochelone pardalis babcocki* (A.M.N.H. 7203); *D, Testudo graeca graeca* (M.C.Z. 4485); *E, Testudo kleinmanni* (Yale Mus. 662); *F, Malacochersus tornieri* (A.M.N.H. 45081); *G, Chersina angulata* (A.M.N.H. 50725).

(P. Washer del.)

the earlier to the later members, e.g. from the emydine hexagonal neural pattern to the advanced testudinine octagonal *cum* quadrilateral condition.

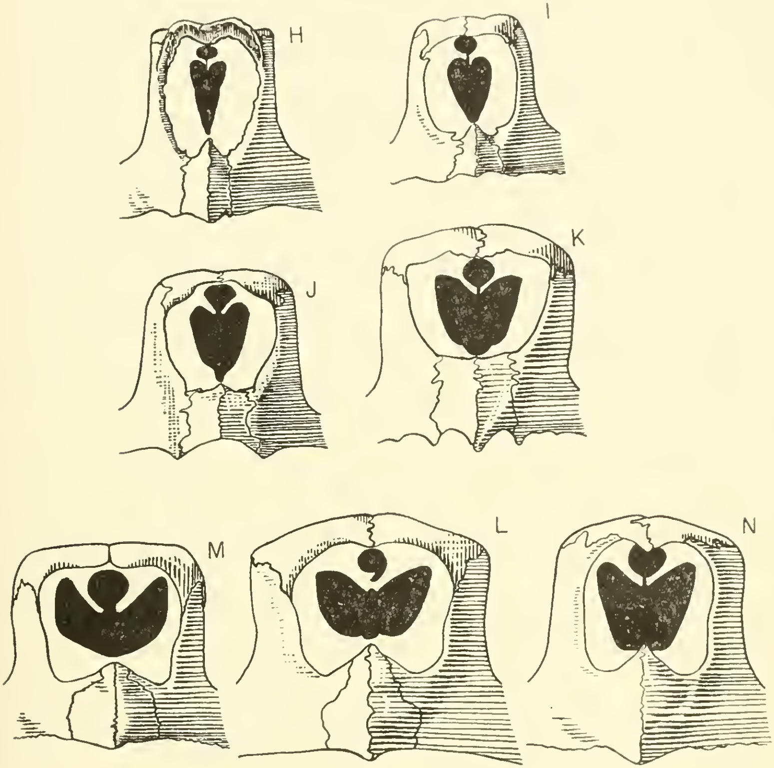

Fig. 11. Interprefrontal space in African testudinids II. *H, Psammobates t. tentorius* (M.C.Z. 3465); *I, Psammobates t. verroxii* (M.C.Z. 21330); *J, Homopus boulengeri* (A.M.N.H. 7107); *K, Homopus areolatus* (A.M.N.H. 17792); *L, Kinixys erosa* (A.M.N.H. 69727); *M, Kinixys homeana* (A.M.N.H. 50725); *N, Kinixys b. belliana* (A.M.N.H. 10029).

(P. Washer del.)

All the osteological characters listed are clearly primitive emydine, with the possible exception of the small, concealed, anterior palatine foramina. The latter feature is considered primitive for testudinines because of its more frequent occurrence in forms regarded as primitive on other grounds. Similarly we treat as primitive for testudinines certain kinds of scutellation unknown in emydines, e.g. complex head scutellation with supranasals, prefrontals and frontals.

No living tortoise exhibits the whole complex of characters[1] here considered primitive. Rather, the members of the Testudininae display various combinations or *mosaics* of primitive and advanced characters, characteristic for each subgroup or lineage.[2]

Superficially considered, the tortoises give a great overall impression of homogeneity — far greater than that provided by the emydines. But when all the evidence is considered and particularly that of the rather good fossil record, it is apparent that this homogeneity is primarily one of *trends* and only secondarily of realized conditions. The records seem to indicate there has been no single sequence, but rather a number of starts from a single point of departure.

The development of advanced characters in the separate lines has been quite independent; the characters have been neither consistently synchronous in appearance nor consistently consecutive nor in any evident way correlated. Each lineage appears to be characterized by the timing of initiation of the several advanced characters, and some lineages indeed are still primitive in certain aspects today, some in others. A discussion of the paleontological evidence supporting these conclusions is not pertinent here and will be presented separately by one of us (EEW). It is however with these considerations in mind that we have framed our diagrams of relationship and based our decisions as to generic rank.

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[1] In our generic definitions we have used many, but not all 27, of the listed characters, or their advanced alternatives. Certain of them have proved too variable within groups, or even within species, to be of taxonomic value. We have also preferred osteological to external characters.

[2] Anyone desiring to check these statements is referred to our numerous figures. Figures 10 and 11 show the condition of the interval between the ventral processes of the prefrontals in most of the African Testudinidae. Figures 19 and 22 furnish examples of head scutellation. Figures 9, 39 and 44 illustrate types of limb scutellation. Figure 12 shows the suprapygal area. Under each genus will be found additional illustrations of, at least, major skull and shell characters. With regard to the latter a warning is necessary. There has been neither the opportunity nor the desire to figure "typical" specimens. Both age and individual variations have been drawn when present in the specimen depicted, and attention has been directed only to the more striking peculiarities or abnormalities.

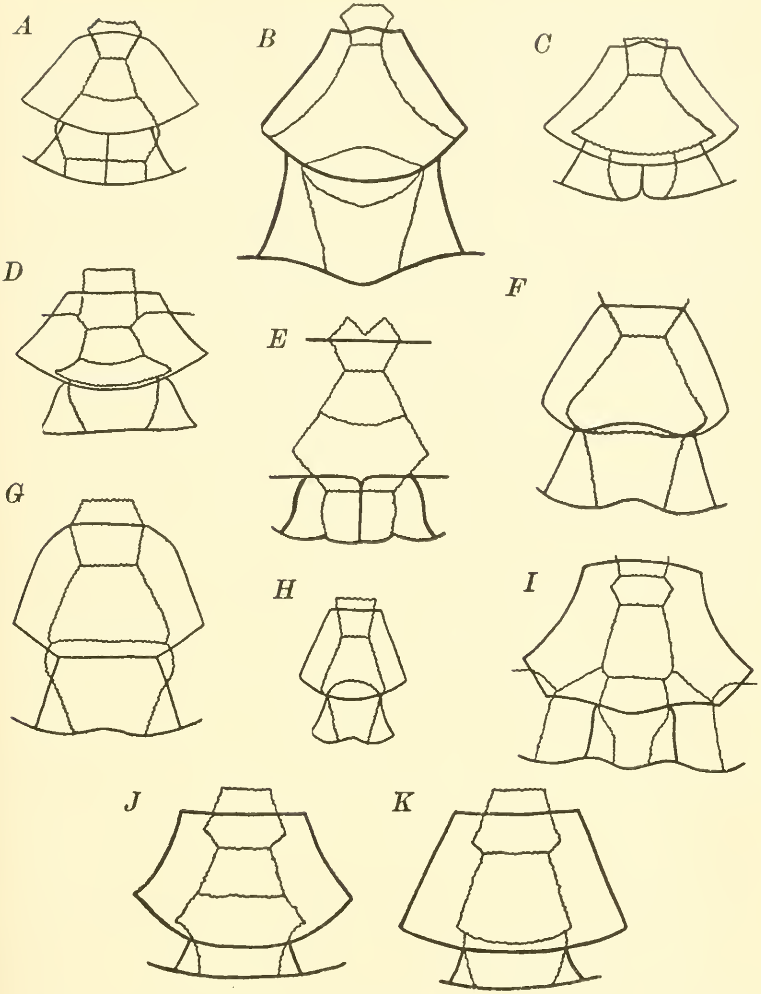

Fig. 12. Pygal patterns in testudinids (diagrammatic). *A, Clemmys caspica leprosa* (Pygal pattern differs within the genus *Clemmys* as currently recognized); *B, Geochelone pardalis babcocki; C, Emys orbicularis; D, Testudo graeca graeca; E, Malacochersus tornieri; F, Psammobates tentorius tentorius; G, Chersina angulata; H. Homopus signatus; I, Kinixys erosa; J, Acinixys planicauda; K, Pyxis arachnoides.*

(P. Washer del.)

In summary, we have come to the following conclusions:

The assemblage that has the Eocene subgenus †*Hadrianus* as its base is a natural grouping and one that appears to us to extend back to the very base of the tortoise line. We have adopted the generic name *Geochelone* for the whole of this rather homogeneous group.

†*Stylemys*[1] and *Gopherus* share a unique specialization — the median premaxillary ridge — and thus clearly belong together but their differences (i.e. in phalangeal formula) point to a very ancient separation at practically the emydine level (see below, p. 255 ff), and we therefore regard them as two quite distinct genera.

Testudo in the strict sense (with *T. graeca* Linnaeus as the type) and *Pseudotestudo* new subgenus (*T. kleinmanni* Lortet type) seem appropriately bracketed together by certain very singular specializations (prootic completely concealed by the parietal,[2] and plastron posteriorly hinged in one or both sexes), but *Pseudotestudo*, which has not been separated from *Testudo* previously, shows some amazing differences in skull structure (see p. 259 and Figs. 20, 24). There are, fortunately, transitional forms in this series and the unity of the genus appears satisfactorily established. The record demonstrates that this lineage is as ancient as that of *Geochelone* (†*Testudo comptoni* of the Eocene of England, see pp. 353 ff below).

For the groups so far mentioned there has been, happily, a fossil record. For the diverse forms of the Ethiopian region there is no such aid. We have proceeded here on the strict ground of degree of morphological difference, influenced, however, by the extra-African evidence that only modest morphological difference may mean very ancient divergence.

We shall argue below that *Acinixys*, *Pyxis*,[3] *Psammobates*, *Chersina*, *Homopus* and *Kinixys* are related. The individual

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[1] As a matter of convention throughout this paper every extinct genus or species is preceded by the symbol †.

[2] This character was first noticed by Baur (1892), who was also the first to point out the "*Testudo leithii*" (i.e. *kleinmanni*) characters that have led us to separate it as a subgenus.

[3] *Pyxis* Bell, 1825, is used rather than *Bellemys* Williams, 1950, 1952, in as much as the supposedly preoccupying name *Pyxis* Chemnitz 1784 is not binomial, and the next use of the name (Humphreys in the "Museum Calonnianum" 1797) has now been outlawed by ruling of the International Commission on Nomenclature (Decision 51).

specializations of each, however, are so marked that we regard each as constituting a separate genus. *Malacochersus* we have found difficult to place, its relationships quite obscure; we suggest that it has branched off at or very near the base of the testudinine series, and we have therefore retained it as a genus also.

Shown on the relationship diagram for the sake of completeness, are two fossil forms of uncertain position. Though imperfectly known, on present evidence they appear to be quite isolated. A few other fossil genera — †*Achilemys* Hay, †*Cheirogaster* Bergounioux, †*Sinohadrianus* Ping — listed in Williams (1952), are impossible to place at this time. Further comment on the African genera will be found under each genus.

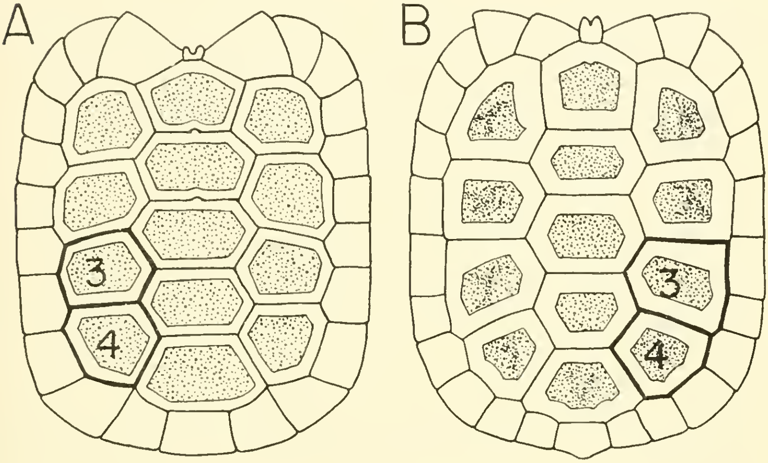

Fig. 13. Third and fourth costals of *Kinixys* for comparison with those of *Homopus*. *A, Kinixys b. belliana* (M.C.Z. 40008); *B, Homopus boulengeri* (M.C.Z. 42231).

(P. Washer del.)

Key to the Genera of Testudininae in Africa[1]

1. Carapace hinged posteriorly *in adults*, usually between 7th and 8th marginals; outer side of fourth costal markedly wider than outer side of third (*in all ages*) (cf. Fig. 13). Range: Africa from 17° north to Bechuanaland and Natal ....*Kinixys* Bell (p. 374)
   Carapace without hinge; outer side of fourth costal subequal to, or smaller than, outer side of third .... 2.
2. Gular single, strongly projecting. Range: South Africa ....*Chersina* Gray (p. 342)
   Gulars paired .... 3.
3. Carapace very flat, flexible, fenestrated; neural bones reduced; plastron with a great fontanelle at all ages. Range: arid areas of Kenya and Tanganyika ....*Malacochersus* Lindholm (p. 283)
   Carapace more or less convex, rigid, solid; neural bones unreduced; plastron with a fontanelle only in hatchlings...................... 4.
4. Maxilla unridged; anterior neurals hexagonal or quadrilateral........ 5.
   Maxilla ridged (except in *Testudo kleinmanni* of Egypt); anterior neurals octagonal and quadrilateral .... 6.

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[1] Some divergence of opinion occurs with regard to the advisability of breaking up *Testudo* into several genera — first attempted by Fitzinger (1835) and more recently by Hewitt (1931: 1933b). Uninfluenced by either of these authors, my colleague, Dr. E. E. Williams, is fully convinced by his own studies that certain structural differences indicate so early a divergence among the several groups as to justify their recognition as full genera. He considers their numerous similarities, when not due to common ancestry, are attributable to parallel evolution or due to convergence. Assumptions as to which characters reflect close affinity, and which are to be discarded as subsequent convergences, seem somewhat speculative to me in view of the fact that the fossil history of five of the seven suggested genera is completely unknown.

More impressed than my colleague by the many similarities (which may be seen by comparing the several generic descriptions), I take a more pragmatic view of the purposes of nomenclature. A multiplicity of genera that are based on single characters, or aggregations of characters that in themselves may be subject to variation, and sometimes difficult to observe or evaluate, tends to nomenclatorial confusion. For an instructive example of the extent to which genera-making can burden posterity, one has only to turn to the 28 synonyms of *Trionyx* (cf. p. 420).

Fragmentation of *Testudo* offers the advantage of separating into groups those species whose characters are believed to indicate close affinities. On the other hand, this result can be achieved by treating such groups as subgenera, an arrangement that has the additional advantage of emphasizing their over-all relationship, though to this my colleague's views naturally prevent him from subscribing (cf. Fig. 8). To me, as a working herpetologist, the desirability of maintaining as stable a nomenclature as possible outweighs the advantages of emphasizing a new theory of phylogeny (that may not find general acceptance or have to be set aside when more is known of the fossil history involved) by raising the several groups to full generic status. In the conservative view, *Geochelone, Psammobates* and *Chersina* would be retained as subgenera of *Testudo*.

Possibly this attitude is a mistaken one, so for the purposes of this revision I defer to a current trend in herpetology. This is done in the confident belief that — as increasing knowledge reveals the disadvantages of a multiplicity of genera that are difficult to define — in due course there will be a return to the larger units as is even now occurring in South African ornithology following an extended period of nomenclatorial chaos. A.L.

5. Carapace somewhat depressed; vertebral shields never conical; each gular usually broader than long (cf. Fig. 14); anterior palatine foramen large, conspicuous; maxillary bone not entering roof of palate. Range: South Africa ....*Homopus* Duméril and Bibron (p. 352)

   Carapace rather convex; vertebral shields sometimes conical; each gular usually as long or longer than broad; anterior palatine foramina small, concealed; maxillary bone entering roof of palate. Range: South Africa ....*Psammobates* Fitzinger (p. 294)

6. Supranasal scales present; nuchal scale present; femoral tubercles absent or only 1; suprapygal single or divided transversely; posterior lobe suprapygals 2, a larger anterior one embracing a smaller posterior one of plastron (in life) more or less clearly movable in one or both sexes; prootic usually concealed dorsally by the parietals. Range: North Africa ....*Testudo* Linnaeus (p. 254)

   Supranasal scales absent; nuchal scale absent; femoral tubercles 2 or 3; suprapygals 2, a larger anterior one embracing a smaller posterior one (cf. Fig. 12B); posterior lobe of plastron never movable; prootic usually well exposed dorsally. Range: Tropical and South Africa.... *Geochelone* Fitzinger (p. 221)

Genus GEOCHELONE Fitzinger

1835. *Geochelone* Fitzinger, Ann. Wiener Mus., 1: pp. 111, 112, 122. Type: *Testudo stellata* Schweigger = *T. elegans* Schoepff (designation by Fitzinger: 1843).

1872c. *Centrochelys* Gray, Appendix Cat. Shield Rept. Brit. Mus., p. 5. Type: *Testudo sulcata* Miller (by monotypy).

1873b. *Stigmochelys* Gray, Hand-List Shield Rept. Brit. Mus., p. 5. Type: *Testudo pardalis* Bell (by monotypy).

1933b. *Megachersine* Hewitt, Ann. Natal Mus., **7**, p. 257. Genotype: *Testudo pardalis* Bell (by original designation).

Definition. Skull with triturating surface of maxilla strongly ridged; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina small, concealed in ventral view; prootic typically well exposed dorsally and anteriorly; quadrate usually enclosing stapes; surangular subequal in height to prearticular; neck with second, third or fourth centrum biconvex.

Carapace never hinged; typically the anterior neurals alternately octagonal and quadrilateral; outer side of third costal scute about as long as, or longer than, that of the fourth; no submarginal scute; suprapygals 2, the anterior larger, bifurcating posteriorly to embrace the smaller posterior element, which (in post-Eocene forms) is crossed near its middle by the sulcus between the fifth vertebral and the supracaudal.

Plastron not hinged; gular region more or less thickened and produced; gulars single or paired, longer than broad.

Range. Galapagos Islands; South America; Africa; Madagascar and other islands of the Indian Ocean (including Ceylon); southeastern Asia (including India).

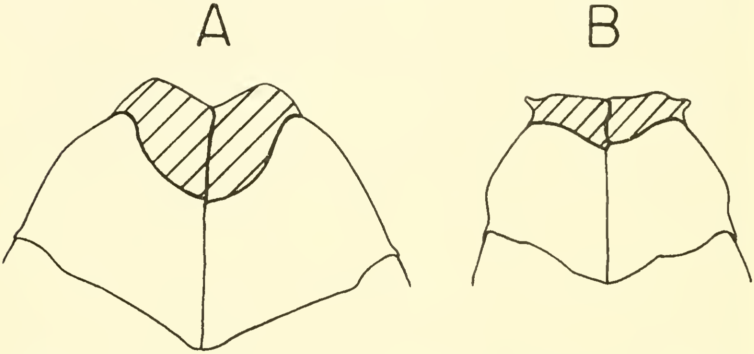

Fig. 14. Typical shape of gular scutes in *Psammobates* for comparison with those of *Homopus*. *A*, *Psammobates t. verroxii* (M.C.Z. 42222); *B*, *Homopus areolatus* (M.C.Z. 17524).

(P. Washer del.)

Fossil record. Well represented in the Tertiary and Pleistocene of North America and the Tertiary of Europe; known from the Oligocene and Pliocene of Asia; from the Oligocene and Miocene of Africa; recorded in South America only since the Miocene, and in the West Indies from the Pleistocene.

Remarks. The genus *Geochelone* tends to large size. In carapace length some fossil and Recent species may exceed a meter in length and none attains to less than 250 mm.

Characteristic of this genus is the fact that the shell takes on certain specializations early in its phyletic history. Earliest of these are a thickened, produced gular region and the peculiar pygal pattern with the first suprapygal embracing a smaller second one, both already present in †*Hadrianus* of the Eocene.

TABLE 3

Characters of the subgenera of *Geochelone:* there are additional habitus features.[1]

Subgenus	Living species	Nuchal present	Supra-caudal divided	Neurals hexagonal	First dorsal vertebra elongate	Gulars single	Gulars bifurcate	Pectorals narrowed	Nares expanded vertically	Postotic fenestra concealed	Entoplastron crossed by humeropectoral sulcus
†*Hadrianus*	0	+	+	+	—	—	—	—	—	—	—
Asterochelys	2	+	—	—	—	±	—	—	—	—	—
Aldabrachelys	2	±	±	—	—	—	—	—	+	—	—
Geochelone	4	—	—	—	—	—	—	+	—	—	—
Cylindraspis	2	—	—	—	—	+	—	—	—	—	—
†*Megalochelys*	0	—			—	—	+	—			—
Manouria	2	+	+	—	—	—	—	+	—	+	—
Indotestudo	4	+	—	—	—	—	—	—	—	—	+
†*Hesperotestudo*	0	+	—	—	—	—	—	+	—	—	±
Chelonoidis	4	—	—	—	—	—	—	—	—	+	—
†*Monachelys*	0				+				—	—	—

[1] For types and content of subgenera here recognized (except *Aldabrachelys* nov.) see Williams (1952).
† Indicates a fossil form or group.

The alternate octagonal-quadrilateral neural pattern arises a little later, but even in †*Hadrianus* one of the neurals may sometimes be octagonal and several of them are often hexagonal short-sided behind. The latter conditions are intermediate, indicating the establishment of a trend which, at least in North America, culminated in the perfected pattern in the Oligocene. An octagonal-*cum*-quadrilateral pattern for the anterior neurals is now very characteristic of the genus, though by no means invariable.

Other shell specializations occur irregularly within the genus. The nuchal scute is lost in many species. The supracaudal is usually single in post-Eocene subgenera with the exception of *Manouria*. The pectoral scutes tend to become narrowed, moderately so in the African species, to an extreme degree in the typical members of the fossil American subgenus †*Hesperotestudo*. In *Cylindraspis,* and independently in *Asterochelys yniphora,* the gulars have fused to form a single scute, while in the subgenus †*Megalochelys* the gular region becomes not merely produced but strongly bifurcate. Variation in height of shell occurs also (contrast *G. radiata* and *G. emys*) as well as striking differences within a species (cf. *G. pardalis*). The humeropectoral sulcus crosses the entoplastron well anteriorly in the subgenus *Indotestudo,* in which this feature was established early (†*G. kaiseni*[1] and †*G. nana*[1] of the Oligocene of Mongolia). The same character occurs irregularly in a number of fossil species elsewhere, e.g. †*G. uintensis*[2] and †*G. costaricensis*[3] of North America.

In contrast to the shell, the skull in most of the subgenera of *Geochelone* is remarkably primitive (for a testudinine) and surprisingly uniform. However, there is a tendency, several times repeated, for a downgrowth of the opisthotic to more or less conceal the postotic fenestra in posterior view. Apart from this the only striking modification occurs in the Seychelles-Aldabra tortoises and †*G. grandidieri* of Madagascar. In these the external naris is extraordinarily extended dorsoventrally in conjunction with a distortion of the whole front of the skull, giving

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[1] C. W. Gilmore, 1931, Bull. Am. Mus. Nat. Hist., **59**, pp. 213-257.

[2] C. W. Gilmore, 1915, Mem. Carnegie Mus., **7**, pp. 101-161.

[3] A. Segura, 1944, Escuela de Farmacia, Guatemala, **6**, Nos. 73-74, pp. 9-29; Nos. 75-76, pp. 16-25; Nos. 77-78, pp. 13-24.

the latter a bulbous appearance. Since this modification appears to be quite as distinctive as any of the features, or combinations of features, that distinguish subgenera of *Geochelone,* and since the minor lineage involved seems to be quite a distinct one, we here propose a new subgenus for *gigantea, sumeiri* and †*grandidieri,* to be called:

ALDABRACHELYS new subgenus

Type species: *Testudo gigantea* Schweigger

Definition. External naris higher than wide; quadrate enclosing stapes or not; postotic fenestra not concealed in posterior view; nuchal present or absent; typically the anterior neurals alternately octagonal and quadrilateral; first dorsal vertebra short and stout; supracaudal divided or undivided; gulars paired but not divergent; entoplastron not crossed by the humeropectoral sulcus.

Range. Aldabra and Madagascar.

The continental African species of *Geochelone* belong to the nominate subgenus, defined as follows:

Subgenus GEOCHELONE Fitzinger

1835. *Geochelone* Fitzinger, Ann. Wiener Mus., 1, pp. 108, 112, 122: as a subgenus. Type species: *Testudo stellata* Schweigger = *T. elegans* Schoepff.

Definition. External naris not higher than wide; quadrate enclosing stapes; postotic fenestra not concealed in posterior view; nuchal absent; anterior neurals alternately octagonal and quadrilateral; first dorsal vertebra short and stout; supracaudal undivided; gulars paired but not divergent; entoplastron not crossed by humeropectoral sulcus.

Distinguishing marks. The African members of this subgenus are easily distinguished from other African tortoises. They are the only ones with 2 or 3 subconical tubercles on the hinder side of each thigh, and are by far the largest in adult size.

Range. Africa; Ceylon; India and Burma.

Fossil record. Not known fossil with any certainty except in the Tertiary of Europe. Probably the fossil giant tortoises of the islands of Malta, Minorca and Teneriffe belong to this subgenus.

Remarks. The living members of the subgenus divide into two species groups, an Asian one consisting of *G. elegans* and *G. platynota,* and an African one comprised of *G. sulcata* and

Fig. 15. Locality records of *Geochelone* in East Africa north of the Equator.

(P. Washer del.)

G. pardalis. The African species are much the larger and differ also in not possessing the tail claw which is present in the Asian forms. Both species groups appear to have been present in Europe during the Tertiary.

The large tortoises of Africa present a relatively simple picture. The largest and most northerly species, *G. sulcata,* is confined to a rather arid belt extending from Senegal to Eritrea, consequently inhabiting mostly the Sudanese subprovince of the Savannah Province of botanists, but also present in the northern portion of the Northeastern subprovince. *G. pardalis babcocki,* relatively uniform in all its characters, occurs southwards from the southern Sudan and Ethiopia throughout most non-forested areas of the eastern half of the continent, westwards into Angola and the northern half of Southwest Africa. Known from very few specimens is *G. p. pardalis,* which occupies, or did occupy (it is perhaps now extinct), a very limited region in western South Africa.

Though available evidence shows *G. sulcata* to be allopatric to *G. pardalis* they have always been separated specifically, a view we see no reason to reverse. *G. sulcata* differs more from the two *pardalis* forms than do the latter from each other. The frontal scute characteristic of *sulcata* is lacking in all the *pardalis* we have seen. While the pale color of *sulcata* is approached by individual *pardalis,* especially those from arid regions that have lost most of their black pigmentation, no *pardalis* is known to us in which the black flecking is entirely absent. More significant is the striking difference in convexity displayed by the much larger *sulcata* when contrasted with its nearest neighbor, *pardalis babcocki.*

The situation in regard to the two subspecies of *G. pardalis* is sufficiently confused to require some extended discussion. The subspecies *babcocki* was separated from the typical race by one of us (Loveridge:1935c) when he discovered that two specimens from Southwest Africa in the collection of the Museum of Comparative Zoology did not correspond to the form known to him in East Africa. Photographs of these two Southwest African tortoises are presented here for the first time and contrasted with East African material. The markings of the adults

TABLE 4

Characters of the African species and subspecies of *Geochelone*

Character	*sulcata*	*p. babcocki*	*p. pardalis*
frontal scute	usually present and large	absent	absent
convexity of carapace	flattened dorsally	very convex	flattened dorsally
shape of gular region	somewhat produced and notched	not or but slightly produced, not or but slightly notched	slightly produced, shallowly notched
enlarged scales on forelimb	juxtaposed	usually not juxtaposed	not juxtaposed
color of adult	uniform horn color	yellow, richly variegated with black; or rarely mostly yellow	yellow to greenish variegated with black
color of hatchling	pale yellow, the dorsal shields edged with brown; plastron pure yellowish white	light brown, the dorsal shields broadly edged with black and typically containing a red-bordered areola within which is a *single* spot centrally located and usually united to the posterior areolae, *or*, in the extreme north, the central spot flanked by two lateral ones[1], plastron as in *p. pardalis.*	dull yellow, the dorsal shields narrowly edged with black and containing a red-bordered areola within which is a *pair* of spots separated by a light vertebral line: plastron dull yellow, sutures of the shields more or less margined with black.
maximum size recorded	762 mm.	585 mm.	432 mm. (type)

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[1] As in a specimen from Mongalla, Sudan, photographed for us by Dr. J. Eiselt of the Vienna Museum; also an Ethiopian tortoise figured by Vaillant (1904a) as *calcarata.* In some Kenya hatchlings the areolar spots may be altogether absent.

are probably indistinguishable, but in juveniles the marked flattening of the carapace is usually correlated with a color pattern so distinctive that the *nomen nudum biguttata*[1] was proposed in a footnote by Cuvier (1829:10; Duméril and Bibron: 1835).

Although twenty years have elapsed since the description of *p. babcocki,* it is still difficult to clearly define the ranges of the two forms because of the paucity of *p. pardalis* material with good locality data. A number of specimens at the British Museum (measured at the time *babcocki* was described) appear to belong to *p. pardalis,* but are labeled only ''South Africa.'' In addition to these the only specimens definitely known to us are the following: Bell's type of *pardalis* with the locality ''Cape of Good Hope''; the adult shell (M.C.Z. 16713) labeled as from Kolmanskop (Dr. W. Beetz coll.); a hatchling (M.C.Z. 22473) from Aroab (W. S. Brooks coll.); the young specimen figured by Duerden (1907b:fig. 7) and Hewitt (1937e:pl. i, fig. 2; pl. ii, figs. 1-2).[2]

We have also hesitantly assigned to the nominate race the Archer tortoise from Keetmanshoop because that locality is so near to Aroab, and, because of their proximity to the type locality of *pardalis,* the Delalande specimens from Oliphants River, Cape Province. However, one Delalande tortoise in the Paris Museum, labeled as the type of *biguttata* Cuvier, with locality ''Cap,'' is an intergrade — being as convex as *p. babcocki* but with the juvenile pattern of *p. pardalis.*

For further remarks on this subject see the footnote on p. 250.

Key to the Species and Subspecies of Geochelone *in Africa*

1. Carapace horn-color or brownish, *uniform;* frontal shield usually present, large. Range: Eritrea and Ethiopia west to Senegal .... *sulcata* (Miller) (p. 230)

   Carapace yellow or olive more or less richly variegated with black; frontal shield absent 2

2. Carapace distinctly convex, its height being included in its length (in a straight line) from 1.61 to 2.11 times; vertebral shields of young with a *central* black spot. Range: Anglo-Egyptian Sudan and Ethiopia

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[1] Erroneously cited as *T. bipunctata* by Gray (1831c:12).

[2] Thanks to Dr. Robert Mertens, we have a photograph of two additional specimens from Rehoboth, south of Windhoek, Southwest Africa.

south to Natal, west through Cape Province to Southwest Africa (where it meets with the typical form, but is dominant north of 27° S.) and southern Angola ....*p. babcocki* (Loveridge) (p. 235)

Carapace distinctly flattened dorsally, its height being included in its length (in a straight line) from 2.02 to 2.62 times; vertebral shields of young with a pair of lateral black spots *separated by a light longitudinal line.* Range: southern Southwest Africa (in former times possibly extending south to the Cape Peninsula, as the type locality was said to be the Cape of Good Hope) ......*p. pardalis* (Bell) (p. 251)

GEOCHELONE SULCATA (Miller)[1]

1780. *Testudo sulcata* Miller, Icones animalium et plantarum (Various Subjects of Natural History . . .), pl. xxvi: "India occidentali" (in error).
1789. Gmelin, 1045.
1792. Schoepff, p. 156 (German ed.).
1796. Shaw, *in* Miller (vide supra), 53, pl. xxvi.
1800. Bechstein, *in* Lacépède, 346.
1801. Schoepff, p. 135.
1802b. Daudin, 313.
1802. Shaw, 39.
1812. Schweigger, 323, 452.
1814. Schweigger, 53, 55 (reprint of 1812).
1831c. Gray, 11.
1835. Duméril and Bibron (part), 74, pl. xlii, figs. 1-1a.
1844. Gray, 7.
1845b. Rüppell, 297.
1851. Guichenot, 189.
1855. Gray, 9.
1860. Duméril, 162.
1862a. Strauch, 78.
1865. Strauch, 22.
1870a. Steindachner, 326.
1872b. Gray, 4, *in* Sowerby and Lear, pls. xvii-xviii.
1884a. Rochebrune, 13 (ignored).
1890. Strauch, 52.
1905. Barbier, 83, pl. iii.
1912. Siebenrock, 214, fig. 2.
1924a. Werner, 263, figs. —.
1928. Flower, 654, figs. 1-2.

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[1] *Testudo Schöpfi* Fitzinger (*nom. nud.*), 1826, sometimes referred to the synonymy of *sulcata*, was subsequently synonymized by Fitzinger with *Kinixys erosa*.

1929. Flower, 32.
1937a. Flower, 9.
1784. *Testudo calcarata* Schneider, Samml. Vermischt. Abhandl. Zool. p. 317, pl. — (based on Miller's figure of *sulcata*).
1835. Rüppell, 4.
1880c. Vaillant, 33, 88, pl. xxvi, fig. 3.
1889a. Boulenger, 159.
1891. Prato (not seen).
1893. Trimen, 79.
1904a. Vaillant (part), 186 (fig. of juv. is *p. babcocki*).
1906. Kammerer, 48, fig. 7.
1906a. Siebenrock, 821.
1908c. Kammerer, 769, figs. 6-7.
1908. Werner (1907), 1826.
1909a. Siebenrock, 521.
1911a. Masi, 34.
1914a. Pellegrin, 122, pl. i, fig. 2.
1925b. Flower, 924.
1928b. Scortecci, 334.
1930a. Scortecci, 215.
1950. Williams, 550.
1820. *Chersine calcarata* Merrem, 32.
1831c. *Testudo radiata* var. *senegalensis* Gray, Syn. Rept., p. 4; Senegal.
1836. *Geochelone sulcata* Fitzinger, 122.
1855. *Geochelone senegalensis* Fitzinger, 251.
1869c. *Peltastes ? sulcatus* Gray, 173.
1870c. Gray, 656.
1870e. Gray, 12.
1873b. *Centrochelys* (*Peltastes*) *sulcatus* Gray, 13.
1873c. Gray, 725.

Further citations of "*sulcata*" and "*calcarata*" will be found under *Geochelone p. babcocki*.

Synonymy. The use of the name *sulcata* has been dealt with at some length by Siebenrock (1912:214). As the copy of Miller's work in the library of the Museum of Comparative Zoology lacks the pertinent part of the text, and plate xxvi bears no name, we appealed to H. W. Parker for help in verifying Siebenrock's conclusions. Dr. Parker replied that though plate xxvi in the British Museum copy is also unnamed, there is a list of plates which states:

"Tabula XXVI

Fig. A. *Testudo sulcata.* Lin. Syst. Nat. Classis III. Ordo I. Genus CXIX. Spec. Habitat in India occidentali.
B. Pars inferior.
C. Caput magnitudine naturali."

Thus no doubt remains as to *sulcata* being the correct name to apply to this species. Furthermore, Parker points out that plate xxvi appeared in Part 5, which, according to Sherborn and Iredale (1921, Ibis:302-309) was published apparently in 1779 or 1780.

Common names. Spurred Tortoise (preferred); Grooved Tortoise (Flower); *abu gatta* (Arabic in Kordofan, *fide* Fitzinger, who translates it as "father of covers"); *abu gefne* (Arabic in Dongola: Rüppell); *gafot* (at Massaua: Rüppell).

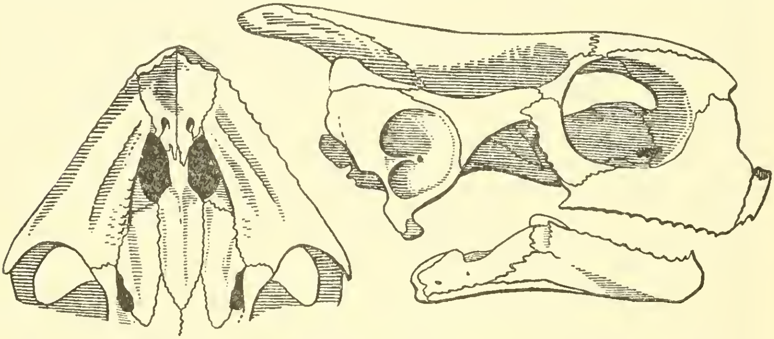

Fig. 16. Skull of *Geochelone sulcata* (B.M. 1904.7.28.1).
(S. McDowell del.)

Illustrations. For most people Miller's fine plate (1780) and its reproductions will be unavailable, but Sowerby and Lear's (1872) (our Plate 1) are equally good. Werner (1924a) and Flower (1928) have figured the young.

Description.[1] Beak weakly hooked, edge of jaws strongly dentate; prefrontal large, divided longitudinally; frontal usually large, rarely broken up; remaining upper head shields small, irregular; forelimb anteriorly with large unequal, *juxta-*

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[1] Based chiefly on the head, limbs and shell of an adult ♀ (M.C.Z. 11975) from Katsina Emirate; together with notes on British Museum material as of 1953, two without data in the A.M.N.H., and one without data in the C.N.H.M.

posed or imbricate scutes, forming 3-6 longitudinal and 6-7 transverse series from elbow to outer claw; claws 5; posterior side of thigh with 2-3 large conical tubercles; heel with large, conical, spurlike, bony tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace flattened dorsally, sides descending abruptly, deeply notched in nuchal region, anterior and posterior margins reverted and serrated, not more than twice as long as deep; dorsal shields concentrically grooved; nuchal absent; vertebrals 5, not convex, the second, third and fifth much broader than long, broader than the costals; costals 4, not forming an angle with the marginals; marginals 11; supracaudal undivided.

Front lobe of plastron somewhat produced and bifid; gulars paired; pectorals very narrow, their anterior border usually straight, widening abruptly towards the axillary notch; axillaries 2; outer moderate to small, inner minute; inguinals 2, outer large to moderate, inner small, meeting femoral; hind lobe deeply notched posteriorly, angular or crescentic.

Plastral formula: Abd>h>f>g>or=p>an.

Color. Carapace of juvenile (50 mm.[1]) pale yellow, the shields with narrow brown sulci. Plastron yellowish white.

Carapace of adult brownish to horn color, uniform. Plastron yellowish, uniform.

Size. Carapace length of ♀ (M.C.Z. 19975) from Katsina Emirate, 670 mm., breadth 470 mm., height 270 mm. Apparently exceeded by that of a specimen mentioned below.

The carapace of a young ♂ hatched at Giza Zoo on 5.x.10, was about 50 mm. long by 45 mm. broad at time of hatching. On 26.iii.28 this tortoise measured 762 mm. (30 inches) in length and weighed 184 lbs. (Flower:1928). The 800 mm. carapace from Eguei mentioned by Pellegrin (1914a) may have been measured over the curve.

Longevity. Two tortoises hatched at Giza Zoo on 5.x.10, lived for 19 years, 9 months, 26 days, and 20 years, 7 months, 22 days respectively, but were possibly surpassed by an adult ♂ measuring "28 inches across the shell" which had been in captivity "over 38 years" when presented to the London Zoo on 3.x.31. It died at Whipsnade on 19.xii.35 when reputedly over 42 years old (Flower:1937a).

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[1] Cf. Flower (1928:654).

Enemies. The flesh of a Spurred Tortoise is "never eaten" by the natives, according to Rüppell (1835). However, his informants may have been Moslems.

Habitat. In the Sudan, according to Werner (1908:1826) *sulcata* extends no further south than Kordofan, being separated by the swamps of the Bahr el Gebel region from the range of *p. babcocki*, still known only from points south of Bor on the White Nile — i.e. about 5° N.

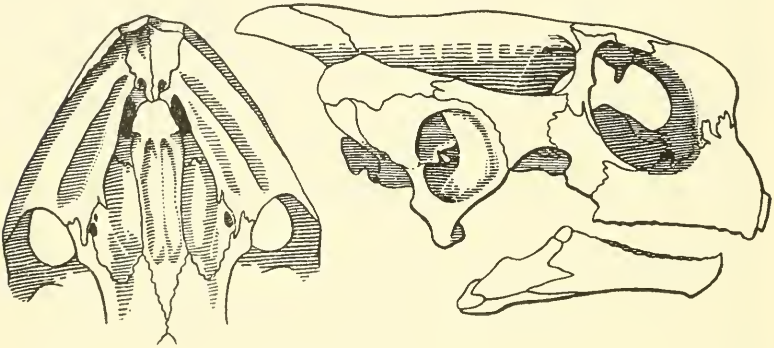

Fig. 17. Skull of *Geochelone pardalis babcocki* (A.M.N.H. 7703). Condylobasal length 81 mm.

(S. McDowell del.)

Localities. Sudan: Dongola;* Jebel Teiga, 30 miles west of Jebel Medob (B.M. specimen seen by E.E.W.); Kordofan; Omdurman (bought in market by Werner:1924a). *Eritrea:* Chenafena; between Cheren (Chire) and Mareb (Marembe) River;[1] Godolefassi; Massaua Coast. *Ethiopia:* Shoa (Chona) near Awash (Heonacha) River;[1] Takkaze [River]. *French Equatorial Africa:* Eguei. *Nigeria:* *Katsina Emirate. *Senegal:* Dagana; near Dakar; Saint Louis. *French West Africa:* Mauretania; Sudan and Niger Territories (*fide* Villiers *in litt.*).

Range. Trans-Africa from Eritrea west to Senegal in the vicinity of 15° N.

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[1] Mons. Paul Chabanaud informs us that Lefebvre left no map of his itinerary that would enable us to fix his localities with precision. Lefebvre's orthography, combined with some misprinting, renders the identification of his place names with currently recognized localities somewhat difficult. Thus "Chona", a misprint for Choua, = Choa or Shoa.

Erroneously reported from Antilles (Merrem); Buenos Aires (A. Duméril); Cape of Good Hope (A. Duméril); Giza, Egypt (Werner); Nyasaland (Johnston); Patagonia (Duméril and Bibron; Port Natal (A. Smith); South Africa (Boulenger). The South American records are due to confusion with *Geochelone chilensis* (see Siebenrock:1912).

GEOCHELONE PARDALIS BABCOCKI (Loveridge)

1831c.	*Testudo pardalis* Gray (part[1]), 12. pl. iii, fig. 3.
1835.	Duméril and Bibron, 71.
1835.	Temminck and Schlegel, 73.
1844.	Gray, 7.
1851.	Duméril and Duméril, 4.
1854a.	Peters, 215.
1855.	Gray, 9.
1862a.	Strauch, 77.
1863b.	Gray, 382.
1865.	Strauch, 22.
1866b.	Peters, 887.
1867a.	Bocage, 217.
1869a.	Peters, 11.
1870c.	Gray, 6.
1872c.	Gray, 4.
1873b.	Gray, 5.
1878.	Fisk, 790.
1878a.	Peters, 202.
1880c.	Vaillant, 8, 33, 88.
1882a.	Peters, 2.
1884a.	Rochebrune, 11 (but in error).
1886.	Vaillant, 137.
1889.	Boettger, 281.
1889a.	Boulenger, 160.
1890.	Strauch, 52.
1893a.	Boettger, 9.
1893b.	Boettger, 113, 122.
1893.	Trimen, 79.
1894c.	Günther, 85.
1895a.	Bocage, 3.
1896a.	Bocage, 97.
1896a.	Boulenger, 546.

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[1] Many of the following references might equally well be considered as "(part)" for they mention Bell's type, though their material is obviously *G. p. babcocki.*

1896c.	Boulenger, 15.
1896.	Tornier, 3.
1897g.	Boulenger, 277.
1897.	Johnston, 361.
1897.	Meek, 184.
1897.	Tornier, 63.
1898.	Jeude, 3.
1898.	Johnston, 361.
1898.	Sclater, W. L., 96.
1898.	Tornier, 282, fig. 1.
1899.	Ansorge, 288.
1899a.	Mocquard, 218.
1899.	Siebenrock, 566, pl. iii, figs. 34-36.
1900.	Peel, 333.
1900b.	Tornier, 582.
1901.	Lampe, 191.
1902d.	Boulenger, 445.
1902.	Scherer, 255.
1905.	Neumann, 389.
1905c.	Tornier, 366.
1906a.	Duerden (not seen).
1906.	Kammerer, 48.
1906a.	Siebenrock, 823, fig. 3.
1907a.	Boulenger, 6.
1907a.	Duerden, 9.
1907.	Lönnberg, 1.
1908.	Chubb, 220.
1908a.	Kammerer, 741, figs. 3-5.
1908b.	Mocquard, 557.
1908.	Werner (1907), 1826.
1909a.	Chubb, 592.
1909b.	Chubb, 34.
1909a.	Siebenrock, 522.
1910.	Siebenrock, 700, 716.
1910a.	Werner, 300.
1911.	Griffini, 3.
1911.	Lampe, 146.
1911.	Lönnberg, 7.
1911a.	Masi, 29.
1911d.	Sternfeld, 49.
1912b.	Boulenger, 329.
1912c.	Sternfeld, 198, 200.
1912b.	Werner, 433.

1913c. Nieden, 54.
1913d. Werner, 40.
1914a. Hewitt, 244.
1915. Werner, 330.
1916. Calabresi, 42.
1919. Schmidt, 600.
1921d. Loveridge, 50.
1922. Falk, 163, fig. —.
1923g. Loveridge, 925, 931.
1924b. Loveridge, 2.
1925b. Flower, 925.
1927. Calabresi, 37.
1928. Cott, 952.
1928d. Loveridge, 49.
1929. Flower, 32.
1929h. Loveridge, 14.
1929. Rose, 188.
1931. Hewitt, 499.
1932b. Parker, 340.
1933h. Loveridge, 206.
1933a. Power, 214.
1934a. Mertens and Müller *in* Rust, 9.
1934. Pitman, 307.
1935b. FitzSimons, 303.
1937. Buxton, 101.
1937a. Flower, 9, 37.
1937b. Monard, 146.
1937. Ruckes, 103.
1939b. FitzSimons, 18.
1940a. Scortecci, 126.
1943. Scortecci, 270, 282.
1944. Leakey, 396, figs. —.
1946. Bally (1945), 163.
1946. Cairncross, 395, pl. i.
1946. Mitchell, 20.
1947. Stevenson-Hamilton, 319.
1950. Williams, 551, 552.
1952. Bally, 236.
1954. Battersby, 248
1954. Noël-Hume, 75, pls. i-iv.
1893a. *Homopus signatus* Boettger (part), 8 (juv. Shell ex Great Namaqualand).
1885. *Testudo sulcata* Smets (not of Miller: 1780), 8.

1904. *Testudo calcarata* Vaillant (part; not of Schneider), 186, figs. (are clearly of a juvenile *p. babcocki*).
1926. Tortoise, Bowker, 37.
1942. Hull, 125.
1948. Cooper, 11.
1933b. *Megachersine pardalis* Hewitt, 257.
1935c. *Testudo pardalis babcocki* Loveridge, Bull. Mus. Comp. Zool., **79**, p. 4: Mount Debasien, Karamojo, Uganda.
1936h. Loveridge, 18.
1936j. Loveridge, 220, pl. i, figs. 1-2.
1937f. Loveridge, 492, 495.
1937d. Mertens, 2.
1947g. Loveridge, 136.
1949b. Loveridge, 19.
1953e. Loveridge, 158.
1955a. Mertens, 35, pl. iii, figs. 9-10; pl. xxii, figs. 129-134.
1955b. Mertens, 52.
1937a. *Geochelone pardalis* Hewitt, 789, pl. x, fig. 6.
1937e. Hewitt, 3 and G; pls. i, figs. 1, 3, 4; ivA, fig. 4; xxvii, fig. 4.
1948a. Archer, 74, figs.
1948b. Archer (part), 75, figs. (omit Keetmanshoop).
1950. Rose, 338, figs. 203-205.
1937b. *Testudo pardalis pardalis* Mertens (not of Bell), 5.
1955. Hellmich, 14, 15 (of reprint).

Common names. Eastern Leopard Tortoise; Mountain Tortoise. The first name, used by Gray (1855:9), is preferable, for the species occurs on the plains as well as on mountains, where it may be more frequently encountered today possibly as a result of its having been killed off on the lowlands. *Akuma*[1] (Karamojong); *anassi* (at Cape Delgado; Peters); *berg-schilpad* (Afrikaans: Bowker); *camba* (at Tete:Peters); *chepkoikochet* (Kipsigis and Nandi:Hull); *ekudu* (Samia:Hull); *ekutu* (Kitosh: Hull); *enkuru* (Kisii:Hull); *fulabomba* (at Capangombe:Bocage); *furgobi*[1] (Swahili); *ikudu*[1] (Gishu); *kamba*[1] (Nyungwe at Tete); *likudu*[1]: (Maragoli; Tereki); *lukutu* (Bunyore and Hanga:Hull); *malugangi*[1] (Gogo); *mfudi*[1] (Ganda); *nguru*[1] (Taita:Peters); *opuk* (Luo:Hull); *prokoch* (Suk:Hull).

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[1] *Fide* Loveridge. Mitchell gives *furu* and *kamba* for tortoises but no evidence that *Geochelone* occurs at Dowa or Fort Maguire.

Description.[1] Beak scarcely to strongly hooked, edge of jaws strongly dentate; prefrontal large, frequently single but usually divided longitudinally; frontal broken up; remaining upper head shields small, irregular; forelimb anteriorly with large, unequal, usually scattered or rarely juxtaposed, generally imbricate

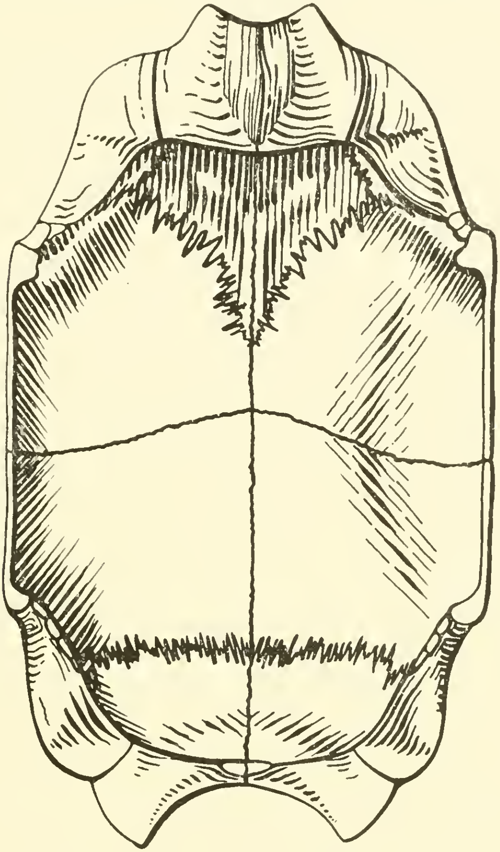

Fig. 18. Internal view of plastron of *Geochelone pardalis babcocki* (M.C. Z. 40004) (x ⅓).

(P. Washer del.)

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[1] Based entirely on material in the M.C.Z. unless otherwise stated.

scutes, forming 3-4 longitudinal and 7-9 transverse series from elbow to outer claw; claws 5; hinder side of thigh with 2 or more very large, rarely small, conical tubercles; heel with large, conical, spurlike tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace very convex, sides descending abruptly, deeply notched in nuchal region except in the very young, anterior margins not, and posterior margins only sometimes, expanded, reverted, and more or less strongly serrated; dorsal shields concentrically striated, sometimes swollen, subconical or convex; nuchal absent; vertebrals 5, rarely 6,[1] more or less convex, first as broad as, or broader than, long, the rest broader than long, broader than the costals; costals 4, rarely 5, not forming an angle with the marginals; marginals 10, 11 or 12;[2] supracaudal undivided, somewhat incurved.

Plastron with front lobe not or but slightly produced and not or but weakly notched; gulars paired; pectorals very narrow, their anterior border usually straight, widening abruptly towards the axillary notch; axillaries 2, one large, the other minute; inguinal moderate, normally in contact with the femoral, rarely separated;[3] hind lobe deeply or slightly notched posteriorly, usually angular, occasionally crescentic,[4] an interanal scute sometimes present.

Plastral formula: Abd > h > or = g > or < f > or = p > or < an.

Color. Carapace of hatchling[5] dull yellow, a broad black border (sometimes mottled with yellow) surrounds each vertebral and costal shield; within this border the ground color is light brown; typically each areola has a reddish brown border of moderate width within which there is *a single* central red-brown spot that usually coalesces posteriorly with the surrounding areolar border; upper and lateral edges of marginals and supracaudal bordered with black within which the areolae are edged with reddish brown. Plastral shields yellow, more or less mottled and edged with blackish brown. Head and limbs yellowish brown, uniform.

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[1] In a juvenile from Artu only, *fide* Tornier (1905c).

[2] In a specimen (A.M.N.H. 50739) from Blanketi River, Tanganyika.

[3] Separated only in a specimen mentioned by Hewitt (1931).

[4] In the holotype ♀ (M.C.Z. 40003) for example.

[5] Chiefly based on a series of specimens (M.C.Z. 42162-7) from Waterberg. Southwest Africa. For illustrations of juveniles from this area see Mertens (1955a:pl. xxii, figs. 129-134).

A juvenile from Ethiopia, referred to "*calcarata*" (=*sulcata*) by Vaillant (1904a) only differs from the Waterberg series in having lateral areolar spots alongside the central ones of the second and third vertebrals. Moreover Tornier (1905c:366) finds a 74 mm. "*pardalis*" (=*babcocki*) from "Artu," Ethiopia, differs but little from one taken in Hereroland, Southwest Africa. A Mongalla juvenile in the Vienna Museum, photographed for us by Dr. J. Eiselt, is very similar to these Ethiopian ones.

Two juveniles from the Ithanga Hills (M.C.Z. 31985) and Southern Guaso Nyiro (U.S.N.M. 41685), measuring 51 and 40 mm. respectively, have yellow carapaces whose shields are devoid of dark spots (except for an azygous spot on the fourth vertebral of the Guaso Nyiro tortoise). Both the dorsal and marginal shields of the latter have an inner dark border, while in the Ithanga Hills juvenile these borders are deep black and cover the sutures, coalescing with the corresponding borders of the adjacent shields.

Carapace of adults yellow with black markings. These are zonary in the young (whose areolae are usually brown) but radially arranged or broken in adults, where they may be so dense as to almost obscure the yellow ground color. Plastrons are invariably yellowish, either uniform or with black radiating streaks and scattered spots.

A Sudanese specimen in the British Museum, accompanied by full MS notes by Flower, is very light in color with very few black flecks. Another from the same locality is more nearly typical. According to Neumann (1905:389) Somali specimens are paler than those from Tanganyika, and Siebenrock (1906a: 823) suggests that tortoises from north of the equator tend to be lighter than those from the south, the coloring of young Sudanese *babcocki* approaching that of *sulcata*. Actually the carapace of a subadult Northern Guaso Nyiro specimen (M.C.Z. 7990) is heavily variegated with black except on the areolae.

The literature teems with descriptions of individual coloring. The pattern is discussed at some length by Duerden (1907b:74).

Size. Carapace length of a ♂ from Albany, 585 mm. (i.e. 23 inches in a straight line); 916 mm. (36 inches[1]) over the cara-

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[1] Possibly it was these figures that gave rise to Stevenson-Hamilton's (1947: 319) misleading statement that leopard tortoises attain a maximum length of "between 2 and 3 feet" (i.e. about 609 to 914 mm.).

pace; girth 1116 mm. (44 inches) (Hewitt:1937e:4). Masi records (1911a:29) an unsexed Ethiopian specimen as 450 mm. Carapace length of a ♂ from Arusha, 340 mm., height 196 mm.; that of the holotype ♀ from Mount Debasien was only 364 mm., height 207 mm., being surpassed by a ♀ from Mount Mbololo with a length of 385 mm., and a height of 208 mm.

A table giving the length, breadth and height of twenty-three tortoises from Southwest Africa is given by Mertens (1955a:35). Length of claws on hind foot, 30 mm. (Cairncross:1946).

Weight. A ♀ from near Aberdeen, weighing about 18 lbs. when captured in 1929, has had its annual growth and fluctuating weight recorded by Cairncross (1946:395) from 3.vii.38 to 7.xii.41 when it attained about 500 mm. (19$\frac{9}{16}$ inches) in length, and weighed 45 lbs. Mrs. Leakey (1944:396) gives the weight of a ♂ as 18 lbs., and those of two ♀♀ as 37 and 45 lbs. respectively. Hewitt (1937c:4) mentions a ♂ of 50 lbs., while Archer (1948a:75) gives 69 lbs. as the maximum but states that some *babcocki* remain at about 10 lbs. while others continue to grow until they reach 30 lbs. Both the heaviest records appear to be those of specimens in the Albany Museum, Grahamstown.

Sexual dimorphism. While some individuals are readily sexed, others are not. Certain characters mentioned by FitzSimons (1935b:304), though doubtless satisfactory for his material, appear quite inadequate when applied to an extensive series. Thus there are exceptions to the general rule that the lower sides of the carapace are almost vertical in ♂♂ and bulging for the accommodation of eggs in adult ♀♀, though it remains a good average character. Again, the notch on the posterior lobe of the plastron is frequently more angular in ♂♂, though in one old ♂ there is scarcely any angle whatever, the sides being almost in a single plane; in the ♀♀ it is widely angular, even semicircular. The shape of the supracaudal, often thought to be diagnostic of sex, is not so in this species. The number of times the breadth of the carapace is contained in the length is largely an age character, ranging from 1.01 to 1.45 times in the young; 1.49 to 1.55 times in our 6 adult ♂♂; 1.45 to 1.68 times in the 10 oldest ♀♀. We are reduced to the following characters, therefore, of which the relative tail length is the surest guide.

Posterior third of plastron slightly concave in adults; tail long . . . . ♂
Posterior third of plastron as flat as the rest in all ages; tail short . . . . ♀

Breeding. When two ♂♂ and a ♀ shared an enclosure at the East London Museum, Archer (1948a:75) observed that the ♂♂ would push and butt one another until one of the combatants was overturned. Then, unless in a depression, the vanquished tortoise would right itself and hurry away. The victorious ♂ then pursued the ♀, which seemingly evinced no interest, bumping against her shell and walking around her — sometimes for hours at a stretch according to P. J. Styrdom (*in* Hewitt:1937e:6) — until pairing took place.

In East Africa, Bally (1952:236), who had a single ♂ confined with two ♀♀ (he has satisfied us as to sexing), states that it was the ♀♀ who butted each other's flanks until one of the contestants was overthrown. Furthermore, so Bally informs us (by mail), the larger ♀, apparently annoyed at the ♂ getting in her way, rammed him also! This seems to refute Hewitt's (1937e:6) statement that ♀ *pardalis* do not butt with the front of their shells.

Mrs. B. E. Leakey (1944:396) records that mating was a common occurrence among her captive tortoises. It began with the ♂ following one of the two ♀♀ around and around, occasionally for several hours, until he was accorded the opportunity to mount. On doing so he would extend his long neck and utter a husky cry that carried for a considerable distance. Hewitt (1937e:6) describes this call as "a peculiar grunting noise."

Nesting. For 2 or 3 days prior to laying, the expectant tortoise walks restlessly about the enclosure, pausing now and again to scratch the ground, while in each eye a frothy white foam[1] gradually accumulates (Cairncross:1946:395).

Apparently Duerden (1906a) was one of the first to record the nesting of this species, but a more detailed account is that given by Loveridge (1923g:926) of the nesting at Kilosa of a captive tortoise from Pwaga. Briefly it may be said that the reptile was first observed to be digging at 5.15 P.M. on May 21. Despite

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[1] Probably an individual characteristic only.

the extreme hardness of the soil, a circular hole about 4 inches in diameter by 2 inches in depth had been dug already. Excavation was accomplished by the insertion of a hind foot which was scraped round and then brought up with a very small quantity of soil precariously balanced upon it; even so, at the last moment, much of the dirt fell back into the hole. The loss would have been even greater had not the tortoise from time to time micturated copiously so that the fluid, besides softening the hard ground, caked and bound the powdery soil. The hind feet were employed alternately with brief pauses for rest between the exchange. On reaching a depth of 4 inches the tortoise undercut the sides to form a gallery round the periphery, then continued excavating until a depth of 5 inches was reached.

Darkness fell at 6.30 P.M. At 7.12 P.M. the first egg was laid, its descent being retarded by an enveloping column of viscous fluid. At 7.24.10 P.M. the seventh and last egg was deposited. As each egg was laid the tortoise put down a foot and felt about for the egg which she then pushed beneath the undercut. At 7.26.10 P.M. the mother began breaking down the sides of the hole after which she proceeded to fill it in with all the recently excavated soil. Not once during the period of approximately three hours that she had expended on the task did the parent face about to examine the progress of her labours, or inspect the eggs which she had buried without ever seeing.

So impressed was Loveridge by the mechanical nature of the entire proceeding that he lifted the tortoise off the nesting site to some hard ground a couple of feet away. There she continued to trample without intermission until returned to the nest site. After a while she began raising herself on all four limbs as high as they would permit, then, suddenly relaxing, she dropped upon the site so that the disturbed soil was flattened by her plastron; this process of pounding the soil was continued for a long time. The following morning she was found to be resting on the site and, though the enclosure was a large one, she returned to sleep upon it that evening and for many subsequent nights. On June 12 Loveridge noted that not only did she sleep on the site but micturated and defecated on it frequently, if not daily. Other observers have reported that the parent tortoise may be so exhausted by her efforts that she can scarcely drag herself away from the site.

Evidently nest holes vary considerably in size, for Archer's had a surface diameter of 6 inches and a depth of 8 inches. Cairncross says that his was 7 inches across at the surface, about 9 inches at the bottom, while the total depth was 9 inches. Mrs. Leakey's flask-shaped cavity was about a foot in depth, but had to accommodate an exceptionally large number of eggs, 30 in all. When numerous, the eggs are arranged in layers that are separated by earth (*fide* Bowker :1926). The number produced at one laying, therefore, ranges from 5 (Cairncross :1946 :395) to 30 (Leakey :1944 :396). Photographs of a nesthole being dug, and of one with eggs *in situ,* have been published by Cairncross (*loc. cit.,* pl. i), one of whose tortoises laid a total of 52 eggs (in 6 installments) during the summer of 1939-40. Their gross weight was 357.48 grams (about 6 lbs.).

Both in appearance and size the egg of a Leopard Tortoise rather resembles a pingpong ball but the porcelain-like shell is very brittle. Occasionally, as with poultry, a double, elongate egg with median constriction (figured by Archer) may be laid. Perhaps a tendency of this kind was exhibited by the Sudanese egg mentioned by Siebenrock (1906a :823) as measuring about 35 or 37 x 43 mm., unless the 43 was a misprint for 33 mm. Loveridge (1936j :220) removed 8 hard-shelled eggs measuring 36 x 38 mm. from a ♀ taken on Mt. Mbololo on April 17, therefore larger than the 7 measuring 32.5 x 35 mm. laid by a Pwaga tortoise on May 21, and smaller than 2, measuring 40 x 40 mm. and 38 x 40 mm., laid by a captive on August 5 and 25 respectively.

Eggs laid very early in the South African spring may hatch in 8 months provided that warm weather continues on into late autumn, but autumn laid clutches may take as much as 18 months to hatch if the following summer is cold (Archer :1948a : 75). Eggs laid in a Grahamstown garden on February 7, hatched on April 23 of the following year, i.e. they took 14 months, whereas two clutches laid in the South African autumn took only 11 and 12 months respectively (Bowker :1926 :37). In South Africa, a presumably captive Leopard Tortoise laid 3 eggs on the ground at Grahamstown (Hewitt: 1937a:6), between July 26 and 28, mid-winter.

Mrs. Leakey (*in litt.*), after removing eggs from the nest, packed them in sand in a gasoline can which she placed on a cement hot-water tank. Nine months later, sometime between December 14 and 21, there emerged a single hatchling weighing half an ounce. As no others appeared during the succeeding 3 weeks the rest of the clutch were examined. Two eggs only held young tortoises, both of which were dead.

As eggs left *in situ* rarely hatched, Cairncross (1946:396) removed many clutches to an incubator where, except for a 10 minute cooling off period each morning, a temperature ranging from 88° to 92° was maintained for 6 months. The results were disappointing as the majority of eggs proved infertile. For further details consult his paper.

In one of Bowker's nests (1926:37) the central clay plug subsided slightly, permitting the hatchlings to squeeze their way out into the sunlight between plug and wall. Normally the young, whose shells are flexible at time of hatching, claw their own way to the surface. Being well supplied with nourishment from the yolk they require no food for several days, despite a display of considerable activity.

Growth. Rate of growth is affected by availability of food coupled with congenial temperatures, being accelerated during warm weather and retarded by cold. Good and bad seasons are reflected in the size of seasonal growth-rings on the shields of the carapace. In immature tortoises these rings furnish an indication of age, but becoming blurred with wear are no longer a trustworthy guide when maturity is reached. Consequently, statements regarding growth which are based on data derived from one or two tortoises, vary widely. P. J. Strydom is quoted by Hewitt (1937e:4) as saying that in South Africa only a few inches in length are gained during the first decade, making a total of 7 inches after 17 years. Archer's (1948a:75) detailed figures seem to support this. He furnished a growth chart of one of many tortoises (No. 64) studied at the East London Museum.

Fisk (1878:790) reports that two fully-grown "*pardalis*" were brought to Clanwilliam in 1846, and there remained without progeny until 1857. In that year 2 young hatched from eggs laid by the ♀ and Fisk assumes this to imply that the parents had only then become adult! In 1877 the parents died within 3 months of each other, at which time, though 20 years old, the young ones were but two-thirds the size of their parents. The young were then deposited in the London Zoological Gardens.

Longevity. According to Flower (1937a:9) the record for known longevity is furnished by the above-mentioned tortoises which lived in captivity for over 30 years (1846-1877).

Diet. Principally grass, though they also feed on various succulents, crassulas, spekboom, thistles, prickly pear, pumpkins, beans and water melons (Hewitt:1937e:5); sweet potato tops or an entire, hard, white cabbage may be consumed at one meal (Leakey:1944:396); verdure of ground nuts, lettuce, and moistened bread (Loveridge:1933h:206); grapes (Rose:1950:339).

Bally (1946; 1952) observed a captive Ethiopian specimen take up and swallow a meatless chicken bone twice as long as its own head. Some days later the reptile was found nosing and pushing around a much larger bone. When Bally smashed this bone the tortoise seized the jagged splinters, one of which was an inch and a half long, and swallowed them one after another until all were gone. Thereafter he supplemented the reptile's vegetarian diet with a daily ration of bone splinters upon which it throve. For several years a companion tortoise from Lake Chala showed no interest in bones; then, in 1947, the Chala reptile also started eating chicken bones and doubled its weight in a year. It almost doubled its weight each succeeding year as the Ethiopian tortoise had been doing.

Bally tabulates the annual growth and his figures show that the Chala tortoise was still about doubling its weight each year in 1950, at which time the Ethiopian reptile's development was slowing down. Bally wondered whether the bone diet was responsible for the Ethiopian specimen's increase in size and weight during the years that the Chala tortoise remained almost static. (We reject the suggestion that Ethiopian tortoises possibly grow larger. There may be some confusion with *sulcata.*) A possible source of calcium for feral tortoises is to be found in the excrement of hyenas and other carnivores for captive specimens have been known to eat the dry dung of dogs as well as owl castings.

After eating, though it may have been on fleshy *Cissus* leaves or lettuce, Bally's tortoises drank regularly and eagerly. Though drinking copiously in summer, leopard tortoises can go for long periods without water (Hewitt:1937e:5).

Even when feeding daily on rich food a lapse of from 2 to 3 weeks occurred between defecations, Bally (1952:236) noted. The volume of such excrement was correspondingly large, frequently exceeding a tenth of the total weight of the depositor.

Parasites. Ticks (*Amblyomma exornatum* and *A. nuttalli,* not *A. marmoreum* as previously reported in error) were present on turtles from many localities.

Enemies. The eggs are dug up and devoured by dogs (Leakey), jackals, meerkats, muishonds. Young tortoises are attacked by crows and ground-hornbills, larger ones by ratels (Hewitt), seemingly by hyenas also; certainly by soldier ants (Loveridge). Nyamwezi tribesmen were seen eating them by Ansorge (1899: 288). Scherer (1902:255), when in the Mkomasi Valley, encountered a couple of Africans carrying a pair of poles to which was attached a huge tortoise about 500 mm. in length that the men said would provide them with a good meal. One of us (Loveridge) was told that in the Iringa Highlands a really large tortoise was considered to be worth 2 goats! According to FitzSimons (1935b:304) Bushmen prize these reptiles both for their flesh and shell. The latter, after removal of the plastron, is used for ladling or holding water, while Dr. R. Pöch states that the shields are made into snuffboxes by the Kalahari Bushmen.

At Magugu, Cooper (1948:11) found a tortoise, apparently of this species, lying on its back and unable to right itself. Surrounding spoor suggested that the reptile had been overturned by a buffalo's nose, after which the ungulate had pawed up the ground in the vicinity.

That many tortoises perish in the annual grass fires is suggested by Ansorge (1899:288) who not infrequently encountered their calcined remains. Many shells and skeletal remains, but no living tortoises, were found at Tsotsoroga by FitzSimons (1935b: 304) who concluded that the reptiles had perished during the extensive flooding of the flats a few years before.

Aestivation and Hibernation. In view of the admitted language difficulties, the alleged burying of this species during dry and cold seasons in Southwest Africa — as reported to Falk (1922:163) by Bushmen, should be received with reserve pending confirmation.

Migration. Peel (1900:333) reports seeing in Somaliland "a whole army of these monsters migrating" across the desert from one patch of grass to another.

Habitat. Leopard Tortoises inhabit the coastal plain and upland savanna, excluding areas of primary forest, in rather sandy, thornbush steppe and on kopjes. Such stone-strewn hills should have scattered scrub to provide shelter from the noonday sun. One tortoise, who skeleton was found between two sloping rocks by Loveridge, had presumably perished through inability to escape from its smooth-walled prison. The seeming predilection of this species for mountain masses (on Mt. Elgon it has been taken between 9,000 and 10,000 feet) may indicate that in such a habitat it is less liable to molestation from man and the larger carnivores. According to Kammerer (1908a:741) low temperatures are resisted better by Leopard Tortoises than by the giant Spurred Tortoise.

Localities. Sudan: Bahr el Ghazal Province (Werner:1924a); Bahr el Jebel (Gebel); Bor; Gondokoro; Lado Enclave; Mongalla; (the Omdurman market record of Kammerer is rejected). *Ethiopia:* Ado-Shebeli (Adoshebai) Valley; Araro (Arero); "Arruena" (?Arenda); Artu; Arussi Gallaland; Boorgha country; Caschei; Dabas (Daba-as); "Ennia Land" (? En); "Farre" (? Erre); Javello; Lake Abaya; Lake Zwai; "Lasman"; Neghelli; Shoa; Sibi; South of Harar (Harrar); "So-Omadu" (? Soddu). *British Somaliland:* Hargeisa; Nogal Valley; Toyo Plain (*ca.* 9°10'N.: 44°45'E.). *Somalia:* "Bambasse"[1] between Berdale (Bardale) and El Condul (Condut); Ircut (Pozzi-Ircudt); Jet; "Sahaieroi."[1] *Uganda:* *Mount Debasien. *Kenya Colony:* Athi Plains; *Guaso Nyiro; *Ithanga Hills; Kabete; Kaimosi; Kedong Valley; Kikuyu Escarpment south of Lake Naivasha; "Kipopotue, Ukamba"; Lekiundu River, Southern Guaso Nyiro; *Meru River Plains; "Mgana" (Betton coll. A locality unknown to L. Leakey and J. G. Wil-

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[1] A Calabresi (1916) report on Stefani and Poli material; many misspellings.

liams); Mount Elgon; Mount Kenya; *Mount Mbololo; Mtito Andei; Murri; Nairobi; Ndi; Ndogo, Lake Baringo; Southern Guaso Nyiro; Turkana; *Wema, Tana River; *Ziwani Swamp, Northeast of Kilimanjaro (C.M.). *Tanganyika Territory:* *Arusha; Blanketi River; Busisi; Dodoma; Irazo; Kahama (Leiden Mus.); *Kilosa; Kondoa Irangi; Korogwe; Lake Eyasi; Lake Jipe; Lindi; Lugno; Magugu;[1] Masai Nyika and Steppe; Mbonoa; Mdjengo's; Mkaramo, near Mombo, Pangani River (1896); Mkomasi River; Moshi; Mtali's; Ruvu River, 33 km. s.e. of Moshi; Mwanza; Namanga; Ngare na Nyuki; Ngoma; Nzinga; *Pwaga; Ruwira; Sagayo; Sanga; *Saranda; Shinyanga; Simbo; *Singida; Tabora; Tambali; *Tukuyu; Ukerewe Id.; Ulugu; Usambara; Wembere; Zengeragusu. *Mozambique:* Cape Delgado Ids.; *Kasumbadedza; Sena; Tete. *Nyasaland:* (occurs south of the Mwanza River and west of the Shire in both Chikwawa and Port Herald districts, according to Mitchell: *in litt.*); Tengani. *Northern Rhodesia:* Luangwa (as Loangwa) River; Petauke. *Southern Rhodesia:* *Birchenough Bridge, Sabi River; near Gwamayaya River; Mount Darwin. *Bechuanaland Protectorate:* Gemsbok; Kalahari; Magalapsi; Makarikari; Maun; Serowe; Shaleshonto; Shorobe; Tsotsoroga Pan, Mababe Flats. *Transvaal:* Mannamead; Naauwpoort; Pietersburg. *Natal:* Durban. *Cape Province:*[1] Aberdeen; Albany; Alexandria district; Algoa Bay; Alice; Bathurst district; Brakkloof; Colesberg; Fort Beaufort district; Grahamstown; Hamburg; Hogsback; Keiskama; Malmesbury; Middleburg; Middleton; Modder River; Mortimer Road; Nonesis; Orange River Station; Port Elizabeth; Queenstown; Saint Clair; Somerset East district; Tarkastad; Tottabi near Alicedale; Uitenhage district; Vryburg; Warrenton; Willowmore. *Southwest Africa:* *Etosha Pan-near; Gibeon; Great Namaqualand; Karibib; Landsberg Farm, Luderitz district; Neudamm Farm; Ogosongomingo; Aus (Oas); Okahandja; Omaruru; Omatjenne; Rietmond near Gibeon; Swakopmund; *Tses (U.S.N.M.); *Waterberg; Windhoek (Windhuk).[2]

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[1] Unidentified "land tortoise" overturned by buffalo (Cooper:1948). Magugu, near Mbugwe, slightly south of Lake Manyara.

[2] Through the courtesy of Mons. J. Guibé we have been able to examine one of Delalande's young tortoises from the "Cap." It is unfortunate that no more precise locality is known. In pattern it is a *p. pardalis* of the *"biguttata"* type, but in proportions is clearly referable to *p. babcocki* for its height of 45 mm. is included in its length of 83 mm., 1.84 times. It must therefore be considered an intermediate.

Angola: Benguela — inland from; Capangombe — some distance from; Cubal; Dombodola; Forte Rocadas; Mossamedes — interior of; Mupa.

Range. Sudan and Ethiopia south to Natal, west through Cape Province to Southwest Africa, where it meets with the typical form, but is dominant north of 27°S. and in southern Angola. It does not occur in northern Angola (*fide* Monard:1937b).

Erroneously reported from Madagascar (1873) and Senegambia (1884a).

GEOCHELONE PARDALIS PARDALIS (Bell)

1828a. *Testudo Pardalis* Bell, Zool. Jour., **3**, p. 420, pl. xxv of Suppl.: "Promont. Bonae Spei," i.e. Cape of Good Hope.

1831b. Gray, 4.

1831c. Gray (part), 12 (omit figs. as these are of *p. babcocki*).

1835. Duméril and Bibron (part), 71 (color of young, etc.).

1836. Bell, text and col. pls.

1849. Smith, A., App., 1.

1851. Duméril and Duméril, 4.

1860. Fitzinger, 411.

1872b. Gray, 3, *in* Sowerby and Lear, pls. ix-x.

1892. ?Müller, F., 214.

1907b. Duerden, 74, fig., pl. vii, fig. 7 (showing juv. markings).

1829. *Testudo biguttata* Cuvier, Regné Animal, ed. 2, **2**, p. 10, footnote (*nomen nudum*): No locality.

1831c. *Testudo bipunctata* Gray, 12 (erroneously attributed to Cuvier mss. and cited with reference to the description of a juvenile in the Paris Museum).

1831b. Gray, 4 (erroneously attributed to Cuvier in Regné Animal).

1831c. *Testudo armata* Boie mss. Gray, 12 (listed as a synonym).

1831b. Gray, 4.

1835. *Geochelone pardalis* Fitzinger, 211.

1937e. Hewitt, pl. i, fig. 2; pl. ii, figs. 1-2.

1948b. Archer (part), p. 77 (Keetmanshoop specimen).

1935c. *Testudo pardalis pardalis* Loveridge, 4 (key).

1955a. Mertens, 35.

Most citations of "*pardalis*," and one of "*pardalis pardalis*," will be found listed under *p. babcocki*, with which race the typical form has been confused for almost a century.

Common names. Southwestern Leopard Tortoise (preferred); Mountain Tortoise.

Illustrations. Excellent colored plates of the ♀ holotype (side and plastral views) appeared in Bell's (1836) rare Monograph of the Testudinata, and were later reproduced by Sowerby and Lear (1872b). The distinctive coloration of the young *p. pardalis* has been figured by Duerden (1907b:fig. 7, based on a specimen beginning to assume the adult coloration), and by Hewitt (1937e:pl. 1, fig. 2, a hatchling closely resembling the Aroab specimen in the Museum of Comparative Zoology).

Description.[1] Beak moderately hooked, edge of jaws not strongly dentate; prefrontal large, divided longitudinally; remaining upper head shields small, irregular; forelimb anteriorly with a few large, unequal, widely separated, non-imbricate scutes, forming 3-4 longitudinal and 7 transverse series from elbow to outer claw; claws 5; hinder side of thigh with 2 large conical tubercles; heel with large, flat tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace flattened dorsally, sides nearly vertical (at least in ♂ adult), sloping gradually in young, deeply notched in nuchal region, in adults the anterior margin not, and lateroposterior margin only slightly, expanded and slightly serrated, its greatest height included more than twice (2.02 to 2.62 times) in its total length; dorsal shields concentrically striated except in young, their areolae slightly raised; nuchal absent; vertebrals 5, more or less (in young) convex, all broader than long, broader than the costals; costals 4, not forming an angle with the marginals; marginals 11; supracaudal undivided.

Front lobe of plastron anteriorly truncate in young, slightly produced and shallowly notched in adults; gulars paired; pectorals very narrow, their anterior border slanting in young, more or less straight, widening abruptly towards the axillary notch; axillaries 2, one small, the other minute; inguinal small, in contact with the femoral; hind lobe deeply notched posteriorly, almost crescentic.

Plastral formula: Abd>h>or=g>or<f>or=p>or<an.

Color. That of a hatchling from Aroab (M.C.Z. 22473) is strikingly different from juveniles of *G. p. babcocki*, viz. carapace dull yellow, black being confined to the narrow sulci surrounding

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[1] Based on original description of ♀ holotype, the shell of an adult ♂ (M.C.Z. 16713) and an alcoholic juvenile (M.C.Z. 22473), together with notes on British Museum material as of 1953.

each vertebral and costal shield; these are edged with yellow, each areola with a reddish brown border, those on the vertebrals flanking a pale cream, broad, median band; upper and lateral edges of marginals and supracaudal bordered with reddish brown. Head and limbs peppered with black. The juvenile tortoise figured by Seba (1735:pl. lxxix:fig. 3), which Bell suggested might be the young of *pardalis,* is more probably a young *P. geometricus* of the *luteola* phase (see below).

The coloring of the adult, as described by Bell, is substantially similar to that of our specimen, also of the eastern race — *p. babcocki.* Carapace light yellow; shields with black, somewhat radiating, markings. Plastron dirty yellow, each shield with black spots, dashes, or radiating streaks extending inwards from the margins. Head, neck, feet and tail, dull brown with some admixture of dull yellow.

Size. Carapace length of type ♀, 432 mm., breadth 280 mm., height 213 mm.; carapace length of ♂ (M.C.Z. 16713), 302 mm., breadth 210 mm., height 147 mm.; carapace length of juv. (Aroab), 55 mm., breadth 42 mm., height 21 mm.

Enemies. Possibly the food value of this large tortoise may have led to its extermination on the Cape for today its range appears to be restricted to a small area in the southern part of Southwest Africa.

Habits. Bell (1828a; 421) states that since the beginning of summer the type had been living in his small orchard, feeding heartily on the grass which it plucked with movements similar to those "of a goose." The strength of an adult Leopard Tortoise is surprising for once it has braced its feet it is next to impossible to pull the reptile backwards. After its death, Bell (1836) dissected the type and found it held an estimated 200 ova ranging in size from those no larger than a pin's head to others equalling a pigeon's egg.

Localities. Cape Province: ? now extinct: Cape of Good Hope[1] (Type); Olifants River (Delalande coll. ? this subspe-

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[1] Walter Rose informs us (6.v.54) that, during thirty years of rambling in the vicinity of Cape Town, he has never encountered a leopard tortoise — except escapees. He believes it formerly occurred 45 miles northwest of Cape Town in the Malmesbury district where one meets with arid conditions resembling those of the Karroo.

cies). *Southwest Africa:* *Aroab; Keetmanshoop[1] *Kolmanskop;[2] Rehoboth.[3]

Range. Southwest Africa possibly as far north as Rehoboth,[3] more certainly south of a line from Kolmanskop (near Luderitz Bay) to Keetmanshoop, south (in former times presumably) to the Cape.

Erroneously reported from Angola (Monard: 1937b).

Genus TESTUDO Linnæus

1758. *Testudo* Linnaeus, Syst. Nat., ed. 10, 1, p. 197. Type: *Testudo graeca* Linnaeus (designation by Fitzinger).

1820. *Chersine* Merrem, Vers. Syst. Amphib., pp. 12, 29. Type: *T. graeca* Linnaeus (designation by Lindholm).

1830. *Chersus* Wagler, Natur. Syst. Amphib., p. 138. Type: *Testudo marginata* Schoepff (by monotypy).

1869c. *Peltastes* Gray (not of Rossi: 1807), Proc. Zool. Soc. London, pp. 167, 171. Type: *T. graeca* Linnaeus (designation by Lindholm).

1870e. *Chersinella* Gray, Suppl. Cat. Shield Rept. Brit. Mus., part 1, p. 8. Type: *T. graeca* Linnaeus (designation by Lindholm).

1870e. *Testudinella* Gray (not of Bory: 1826), Suppl. Cat. Shield Rept. Brit. Mus., part. 1, p. 12. Type: *T. horsfieldi* Gray (by monotypy).

1872c. *Peltonia* Gray, App. Cat. Shield Rept. Brit. Mus., part 1, p. 4. Nom. nov. for *Peltastes* Gray (preoccupied).

1916. *Medaestia* Wussow, Wochenschr. Aquar.-Terrar. Kunde, 13, p. 170. Type: *T. graeca* Linnaeus (designation by Mertens).

Definition. Skull with triturating surface of maxilla moderately or weakly ridged or without ridging; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina small, concealed or large and conspicuous; *prootic typically concealed dorsally and anteriorly by parietal;* quadrate enclosing stapes or not; surangular subequal in height to prearticular; neck with third or fourth centrum biconvex.

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[1] This Keetmanshoop record is assumed solely on geographical grounds, being taken from Archer (1948b;77) who lists it with many others as *Geochelone pardalis.*

[2] It is only right to mention that in the Vienna Museum there is a specimen allegedly from Swakopmund (Poch coll.) whose breadth is contained in its length 2.10 times, and another of 2.11 times from Aus where Poch collected many *G. p. babcocki.* We propose regarding these two individuals as intermediates between the two races which meet in the Luderitz Bay region.

[3] The Rehoboth record is based on a photograph of two young specimens kindly sent to us by Dr. Robert Mertens in a letter of 18.v.56.

Carapace never hinged; typically the anterior neurals alternately octagonal and quadrilateral; outer side of third costal scute about as long as, or longer than, that of fourth; submarginal scute absent; frequently a single suprapygal, if two, they are typically separated by a straight transverse suture.

Plastron with posterior lobe more or less hinged in one or both sexes; gular region but little thickened or produced; gulars paired, longer than broad.

Range. Northern Africa, southern Europe, and western Asia.

Fossil record. Extensively known from the Cenozoic of Europe, and since the Pliocene from North Africa.

Remarks. The genus *Testudo* includes forms of moderate to small size, the living species attaining as much as 280 mm. in some cases, as little as 120 mm. in one instance.

Testudo graeca, though technically the type of *Testudo,* is not typical of the Boulengerian grouping which has gone under this generic name. In our belief, as indicated in the diagram of relationships above (Fig. 8), *Testudo graeca* and its immediate relatives are not closer to the species *pardalis* or *elegans* or *denticulata* or *gigantea* or *emys* or *radiata* than are the species of *Gopherus* or of *Homopus,* forms which have long been put in distinct genera. Though conventionally the *graeca* group, at best, has been one subgenus among many subgenera, an inspection of the characters by which the subgenera that we unite under *Geochelone* are separated, and a comparison of these with the peculiarities of the *graeca* group, makes it plain that different orders of magnitude of divergence are involved.

We have here suggested the separation of two larger genera *Geochelone* and *Testudo* — as well as the smaller units *Malacochersus, Psammobates* and also *Chersina,* the latter all Ethiopian endemics. We have considered another possibility, that, while the Ethiopian endemics might still be separated, *Geochelone* and *Testudo* might be regarded as subgenera within a larger concept of *Testudo.* This would have the apparent merit of removing from the Boulengerian genus *Testudo* only the Ethiopian forms that have never fulfilled the Boulengerian definition of the genus But it appears to us that this suggestion founders when the *Gopherus-Stylemys* lineage is taken into account. The *Gopherus-Stylemys* line has quite as much in common characterwise with *Testudo* and *Geochelone* as these have with each other. Recent *Gopherus* has the maxillary ridging, the concealed anterior palatine foramina and the octagonal and quadrilateral neurals that occur, though not quite invariably, in the other two groupings. The *sole* conspicuous distinction is the median premaxillary ridge, seemingly a triviality. Considering only Recent material, as Boulenger did, it was entirely logical for him to include *Gopherus* in *Testudo*.

But the evidence now available from the fossil genus †*Stylemys,* which has the gopheride premaxillary ridge and is clearly a close cousin of *Gopherus,* transforms the entire picture and reveals that the roots of the gopheride lineage go back to forms with many emydine characters. Thus it has been demonstrated (Case 1936 [1]; Williams:1952) that the North American Oligocene species †*Stylemys nebrascensis* had neurals with the primitive emydine shape (hexagonal, short sided in front), and in both fore- and hind feet the emydine phalangeal formula of 2,3,3,3,3.

Thus it is necessary to face the fact that *many of the characters common to modern land tortoises*—for example, *Geochelone, Testudo, Gopherus* and *Pyxis* share the octagonal and quadrilateral neural pattern — *have been acquired in parallel.* Formerly this fact so impressed one of us (Williams:1950; 1952) that *he questioned the naturalness of the subfamily Testudininae.* Further investigation and consideration has convinced him that all the land tortoises do spring from a common root within the Emydinae. He now believes that the major lines within the land tortoises had their start in the beginning of the Tertiary with an ancestral form that in terms of its characters was then only a slightly divergent emydine and only prospectively a testudinine. It appears to him that as a correlative of this view, it is desirable to recognize at least one genus for each of the major lineages that go back to the postulated ancestral testudinine.

It is on the basis of this interpretation that we venture to break up the Boulengerian genus *Testudo* and restrict its concept to the *graeca* group. Previously (p. 218), we have mentioned two distinctive characters of this genus — the posterior plastral hinge (present in one or both sexes), and the concealed prootic. A third, heretofore neglected, character which we have found

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[1] Case, E. C., 1936, Contrib. Mus. Paleont. Univ. Michigan, 5, pp. 69-73.

useful enough to employ in the key (p. 221), is the presence of distinct supranasal scales (Fig. 19) otherwise occurring only in *Malacochersus.* Perhaps this implies affinity between these two genera. However, we are inclined to believe that a rather elaborate head squamation was primitive for tortoises, and that breakdown of this condition has occurred to a greater or lesser extent in many lines. In any event, and in spite of a certain amount of variation (Fig. 22), this character proves a valuable external indicator for the genus.

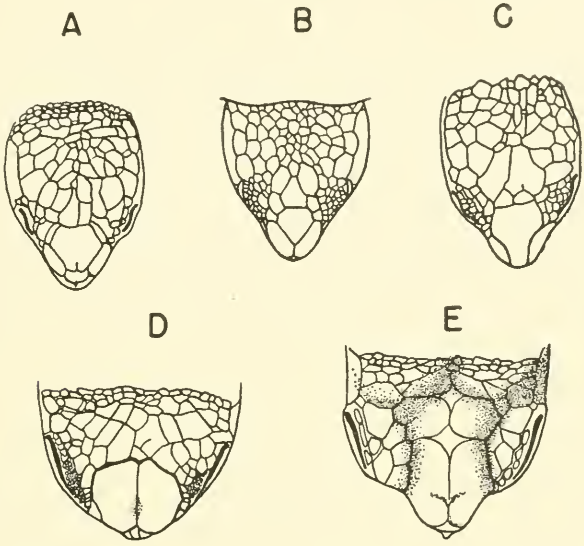

Fig. 19. Head scalation in certain testudinines (cf. Fig. 22). *A, Testudo hermanni* juv. (M.C.Z. 3063); *B, Malacochersus tornieri* (after Procter: 1922b); *C, Testudo g. graeca* juv. (M.C.Z. 1497); *D, Geochelone p. babcocki* juv. (M.C.Z. 40005); *E, Kinixys erosa* juv. (M.C.Z. 12583).
(P. Washer del.)

Within the restricted genus *Testudo* there are groupings at various levels. We recognize two subgenera, both African, which may be defined as follows:

Key to the Subgenera of TESTUDO

Maxillary with weak to moderate ridges; quadrate enclosing stapes. Range: Northwest Africa; southern Europe; western Asia ....
Testudo Linnaeus (p. 261)

Maxillary without ridges; quadrate not enclosing stapes. Range: Northeast Africa (Tripoli and Egypt only) ....
Pseudotestudo new subgenus (p. 276)

The subgenus *Testudo sensu stricto* is here interpreted to include only *graeca, marginata, horsfieldi* and *hermanni.* Of these *hermanni* appears to be the most primitive, possibly the most primitive in the entire genus. Both its external and internal characters testify to this. Externally the forelimb has relatively small and numerous scales (in as many as ten longitudinal rows) the larger ones mostly toward the outer side, and the supracaudal is divided. The presence of a tail claw may also be primitive for the genus. Internally the skull shows relatively strong ridging on the maxilla and the anterior palatine foramina are fully concealed. The trachea (*fide* Siebenrock) is unspecialized in not being excessively long and coiled as in the two other members of the subgenus in which this character has been studied. In all these respects *graeca* is more specialized than *hermanni;* while *marginata,* as Siebenrock (1910) has shown, is extremely close to *graeca.* The two form a transition to the very specialized dwarf species *kleinmanni, graeca* in particular being close enough to suggest that *kleinmanni* was ultimately derived from it.

Testudo graeca has the scales of the forelimb enlarged and forming 4 to 6 longitudinal rows, a trend continued by *kleinmanni* in which there are usually only 3 in longitudinal series. In both *graeca* and *kleinmanni* the supracaudal is usually single, and the tail claw is rudimentary or absent in both species. As compared with *hermanni* the maxillary ridging is reduced in *graeca,* absent in *kleinmanni.* The anterior palatine foramina, more exposed in *graeca* than in *hermanni,* are fully exposed in *kleinmanni.* In possessing a long and coiled trachea, *graeca* is more specialized than *kleinmanni;* however, it is in the *largest* individuals of *graeca* and *marginata* that this condition is most pronounced (Siebenrock:1910). In one respect *kleinmanni* differs from other members of *Testudo* in a way not approached by *graeca,* i.e., in having the quadrate open behind, not enclosing the stapes. In size the two species differ radically, *graeca* being one of the largest members of the genus and *kleinmanni* decidedly the smallest. However, this disparity is bridged by an allegedly dwarf subspecies, if valid, *T. graeca floweri* of southern Palestine (cf. Flower:1933:745).

Testudo kleinmanni, despite the numerous ways in which it is approached by *graeca,* from which in all probability it is directly derived, is still a species rather sharply set apart. It might be said to represent only the extreme of trends within *graeca,* but the differences are abrupt and very striking. The end result is a species which, in many of the characters considered of taxonomic value by Boulenger (and for the most part so considered by us), parallels forms that are almost certainly not closely related. In the absence of maxillary ridges it parallels *Pyxis, Psammobates, Chersina, Homopus* and *Kinixys,* and parallels as well the last two in its fully exposed anterior palatine foramina. In the quadrate failing to enclose the stapes it displays an emydine character (probably secondary) elsewhere found in testudinines only in *Pyxis arachnoides,*[1] and *Geochelone sumeiri* (type specimen examined at the Tring Museum).

If as we suspect it is a derivation of *graeca, Testudo kleinmanni* must surely have been at one time only a geographical form of *graeca.* It is still allopatric to that species, dividing the present range of *graeca* in two. This singular fact of distribution is indeed our only clue, for in Africa there is no fossil evidence on which to found an opinion on the circumstances of *kleinmanni's* origin, and the evidence from Europe has not been sufficiently analyzed.

Testudo graeca of North Africa and southern Spain is probably racially distinguishable from the populations of eastern Europe and Asia. However, Mertens (1946d) who separated it as *g. graeca,* found only minor differences in shell proportions between the typical form from North Africa and his *g. ibera* ranging from the Balkans to Persia. Certainly the populations of eastern Europe and Syria do not differ greatly from those in Africa. If one may deduce from this that the separation of the African and east European races has not been of long standing, it is natural

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[1] In *Pyxis* the condition is quite different and not primitive. The skull structure of this genus and of *Acinixys* is to be described in a separate paper by one of us (E.E.W.).

to infer that formerly a continuous population extended across southern Europe whence the invasion of western North Africa occurred via Spain and *not* across Egypt. In this view the southern Spanish population of *g. graeca* would be a relict one, persisting after the general extinction of the species in western Europe. This might be due to an invasion by *hermanni* which now occupies much of the region separating the two ranges of *graeca* in southern Europe.

If this hypothesis is correct, then *Testudo kleinmanni* is not a peculiar form that has differentiated in the middle of the geographic range of its parent species. Instead, at the time of its origin, it was the most westerly form of the *graeca* complex on whose periphery it developed. If in southern Palestine there is really a dwarf race (*T. g. floweri* Bodenheimer: 1935[1]) resembling *kleinmanni* in coloration — and a single shell[2] in the British Museum seems to support this view — the case for our hypothesis respecting the mode of origin of *kleinmanni* will be strengthened.

Key to the Circum-Mediterranean Species of TESTUDO

1\. Forelimb anteriorly with 7-10 small scales across it; hinder side of thigh without enlarged tubercle; tail terminating in a distinct claw, always present; supracaudal usually divided. Range: southern Europe[3]...... *hermanni* Schneider

Forelimb anteriorly with 3-6 larger scales across it; hinder side of thigh with or without a large tubercle; tail claw present or absent in all three species; supracaudal usually undivided 2

2\. Forelimb anteriorly with 3-6 scales across it; hinder side of thigh with a large tubercle. Range: western North Africa and southern Spain (with races in extreme southeastern Europe and western Asia) ...... *g. graeca* Linnaeus (p. 261)

Forelimb anteriorly with 3-5 scales across it; hinder side of thigh without enlarged tubercle 3

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[1] Bodenheimer, F. S., 1935, "Animal Life in Palestine" (*fide* Mertens :1946d). We have also found the name referred to in Mém. Inst. Egypt, 1937, **33**, p. 71.

[2] While the carapace of this specimen (examined by us) has the predominantly yellow hue of *kleinmanni*, the plastron was much blacker than in that species; also the pectoral shields were larger than the femorals, the reverse of the *kleinmanni* condition. While having the appearance of an adult, the length of its carapace is only 114 mm., that of its plastron 97 mm.

[3] As Lortet (1887 :6) distinctly states that he never collected this species in Syria, the specimen from Antakia, Syria, allegedly collected by Lortet, and recorded as *"graeca,"* i.e. *hermanni* by Boulenger (1889a :177) requires confirmation.

3. Forelimb anteriorly with 5, rarely 4, scales across it; supracaudal and posterior marginals spread out; coloration predominantly black; size moderately large, maximum length of carapace about 280 mm. Range: Greece only .... *marginata* Schoepff

Forelimb anteriorly with 3, rarely 4, scales across it; supracaudal only spread out; coloration predominantly yellow; size small, maximum length of carapace not exceeding 127 mm. Range: eastern North Africa (Tripoli and Egypt) ....*kleinmanni* Lortet (p. 276)

Subgenus TESTUDO Linnæus

1835. *Testudo* Fitzinger, Ann. Wiener Mus., 1, pp. 108, 113, 122: Type species: *Testudo graeca* Linnaeus.

Definition. Supracaudal divided or single. Maxillary weakly to moderately ridged; anterior palatine foramina at least partly concealed in ventral view; quadrate enclosing stapes. Plastron of adults with a more or less movable posterior lobe in one or both sexes. Tail claw present or absent.

Range. Northern Africa, southern Europe, western Asia.

TESTUDO GRAECA GRAECA Linnaeus

1758. *Testudo graeca* Linnaeus, Syst. Nat., ed. 10, 1, p. 198: Africa.
1774. Müller, S., 44.
1789. Poiret, 358.
1804. Blumenbach, 66 (illus. no.).
1828. Bory de St. Vincent (part), 73.
1833. Rozet, 232.
1835. Temminck and Schlegel (part), 70.
1860. Tristram, 405.
1867a. Steindachner, 4.
1872b. Gray, 4, *in* Sowerby and Lear, pl. xvi (but omit "Asia Minor").
1880c. Vaillant, 8, 33, 88, pls. xxv; xxvii, fig. 5.
1886. Eade, 316.
1893. Eade, 368.
1924a. Flower, 921.
1925. Flower, 929.
1926. Flower, 133.
1929. Flower, 28.
1932. ?Thomson, 362, pls. —.

1933. Flower, 744.
1934a. Mertens and Müller *in* Rust, 9 .
1936b. Mertens, 15, figs. 2-3.
1937a. Flower, 6-9, 36.
1937. Hediger, 187, 191.
1946d. Mertens, 112.
1948. Astré, 60.
1949. Moyle, 582.
1950. Williams, 550.
1951. Aellen, 167, 195.
1952. Williams, 555, 556.
1954. Noël-Hume, 20, figs. 5-6.
1766. *Testudo pusilla* Linnaeus (part: not of 1758), 353.
1802. Shaw (not of Linnaeus: 1758), 53.
1862a. Strauch, 67.
1862b. Strauch, 14.
1865. Strauch, 14.
1874. Boettger, 123.
1880c. Vaillant, 8, 26, 88.
1886. Vaillant, 135.
1890. Strauch, 45 (but omit Asiatic localities).
1898. Jeude, 2.
1835. *Testudo Mauritanica* Duméril and Bibron (part), Erpèt. Gén., 2. p. 44: Mauritanica; Algeria (omit coasts of Caspian Sea, etc.).
1850. Guichenot, 1.
1854. Eversmann, 443.
1857. Jan, 35.
1875. Kercado, p. xxxv (*Tistudo Mauritonica*).
1894. Oliver, 102.
1896b. Oliver, 118.
1897. Bateman, 48.
1904. Chaignon, 2.
1905. Barbier, 78, pl. iii.
1907. Le Cerf, 22.
1912. Kollman, 103 footnote.
1919. Leblanc, 178, figs. 1, 5, 6.
1920. Mourgue, 233.
1836. *Testudo marginata* Gervais (not of Schoepff), 309.
1841. Schlegel, 138.
1848. Gervais, 204.
1884a. Rochebrune (erroneous report of occurrence in Senegambia) 15.
1898. Jeude (erroneous listing of skeletal material from Cape) 2.
1836. *Testudo ibera* Gervais (not of Pallas), 309.

1848.	Gervais, 204.
1851-64.	Blanchard, 72, pls. i-ii (skull, carapace, etc.).
1851.	Eichwald, 414.
1877.	Camerano, 97, pl. iv.
1883a.	Boettger, 130.
1885b.	Boettger, 472.
1887.	Lortet (part), 3, pl. i.
1889a.	Boulenger, 176.
1891c.	Boulenger, 96, 104.
1892.	Anderson, 11.
1892.	Koenig, 15.
1892a.	Werner, 354.
1892b.	Werner, 269.
1893a.	Boettger, 11.
1894.	Werner, 75.
1895.	Koenig, 403.
1895c.	Werner, 127.
1896.	Anderson, 111.
1896.	Escherich, 278.
1899.	Doumergue, 243.
1900.	Boettger and Tornier, 64.
1901.	Gadow, 369.
1901.	Lampe, 193.
1903.	Mayet, 10.
1906c.	Siebenrock, 847.
1908.	Kerville, 96.
1908.	Zulueta, 451.
1909a.	Siebenrock, 540.
1909a.	Werner, 597, 628.
1911.	Lampe, 147.
1912a.	Pellegrin, 256.
1912b.	Werner, 448.
1913.	Ghigi, 266, 283.
1913b.	Siebenrock (part), 24, figs. 10-19.
1919.	Leblanc, 177.
1922b.	Procter, 493, figs. 1a, 11b.
1922.	Zavattari, 15.
1923a.	Calabresi, 7.
1924a.	Flower, 920.
1924.	Zavattari, 15.
1926a.	Pellegrin (1925), 315.
1927a.	Pellegrin, 261.
1928.	Hediger, 408.

1929. Lindholm, 295.
1929b. Werner, 15, 21.
1929. Zavattari, 86.
1930a. Zavattari, 263.
1931c. Werner, 275.
1932. Thomson, 363, pls. —.
1935. Hediger, 3.
1935. Laurent, P., 345.
1937. Zavattari, 530.
1944b. Kehl, 166.
1948. Astré, 60.
1953. Burton, 34, fig., photo.
1836. *Testudo Whitei* Bennett, in White, Nat. Hist. Selborne, p. 361, fig.: No locality given, but type in British Museum.
1841. *Testudo graeca* var. *mauritanica* Schlegel, 106.
1857. *tortue terrestre* Labouysse, 86.
1870e. *Peltastes marginatus* var. *whitei* Gray, 11.
1873c. *Chersinella graeca* Gray, 725, pl. lx, fig. 4 (skull: African).
1880d. *Testudo campanulata* Peters (not of Strauch)[1], 305.
1881a. Peters, 365.
1928. *tortue d'Algerie* Bailly-Maitre, 111.
1946d. *Testudo graeca graeca* Mertens, 112.

Further citations of "*graeca*," "*mauritanicus*," "*marginata*," and "*campanulata*," will be found under *Testudo kleinmanni*. Owing to the composite and frequently involved nature of many of the early references to "*graeca*," we have preferred to omit them unless they definitely mentioned a North African locality.

Synonymy. The name *graeca* (according to Statius Müller: 1774, as quoted by Siebenrock :1913 :26) was given to this tortoise by Linnaeus on account of its carapacial pattern resembling Grecian mosaic work. It was entirely without reference to its place of origin which Linnaeus quite definitely stated to be Africa, after Edwards (*circa* 1743-8: Nat. Hist. Birds, part iv). In this work the life-sized colored plate carries this caption:

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[1] Strauch (1862b, Mem. Acad. Imp. Sci. St.-Pétersbourg, (7), **4**, No. 7, p. 14) lists *campanulata* as occurring in Algeria though not seen by him. His description is of *marginata*. Strauch attributes the authorship of *campanulata* to Walbaum (1782, Chelonogr. Beschr. Schildkröten, pp. 80, 124), but Walbaum's name — "*Lorica varietatis tabulatae testudinis campanulata*" — is not binomial and consequently invalid; furthermore, it apparently does not refer to an African species.

"No. 204. The African Land-Tortoise.
Loc. Santa Cruz in West Barbary."

i.e., the old Spanish fort of Santa Cruz near Oran, Algeria (*fide* Strauch :1862a), and the reptile figured is quite identifiable.

Strauch (1862a :67) points out that *graeca* Linnaeus, 1758, and *pusilla* Linnaeus, 1758, are not specifically the same, the latter being a composite; but *pusilla* Linnaeus (in part), 1766, and *pusilla* Shaw, 1802, were both based on Edward's specimen and are consequently synonymous with *graeca* Linnaeus, 1758.

The first to point out that *graeca* was the correct name to apply to the African species, was Siebenrock (1913, Ann. k.k. Naturhist. Hofmus. Wien., 196-197) but because *ibera* Pallas 1831 had long been employed for this species, he preferred to continue use of the latter name. Subsequently Flower (1925b; 929) pointed out that the type of *ibera* came from Iberia in Transcaucasia (cf. Pallas, 1811, Zoogeographia Rosso-Asiatica, **3**, p. 18, pl. ii, figs. 2-3). Specimens (M.C.Z. 5301-2) from Tiflis, Transcaucasia, suggest that this is a race of *graeca*, recognizable by its broad and low-vaulted carapace. *T. g. ibera* has been considered by Mertens (1946d :112) as one of several races inhabiting Asia Minor, their range separated from that of *T. g. graeca* by Egypt.

Testudo graeca bettai Lataste, based on an old specimen of unknown origin, having a divided supracaudal and a caudal spur, but lacking a conical tubercle on the hinder side of the thigh, appears to be a straight synonym of *hermanni* Gmelin, 1789, except for its allegedly 4-clawed forefeet and 3-clawed hind feet.

Common names. Western Spur-thighed Tortoise (preferred); Mosaic Tortoise (Müller :1774); Moorish Tortoise (Bateman: 1897): Spur-thighed Mediterranean Land-Tortoise (Flower: 1925); *Fakroun* (Tunisian Arabic: Mosauer); *makroona* (Algerian Arabic :Koenig); *zolhafie* (Arabic :Forskål).

Illustrations. The finest colored representations of this tortoise are those to be found on plate xvi of Sowerby and Lear (1872b), correctly labeled *graeca;* and on plate i of Lortet (1887) where it is miscalled *ibera.*

Description. Beak weakly hooked, tricuspid; edge of jaws not dentate; supranasals present, not meeting medially; prefrontal entire, rarely divided longitudinally;[1] frontal large,

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[1] Occasionally divided longitudinally in "*ibera*" according to Boulenger (1889a).

occasionally broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with large to very large, unequal, juxtaposed, more or less imbricate, rounded (young) to pointed (adult) scutes forming 3-6[1] longitudinal and 4-7 transverse series from elbow to outer claw; claws 5;[2] hinder side of thigh with a very large flat or subconical tubercle; heel with or without an indefinite spurlike tubercle; claws 4; tail without, or with a poorly developed terminal clawlike tubercle.

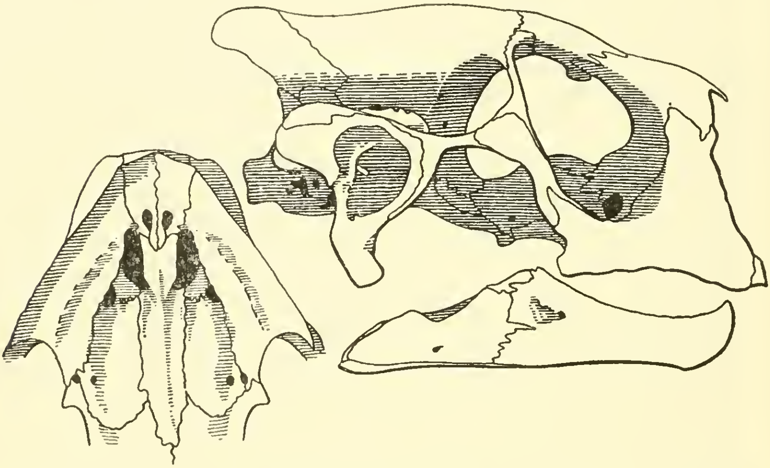

Fig. 20. Skull of *Testudo graeca graeca* (M.C.Z. 4485). Condylobasal length 26 mm.

(S. McDowell del.)

Carapace convex, slightly depressed in young only, sides descending abruptly, broadly notched in nuchal region, anterior and posterior margins not expanded, not or but slightly reverted, not or but slightly serrated; dorsal shields concentrically striated, not or but slightly swollen; nuchal moderately elongate, often broader behind, rarely divided longitudinally;[3] vertebrals

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[1] Three on left, four on right of an Algerian specimen (M.C.Z. 4485).

[2] Flower remarks (1924:921) that of 31 tortoises of unknown parentage (though presumably of Mediterranean origin) hatched in Giza Zoological Gardens between the years 1907-192 , 12 had 4 claws on their forefeet, 7 others bore 5 claws, and the condition in the remaining 12 was not noted.

[3] Divided in a North African tortoise (Lampe:1901).

5, rarely 6,[1] the first as broad as or broader than long,[2] second to fifth narrower or broader than the costals; costals 4, rarely 7 or 8,[1] not forming an angle with the marginals; marginals 11, rarely 10; supracaudal undivided, rarely divided;[3] not projecting beyond the marginals, slightly incurved in ♂♂, occasionally in ♀♀.

Front lobe of plastron anteriorly truncate, not or but slightly produced and not or but slightly notched; gulars paired; pectorals moderate, their anterior border usually curved and widening towards the axillary notch; axillary 1, small or moderate; inguinals (apart from some accessory scales) 2, outer moderate.

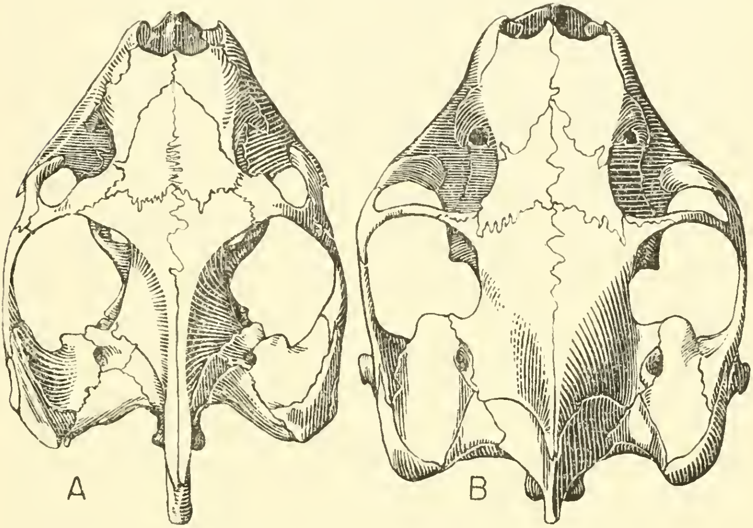

Fig. 21. Typical condition of prootic in dorsal view of skulls. *A*, *Geochelone p. babcocki* (A.M.N.H. 7203) showing prootic exposed; *B*, *Testudo g. graeca* (M.C.Z. 4485) showing prootic concealed.

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[1] Six in an abnormal living individual which had 7 costals on the right and 8 on the left (Mertens: 1936b: figs. 1-2).

[2] The third vertebral was always broader than or equal to the fifth in young Giza-bred tortoises, in older ones the third was narrower than the fifth (Flower: 1924a).

[3] Occasionally divided in young (*fide* Kœnig: 1892) or adults (Doumergue: 1899).

triangular, inner small, quadrate and in contact with the femoral; hind lobe broadly notched posteriorly, especially so in ♂♂, immovable in juveniles[1] but in life more or less movable in adults of both sexes.[2]

Plastral formula: Abd > (g. h. p. f. an: very variable).

Color. Carapace of young yellowish or pale olive, each shield bordered with black and brown and usually bearing a central black spot.

In adults yellowish, pale olive, brownish to reddish brown, rarely uniform; the darker pattern as described for the young but much more irregular with black predominating. Plastron usually yellow or greenish yellow, occasionally light brown, most or all of the shields bearing a blackish blotch. In ♂♂, according to Doumergue (1899), the plastron has a tendency to be more melanistic than in the ♀♀.

Size. Carapace length of a ♂ (M.C.Z. 18161) from Bone (which lived for over twenty years — 10.vii.1890 to 3.vi.1913 — in the Loveridge garden), 145 mm., breadth 109 mm., height 73 mm.

Carapace length of a ♀ (M.C.Z. 1498) from Algeria, 192 mm., breadth 133 mm., height 100 mm., far surpassed by an Algerian ♀ 276 mm. (see below) mentioned by Flower (1945:452) who points out that the largest examples of this species may not be more than 35 years old, though attaining a much greater age. Moreover, he says that very large individuals of this *species* need not necessarily have come from the Balkan Peninsula or Asia Minor, but may sometimes be of the typical North African race.

Growth and Weight. The carapaces of two tortoises of uncertain origin (purchased from a dealer in Norwich, England) increased during a seven-year period from 7 to 9, and 7½ to 9½ inches, respectively, when measured over the curve. Their weight, recorded every six months from 1886-1892, showed a gain of 11 and 12 oz., respectively. Occasional fluctuations in the carefully tabulated figures were attributed to variations in the

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[1] Under 65 mm. according to Strauch (1862b:15); occasionally movable in young (Koenig:1892).

[2] Very slightly (Schlegel:1841); observable in the largest adults (Strauch: 1862b); sufficiently movable in ♀♀ to facilitate enlarging the opening (Doumergue:1899); movable in both sexes (Siebenrock:1906c).

climatic conditions, hot summers and cold winters being considered as the most favorable for growth by Sir Peter Eade (1893) whose papers contain a wealth of detail.

Flower (1945:451) furnishes the annual weights and measurements of two female Algerian *graeca* that were hatched in September, 1905, from a batch of 14 eggs laid the previous May. Of the 14 hatchlings, two were acquired by C. F. Moysey on 22.ii.06. The following day he weighed and measured them for the first time and gave them the names of "Daimler" and "Panhard." Their respective weights were then .008 (Daimler) and .012 kgm. (Panhard), their carapacial lengths *over the curve* 47 and 49 mm. respectively. During the succeeding 39 years (in Somersetshire and Devon gardens) a fairly regular rate of growth (measurements were not taken from 1921 to 1937) was maintained while, except on two occasions, each tortoise registered an increase in weight *every* year from 1906 to 1944. In the latter year their respective weights were 1.814 and 3.969 kgm., their corresponding lengths over the curve 279 (11 inches) and 365 mm. (14⅜ inches). In a straight line the length of the latter (Panhard) was 276 mm. (10⅞ inches) on 22.v.44. Of its weight Flower remarks that it was (almost) the same as that of the heaviest *graeca* in the Giza Zoological Gardens, which he recorded as 4 kilos (8 lbs. 13 oz.).

Following the exceptionally fine and dry summer of 1955, which probably stimulated the tortoises' appetites, Daimler and Panhard were weighed on September 1st *for the fiftieth successive year* of their captivity. At that time Daimler weighed 2.629 kgm., and measured 298 mm., having ceased growth in 1949 at 44 years, while Panhard weighed 4.252 kgm., and measured 365 mm., having ceased growth in 1942 at 37 years. The weight of the larger tortoise may well constitute a record for a North African *graeca*. Certainly Mr. Moysey's achievement in weighing these animals monthly, except when hibernating, for half a century is something for which all herpetologists should be grateful. For the supplementary data contained in this paragraph we personally are indebted to Mr. Moysey (in letter of 14.i.56).

Mr. Moysey suggests that the difference in size of his two female tortoises is possibly attributable to the sharper-edged beak of the larger. With a single snap this reptile would sever a piece of leaf, whereas the smaller specimen often made several abortive attempts before succeeding in separating a piece for mastication and swallowing.

Sexual dimorphism. Eighteen alleged secondary sexual characters are discussed and illustrated by Camerano (1877:pl. lv). Most, if not all, are highly questionable. Werner (1895c) states that sex cannot be determined by plastron for he says it may be concave, flat, or slightly convex in either sex.

Courtship. Burton (1953:34) quotes C. H. Lay as saying that sometimes between mid-May and mid-June a thirty-year-old captive "*ibera*" male annually executes a series of rhythmic convolutions which leave a definite and regular pattern (cf. fig. in Burton) on the bare soil over an area of about forty feet square. The course taken is not so obvious in years when grass or weeds cover the plot. If this is indeed a courtship performance, supplementary to the oft-recorded butting described below, then further information should be gathered by persons resident in Africa.

Breeding. Possibly the fullest account of the breeding of a Moroccan tortoise is furnished by Gaston Astre (1948:60-64), based on a young and an adult ♂ and an old ♀ that had lived in his garden at Toulouse for twenty years. Owing, perhaps, to the difference in age and size of the ♂♂, no combats were observed between them. However, each spring the adult ♂ assiduously pursued the ♀. Then, rising on his four feet and withdrawing his head, with the front of his carapace he would deliver a smart blow on the back of hers. This performance would be repeated at the rate of one or two blows every two seconds. Should the ♀ hurry away the ♂ would give chase and, passing, bring her to a halt by biting at her head and forelimbs until she withdrew them within her shell, or, more usually, he would seize her carapace in his jaws and shake it with a range of as much as one or two centimetres. During copulation, according to Bailly-Maitre (1928), the male gapes widely and emits a muffled whistling cry.

From mid-May to mid-June the instincts of the ♀, rather than necessity, caused her to excavate with her hind feet a number of shallow troughs — about 34 mm. deep. These she soon abandoned, making no attempt to fill them in. Eventually, about the 10th to 15th of June, she would select a sunny spot with southern aspect, most frequently at the foot of a wall where the soil was sandy or loose and the ground likely to remain dry. There, using her hind feet, she would dig a conical, somewhat bell-shaped, pit. though its sides might be almost vertical if the earth happened to be well packed, to a depth of 70 or 100 mm. and a surface diameter of 120 to 140 mm.

On the bottom of this funnel she usually deposited 2, though occasionally 3, white, ellipsoidal eggs measuring 25 x 30 mm. and weighing from 13 to 14 grams. Next she proceeded to cover them to a depth of about 30 mm. with loose earth taken from that heaped around the periphery of the excavation. The hole was never entirely filled, for after the tortoise had smoothed over the surface a slight concavity of from 5 to 10 mm. remained. Having finished her task the tortoise would unconcernedly walk away.

On one occasion Astre noted the time expended on nest-making and egg-laying. Digging commenced at 12 noon and was completed at 17.30 hours. Laying began at 17.30 and continued until 18 hours. Covering the eggs and filling in the hole with earth took until 18.30, after which the tortoise made for the far end of the garden, where she customarily spent the night beneath a heap of dry vegetational debris, and went to sleep.

Though eggs were laid each summer for a period of twenty years they never hatched owing to the Toulouse climate. Following the unusually hot summer of 1947, however, when the average temperature for July was 23.02° C., for August 23.81° C., with a maximum of 42° on August 1st, and averaging 19.7°C. during September, two eggs hatched. It may be assumed that the temperature of the soil when directly exposed to the sun was possibly 20° higher than the shade temperatures cited above.

If the eggs benefited by the exceptionally warm summer, the hatchlings were favored by the unusually mild winter that followed. The average temperatures were 7.76°, 7.25° and 12°C. respectively for the months of January, February and March, 1948. In April, when the young tortoises would be about 6 months old, they weighed 9 grams apiece and their carapaces measured 30 mm. in length by 25 mm. in breadth.

In October, Bailly-Maitre (1928) found a hatchling Algerian tortoise in his Narbonne garden and, on examining the nest, a freshly dead embryo in an egg. Astre mentions that in September, 1944, M. LeCompte discovered in his Gironde garden a small tortoise that appeared to have been hatched there.

During the Tunisian rainy season in early spring, these tortoises are rarely in evidence unless the sun is powerful. When this happens the reptiles begin to wander about in search of each other (Chaignon :1904). On March 12th, in Algeria, tortoises were observed fighting and mating among the bushes (Doumergue :1899).

In May, 3 ellipsoid eggs, each the size of a pigeon's, were present in a Tunisian tortoise eaten by Chaignon (1904). An old ♀, captured in the Macta (Mactra) region on 19.v.1890, laid an egg on June 25th; on July 4th two more eggs were found, and laying continued until 7 eggs had been deposited (over how long a period is not stated). These eggs measured 28 x 36 mm. (Doumergue :1899). In August an Algerian tortoise laid 2 eggs measuring 24 x 33 mm. (Werner :1894), while others laid by a 202 mm. Tunisian reptile measured 24.5 to 31 x 31.5 to 38.5 mm. (Gadeau de Kerville :1908). An egg in our possession (M.C.Z. 19003) measures 26 x 37 mm. The remarks by Kercado (1875) are intentionally omitted as being based on untrustworthy hearsay.

Longevity. The record is given by Flower (1925b and 1937a) as being 102 or 125 years, depending on whether Archbishop Laud's tortoise died in 1730 or 1753. This reptile, whose shell was examined and identified by Flower at Lambeth Palace where it is preserved, was at Fulham Palace in 1628 when Laud was Bishop of London. He took it with him to Lambeth Palace when he became Archbishop of Canterbury in 1633. Much supplementary information regarding this and other historical tortoises will be found in the references given above.

Possibly more reliable records are those of 96 and 54 years down to one of 22 years, 10 months and 23 days for a tortoise (M.C.Z. 18161) already adult when brought back from Bone, Algeria, on 10.vii.1890. The latter lived until 3.vii.1913 when one of us (A.L.) chloroformed him because he was so weak and moribund that flies were buzzing around him and depositing their eggs about his tail. Each winter during his life in a South Wales garden, he had dug himself under the surface in a strawed-over strawberry bed.

Diet. Food is taken with a snapping movement or torn away, being swallowed with little or no mastication. When not fed, Eade's two tortoises sought, not grass but clover, trefoil and fleshy-leaved plants such as *Echweria* or *Sedum.* They displayed a marked preference for yellow blossoms, consuming quantities of buttercups, dandelions, French beans and lettuce. Both would leave all other food for a green pea, a vegetable of which they were so fond that they would follow anyone who would feed them peas and clamber up his legs in their eagerness to reach them. One would take sliced apple, the other not. While a neighbor's tortoise fed on milk-soaked bread, Eade's two could not be tempted with milk and never drank water (Eade:1886). Captive tortoises at St. Petersburg were fed cabbages and potatoes (Eichwald:1851).

Though essentially vegetarian, according to Doumergue (1899) they will take insects, mollusks and worms during the Algerian dry season! Street vendors are apt to advertise these tortoises as useful in ridding a house of cockroaches or a garden of slugs. As a result many perish of starvation unless liberated in a garden where they can help themselves to lettuce and strawberries.

Parasites. Ticks (*Hyalomma aegyptiacum* Linnaeus) from a Rabat tortoise were identified as its synonym (*Hyalomma syriacum* C. L. Koch) by Dr. R. Schweizer (Hediger:1935).

Enemies. Tortoise eggs are richer in albumen than those of birds; the flesh also is edible and tortoise broth is recommended for the feeble (Doumergue:1899). The flesh is like that of a chicken and many were eaten by the French soldiers, though not by the Arabs and Moors (Rozet:1833), for the latter fear them, imagining that they are evil spirits (Poiret:1789).

Formerly it was, and possibly still is a common sight in early summer in the larger cities of Europe, especially maritime ones, to see barrow loads of these helpless reptiles being offered for sale by street vendors, or crawling aimlessly about in the windows of so-called pet shops.

Temperament. Of three purchased from a hawker on a Norwich street by Eade (1886:316-322) one died, the others appeared ill but recovered. They showed little evidence of *hearing,* but their *sight* was acute and their sense of *taste* well developed, enabling them to "discriminate instantly." As Lady Eade was apt to indulge them with their favorite foods, upon her arrival they would leave Sir Peter — even though he might be feeding them at the time — and go to her to be fed. They ate only once a day, if at all, during cool weather.

On the finest summer days, however, they were early astir and by 6 or 7 A.M. might be found nibbling at trefoil. Normally they did not venture abroad until between 8 and 10 o'clock, and not then if it happened to be raining or overcast. Should a cloud obscure the sun when they were feeding, both would promptly withdraw their heads. In thundery weather, even though there might be hot and sunny intervals, the tortoises remained quiet and indifferent to food. When the solar rays were insufficiently hot the reptiles would tilt themselves against the south wall of a greenhouse in order to enjoy the maximum warmth. When too hot they would bury their heads beneath leaves while leaving the carapace exposed.

They objected to being placed in a sleeping place other than the one to which they customarily resorted. In cool weather, however, Sir Peter habitually placed them under a mat in the greenhouse; next morning they would be at the door waiting to be let out. When shut up in a greenhouse one tortoise was frequently found mounted on the other's back or on an inverted flowerpot. Apparently both were ♂ ♂ but they did not fight or display any interest in each other's society; when one got in the way its companion would attempt to clamber over it. Both evinced a love of climbing; when one tried to ascend some sticks that were resting against a wall, it slipped and was found sprawling on its back, three legs waving helplessly in the air while only one hind limb rested on the ground.

If carried from some spot they liked, they would make straight for it again as soon as released. When timed it was found that one took a minute to walk 10 feet, while the other could do 20 feet in this period; at this rate they would take between 4 and 5 hours to cover a mile. Their *memories* appear good, for immediately after emerging from a hibernation of 7 to 8 months' duration, they would set off for their old haunts as if only a day had intervened.

Aestivation and Hibernation. Both aestivation and hibernation are intermittent in North Africa. During the Algerian summer these tortoises normally seek shelter from the sun by burying themselves, and consequently are rarely encountered (Doumergue:1899), but in July and August two were collected in the early morning by Hediger (1928).

They reappear in September only to vanish again at the approach of winter by concealing themselves in burrows or beneath a large stone. Even in the depth of winter, however, when the ground has been sufficiently heated by the sun, individual tortoises emerge for a time. In the hot coastal dunes and hills they come out again in February (Doumergue:1899).

Habitat. In Algeria these tortoises are extremely common throughout the region from Oran to the Petit Atlas (Rozet:1833), where they occur among the dwarf palms (*Chamaerops humilis*) beneath whose fronds they conceal themselves (Schlegel:1841). They are numerous among the bushes (*Zizyphus jujuba*) that are scattered throughout the waste lands (Eversmann:1854), where they are more plentiful among the dunes than on the edges of the plains (Le Cerf:1907). Scarce, though widely distributed throughout the mountainous regions and all the high plateaus, this species is apparently absent from the oases, its most southerly records being Beguira; El Aricha, and Geryville (Doumergue:1899). Absent south of El Kantara (Kantarah), which is also the most southerly limit for the lizard genera *Lacerta*, *Ophisops* (*Ophiops*) and *Psammodromus* (Werner:1894).

Common on the plains of Tunisia (Olivier:1896b).

Localities. Spanish Morocco: Tangier (Tanger). *French Morocco:* Azemmour (Azimor); Azrou; *Beni Snassene; Berguent; Casablanca; Dar el Beida, Casablanca; El Marit, Casablanca; Fes (Fez); Karia ba Mohammed; Maarif near Casablanca; *Mamora (Marmorea) Forest; Mogador; Moghran, a confluent of Sebou west of Beht; Oued Akrech, south of Rabat; Oued Mella north of Mogador; Ouezzane; Rabat (Aïn el Anda and La California); *Sefrou; Sidi Amar; *Sidi Yahia (U.S.N.M.); Souk el Arba; Taourirt. *Algeria:* Aumale, Guyotville; Bainen Forest near Algiers, Batna; Beguira; Biskra; *Bone; Boudsareah near Algiers; Bou Saada; Constantine; El Aricha; Geryville; La Calle; Lambeze (Lambesa); Macta; Maison Caree near Algiers; Medea (Medeah); Metidja near Algiers; Nemours; Palestro; on mountains between Rosmarin and Thymian; Santa Cruz=Oran. *Tunisia:* Aïn Draham; Bir Mcherga; Djebel Achkel (? Ischkeul); Djebel Rsass (*sic*); Douirat (Duirat); Graiba; Kairouan (Kairwan); Maxula Rades; Sidi bou Ali; Tunis; Utique ruins; Zarzis. *Libya:* Barce (= El Merg); Bengasi; Bir (Bil) Milrha; Marmarica; Merg (= Barce); Tobruk (Tobruch); Tolmeta (Tolmetta); Tripoli.

Range. Morocco to Cyrenaica; Pityusen Islands and southern Spain.

PSEUDOTESTUDO new subgenus

Type species: *Testudo kleinmanni* Lortet

Definition. Supracaudal usually single. Maxillary without ridges; anterior palatine foramina large, not at all concealed; quadrate not enclosing stapes. Plastron of adults with a clearly movable posterior lobe in both sexes. Tail claw absent.

Range. Northeast Africa.

TESTUDO KLEINMANNI Lortet

1823. *Testudo graeca* Lichtenstein (not of Linnaeus), 91.
1835. Rüppell, 4.
1880d. Peters, 305.
1881a. Peters, 365.
1835. *Testudo marginata* Duméril and Bibron (part: not of Schoepff), 37.
1844. Gray, 9.
1855. Gray, 11.
1857. Jan, 35.
1855. *?Chersus mauritanicus* Fitzinger (not of Duméril and Bibron), 252 (Egypt).
1869a. *Testudo leithii* Günther, Proc. Zool. Soc. London, p. 502, figs. 1-4: "Sindh" (error); preoccupied by *T. leithii* Carter, 1852.
1869b. Günther, 110.
1880c. Vaillant, 32, 88.
1889a. Boulenger, 175.
1890. Boulenger, Fauna British India. Rept. and Batr., p. 20.
1890. Strauch, 45.
1892. Baur, 156.
1893a. Boettger, 11.
1896. Anderson, 77, 95.

1898. Anderson, 28, col. pl. ii.
1901. Steindachner, 326.
1904. Andersson, 9.
1908b. Kammerer, 757.
1908c. Kammerer, 772, figs. 9-10.
1909a. Siebenrock, 540.
1909a. Werner, 596, 628.
1912b. Werner, 452.
1913. Ghigi, 283.
1923a. Calabresi, 7.
1924a. Flower, 920.
1925b. Flower, 928.
1926. Flower, 133.
1927. Vinciguerra, 328.
1929. Flower, 29.
1929. Zavattari, 86.
1930a. Zavattari, 263.
1931. Gestro and Vinciguerra, 538.
1933. Flower, 745, fig. 1a.
1934a. Mertens and Müller *in* Rust, 9.
1937. Zavattari, 530.
1950. Williams, 551.
1870c. *Peltastes leithii* Gray, 657.
1870e. Gray, 11, fig. 6.
1873b. Gray, 11.
1883. *Testudo Kleinmanni* Lortet, Arch. Mus. Hist. Nat. Lyon, **3**, p. 188: Lower Egypt and environs of Alexandria, Egypt.
1887. Lortet, 11, pl. v.
1894. *Testudo campanulata* d'Aubusson (not of Strauch), for 1893, 230.

Synonymy. Mons. Kleinmann, after whom the species is named, was Director of the Crédit lyonnais en Égypte (Lortet: 1887 :13). *Testudo leithii,* named for Dr. A. H. Leith by Günther (1869a), is preoccupied by *Testudo leithii* Carter 1852 proposed for a fossil turtle from Worli Hill, Bombay, India, which Williams (1953)[1] has shown to be that of a pelomedusid and assigned to a new genus — *Carteremys.*

Common names. Egyptian Tortoise (suggested); Leith's Tortoise (Flower); *solhalfa* or *zihlifa* (Innes *in* Anderson 1898).

Illustrations. Exceptionally fine colored figures of this species (dorsal, lateral and ventral views) are given by Lortet (1887 :pl. v) and Anderson (1898 :pl: ii).

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[1] Williams, E. E., 1953, Breviora (Mus. Comp. Zool.), No 13, p. 5.

Description. Beak feebly or moderately hooked, tricuspid; edge of jaws not dentate; supranasals present, sometimes meeting mesially; prefrontal entire. divided longitudinally, or broken up; frontal large or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with a few, contiguous, extremely large, imbricate, rounded or pointed scutes forming 3, rarely 4, longitudinal and 4-7 transverse series from elbow to outer claw; claws 5, rarely 4;[1] hinder side of thigh without enlarged tubercles; heel with large, conical, spurlike tubercle; claws 4; tail with or without a terminal clawlike tubercle.

Carapace convex, slightly depressed in young only, sides descending abruptly, deeply or broadly notched in nuchal region, anterior and posterior margins not expanded, not, or but slightly, serrated; dorsal shields concentrically striated, not or but slightly swollen; nuchal moderate or large, triangular, rectangular or exceptionally elongate;[2] vertebrals 5, rarely 6 or 7,[3] the first as broad as, or much broader than, long, smaller than the second to fifth which are narrower than, as broad as, or broader than, the costals;[4] costals 4, rarely 3 or 5,[5] not forming an angle with the marginals; marginals 11 or 12, rarely 10;[6] supracaudal usually undivided, less frequently divided, spread out like, but projecting angularly beyond, the marginals.

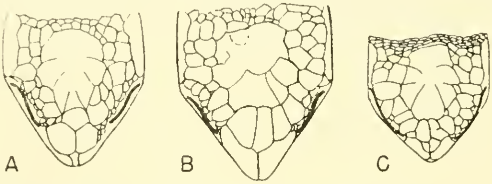

Fig. 22. Head scalation in *Testudo kleinmanni* (x 1). *A*, Salum specimen (M.C.Z. 54045); *B*, Salum specimen (M.C.Z. 54044); *C*, Alexandria specimen (M.C.Z. 5081), Cotype.

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[1] Four in a tortoise bred at Giza Zoo from El Arish parents, both of whom had four claws only on each forefoot (Flower :1933 :747).

[2] In a ♂ from El Arish in which it was 6 mm. x 2.5 broad mm. (Flower :1933 : 747).

[3] Six in a hatchling and also in a 95 mm. ♂ from El Arish (Flower :1933 :747) ; seven in a cotype (U.S.N.M., 10979) seen by E.E.W.

[4] In a 95 mm. Derna tortoise the third vertebral has given rise to a couple of supplementary shields lying between the 3rd and 4th costals (Calabresi : 1923a).

[5] Three in one seen by Flower (1953 :748) ; 5 on right side of a carapace (Y.P.M. 672) seen by us.

[6] Ten on one side of a cotype (U.S.N.M. 10979) and a specimen (B.M. 1922.5.23.2), both seen by E.E.W. ; 12 in a 95 mm. ♂ from El Arish, while others from this locality had 11 on one side and 12 on the other (Flower :1933 :747).

Front lobe of plastron anteriorly truncate, not or but slightly produced, somewhat notched and each lateral point itself very slightly toothed; gulars paired, rarely absent;[1] pectorals moderate, their anterior border usually widening towards the axillary notch; axillary 1, moderate; inguinals 1 or 2, small or moderate, in contact with, or separated from, the femoral; hind lobe very broadly notched posteriorly, slightly movable in adults of both sexes but especially in the ♀.

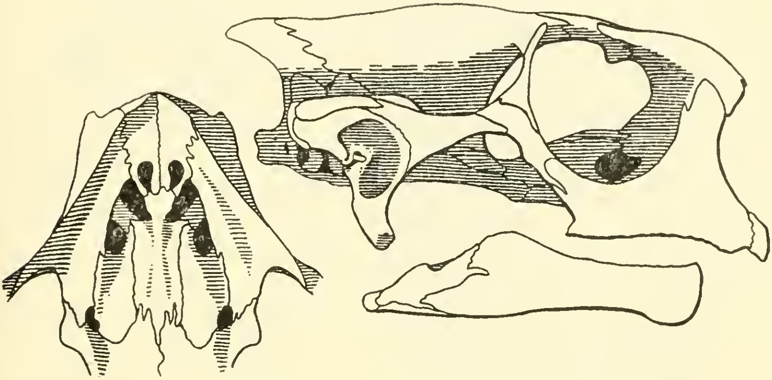

Fig. 23. Skull of *Testudo kleinmanni* (Yale Mus. 667). Condylobasal length 21 mm. The entrance of the parietal into the orbit is an individual peculiarity.

(S. McDowell del.)

Plastral formula: Abd > (g, h, p, an, subequal) > f.

Color. Carapace greenish yellow to pale yellow, uniform, or each shield more or less edged with black or brown. Plastron greenish to yellow, each abdominal shield with a dark brown to black, triangular or cuneiform patch, which is usually conspicuous and never entirely absent; pectorals occasionally margined anteriorly with dark brown; remaining plastral shields uniform. Hatchlings are completely yellow, according to Lortet (1887).

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[1] Absent in a Giza tortoise (U.S.N.M. 55758) in which the anterior lobe is abnormally shortened though apparently *not* the result of an injury.

Head, neck, limbs, feet, nails and tail, yellow; rarely a black spot on crown of head posterior to the eyes; the buttonlike eyes strikingly black, the irides in both sexes being shining black and very conspicuous according to Flower (1933:748) who should be consulted for further details on coloration. His paper, based on 159 living tortoises, contains far more information about "*leithii*" than all of the other citations combined.

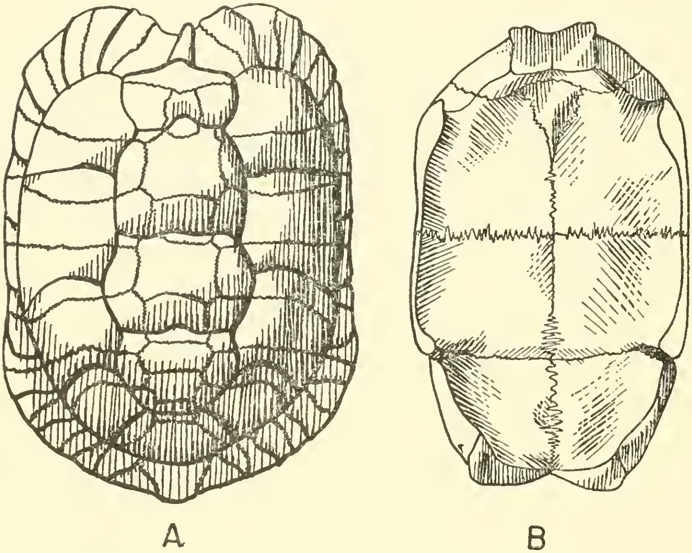

Fig. 24. *Testudo kleinmanni*. *A*, Dorsal view of carapace (M.C.Z. 1499) (x ⅔); *B*, Internal view of plastron (Yale Mus. 667). Note hinging of the posterior lobe (x ⅔).

(P. Washer del.)

Size. Carapace length of adult ♂♂ is from 86 to 110 mm.; the last mentioned, coming from El Arish, is exceptional for a ♂. Carapace length of adult ♀♀ is from 113 to 127 mm., the latter from Mersa Matruh (cf. Flower:1933:746). Carapace length of a ♀ (M.C.Z. 1499) 100 mm., breadth 72 mm., height 57 mm. Carapace length of a *kleinmanni* cotype, 100 mm., of the *leithii* holotype 120 mm.; of a juvenile *kleinmanni* cotype (M.C.Z. 5081) 55 mm., breadth 45 mm., height 28 mm.

Weight. Adults average 7 to 9 oz. (.198 to .255 kgm.), the largest attaining 13 or 14 oz. (.35 to .4 kgm.), *fide* Flower (1933:746).

Sexual dimorphism. Tail of ♀ short and pointed, that of the ♂ very long, yet exceeded by the fully extended penis which, though normally pink, then turns to a rich purple (Flower: 1933:746).

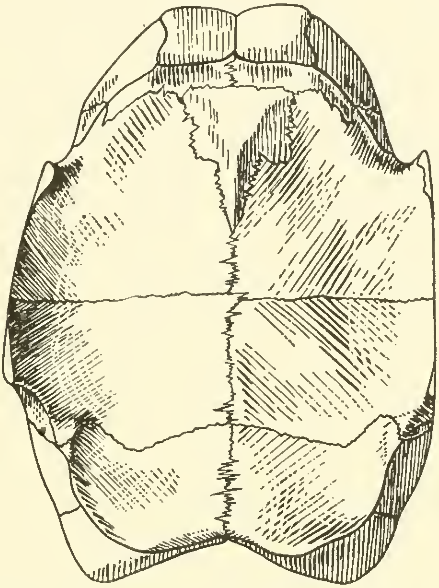

Fig. 25. *Testudo hermanni* ♂ (M.C.Z.). Internal view of plastron to show absence of hinging.

(P. Washer del.)

Breeding. Mating at the Giza Zoological Gardens, Cairo, took place in September and October (Flower). March and April among captive tortoises (Lortet:1883), while a ♂ that Kammerer (1908c) kept for five years, repeatedly copulated with captive *hermanni* (miscalled *graeca*) but, possibly because the ♀♀ were subadult, they remained infertile. Flower describes the voice of the mating ♂ as sounding like the intermittent winding-up of a metal spring.

Eggs with a rosy blush and measuring 23 x 30 mm., were deposited in May and abandoned on the surface, according to Lortet (1887), who adds that when the temperature is sufficiently high the young may emerge in 20 days after laying. Such hatchlings were completely yellow.

On two occasions eggs were laid at Giza in June, one laid on the 17th measured 22.75 x 29 mm. No records were kept as to when the majority of the eggs were laid, but 69 hatchings took place as follows: September (6); October (37); November (17); January (3); February (6).

Kammerer (1908b) somewhat vaguely refers to a dozen eggs measuring 22 x 28 mm., some of which were laid on July 6 by a tortoise having a carapace length of 104 mm. After 125 days[1] all allegedly hatched on November 8 but, refusing food, died within a few weeks of emergence. The dimensions of these hatchlings, stated to be from 18 to 19 mm., are at variance with those furnished by Flower (1933:748) for one which was 33 mm. in carapace length and 28 mm. in breadth.

The outline of *kleinmanni* hatchlings is quite different from that of the more spherical *graeca*. Contrasting figures to illustrate this are furnished by Flower (1933:748).

Longevity. Twenty-one years and 25 days. Average longevity of twenty tortoises still living in the Giza Zoo in 1925, was 16 years, 7 months, and 6 days (Flower:1925b).

Diet. Largely Saltwort (*Salsola* sp.) and Sea Lavender (*Limonium* sp.) according to Lortet (1887:14).

Hibernation. Active throughout the Egyptian winter though more sensitive to low temperatures than either *graeca* or *marginata*, according to Lortet (1887:14).

Habitat. In Egypt it is very restricted, being absent from the deserts around Cairo, and present only in two districts which are about 180 miles apart, viz. the northwestern deserts of the Nile delta and region of Suez Canal where, as well as in northern Sinai, it may be found among the bushes growing in the vicinity of brackish lagoons.

Localities. *Libya:* Barca; between Bir Sceferzen and Esc-Seegga on the Giarabub to Tobruk road; Sirtica; Wadi Tessina in Kufra Oasis. *Egypt:* *Alexandria; Bir el Abd; Damietta; El Arish (Arisc); *Giza (Gizeh); Ismailia; Kantara (Kantareh);

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[1] Compare with Lortet above!

Khabra Abu Guzoar; Katia; Lahfan; Mariut (Maryut); Mersa Matruh; Port Said; Romani; Salmana; *Salum; Wadi el Amr; Wadi Hareidhin.

Range. Western Cyrenaica and northern Egypt (including northern Sinai).[1]

Genus MALACOCHERSUS Lindholm

1929. *Malacochersus* Lindholm, Zool. Anz., **81**, p. 285. Type: *Testudo tornieri* Siebenrock (by original designation).

Definition. Skull with triturating surface of maxilla strongly ridged; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina small, concealed in ventral view; prootic well exposed dorsally; quadrate enclosing stapes; surangular sometimes markedly lower than prearticular, exposing the latter to view externally; neck with third or fourth centrum biconvex.

Carapace never hinged, *persistently fenestrated; neurals attenuated and greatly reduced;* outer side of third costal scute about as long as, or longer than, that of fourth; submarginal scute absent; a single suprapygal.

Plastron never hinged, persistently fenestrated; gular region neither thickened nor produced; gulars paired, broader than long.

Distinguishing marks. No other tortoise is so nearly flat or has a shell so flexible that it may be compressed between finger and thumb. Carapace length not known to exceed 177 mm.

Range. Apparently restricted to certain rocky regions of Kenya and Tanganyika.

Fossil record. None.

Remarks. The relationships of *Malacochersus* are far from clear. At first glance the shell seems anomalous and unique, yet its fenestration, as has been made clear by Miss Procter (1922b), is similar to that of some adult *Gopherus polyphemus* and to the hatchling stages of every tortoise (cf. Procter: fig. 21b of a young *Testudo horsfieldi* and the figures in Gray: 1873e). In *Malacochersus* we find persisting into adult life a stage in shell

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[1] Tristram's statement (1884. The Survey of Western Palestine. The Fauna and Flora of Palestine, 156) that *kleinmanni* ranges northwards in suitable localities to the western side of the Black Sea (in the vicinity of Hebron), Palestine, was based on a misidentification as shown by Flower (1933:745).

ontogeny usually present only for a short time after hatching. At least this is true of the dermal shell. There is, however, some resorption of the endochondral ribs, but this also is paralleled in other land tortoises, in which reduction of the ribs is a very common condition. Apart from fenestration, the shell is rather primitive, i.e. essentially emydine, in its single suprapygal, the hardly developed gular lip and the broad transversely extended gular scutes.

However, skull, vertebrae and limbs are thoroughly testudinine and differ but little from those of *Geochelone.* Limbs and vertebrae are in fact in no way distinctive, but the skull has certain discernible but rather subtle peculiarities, and the mandible is more conspicuously distinct in a dorsal emargination of the surangular. This is not consistently present and while it is tempting to ascribe such an emargination to a general weakness of ossification in this form, such a suggestion is not borne out by the very solidly built skull in which even the anterior palatine foramina are not at all enlarged.

In external features *M. tornieri* is somewhat peculiar. The transversely, rather than longitudinally, developed gulars recall *Homopus,* while the head scutellation with its large supranasals along with the prefrontals and frontal, is more elaborate, so possibly more primitive, than that in any other form except *Testudo.* Miss Procter would call an azygous scute, occasionally occurring on the anterior plastron, an intergular, comparable to that of primitive turtles; it may be doubted that these anomalies have any atavistic or phylogenetic significance. The flatness of the shell is extraordinary and, as Dr. Procter comments, is unrelated to the fenestration but appears to be a special development correlated with the reptile's habits. Miss Procter believed the feet to be more supple at wrists and ankles and less club-shaped than in most testudinines.

Because of the nature of the shell the paleontology of this form is unlikely to become known soon. The best hope would appear to be a skull, since that is rather solidly built, but even this would have to be well preserved, and, as is well known, well-preserved turtle skulls are paleontological rarities.

In the preceding diagram of relationships (see p. 210) we have tentatively suggested *Malacochersus* as arising quite independently from the ancestral stock of the testudinines. It would seem that the characters possessed by *Malacochersus*, other than specializations peculiar to itself, are primitive for the subfamily. This opinion, while the best we can offer, is a guess, but on the basis of the data available no other conclusion seems likely.

Fig. 26. Distribution of *Malacochersus tornieri* in East Africa. The hollow circle indicates the type locality of *procterae*. (P. Washer del.)

The distribution of this peculiar genus, dependent on a rocky habitat, is not merely limited but discontinuous if judged by present records. The presence of such a shy and cryptozoic creature may well have been overlooked, however, and some of the gaps in its range are certain to be closed when intervening areas are carefully searched.

The southernmost record, Lindi, whence came the second known specimen, is on the southeast coast of Tanganyika Territory almost 400 miles southeast of Dodoma, which appears to be the chief center of distribution. From Dodoma the species extends west to Tabora and north to Busisi (the original type locality of *tornieri*) at the southern end of Lake Victoria, and east to Lake Eyasi which is due north of Dodoma.

The most northerly record for which a specimen is available, Njoro, Kenya Colony, is approximately 200 miles due north of Lake Eyasi. Another record in Kenya is Malindi about 360 miles southeast of Njoro on the Kenya coast and as far from Dodoma as it is from Njoro. But *Malacochersus* is to be looked for still further north, for in 1914 the late R. B. Woosnam, when asked by Loveridge whether undescribed reptiles were still to be found in Kenya, replied that he had once come across two strange soft-shelled land-tortoises when on safari in the Northern Frontier District. Being on the march at the time, and having nowhere else to put them, he had popped them into a cooking pot being carried by one of the bearers. Later, on enquiring for them, he found they had been turned loose by his indignant cook. Woosnam added that he had never seen any similar tortoises during the many years he had spent in Africa.

MALACOCHERSUS TORNIERI (Siebenrock)

1896. *Cinicys* (*sic*) *belliana* Tornier (part: not of Gray), 2.
1903. *Testudo tornieri* Siebenrock, Anz. Akad. Wiss. Wien, 40, p. 185: Busisi, s. end of Lake Victoria, Tanganyika Territory.
1903b. Siebenrock, 442, pl.
1904a. Siebenrock, 29, fig.
1909a. Siebenrock, 538.
1911. Lönnberg, 7.
1913c. Nieden, 54.
1922d. Loveridge, 522.
1923g. Loveridge, 931.
1924b. Loveridge, 2.
1924. Wettstein, 201, figs. 1-2.
1928d. Loveridge, 49.
1929. Flower, 32.

1933h. Loveridge, 207.
1936. Kanberg, 187, photo.
1936h. Loveridge, 19.
1936j. Loveridge, 221.
1937f. Loveridge, 492, 495.
1937. Ruckes, 103.
1940. Conant and Downes, 48.
1950. Williams, 550, 551.
1954. Noël-Hume, 76 (numerous misstatements).
1920c. *Testudo Loveridgii* Boulenger, C. R. Acad. Sci. (Paris), 170, p. 263: Dodoma, Ugogo, Tanganyika Territory.
1920d. Boulenger, 68.
1920. Boulenger, E. G., 190.
1921d. Loveridge, 50.
1922b. Procter, 483, figs. 1b, 2-11a, 12-21a, pls. i-iii.
1922d. Loveridge, 522.
1923g. Loveridge, 928.
1924b. Loveridge, 2.
1924b. Mertens, 71.
1924. Wettstein, 201, figs. 1-2.
1924d. Witte, 48, 61.
1925b. Flower, 925.
1922b. *Cinixys belliana* Procter (not of Gray), 515.
1923g. *Testudo procterae* Loveridge, Proc. Zool. Soc. London, p. 928, pls. i-ii: Ikikuyu, s. of Gulwe, Tanganyika Territory.
1924b. Loveridge, 2.
1924b. Mertens, 72.
1924d. Witte, 48, 62.
1937f. Loveridge, 495.
1929. *Testudo (Malacochersus) tornieri* Lindholm, 285.
1934a. *Malacochersus tornieri* Mertens and Müller *in* Rust, 9.
1937d. Mertens, 3.
1939. Zangerl, 355, 399, pl. ii.
1942d. Mertens, 245-251, figs. 1-4.
1949. Conant and Hudson, 4.
1949b. Loveridge, 19.
1934a. *Malacochersus procterae* Mertens and Müller *in* Rust, 9.

Further citations of "*tornieri*" will be found under *Kinixys b. belliana.*

Common names. Soft-shelled Tortoise (Flower); Pancake Tortoise (W. M. Mann).

Illustrations. Siebenrock (1903:pl. –) furnishes a dorsal view of the type of *tornieri,* together with detailed drawings of the beak and scaling on the forelimb. Procter (1922:pl. i) has a colored plate of topotypical *loveridgii,* which should be contrasted with that of *procterae* as shown by Loveridge (1923g: pl. i). Siebenrock (1904a:fig. –) pictures the skeletal carapace from below; x-rays of ♂ and ♀, besides numerous developmental figures, will be found in Procter (1922b), Loveridge (1923g:pl. ii), and Zangerl (1939:pl. ii).

Types. The Berlin type, collected by Stuhlmann, was at first referred to *Kinixys* by Tornier under the impression that the paperlike consistency of its carapace was abnormal, perhaps a case of arrested development. Later Siebenrock (1903a), discovering this Berlin specimen was not a *Kinixys* but an undescribed species of *Testudo,* named it *tornieri,* though still attributing its peculiar softness and flatness to pathological defects which had retarded the development of the bony carapace and plastron; alternatively he postulated faulty preservation. The receipt of a second specimen from Lindi, enabled him (1904a:29) to amplify his original description and give a detailed account of the fenestration of the shell.

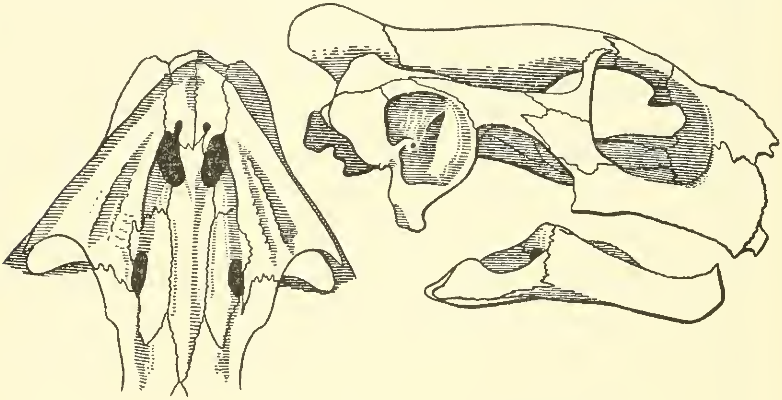

Fig. 27. Skull of *Malacochersus tornieri* (A.M.N.H. 45081). Condylobasal length 30 mm. The lateral exposure of the prearticular is not constant. (S. McDowell del.)

When five specimens collected by one of us (A.L.) and labeled "*Testudo tornieri*" in the field, were submitted to Boulenger, he regarded them as separable and distinct. Included in the shipment were other tortoises including a young *Kinixys belliana* from another locality which Boulenger (1920c) unfortunately assumed was the young of his *loveridgii.*

The disposition of *Testudo procterae* Loveridge, poses something of a problem. Its type locality — Ikikuyu (not to be confused with the place of the same name on the outskirts of Dodoma) south of Gulwe (Igulwe) Station on the Central Railway — is about 75 miles southeast of Dodoma, type locality of *loveridgii* Boulenger (=*tornieri*).

The supposed structural differences offer but weak support (cf. comments under Size) to the idea that the very distinctively colored (cf. Loveridge :1923g :col. pl. i.), but still unique, type of *procterae* in the British Museum is a distinct species. In the absence of more material, therefore, we incline to the view that *procterae* may be only a very striking color variant of *tornieri.* This view, if correct, is paralleled by the somewhat similar case of ''*Homopus*'' *bergeri* Lindholm, which we regard as merely a color variety of *Psammobates tentorius verroxii* (Smith). In both instances pattern reduction has taken place; in *bergeri* there has been a melanistic simplification; in *procterae* brown pigmentation has become dominant to the exclusion of all other markings.

However, in its *elongate* and large prefrontals with correlatively absent supranasals (cf. Plate 6), the head scalation of *procterae* differs strikingly from, and is not approached by, any of the many *tornieri* we have examined (cf. characteristic scutellation of *tornieri* in Fig. 19). Symmetrical as is the arrangement in the holotype of *procterae* there remains the possibility that it is an individual variation. Variation in head scalation, common though it is among tortoises, usually consists in a breakdown of the normal arrangement, *not in the appearance of an alternative pattern.* In this instance, with only a single specimen available, it is impossible to evaluate the importance of this character. It emphasizes the importance of securing further *Malacochersus* from the type locality of *procterae;* we have attempted to have such material obtained for us, but the attempt was unsuccessful.

Description. Beak weakly or moderately hooked, bi- or tricuspid, edge of jaws minutely denticulate; a pair of supranasals in contact, very rarely separated; prefrontal entire or divided longitudinally or somewhat broken up; frontal large, small, or broken up; remaining upper head shields small, irregular; forelimb along anterior edge with some moderately enlarged, more or less imbricating scutes[1] forming about 5-10[2] transverse series from elbow to outer claw; on inner aspect of forelimb are 2-4 prominent, enlarged, separated or juxtaposed, pointed scutes; claws 5, occasionally 4 through accident; hinder side of thigh with a rosette of enlarged scales surrounding a somewhat larger subconical tubercle; heel sometimes with trace of a spurlike tubercle; claws 4; tail without terminal clawlike tubercle.

Carapace very much flattened dorsally, flexible, its sides either straight and parallel or oblique, perpendicular or steeply sloping, scarcely notched in nuchal region, anterior margin flat and weakly serrate, lateral margins sometimes reverted, gutter-like, posterior margin flat, rarely reverted, slightly serrated; dorsal shields concentrically striated, sometimes swollen;[3] nuchal somewhat broader than long in young, usually elongate in adults, anteriorly indentate and projecting, usually broader posteriorly, occasionally completely divided;[4] vertebrals 5 rarely 4,[5] 6,[6] or 7,[7] sometimes flat, very rarely divided longitudinally[8] or transversely,[9] the contact between fourth and fifth frequently very narrow, first vertebral slightly broader than long or as broad as long and smaller than the second to fifth, which are much broader than long, as broad as, or broader than, the costals; costals 4, rarely 5,[10] sometimes forming an angle with the lateral marginals; marginals 11, sometimes 12; supracaudal divided, sometimes above only, rarely undivided, downwardly directed or outwardly flared irrespective of sex.

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[1] These enlarged scutes are both more numerous and strongly imbricating in the Njoro tortoise (Stockholm Mus.).

[2] Twelve on both sides of the Njoro specimen (Stockholm Mus.).

[3] Swollen in only one Dodoma individual (M.C.Z. 24912).

[4] Divided in a ♀ (M.C.Z. 30009) from Mangasini, and in U.S.N.M. 72505, probably from Dodoma.

[5] Four in a ♂ cotype of *loveridgii* (cf. Procter :1922b :fig. 4).

[6] Six in a ♀ (M.C.Z. 23000) from Kondoa Irangi.

[7] Seven in U.S.N.M. 73934, probably from Dodoma.

[8] Fourth vertebral is longitudinally divided in U.S.N.M. 72497, probably from Dodoma.

[9] Fifth vertebral is transversely divided in U.S.N.M. 73943, probably from Dodoma.

[10] Five in U.S.N.M. 72522, 73934, etc.

Front lobe of plastron anteriorly truncate, more or less produced, openly notched; gulars paired, as wide as, or wider than, long; exceptionally an intergular;[1] pectorals moderately broad, not or but slightly narrowed medially, their anterior border usually straight, widening gradually towards the axillary notch; axillaries 2, rarely 3, small; inguinals 2 to 4, outermost normally triangular, the others transverse, the innermost in contact with the femoral; hind lobe more or less deeply notched posteriorly.

Plastral formula: Abd>h>p>or<f>or=g>or=an.[2]

Color of a hatchling (M.C.Z. 18167). Ground color of carapace pale yellow; sutures between dorsals irregularly, but broadly, bordered with dull brown though frequently interrupted at one or more points on each shield; vertebrals 2 to 4 have a median brown spot, while the first and fifth vertebrals and each of the costals have a fainter, less regular, brown spot; dorsal edge of marginals with a less well-defined brown border tending to extend downwards between each marginal, free edge of marginals without markings. Plastron pale yellow, immaculate.

Color of juveniles. No two specimens are quite alike. Ground color of carapace pale yellow; brown borders covering the sutures become black, and both these and the inner brown borders tend to be interrupted to a varying extent by yellow rays, the brown spots on the vertebrals and costals may, or may not, persist. Plastron pale yellow, all the sutures, except those between the gulars and anals, dark brown crossed by light rays, while the gulars and anals may show a trace of such pigmentation. Plastron substantially as described below for adults.

Color of adults. Ground color of carapace pale yellow to horn with variable markings so that scarcely two are alike; dorsal pattern almost always more or less distinctly rayed like members of the *Psammobates geometricus* group with the rays tending to be much less regular, center of areola yellow surrounded by very irregular traces of brown while immediately outside the areolar area is a narrow zone of yellow, beyond which to the periphery of the shield is a broad black border broken by fine or broad yellow rays, sometimes one color, sometimes the other predominating according as the light rays are broad or narrow,

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[1] Figured by Procter (1922b:495:fig. 7), also present in U.S.N.M. 72530 and 72547, probably from Dodoma.

[2] Gular smaller than the anal in the Njoro tortoise (Stockholm Mus.).

heavy or faint. Plastral shields with yellow areolae which may be smudged with brown; around the areola a broad zone of black, broken to a greater or lesser extent by yellow rays, in some cases, extends to the periphery of the shield, while in others it is separated from the periphery by a narrower or wider zone of yellow. In certain extreme cases the plastral shields appear almost black, in others mostly yellow. Very rarely a specimen may be almost uniform horn color both above and below.[1]

Size. Carapace length of a large ♂ (M.C.Z. 30008) 145 mm., breadth 102 mm., height 32 mm.; the corresponding figures for a ♂ cotype of *loveridgii* (Brit. Mus.) being 140 mm., 100 mm., and 27 mm. Carapace length of largest ♀ (M.C.Z. 23024), 177 mm., breadth 131 mm., height 40 mm.; the corresponding figures for the ♀ type of *tornieri* (Berlin Mus.) being 160 mm., 110 mm., and 35 mm., while those of the juvenile type of *procterae* (Brit. Mus.) are 85 mm., 72 mm., and 40 mm.

When *procterae* was compared with a *tornieri* of exactly the same carapace length, a difference in its relation to the breadth (84.5%) and depth (47%) was noted, the same figures for the *tornieri* being 90.5% and 26% respectively. However, at least in the breadth/length ratio *procterae* is within the range of Dodoma *tornieri* which ranged from 71 to 83.8% in seventeen specimens measured by Procter, and from 69.1 to 94.2% in twenty-five others measured by Loveridge.

Breeding. Courtship consisted in the ♂ impatiently snapping at the limbs of the ♀ as he followed her about, at times clambering on her back and biting viciously at her head whenever she ventured to thrust it out. Two ♂♂ were so ill-tempered as to seize the edges of the ♀♀ carapaces in their jaws, drag them along and eventually get beneath as they apparently attempted to overturn them. One ♂ persistently, though unsuccessfully, endeavored to mate with a ♀ *Kinixys b. belliana* which shared the enclosure. Pairing took place in January and February, as early as 9 A.M. and as late as 4.30 P.M.

Females appeared gravid in April. A single elongate egg is laid in July or August in East Africa, but Conant and Downs (1940:48) record an egg weighing 33.5 gm., and measuring 28 x 48 mm. being laid in the Philadelphia Zoo on January 9, 1937.

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[1] As in U.S.N.M. 73945.

Two eggs removed from the enclosure at Kilosa, where they had been buried beneath a rockery, measured 26 x 42 mm. and 28 x 44 mm. The shells were extremely thin and brittle but one (M.C.Z. 43834) was successfully drilled and blown. On December 19, 1922, an embryo on the point of hatching was removed from another egg and preserved (M.C.Z. 18167).

Longevity. The Soft-shelled Tortoise is very hardy in captivity. One captured December 8, 1918, and taken to England in midwinter, lived in the Zoological Gardens, London, until July 2, 1927, i.e. 8 years, 6 months and 24 days in captivity (Flower, 1937, records only its stay at the zoo). Conant and Hudson (1949) mention one that lived at Philadelphia Zoo for 7 years, 5 months and 6 days.

Diet. Apparently Soft-shelled Tortoises emerge to feed only during the early morning hours. At Tabora one was found nibbling dry grass. In captivity they throve on lettuce and tender cabbage leaves or, for long periods, were fed on bread soaked in jam (Loveridge). Bread soaked in milk was taken, also clover, dandelion and lettuce; fruit only sparingly and they refused bananas altogether. The species is exclusively vegetarian (Mertens: 1942d).

Parasites. A tick (*Amblyomma nuttalii*[1]) was on the type of *procterae* when found. None of the extensive Dodoma series was so affected but soon acquired ticks when transported to Kilosa.

Habits. At 9 A.M. some young were found basking on a rock slab, though usually during daylight these tortoises spend their time in rock crevices into which they climb. Their depressed shells enable them to push their way farther into such retreats than if they were convex. When surprised suddenly the reptiles may be removed with ease, but if warned by a shadow falling across the entrance, they inflate their lungs so that their shells press upon the rock both above and below as they brace their legs like struts. Under these conditions it frequently took as much as an hour to work a single tortoise loose (Loveridge).

Eleven were found beneath one flattish slab of rock in January, possibly aestivating as that and February are the hottest months at Dodoma. In conformity with their structure, these tortoises are far more active than their allies of the genus *Geo-*

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[1] Originally identified as *marmoreum* by S. Hirst; identification corrected by J. C. Bequaert.

chelone, while their predilection for clambering up and falling off rocks calls for rapid recovery in turning over should they land on their backs. In captivity they displayed surprising agility in climbing up vertical wire netting two feet in height, and many escaped. At night shelter was sought beneath the rockery where they would pile up on top of one another (Loveridge).

Mertens (1942d) found his captive specimens, though not nocturnal, spent most of the daylight hours in their hiding place. Even when feeding they did not venture more than nine metres from their retreat, which is definitely selected and constantly used thereafter. To it the tortoise hastens when surprised in the open, for *M. tornieri,* unlike most tortoises, does not, or only momentarily, withdraw its head inside its shell, preferring to make a dash for its home. This it locates in a matter of minutes if taken to a distant corner of the enclosure and then released. Also, after being removed to winter quarters, when liberated in the spring it readily located its ''home.''

Habitat. Small hills with rocky outcrops in arid thornbush or savanna, at altitudes from about 100 to 4000 feet. The most unusual habitat record was that of a tortoise taken by an African when ''cleaning round his rice plants about a hundred yards from'' Allen Turner's camp at Mida Creek.

Localities. Kenya Colony: 10 miles south of Malindi at Mida Creek; Mathews Range (*fide* J. G. Williams); Njoro. Tanganyika Territory: Busisi (Bussisia); Dodoma; Ikikuyu; Kibakwe; Kidengi; Kikombo; Kondoa Irangi; Lindi; near Lake Eyasi (as Njarassa); Mangasini; Matete; Mfilima; Tabora; Usandawi.

Range. Kenya Colony (in suitable terrain from Njoro east to Malindi) south to Tanganyika Territory (from Busisi, Smith Sound, Lake Victoria southeast through Ugogo to Lindi on the southeast coast).

Genus PSAMMOBATES Fitzinger

1835. *Psammobates* Fitzinger, Ann. Wiener Mus., 1, pp. 108, 113, 122. Type: *Testudo geometrica* Linnaeus (designation by Fitzinger, 1843, Syst. Rept., part 1, p. 29).

1933b. *Chersinella* Hewitt (not of Gray: 1870), Ann. Natal Mus., 7, p. 259. Type: *Testudo geometrica* Linnaeus (by original designation).

Definition. Skull with triturating surfaces of maxilla and premaxilla without ridging; maxillary participating in roof of palate; anterior palatine foramina small, concealed in ventral view; prootic narrowly exposed dorsally; quadrate enclosing stapes; surangular subequal in height to prearticular; neck with third or fourth centrum biconvex.

Carapace never hinged; normally the anterior neurals hexagonal; outer side of third costal scute about as long as, or longer than, that of the fourth; submarginal scute absent; suprapygals 1 or 2, if 2 they are separated by a straight transverse suture.

Plastron not hinged; gular region scarcely thickened and produced; gulars paired, longer than broad.

Range. Bechuanaland Protectorate; Union of South Africa (Orange Free State and Cape Province); Southwest Africa.

Fossil record. None.

Remarks. When Lindholm (1929:284, footnote) stated that the genus *Testudo* (*sensu* Strauch, Boulenger and Siebenrock) was unique, not only among reptiles and vertebrates but in the entire Animal Kingdom, he was referring to the fact that it contained some species (citing *Geochelone gigantea*) that in volume and weight were several hundred times greater than such alleged congeneric species as "*fiski*" (i.e. *Psammobates tentorius verroxii*). This is one of the tortoises of the *geometricus* group, none of whose members is known to exceed 150 mm. in carapace length.[1] Re-examining the case, we have found that in addition to size the other characters of the *geometricus* group require its separation as a genus distinct from both *Testudo* and *Geochelone.*

The *geometricus* group is emydine-like in maintaining as a normal condition the hexagonal neural pattern that *Geochelone, Testudo* and *Gopherus* — all three independently — abandoned (except as an occasional variant) 30 or more million years ago. In the general discussion of testudinine genera above (p. 218) the *geometricus* group (as *Psammobates*) was assigned to the larger assemblage of which *Homopus* is a central member. The character of hexagonal neural pattern has been one reason for this assignment, but several other considerations have entered

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[1] We have not seen any larger than this, but larger specimens of *geometricus* itself have been reported (p. 323).

into this decision. A discussion of the problems involved seems pertinent here.

Among African tortoises several groups of species occur which are evidently endemic, as species groups, to this continent. Neglecting *Malacochersus* which seems quite isolated, the rest have several features in common. None of them has any close relative or representative outside Africa or even in North Africa. All have the neural bones hexagonal or vaguely quadrate or irregular, never with the regular octagonal and quadrilateral pattern that is characteristic of all Recent tortoises outside the Ethiopian region. *Chersina* approaches the advanced pattern more closely than any other of this group but still only occasionally and imperfectly. In all, the maxillary triturating surfaces are without definite ridging. *Chersina* again is atypical but it has only a very feeble ridge which is more easily felt than seen. All except *Homopus* have the primitive single or transversely divided suprapygal, not the geochelonide type. In addition all are of only small to moderate size.

Against these general resemblances are to be set the striking peculiarities which separate the African endemic species groups not only from each other but from everything else. We evaluate these peculiarities, as we have stated elsewhere (p. 218), as implying generic distinction. Yet it may be worth consideration that despite these peculiarities there have been instances of taxonomic confusion. For example, a color variant of a member of the *geometricus* group was described as a species of *Homopus* (*H. bergeri* Lindholm), and juvenile specimens of *Kinixys* with the carapacial hinge still undeveloped have been twice confused with *Homopus* (*H. nogueyi* Lataste and *H. darlingi* Boulenger). Though inability to separate forms is not always indicative of relationship, such errors at least make clear that the characters used to separate generic groups are not conspicuous always or at all ages. On our part, we believe that the resemblances of the African endemics to one another are really indicative of close relationships among them. We regard these endemics as a true autochthonous African group.

At this point it is necessary to mention the two endemic Malagasy tortoises — *Acinixys* and *Pyxis*. The skull of *Acinixys* has maxillary triturating ridges and its carapace has hexagonal neurals. In *Pyxis* this situation is reversed, its skull lacking triturating ridges while its carapace shows the octagonal and quadrilateral neural pattern; in addition there is in *Pyxis* the obvious specialization of a very peculiar plastral hinge. Both possess the primitive pygal pattern, and in size they fit in the middle of the continental African series. Thus while seeming to resemble the continental African endemics, each of the Malagasy endemics differs from that series in a single character — in each case a different one. Note, however, that *Chersina* of continental Africa approaches each of these in precisely its aberrant character — *Acinixys* in its maxillary ridge and *Pyxis* in its approximations of an octagonal and quadrilateral neural pattern.

We interpret this case, as we have others, in terms of a conception of the evolution of tortoises as resulting from modifications in parallel occurring at very different tempos in the separate lineages and sub-lineages. Thus for the most part the Ethiopian endemics (including now the Malagasy with the continental African forms) have been slow to modify the primitive (emydine) neural and pygal patterns at the same time that most of them have gone the whole distance in the loss of maxillary ridging. *Acinixys* has been slow to evolve both maxillary and neural advanced features, while *Pyxis* has been ''progressive'' in both these details, but both *Acinixys* and *Pyxis* remain primitive in the pygal pattern in which *Homopus* has gone on to an advanced condition.

We see the Malagasy endemics therefore as part of one series with the African endemics — part thus of a larger autochthonous Ethiopian group. Recognition of such a group has a certain geographical tidiness, but there is very much more to support this conception than just this tidiness. We may argue from any one of the resemblances shared by these Ethiopian forms. Thus the primitive pygal pattern in an Ethiopian tortoise can be explained in one of three ways: (1) as an emydine inheritance going back to a separate emydine ancestor; (2) as an emydine inheritance shared with other Ethiopian tortoises and going back to a common ancestor; (3) a secondary reversion to a primitive condition. The likelihood of the first and third of these possibilities is much diminished by the occurrence of several forms with the same condition in one region, still further reduced by other resemblances among the forms. Thus, by elimination, the second of these suggestions appears to be the most likely. On the basis of primitive neural pattern an argument essentially identical may be set up, and a very similar argument will apply for the unridged maxilla. All of these taken together and considered along with the subtler cross resemblances among the forms would seem to strongly support the naturalness of our postulated group.

If this reasoning is valid and the Ethiopian endemics as a group do have a common ancestor independently of the other tortoises, then the *geometricus* group as one of this series cannot be retained in *Testudo*, at least not in any conception of tortoise genera short of an inclusive genus that would embrace the entire subfamily. *Below that level no inclusive genus would be at once definable and natural.* We do not argue against the genus-subfamily concept on grounds of merit, but to apply this viewpoint in only one subfamily would be to create a genus whose dimensions and variability are not consonant with those of the genera of any other subfamily or family in the order.

The argument that *Psammobates* must be separated from *Testudo*, as typified by *T. graeca*, does not automatically imply its distinctness from every other genus. We maintain it as separate because of its morphological distance from its closest relatives. Thus in skull structure *Psammobates* shows one feature in which it is distinctive within its lineage, and one that is altogether unique.

(1) The space between the ventral processes of the prefrontals is more restricted and, consequently, more emydine-like than in any other testudinine (Fig. 11 *H*, *I*). Indeed the opening in *Psammobates* approaches, but is still not quite as narrow as the widest narial apertures in emydines, e.g. *Hieremys* and *Siebenrockiella*. Since at least a moderate restriction of the narial aperture is probably primitive for all the Testudinidae (the emydine condition occurs in *Platysternon*), in this feature *Psammobates* is probably more primitive than any other living group of testudinines.

(2) Behind the anterior palatine foramina of *Psammobates* the maxillary bones send up into the roof of the palate more or less sizable wings which, from each side, approach, but never join, the vomer. This is decidedly a specialization.

In its shell structure, *Psammobates* displays a condition (in certain subspecies in very exaggerated form) unique among the African endemic genera — conically raised vertebrals. This condition, together with a very similar color pattern, occurs in some *Geochelone*, notably in *G. elegans* of Asia, but conical vertebrals also occur in *G. pardalis babcocki* and some South American tortoises. We consider this similarity convergent only, not more significant than the superficial similarity of *Emydoidea* with *Emys*, or the convergent resemblance of various agamid and iguanid lizards.

Differences in skull and shell as great as these seems to merit generic separation. Such recognition has already been accorded the group by Hewitt and other students of South African tortoises. The name *Chersinella* Gray, 1870, was at first employed by Hewitt. Unhappily this is doubly invalid, first because its genotype, as selected by Lindholm in 1929, is *Testudo graeca* Linnaeus, and also because a much older name is available. The correct name *Psammobates* Fitzinger, 1835, with *T. geometrica* Linnaeus as genotype, was subsequently adopted by Hewitt (1937e). The gender of *Psammobates* being masculine, it compels changes in termination of all the familiar names of the *geometricus* group.

General Survey of the *Psammobates* Species

No group of tortoises has fostered the making of so many specific names as has *Psammobates*. For the three species that we recognize there are 32 names available (see following list). This plethora of names provides examples of nearly every kind of taxonomic error. Names have been applied to adults and young separately (*geometrica* and *luteola; semiserrata* and *oculifera*). Names have also been erected: (1) due to the misreading of a type description (*smithi* Boulenger); (2) for striking color variants (*bergeri* Lindholm); (3) for striking scute variants (*strauchi* Lidth de Jeude); (4) for minor scute variants (*boettgeri* Siebenrock); (5) for ill-defined local populations (various names of Hewitt); (6) for selected series within a single local population (other names by Hewitt); (7) for intergrading populations (names by Hewitt).

Most of these unnecessary names apply to a single species — *tentorius* — individuals of which show an astonishing range of pigmentary and morphological variation. The errors of such earlier workers as Boulenger and Siebenrock resulted primarily from a lack of adequate series with definite locality data, their "new species" being based on one or very few specimens.

The extraordinary multiplication of names by Hewitt had a very different foundation — a philosophy of naming which we regard as unfortunate. Finding, when dealing with fairly large local collections, that he was more or less able to recognize members of these local series, Hewitt provided each such population with a formal Latin name. When these populations proved less homogeneous than usual, Hewitt proposed additional names for the extreme types, e.g. the three names given variants within the Hanover District population.

A list of names proposed for members of the genus *Psammobates* (Table 5) is offered as a ready means of recognizing the status assigned to each in this revision.

Grouping of Species

As suggested by Siebenrock (1904 and 1910), the species of *Psammobates* fall into two groups distinguished by the size of the nuchal, the number of the axillaries, and the plastral pattern. As is usual in testudinines every one of these characters is subject to individual variation, so that occasional individuals appear to transgress their group boundaries in one or another of these characters.

The first species group within *Psammobates* consists of two allopatric forms — *geometricus* and *oculifer*. Both differ from the *tentorius* complex in having a plastral pattern that covers the entire plastral area. Typically it is an elaborate rayed pattern in both *geometricus* and *oculifer*, but in the first it may sometimes be simplified (see Hewitt :1933b, pl. 14, fig. 6), and in the second it is sometimes indistinct. Both forms have only one axillary, but in *oculifer* it is almost always fused with the humeral (Fig. 30*B*).

Normally the nuchal shield is well developed and longer than broad in both species, more consistently in *oculifer* where it is regularly large and subtriangular. In *geometricus,* while usually

TABLE 5

Chronological List of Specific and Subspecific Names Proposed for Members of the "*geometricus* Group," (i.e. *Psammobates*), and their suggested Synonymy.

C. = *Chersinella*; *H.* = *Homopus*; *P.* = *Psammobates*; *T.* = *Testudo*

1. *T. geometrica* Linnaeus, 1758 = *P. geometricus*
2. *T. luteola* Daudin, 1802 = *P. geometricus*
3. *T. oculifera* Kuhl, 1820 = *P. oculifer*
4. *T. tentoria* Bell, 1828 = *P. t. tentorius*
5. *T. verroxii* Smith, 1839 = *P. t. verroxii*
6. *T. semiserrata* Smith, 1839 = *P. oculifer*
7. *T. geometrica* var. *tentoria* (*non* Bell) Gray[1] = *P. geometricus*
8. *T. geometrica* var. *nigriventris* Gray, 1855 = *P. t. tentorius*
9. *T. trimeni* Boulenger, 1886 = *P. t. trimeni*
10. *T. smithi* Boulenger, 1886 = *P. t. verroxii*
11. *T. fiski* Boulenger, 1886 = *P. t. verroxii*
12. *T. strauchi* Lidth de Jeude, 1893 = *P. geometricus*
13. *T. seimundi* Boulenger, 1903 = *P. t. verroxii*
14. *T. boettgeri* Siebenrock, 1904 = *P. t. verroxii*
15. *H. bergeri* Lindholm, 1906 = *P. t. verroxii*
16. *T. oscarboettgeri* Lindholm, 1929 = *P. t. verroxii*
17. *C. tentoria albanica* Hewitt, 1933 = *P. t. tentorius*
18. *C. tentoria tentorioides* Hewitt, 1933 = *P. t. tentorius* × *verroxii*
19. *C. tentoria piscatella* Hewitt, 1933 = *P. t. tentorius*
20. *C. tentoria subsulcata* Hewitt, 1933 = *P. t. tentorius*
21. *C. tentoria karuica* Hewitt, 1933 = *P. t. tentorius* × *verroxii*
22. *C. tentoria duerdeni* Hewitt, 1933 = *P. t. tentorius* × *verroxii*
23. *C. tentoria lativittata* Hewitt, 1933 = *P. t. tentorius*
24. *C. tentoria karuella* Hewitt, 1933 = *P. t. tentorius*
25. *C. tentoria hexensis* Hewitt, 1933 = *P. t. trimeni*
26. *C. schonlandi* Hewitt, 1934 = *P. t. verroxii*
27. *C. fiski cronwrighti* Hewitt, 1934 = *P. t. verroxii*
28. *C. fiski orangensis* Hewitt, 1934 = *P. t. verroxii*
29. *C. fiski colesbergensis* Hewitt, 1934 = *P. t. verroxii*
30. *C. fiski grica* Hewitt, 1934 = *P. t. verroxii*
31. *C. fiski gricoides* Hewitt, 1934 = *P. t. verroxii*
32. *C. verroxii amasensis* Hewitt, 1934 = *P. t. verroxii*
33. *P. depressa* FitzSimons, 1938 = *P. t. verroxii*

[1] Though not a new name, this synonym is included here because of its importance, due to misuse at so early a date (1855).

a moderate sized though slender scute, it is sometimes absent — as in the type of *strauchi* v. Lidth de Jeude and another specimen in Leiden. In such cases of absence the first marginals meet medially, thus seeming to imply that the nuchal has been lost by extreme attenuation.

The scalation of the forelimb differs in the two species (Pl. 7*A*, *B*), but in both there are only a few enlarged scales and many small ones. This is in contrast to the situation in the *tentorius* group where there are more enlarged scales in rather definite rows, and fewer smaller ones.

Though *P. oculifer* has a very extensive range, it seems not to extend south of the Orange River. Boulenger's record of this species from "between Richmond and Victoria West" (questioned by Hewitt:1934) was based on a misidentified *tentorius verroxii*.[1] On the other hand, *geometricus* is, or was — it is now very rare or extinct — confined to a few districts in the vicinity of the Cape Peninsula. Though these are well-marked forms, readily distinguishable on color, shape of nuchal, scalation of forelimb, etc., in view of their geographic separation it is difficult to evaluate the differences in terms of species versus subspecies distinction. It is always possible to claim that these are clinal extremes of a formerly intergradient population. However, since distance has been demonstrated on more than one occasion to mean reproductive isolation, even when morphological difference is not great, and since the two forms are separable on many characters and cannot intergrade in nature, we have conservatively maintained them as full species. In modern systematic terms, however, they certainly belong to one superspecies.

In this connection a further point may be mentioned. North of the Orange River *oculifer* occurs over part of the range of *tentorius verroxii*. Differences beyond sympatric species are commonly used as a measure of the specific distinctness of allied allopatric forms. With this in mind a comparison reveals that the populations of *oculifer* that coexist with the far more vâriable *t. verroxii*, resemble the latter more than do the more distant *t. tentorius* and *t. trimeni*. Both sympatric populations are relatively dull colored and have large femoral tubercles; neither have high conical vertebrals. Usually *oculifer* has a very serrate

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[1] Specimen examined at the British Museum by E.E.W.

margin but sometimes varies towards a non-serrate condition; while *t. verroxii* is normally not serrate, occasionally within the range of *oculifer* it may be strongly serrate (Power :1932b). Also in some specimens of *t. verroxii* the nuchal shield may be rather large, in size and shape approaching the nuchal of *oculifer*. In general the differences between these sympatric species, while perfectly clear-cut, are no stronger than those between *geometricus* and *oculifer*. On this criterion also these two last may be regarded as full species.

The second species group is interpreted by us to consist of a single highly variable species — *tentorius* — of complex population structure. Reference has frequently been made to individual variability among testudinines but — measured by the variation seen within a single small local population — probably no one species exhibits greater variability than does *tentorius*. Two excellent studies of such variation in *tentorius verroxii* have already been published. That of Power (1932b) on a series of 25 from, or near, Niekerks Hope, just north of the Orange River, and another by Lorenz Müller (1939a) on 45 individuals of the same race from Carmel Rust, near Phillipstown. Much further information on variation can be found in Hewitt's several papers, also in Duerden's (1907c) review of the "*geometricus* group." The last two authors have seen far more material than anyone else, and therefore should have had a better general view of both individual and geographical variation, but we must add that each of these authors has, in his own way, diminished the value of his work for subsequent investigators.

Far more unfortunate than Hewitt's peculiar taxonomic concepts are the unsystematic and erratic nature of his descriptions. A great many individual specimens are described in some detail, but the descriptions are not comparable, i.e. do not consistently deal with the same characters; consequently they are not usable by anyone lacking access to his material.

Duerden's fault springs from an opposite prejudice to that of Hewitt — denigration of all local varieties — and with it a tendency to suppress all locality data. Thus in Duerden's paper there are many general statements about variation, but too often these statements are not tied to specimens with specific localities.

Comments such as these on Hewitt's and Duerden's work would be neither necessary nor appropriate if theirs were not the major works on this whole group, done on the spot and with abundant collections. Although one or both of us have seen much material, including types, in the British Museum, in Leiden, in Frankfurt, Lorenz Müller's series in Munich, cotypes of several of Hewitt's forms in the Museum of Comparative Zoology and certain material generously loaned by the Transvaal Museum, we have not seen all of this material at one time or in one place. Nor have we seen the animals alive, and we are in no position to solve by judicious collecting in critical localities any of the many problems that have become evident to us. It remains an inescapable fact that these tortoises are forms of Southern Africa which are not too profitably studied at a distance of many thousand miles. The complex relationships will be satisfactorily resolved only when South African workers, utilizing all the material available to them, undertake studies of variation as meticulous as those of Power and Lorenz Müller.

Owing to the distance separating us from the principal South African collections, and because of our inability to explore the intricacies of local variation, we have been compelled to take a broad view of the *tentorius* complex. While not fully satisfied with our interpretation, we present the following picture:

In the vicinity of Grahamstown, in southeastern Cape Province, a *Psammobates* population occurs that is characterized by:

(1) high conical vertebrals;

(2) a strongly contrasting dorsal pattern of narrow yellow or orange rays on a dark ground;[1]

(3) a plastral pattern consisting of a dark central figure with sharply defined boundaries that are not broken up by lateral rays, the whole surrounded by a broad yellow border;

(4) the scalation of the forelimb from elbow to wrist, usually with three longitudinal rows of enlarged scales, none of which is conspicuously disparate in size;

(5) hinder side of each thigh with a very large, sharp, subconical tubercle.

In the northwest corner of Cape Province, including western Little Namaqualand near the mouth of the Orange River, and in

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[1] However, we figure a specimen (Pl. 10D) in which the relative width of black and yellow rays is reversed. This lighter pattern is still very different from anything that has been observed in other populations.

nearby localities on the slopes behind the high plateau, there is present a second population characterized by:

(1) high conical vertebrals;

(2) a strongly contrasting dorsal pattern of moderately wide yellow or orange rays on a black ground;

(3) a plastral pattern consisting of a dark central figure with sharply defined boundaries broken through by numerous yellow rays, the whole surrounded by a broad yellow border;

(4) the scalation of the forelimb from elbow to wrist without three longitudinal rows of enlarged scales; instead, either a single scale greatly enlarged in relation to the others, or else a single row of especially enlarged scales;

(5) hinder side of each thigh without any very large, sharp, subconical tubercle, though small inconspicuous tubercles may be present.

On the plateau of eastern Little Namaqualand, just east of the last population, is one that differs from both the preceding groups. Its characters are:

(1) vertebrals quite flat, not in the least conical;

(2) a dorsal pattern that is not so strongly contrasting, its rays broader, its coloring duller;

(3) a plastral pattern consisting of a dark central figure, as in the preceding groups, but paler and characterized by the indistinctness of its boundary with the surrounding broad yellow border;

(4) the scalation of the forelimb from elbow to wrist consists of relatively few scales variously enlarged;

(5) hinder side of each thigh with a very large, sharp, subconical tubercle.

These are the three peaks of character differentiation which are to be found within the *tentorius* complex. All three populations share certain characters:

(1) the plastral pattern never covers the entire plastral area, which always has a broad clear border;

(2) usually two axillaries present, sometimes more, rarely one;

(3) the nuchal shield is usually broader than long, frequently minute, occasionally absent, in the latter event the first marginals do not meet.

With these characters uniting them in a species group, what

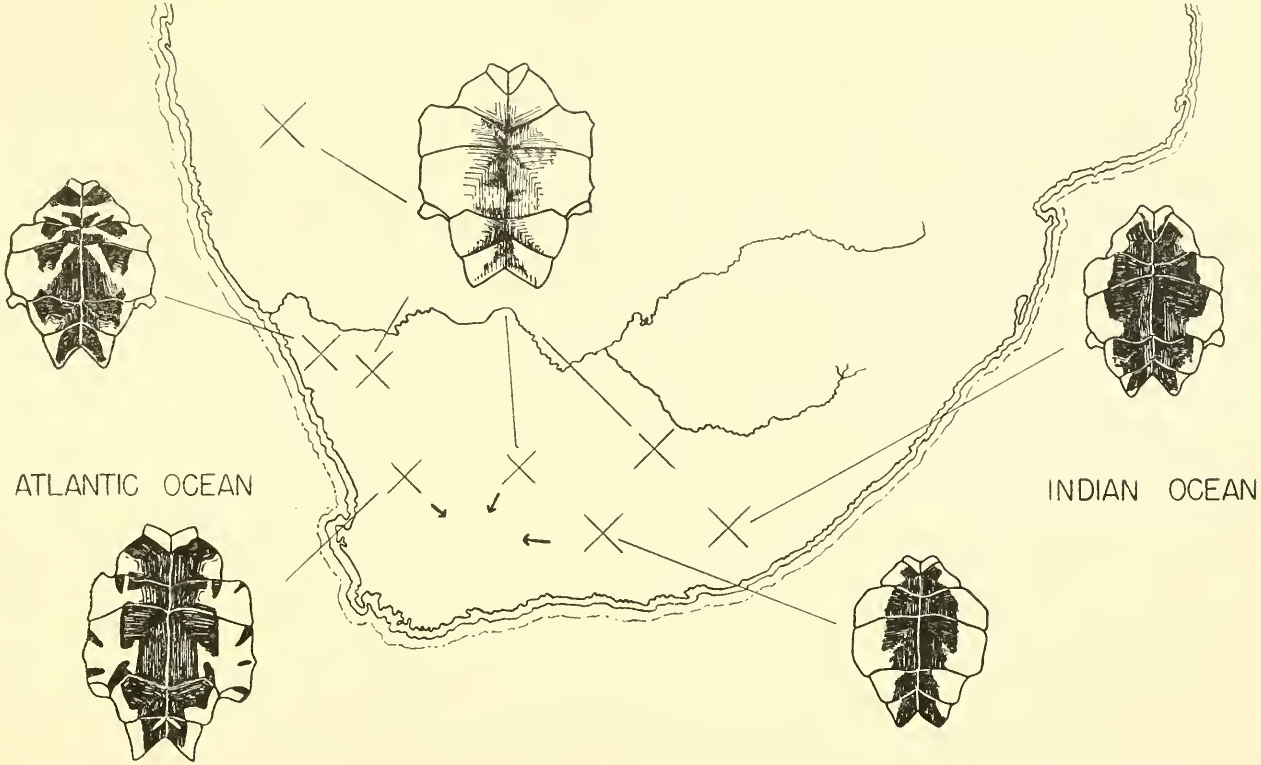

Fig. 28. Distribution of plastral patterns in *Psammobates tentorius*. The area of converging arrows indicates the district in which all types of plastral patterns occur together (see Pl. 11). Plastral patterns drawn from specimens. (P. Washer del.)

do the three populations represent — species, subspecies, or local assemblages unworthy of nomenclatorial recognition?

So far as we are aware no intergradation occurs between the Orange River mouth population and the one on the plateau to the east of that area. In fact, representatives of both populations labeled "Steinkopf" are present in the Museum of Comparative Zoology collection. Hewitt (1934:308-309) has suggested that the populations are probably allopatric; an opinion with which we concur though apparently the evidence is not positive. However, whether the populations overlap or not is relatively unimportant. They are adjacent; they are strikingly different, and they show no sign of interbreeding. In short they are behaving like good species.

But these populations in northwestern and northeastern Little Namaqualand are the only adjacent populations in the *tentorius* complex that are sharply distinct. Everywhere else contiguous populations of the *tentorius* complex merge into one another. Less strongly differentiated populations cluster around the three peaks of difference already described and, wherever they meet, coalesce by rather gradual transitions.

At this point, in order to facilitate ready reference to the concepts involved, we propose applying the available scientific names, using for this purpose topotypical ones that may ultimately be synonymized. Thus *trimeni* Boulenger, whose concept is substantially the same as ours, can be applied to the Orange River mouth population in which the plastral pattern is broken into sharply distinct fragments.

For the moment *schonlandi* Hewitt may be applied to the neighboring population in eastern Little Namaqualand. The precise locality of the ♂ type is unknown, but a ♀ paratype was suspected to have come from O'okiep. The type locality may confidently be restricted to O'okiep as the population of this and surrounding localities is clearly what we understand by *schon-*

landi. Our conception is based on three paratypes from Steinkopf (M.C.Z. 4222-4).

The name *tentoria* Bell may be applied to the population centering around Grahamstown. Here again the type has imprecise locality data, merely "South Africa," but we may with confidence restrict the type locality to Grahamstown, as the type conforms satisfactorily to that population.

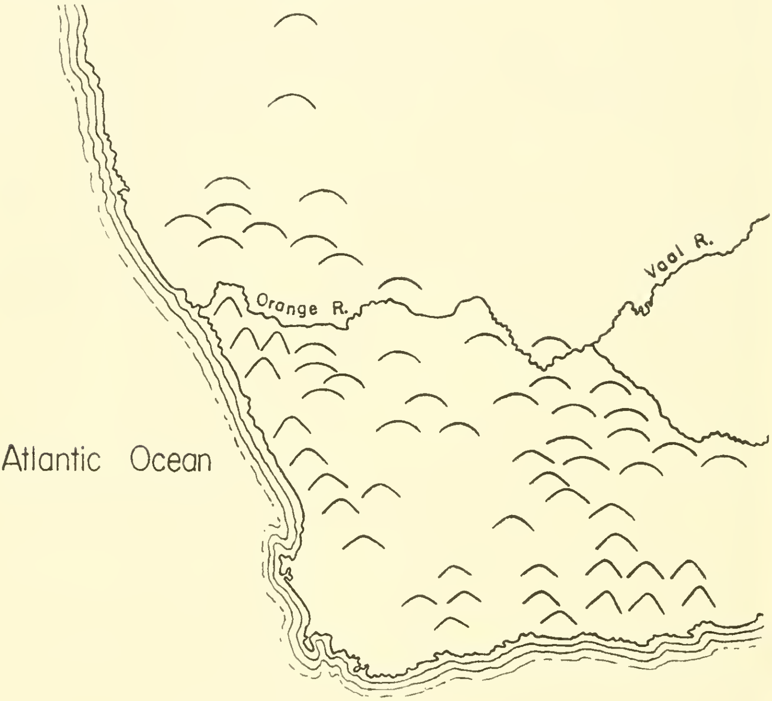

Fig. 29. Distribution of vertebral height in *Psammobates tentorius.* Subjective estimates of average height in the various populations.

(P. Washer del.)

It is now necessary to discuss the populations satellite to those which constitute peaks of difference.

To the south of typical *trimeni* in northeastern Little Namaqualand is a population displaying the characters of *trimeni* in much reduced intensity. The vertebrals instead of being conical are relatively low. The forelimb no longer possesses any scale that is strikingly larger than its fellows. The dorsal coloration is duller, the rays wider. The plastral pattern is interrupted by yellow rays but is no longer separated transversely. We have an example of this sort from Bitterfontein (M.C.Z. 33451), and have seen others from near Calvinia (T.M. 18258) and Nieuewerust (T.M. 18257). Similuar specimens from Hex River Valley were named *tentoria hexensis* by Hewitt.

To the north and west the typical population of *tentorius* grades into others that possess its characters in an attenuated degree. The vertebrals are less conical; in this character there is a considerable range of variation but it centers about a different and lower mode. The dorsal pattern becomes less sharply defined and may have broader rays. The plastral pattern changes very little but occasionally may be very faint, even though still sharply bounded. Still farther north on the Karroo plateau the populations progressively lose *tentorius* characters and approximate those of *schonlandi.* The vertebrals are only slightly and occasionally raised. The dorsal pattern is very variable but usually broad rayed. The plastral pattern is extraordinarily variable, sometimes almost a faded, vaguely outlined, *tentorius* pattern, or an indefinite rayed pattern, in others just an indistinct central infuscation, or entirely absent.

It is for these populations to the north and northwest of *tentorius* that extreme variability has been recorded by Power and Lorenz Müller. Of them it is said that no one individual is like another, and the amplitude of variation is indeed such that from one locality Boulenger described two full species, while from the same place Hewitt described still a third form; all regarded by us as strict synonyms. These plateau populations appear to be really more variable than typical *trimeni* or typical *tentorius,* their characters only attaining some degree of definition and constancy where. as *schonlandi* Hewitt, their ranges abut on that of *trimeni.*

The variable populations of the Karroo plateau extend north of the Orange River into Great Namaqualand. Here a distinct variant occurs. This is the melanistic unicolored variety named *bergeri* by Lindholm. So far, only single specimens have been recorded, viz. the type from Gibeon; another from "Herreroland" (Werner:1910a); a third from Upington in Gordonia district (Siebenrock: 1910). Also referred to *bergeri* by Mertens (1955a: 37) is a specimen without exact locality identified by Sternfeld (1911d:49), and one in his own collection obtained at Klein Windhoek but believed to be an escaped captive not native to the locality. We have also seen a British Museum example from Barby, Tiraz Mountains, Southwest Africa.[1]

Since in each instance these *bergeri* individuals appear to differ from surrounding populations only in color, and their distribution so far as known is quite erratic, we have regarded *bergeri* as merely a color phase occurring in, but nowhere characterizing, the northern populations of the plateau tortoises of this complex. On the other hand, when Mertens (1955a:37) was in Southwest Africa he was told that all the tortoises in one part of Great Namaqualand were of a uniform red-brown color. Such a report requires verification, for of the "*bergeri*" localities only Gibeon and Barby are relatively near one another. Not only is Upington remote from both, but it is separated from them by localities (e.g. Keimoes, Lower Molopo River; Klein Karas Mtns.) in which patterned tortoises occur.

Whether the Great Namaqualand populations allied to *schonlandi* meet *trimeni* on the south, or whether they are separated from the latter by the Orange River, is uncertain. From north of the Orange the only records of *trimeni* worth attention are those of Werner (1910a) and Mertens (1955a). Werner (1910a) presents a photograph of the specimen from Keetmanshoop, but this is too poor to permit of reappraisal. The descriptions and photographs of Mertens (1955a) are more satisfactory and indicate that *trimeni* may really coexist with *schonlandi*-like forms north of the Orange River.[2]

Summarizing the information so far presented, we postulate the following:

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[1] The skull of this specimen has been prepared and confirms the assignment to *Psammobates* on three grounds: (1) the characteristic maxillary projection extends on to the roof of the palate; (2) the ventral processes of the vomer are approximated; (3) the anterior palatine foramina are small and inconspicuous.

[2] Dr. Mertens states (in a letter of 19.xii.55) that the plastral patterns of the Southwest African specimens referred by him to *trimeni* (1955a: 36), agree "sehr genau" wih the pattern of the type of *trimeni* as figured by Boulenger.

The northwest form (typical *trimeni*) grades southward into a less distinctive population that approaches more closely the other assemblages of the *tentorius* complex. The southeast form (typical *tentorius*) grades in almost clinal fashion northward and northwestward into populations again less and less like the topotypes and increasingly like a third distinctive group. This third population, nearly or entirely confined to the inland plateau (whereas the other assemblages are more nearly coastal), is over most of its range very variable (to a limited extent geographically, to a much greater extent individually) and is only sharply distinct and relatively uniform where, as *schonlandi,* it meets the northwest population.

Undiscussed so far is the southwest area that the southern population of *trimeni,* and that allied to *schonlandi,* approach from the north, and which the populations of *tentorius* enter from the east. This is the meeting place of all three of the major series of assemblages of the *tentorius* complex, and adjacent to this meeting place the representatives of all three have already lost every distinctive character except plastral pattern. All are relatively dull in color, without very convex vertebrals and with rather uniform forelimb scalation, i.e. three longitudinal rows from elbow to wrist.

Through the courtesy of the Transvaal Museum we have been able to examine a series of nine specimens from Matjesfontein, which is in this critical area. All three types of plastral pattern, as well as intermediates between them, occur in this small sample (Pl. 11).

This then is the picture which has emerged for us as a broad and general view of the *tentorius* complex. It remains to be considered how this situation is to be interpreted biologically and treated taxonomically.

Despite the lack of any evidence of introgression or intergradation between typical *trimeni* and adjacent *"schonlandi,"* the *tentorius* complex taken as a whole appears to be a reproductive unit. By the indirect route of a chain of allopatric populations which appear to interbreed freely at their points of contact, it seems clear that even *trimeni* and *"schonlandi"* must be able to exchange genes. We may, therefore, consider that the whole complex constitutes one species for which the name *Psammobates* *tentorius* (Bell) is available. The question arises as to whether this species should be subdivided; if so, how minutely?

The problem of species subdivision is only partly a biological one. To describe the biological situation completely would require a far more elaborate analysis than that provided above and a knowledge that no one now possesses. No series of names can prove a satisfactory substitute for such a biological description. If it is admitted that names cannot tell the full story, is there any use or purpose in applying subspecific names?

We believe that the three well-differentiated centers or peaks already described, around which other populations cluster, merit recognition, especially in view of the fact that two of them behave toward one another as if they had already reached the specific level. By granting these populations names we are endeavoring to indicate something both in regard to their past and to their potential history. We believe that the typical populations of *trimeni, "schonlandi,"* and *tentorius,* represent the focal *loci* of the *tentorius* complex during a previous fragmentation of its range; that during this former separation these three populations built up the system of features that now distinguish them as peaks of difference within the complex. In terms of characters they are even now almost at the specific level, but the satellite populations surrounding them — showing as they do every apparent evidence of intergradation — testify that reproductive isolation has not been achieved. Still the process of differentiation has gone so far that we may rather confidently assert that if fragmentation and isolation again occurred, these populations showing peaks of difference are the best candidates to pass the species threshold. As true "incipient species," we believe they may legitimately receive names.

Our subspecies are to be conceived of primarily in terms of the peaks of difference — the three topotypical populations of *trimeni, "schonlandi,"* and *tentorius.* Simply for convenience in demarcating subspecific boundaries, we attach to each of these central populations its satellite groups, without granting any of these separate nomenclatorial recognition. We agree with Hewitt that each of these satellite local populations may be recognized by modal tendencies, though probably not by any constant feature, but we also think that, without extreme artificiality, it will never be possible to set limits to these populations. To accept or erect names for these local groups would be to multiply boundaries that, by reason of intergradation, are vague at every level.

We have chosen to recognize only three somewhat arbitrary ranges which are based on the convenient character of plastral pattern. All populations possessed of a plastral pattern that is sharply bounded, but indented or broken through by a series of yellow rays, we assign to *trimeni*. All populations possessed of a plastral pattern sharply bounded, but very little indented or quite intact, we refer to *tentorius*. All populations with a plastral pattern that is both indistinct and variable, we group under the name *verroxii* A. Smith which antedates *schonlandi* Hewitt. The population around Matjesfontein we cannot allocate since it comes from an area of intergradation between all three forms.

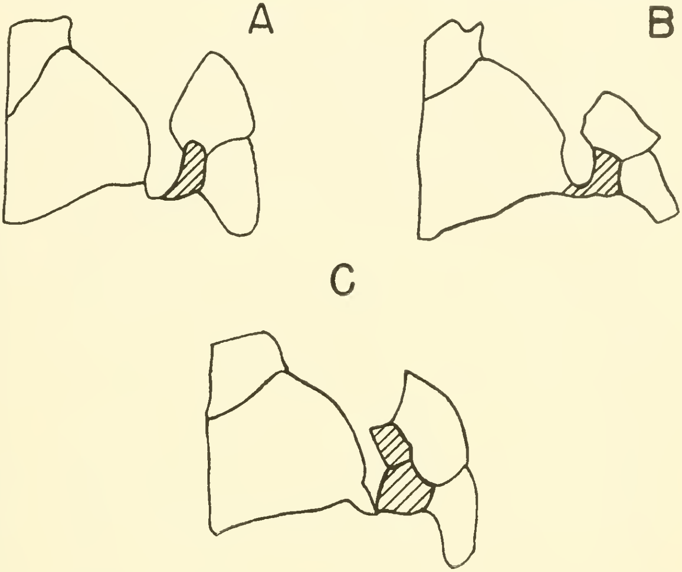

Fig. 30. Axillaries in various species of *Psammobates*. *A, P. geometricus* (M.C.Z. 32184); *B, P. oculifer* (M.C.Z. 42158); *C, P. t. verroxii* (M.C.Z. 42224).

(P. Washer del.)

We have felt that the complex geographical variation of these forms was a phenomenon meriting rather full discussion and, indeed, further investigation. It may be noted that during this discussion we have arrived at substantially the same taxonomic allocations proposed by Duerden in 1907. It is hoped that by dealing with the problem of geographic variation more elaborately than he did, the conclusions are placed on a firmer footing.

Key to the Species and Subspecies of PSAMMOBATES

1. Plastral pattern dark brown or yellow brown, highly ornate, covering entire plastral area; anterior and posterior margins of carapace typically *very* sharply serrate, even spinose; nuchal large, usually subtriangular; axillary single, normally fused with humeral; forelimb with a few large scales on its anterior surface. Range: north of the Orange River, viz. Southwest Africa; Bechuanaland; Transvaal; Orange Free State; and Griqualand West in Cape Province .... *oculifer* (Kuhl) (p. 315)

Plastral pattern, if covering entire plastral area, black on yellow, otherwise restricted to central area of plastron or absent; anterior and posterior margins of carapace typically *not* sharply serrate, never spinose; nuchal, if present, smaller, either elongate or broad; axillaries 1 or 2, not united with the humeral; forelimb with variable scaling anteriorly 2

2. Plastral pattern never absent, black on yellow; margins of the plastral shields, even laterally and on the bridge, either wholly black or black broken by yellow rays; nuchal very variable in size but typically elongate, occasionally absent; axillary 1; forelimb anteriorly with a few large scales which are *not in contact* but separated by smaller ones. Range: extreme southwest Cape Province within a 100 mile radius north and east of Cape Town. .*geometricus* (Linnaeus) (p. 319)

Plastral pattern sometimes absent, otherwise black or brown and yellow, peripherally a more or less broad zone of yellow that is usually *entirely devoid of markings;* nuchal very variable in size but typically broader than long, often minute, rarely absent; axillaries 2 or 3, rarely 1; forelimb anteriorly with large juxtaposed scales, not separated by smaller ones 3

3. Plastral pattern, when present, without a well defined outline; dorsal shields never strongly conical. Range: Orange Free State (possibly) and northern Cape Province north through Southwest Africa, occurring mostly at elevations above 3000 feet....*t. verroxii* (A. Smith) (p. 324)

Plastral pattern with a well defined outline; dorsal shields more or less strongly conical; occurring mostly at elevations below 3000 feet.... 4

4. Plastral pattern broken through by light rays and/or its outline indented by a series of encroachments of the pale ground color. Range: Cape Province (Little Namaqualand south to near Touw's River) north to Southwest Africa (Keetmanshoop, the only record) .... *t. trimeni* (Boulenger) (p. 333)

Plastral pattern without light rays crossing and with few or no indentations. Range: Cape Province (mostly south of 33° parallel) from vicinity of Fish River west to beyond Uniondale and Willowmore *t. tentorius* (Bell) (p. 336)

PSAMMOBATES OCULIFER (Kuhl)

1820. *Testudo oculifera* Kuhl, Beitr. Zool. Anat., p. 77: Cape.
1831c. Gray, 22.
1865. Strauch, 61.
1889a. Boulenger (part), 165 (omit specimen Richmond to Victoria West).
1890. Strauch, 54.
1893a. Boettger, 10.
1897. Siebenrock, 247.
1898. Sclater, W. L., 97.
1898. Siebenrock, 425.
1899. Siebenrock, 566.
1901. Lampe, 192.
1902a. Werner, 341.
1904c. Siebenrock, 307.
1907a. Duerden, 9.
1907b. Duerden, 76, pl. viii, fig. 12.
1907c. Duerden, 196.
1909a. Siebenrock, 524.
1910. Siebenrock, 704.
1910a. Werner, 301.
1911. Lampe, 147.
1911b. Sternfeld, 409.
1911d. Sternfeld, 49, fig. 61.
1912b. Werner, 434, pl. —.
1914a. Hewitt, 247.
1929. Flower, 31.
1931. Hewitt, 499.
1931. Power, 44.
1932b. Power, 467.
1934a. Mertens and Müller *in* Rust, 9.
1935b. FitzSimons, 304.

1937b. Mertens, 5.
1939a. Müller, L., 129, pl. xi, fig. 7.
1950. Williams, 550, 551.
1955a. Mertens, 34, pl. iii, figs. 7-8.
1839. *Testudo semiserrata* A. Smith, Ill. Zool. S. Africa, Rept., pl. vi aa: ''between Latakoo and the Tropic of Capricorn.''
1844. Gray, 8.
1851. Duméril and Duméril, 3.
1855. Gray, 9.
1880c. Vaillant, 25.
1886b. Boulenger, 542.
1887b. Boettger, 138.
1844. *Emys oculifera* Gray, 28.
1862a. *Clemmys oculifera* Strauch, 32.
1870c. *Peltastes semiserratus* Gray, 656.
1870e. Gray, 9.
1872c. Gray, 5.
1873b. Gray, 10.
1893a. *Homopus signatus* Boettger (part), 8 (juv. ex. ''Namaland'').
1894a. Boettger, 88.
1894. Fleck, 83.
1933b. *Chersinella oculifera* Hewitt, 263.
1934. Hewitt, 337.
1935a. FitzSimons, 520.
1937a. *Psammobates oculifera* (*sic*) Hewitt, 791, fig. 2.
1938. *Testudo geometrica* Schepers (not of Linnaeus), 535-555, figs. 1-5.
1939. Schepers, 451-495, 1-8.
1948a. Schepers, 9-11, figs. 1-4.
1948b. Schepers, 1-212, figs. 1-250.

A further citation of ''*oculifera*'' will be found under *Psammobates tentorius verroxii*.

Common names. Serrated Tortoise (preferred) ; Toothed Cape Tortoise (Gray :1844) ; Kuhl's Tortoise (Flower :1929).

Illustrations. Excellent figures (lateral and plastral views) copied as our Plate 7 are furnished by Sir Andrew Smith (1839 :pl. vi), who contrasts the nuchal and forelimb (figs. aa) with those of *geometricus* (figs. bb). Siebenrock (1910) shows the carapace and plastron of a hatchling. Sternfeld (1911d :fig. 61) provides a sketch of the buttock tubercle. Werner (1912b) has a colored plate of both adult and juvenile.

Types. The principal discussions on the status of this species and its synonym have been by Strauch (1865; 1890), Boulenger

(1889a), Duerden (1907c), and Siebenrock (1940c; 1910).

Description. Beak more or less strongly hooked, tricuspid, edge of jaws more or less serrate; prefrontal divided longitudinally or broken up; frontal broken up; upper head shields small, irregular; forelimb anteriorly with a few unequal (one extremely large) tubercular scutes (but area distal to the largest formed of small scales), forming 2-4 longitudinal and 4-6 transverse series from elbow to outer claw; claws 5; hinder side of thigh with a large, and occasionally a few subsidiary, subconical tubercles; heel with or without [1] conical, spurlike tubercles; tail in both sexes devoid of tubercles on sides and without a terminal claw-like tubercle.

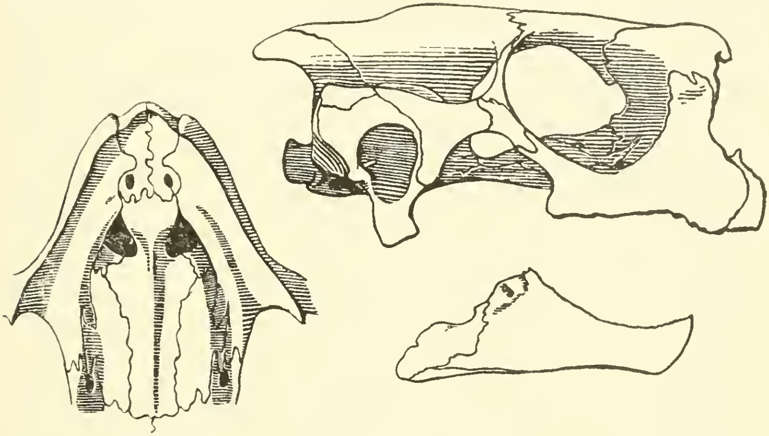

Fig. 31. Skull of *Psammobates oculifer* (A.M.N.H. 7094). Condylobasal length 23 mm.

(S. McDowell del.)

Carapace convex, sides descending abruptly, shallowly notched in nuchal region, anterior and posterior margins more or less expanded, sometimes reverted, and strongly (rarely weakly) serrated; dorsal shields concentrically striated; nuchal present, usually large, subtriangular, more or less projecting into nuchal notch; vertebrals 5, rarely 4, 6, or 7,[2] more or less swollen,

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[1] Both present and absent in United States National Museum material.

[2] Four in a tortoise from Kooa (*fide* Werner:1910a); 6 in Keetmanshoop specimen; 7 in one (U.S.N.M. 63021) from Bechuanaland.

typically *not* conical, broader than long, about as broad as, or broader than, or narrower than, the costals; costals 4, not forming an angle with the lateral marginals; marginals 11, rarely 10 or 12; supracaudal undivided, incurved in ♂♂, downwardly directed in ♀♀.

Front lobe of plastron anteriorly more or less produced and openly notched; gulars paired; pectorals narrow where they meet, sometimes even separated,[1] their anterior border sloping towards the axillary notch; axillary 1, almost always fused with the humeral; inguinal moderate, meeting femoral;[2] hind lobe deeply notched posteriorly.

Plastral formula: $Abd>h>(g, f, an)>p$; g usually$>$an, though sometimes$=$or$<$.

Color. Carapace brownish yellow or horn color (♂), with a very variable pattern of dark brown or black rays of more or less equal width, numbering 6-10 on the vertebrals and costals. Plastron yellowish with light or dark brown (black, *fide* Gray: 1844) rays.

For lengthy discussion of ontogenetic changes in coloration see Siebenrock (1910); for detailed individual variations Hewitt (1933b) and FitzSimons (1935b).

Size. Carapace length of a ♂ (T.M. 15999) from near Kimberly, 118 mm., breadth 82 mm., height 61 mm. Carapace length of a ♀ (T.M. 15998) taken with above, 133 mm., breadth 99 mm., height 70 mm. (FitzSimons:1935a).

Sexual dimorphism. Siebenrock (1910) states that in ♂♂ the vertebrals are flatter than in the ♀♀, but our meagre material scarcely bears this out. However, Siebenrock is correct in stating that the ♀ carapace is relatively higher than that of the ♂. Unlike most species, according to Hewitt (1933b), there is no disparity in size between the sexes.

Breeding. On November 29, 1933, a pair were engaged in courtship on the Kimberly to Schmidtsdrift road, the ♂ scuttling around the ♀, butting against her shell, and periodically emitting short, low, grunting coughs. Though approached closely by FitzSimons (1935a), the ♂ only ceased his activities when actually picked up.

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[1] As in the type and a Waterberg tortoise (M.C.Z. 42158).

[2] Except in a Quickborn specimen mentioned by Hewitt (1931).

The egg of a Kimberly tortoise measured 31 x 39.5 mm (Hewitt:1934).

Enemies. Jackals, ratels and the brown hyena will all break open the plastron to get at these tortoises (R. D. Bradfield in Hewitt:1934); Bataleur Eagles also prey upon them according to the Hereros (Hewitt:1934).

Habitat. Frequents sandy plains and grassgrown flats (Power: 1931; 1932b); grassland savannas of the inland plateaus according to Bradfield (in Hewitt:1933b).

Localities. Bechuanaland: Gemsbok; *Gomodimo; *Kalahari; Kamelslip; Kaotwe; Kooa; Lake Ngami; Lehututu (as Lekutu) to Kang; Makarikari; Mookane (Moocane); Palapye Road; *Serowe (U.S.N.M.); Vlei Topan. *Transvaal:* Jamestown; Linokana. *Orange Free State:* Bothaville; Modder River. *Cape Province:* as "Cape" (type locality); Danielskuil (Daniel's Kuil); *Kimberly; Kuruman; "Latakoo to Tropic of Capricorn" (type locality of *semiserrata*); Niekerkshoop (Niekerk's Hope); Schmidtsdrift to Kimberly; Saint Clair; Douglas; Warrenton; Witput Siding; Zoetvlei near Vryburg. *Southwest Africa:* Aukeikas, 25 km. west of Windhoek; Aus (Auas; Oas); *Etosha Pan-near; *Gaucha (U.S.N.M.); Gibeon; Gobabis; Grootfontein; *Nama (U.S.N.M.); Ogosongomingo to Great Waterberg; Omaruru; Ondonga; Quickborn Farm, Okahandja; Rehoboth; Rietmond; Sandup; Swakopmund; *Waterberg; Windhoek (Windhuk).

Range. Extreme western Transvaal and western Orange Free State northwest through Bechuanaland and Southwest Africa almost to the frontier of Angola.

Clanwilliam, we believe, was not the true source of the specimen but the donor's address cited by Duerden (1907a). It is probably responsible for Little Namaqualand being included in the range by FitzSimons (1935b:305) and Mertens (1955:35).

PSAMMOBATES GEOMETRICUS (Linnaeus)

1734. *Testudo minor, amboinensis* Seba, Rerum Naturalium Thesauri . . . 2, p. 130, pl. lxxx, fig. 8: "Amboina" (in error).

1758. *Testudo geometrica* Linnaeus, Syst. Nat., ed. 10, 1, p. 199: "Asia" (in error).

1766. Linnaeus, 353.

1784.	Daubenton, 628.
1788.	Lacépède, 157, pl. ix and Synopsis.
1789.	Bonnaterre, 24, pl. vi, fig. 1.
1792.	Schoepff, 55, pl. x.
1793.	Schoepff, 49, pl. x.
1797.	Shaw and Nodder, pl. cccvi.
1802b.	Daudin, 260, pl. xxv, fig. 1.
1802.	Shaw, 20, pl. ii.
1812.	Schweigger, 325, 424 (omit non-African localities).
1814.	Schweigger, 56.
1828.	Bory de Saint Vincent, 73 (omit Asia occidentale).
1831.	Griffith, 10, 54.
1831b.	Gray, 5.
1831c.	Gray, 12.
1835.	Duméril and Bibron, 57.
1835.	Temminck and Schlegel (part), 73.
1836.	Bell, text, col. pl.
1838.	Cuvier, pl. i.
1844.	Gray, 8.
1845b.	Rüppell, 297.
1849.	Smith, A., App., 1, pl. vi, bb only.
1855.	Gray (part), 8.
1857.	Jan, 35.
1862a.	Strauch, 74.
1865.	Strauch, 19.
1867a.	Steindachner, 3.
1872b.	Gray, 3, *in* Sowerby and Lear, pl. xiii.
1882a.	Müller, F., 165.
1882a.	Peters, 3.
1884a.	Rochebrune, 12 (in error).
1886b.	Boulenger, 541.
1889a.	Boulenger, 162.
1890.	Strauch, 56.
1893a.	Boettger, 10.
1893.	Trimen, 79.
1896.	Lönnberg, 11.
1898.	Jeude, 4.
1898.	Johnston, 361.
1898.	Sclater, W. L., 96.
1901.	Lampe, 192.
1904c.	Siebenrock, 309 (key).
1907c.	Duerden, 195.
1909a.	Siebenrock, 524.

1910. Siebenrock, 702.
1911. Lampe, 146.
1911d. Sternfeld, 49.
1914a. Hewitt, 247.
1929. Flower, 30.
1929. Rose, 189.
1934a. Mertens and Müller *in* Rust, 9.
1938. Bernstein, 327 (det. doubtful).
1939a. Müller, L., 129.
1954. Noël-Hume, 74.
1767. *Tortuc* Knorr, 127, pl. iii, fig. 3 (clearly *geometricus* from this fine colored figure).
1802b. *Testudo luteola* Daudin, Hist. Nat. Rept., **2**, p. 277, pl. xxv, fig. 3: (purchased in Dieppe) No locality.
1820. *Chersine geometrica* Merrem, 32.
1829. Gravenhorst, 20.
1843. *Psammobates geometricus* Fitzinger, 29.
1861. Fitzinger, 411.
1844. *Testudo geometrica* var. *tentoria* Gray (not of Bell), 8.
1855. Gray, 8.
1869c. *Peltastes geographicus* Gray (lapsus: *fide* Gray), 173.
1870c. *Peltastes geometricus* Gray, 655, pl. xiii.
1870e. Gray, 9.
1873b. Gray, 8.
1893. *Testudo Strauchi* Lidth de Jeude, Notes Leyden Mus., **15**, p. 312, pl. ix: Cape of Good Hope.
1907c. Duerden, 201.
1909a. Siebenrock, 523.
1934a. Mertens and Müller *in* Rust, 9.
1933b. *Chersinella geometrica* Hewitt, 260, pl. xiv, figs. 1-7.
1934. Hewitt, 336.
1933b. *Chersinella strauchi* Hewitt, 262.

Further citations of "*geometrica*" will be found under *oculifer*, *t. tentorius* and *Kinixys b. belliana*.

Common Names. Geometric Tortoise (Lacépède); seerpootjies (*fide* Peers in Hewitt :1934 :336).

Illustrations. For a side and plastral view in color cf. Schoepff (1792 :pl. x). A. Smith (1839 :pl. vi, bb) contrasts the forelimb and nuchal with those of *oculifer*. Photographs of variants are furnished by Hewitt (1933b :pl. xiv, figs. 1-7).

Types. *Testudo luteola* was synonymized with *geometricus* by Gray (1831b), a disposition with which we are in accord. Lidth de Jeude separated *strauchi* (still in Leiden Museum where it has been studied by one of us — E.E.W.) because it lacked a nuchal and on the proportions of its gulars, characters that are demonstrably inconstant. It was synonymized with *geometricus* by Duerden (1906), and there seems no justification for its revival by Siebenrock (1909; 1910) and Hewitt (1933b).

Description. Beak moderately or strongly hooked; prefrontal divided longitudinally or broken up; frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few large, unequal, scattered tubercular scutes, forming 6-7 longitudinal and 7-10 transverse series from elbow to outer claw; claws 5; hinder side of thigh without large conical tubercles; tail in both sexes devoid of tubercles on sides and without a terminal clawlike tubercle.

Carapace very convex, sides descending abruptly, deeply notched in nuchal region, posterior margins not or but weakly expanded, slightly reverted, and but rarerly serrated; dorsal shields concentrically striated; nuchal present, typically elongate, occasionally triangular, sometimes minute, rarely absent, when present more or less projecting into nuchal notch; vertebrals 5, rarely 4 or 6,[1] sometimes swollen as truncate pyramids, much broader than long, as broad as, or broader than, or narrower than, the costals; costals 4, rarely 5, usually not forming an appreciable angle with the lateral marginals; marginals 11 or 12; supracaudal undivided, more or less incurved in both sexes.

Front lobe of plastron anteriorly truncate, not or but slightly produced and very shallowly notched; gulars paired; pectorals broadly in contact, their anterior border sloping towards the axillary notch; axillary 1, small; inguinal moderate, meeting femoral; hind lobe deeply notched posteriorly.

Plastral formula: Abd $>$ g $>$ or $<$ h $>$ or $=$ f $>$ or $=$ an $>$ or $=$ p; f usually $>$ an.

Color. Carapace with yellow areolae from which radiate yellow rays (8-15 on vertebrals, 9-12 on costals, 2-4 on marginals) separated by black. Plastron yellow with more or less ill-defined black rays and bands.

The juvenile coloring is substantially the same as that of the adult, according to Siebenrock (1910); however, hatchlings in

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[1] Six in figure on plate of Shaw and Nodder (1797).

the Paris Museum seen by E. E. W. possess the *luteola* pattern (cf. Plate 8A, B).

Size. Carapace length allegedly attains to 240 mm. (*fide* Duerden:1907c); one of 135 mm. is mentioned by Strauch (1862a) with a breadth of 95 mm., and height of 76 mm. Carapace length of type ♀ of *strauchi* was 140 mm.

If correctly identified, a specimen recorded by Daudin (1802b) far surpasses all recent records. In *French inches* it is said to have a length (possibly over the curve ?) of 10″ 6‴=283.6 mm.
breadth .... 8″ =208.5 mm.
height .... 3″ 9‴=101.5 mm.

Breeding. Twelve to fifteen eggs are laid according to Bruyere (Lacépède:1788).

Enemies. In all probability mankind is responsible for the extermination, or near extermination, of this handsome little species. Writing of his journey into Caffraria in 1772, the botanist C. P. Thunberg made the following observations.

"Instead of China-vessels and calabashes, poverty had taught them [the Hottentots] to use the shells of the tortoises, which frequent the bushes in the sandy plains, particularly the *Testudo minuta* and *geometrica*" (1795:**1**:182).

"The *Testudo Geometrica* was known here (vicinity of the Cape) by the appellation of the *Syren* (*Syrentie*). This land-tortoise, which probably is the most beautiful of its kind, was found very common in the sandy downs among the bushes. The shells of such as were very small, and consequently the most beautiful, were used for making snuff boxes" (1795:**1**:243).

"Some of the women . . . had a tortoise-shell hanging at their backs, in which they preserved either their tobacco or bucku (*diosma*). For want of clay tobacco-pipes they use wooden ones" (1795:**1**:194).

"Some of them [Kaffirs] wore about their necks a necklace made of small shells, called serpents skulls (*Cypraea moneta*) strung upon a string, and to this hung a tortoise-shell, for keeping the bukku ointment in" (1795:**2**:82).

"Among their [Hottentots] ointments they mix the powder of a strong smelling herb, which they call Bucku (a species of *Diosma,* frequently the *Pulchella*), and which gives them so disagreeable, so fetid, and at the same time so rank an odour, that I sometimes could not bear the smell of the Hottentots that drove my wagon" (1795:**2**:187).

Localities. Cape Province: Cape Peninsula; Ceres; Darling; Eendekuil (as Eendekind) district; Klapmuts; Moorreesburg district; Porterville district; Riebeeck Kasteel. (Williston—as Amandelbom Mission on Zak River—we reject on the grounds that it is too far west, and because other species recorded from the mission lead us to suspect it was merely a collecting center for shells brought in by pupils).

Range. Cape Province (Tulbagh, Paarl and Malmesbury districts of the extreme southwest, in former times possibly extending to the Cape Peninsula).

Reported in error from Ascension Id. and Madagascar (Lacépède:1788); Mauritius (Gray:1855); Mozambique (Bianconi:1851); Nyasaland (Johnston:1898); Great Namaqualand (Sternfeld:1911b) and Senegambia (Rochebrune:1884a).

Psammobates tentorius verroxii (Smith)

1839. *Testudo verroxii* A. Smith, Ill. Zool. S. Africa, Rept., pl. viii: Near the sources of the Orange River (probably in Cape Province, rather than in Basutoland where it has not been taken. See remarks under *Type*).
1844. Gray, 9.
1855. Gray, 8.
1909a. Siebenrock, 525.
1910. Siebenrock, 710 (but Transvaal locality erroneous).
1910a. Werner, 302, pl. x, figs. 15a-b, 16a-b.
1911d. Sternfeld, 50, fig. 62.
1915. Werner, 330.
1934a. Mertens and Müller *in* Rust, 9.
1939a. Muller, L., 129, pls. x-xi.
1870c. *Peltastes verreauxii* (editor's emendation) Gray, 656.
1870e. *Peltastes verroxii* Gray, 9.
1872c. Gray, 5.
1873b. Gray, 10.
1884a. *Testudo verreauxii* Rochebrune (in error), 13.
1886b. Boulenger, 541.
1887b. Boettger, 139.
1889. Boettger, 282.

1889a. Boulenger, 163.
1892. Müller, 214.
1893a. Boettger, 10.
1895. Oudemans, 323.
1904c. Siebenrock, 313, pl. iv and v, fig. 5.
1907c. Duerden, 198.
1911. Lampe, 146.
1914a. Hewitt, 247.
1932b. Power, 466.
1933a. Power, 211.
1886b. *Testudo smithi* Boulenger, Proc. Zool. Soc. London, p. 542: South Africa.
1889. Boettger, 285.
1889a. Boulenger, 165, pl. iv.
1892. Müller, 215.
1893a. Boettger, 10.
1894a. Boettger, 88.
1894. Fleck, 83.
1898. Sclater, W. L., 97.
1904c. Siebenrock, 318, pl. iii.
1904b. Tornier, 304, figs. 12, 14, 15.
1907c. Duerden, 200.
1909a. Siebenrock, 526.
1910. Siebenrock, 712.
1911. Lampe, 147.
1911b. Sternfeld, 410.
1911d. Sternfeld, 50.
1915. Werner, 330.
1934a. Mertens and Müller *in* Rust, 9.
1886b. *Testudo fiski* Boulenger, Proc. Zool. Soc. London, p. 542, col. pl. lviii: De Aar, near Hopetown, Cape Province.
1889a. Boulenger, 165.
1898. Sclater, W. L., 97.
1904c. Siebenrock, 322, pl. v, fig. 6.
1907a. Duerden, 10.
1907c. Duerden, 200.
1909a. Siebenrock, 527.
1910. Siebenrock, 716.
1929. Flower, 31.
1933a. Power, 214.
1934a. Mertens and Müller *in* Rust, 9.
1939a. Müller, L., 129, pl. ii, fig. 1.
1889. *Testudo tentoria* Boettger (not of Bell), 284.

1893a. Boettger, 10.
1894a. Boettger, 88.
1894. Fleck, 83.
1903e. Boulenger, 217.
1889a. *Testudo oculifera* Boulenger (part: not of Kuhl), 166 (specimen ex Richmond to Victoria West).
1903e. *Testudo Seimundi* Boulenger, Ann. Mag. Nat. Hist. (7), **12**, p. 216, pl. xvii: Three miles east of Deelfontein, Cape Province.
1907c. Duerden, 201.
1909a. Siebenrock, 527.
1934a. Mertens and Müller *in* Rust, 9.
1904b. *Testudo boettgeri* Siebenrock (not of Mojsisovics), Anz. Akad. Wiss. Wien, **41**, p. 194: Great Namaqualand, Southwest Africa.
1904c. Siebenrock, 310, pls. i-ii.
1907c. Duerden, 202.
1909a. Siebenrock, 525.
1911d. Sternfeld, 49.
1922a. Mertens, 168.
1906. *Homopus bergeri* Lindholm,[1] Jahrb. Ver. Nat. Wiesbaden, **59**, p. 348: Gibeon, Southwest Africa.
1907b. *Testudo tentoria* var. *fiskii* Duerden (part), 88 (fig. is of *tentoria trimeni*).
1909b. *Testudo bergeri* Siebenrock, 623.
1910. Siebenrock, 713, pls. ii and iv.
1910a. Werner, 304, pl. ix, figs. 14a-c.
1911. Lampe, 146.
1911d. Sternfeld, 50.
1929. *Testudo oscarboettgeri* Lindholm, Zool. Anz., **81**, p. 295; n.n. for *boettgeri* Siebenrock, preoccupied.
1934a. Mertens and Müller *in* Rust, 9.
1934. *Chersinella schonlandi* Hewitt, Ann. Natal Mus., **7**, p. 303, pl. xvi, figs. 46-50: Little Namaqualand, Cape Province.
1934. *Chersinella fiski* Hewitt, 309, pl. xvi, figs. 51-56.
1934. *Chersinella fiski seimundi* Hewitt, 314, pl. xvi, fig. 57.
1934. *Chersinella fiski cronwrighti* Hewitt, Ann. Natal Mus., **7**, p. 317, pl. xvi, fig. 58: Hanover, Cape Province.
1934. *Chersinella fiski orangensis* Hewitt, Ann. Natal Mus., **7**, p. 319, pl. xvi, figs. 59-60: Between Phillipstown and Petrusville District, Cape Province.
1934. *Chersinella fiski colesbergensis* Hewitt, Ann. Natal Mus., **7**, p. 321, pl. xvi, figs. 61-62: Colesberg, Cape Province.

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[1] Erroneously synonymized with *Homopus boulengeri* by Siebenrock (1909: 515), who later (1910) correctly assigned it to the *geometricus* group.

1934. *Chersinella fiski grica* Hewitt, Ann. Natal Mus., **7**, p. 323, pl. xvi, figs. 63-66; pl. xvii, figs. 67-71: Marydale, Prieska District, Cape Province.

1934. *Chersinella fiski gricoides* Hewitt, Ann. Natal Mus., **7**, p. 326, pl. xvii, figs. 72-75: Nickerks Hope (= Niekerkshoop), Hay District, Cape Province.

1934. *Chersinella verroxii* Hewitt, 328, pl. xvii, fig. 78.

1937a. FitzSimons, 260.

1934. *Chersinella verroxii smithi* Hewitt, 331, pl. xvii, figs. 76-77.

1934. *Chersinella verroxii boettgeri* Hewitt, 333.

1934. *Chersinella verroxii amasensis* Hewitt, Ann. Natal Mus., **7**, p. 333: Ukamas District, Cape Province.

1934. *Chersinella verroxii bergeri* Hewitt, 335.

1935a. *Chersinella boettgeri* FitzSimons, 520.

1935a. *Chersinella fiskii* ? FitzSimons, 520.

1937c. *Psammobates fiski colesbergensis* Hewitt, 8, pl. iii, fig. 6.

1937c. *Psammobates fiski cronwrighti* Hewitt, 9, pl. iii, fig. 5.

1938. *Psammobates depressa* FitzSimons, Ann. Transvaal Mus., **19**, p. 154, pl. ii, figs. 1-4; pl. iii, figs. 1-2: Aus, Southwest Africa.

1938. *Psammobates fiskii* FitzSimons, 155.

1946a. *Psammobates fiskii fiskii* FitzSimons, 354.

1955a. *Testudo verroxii bergeri* Mertens, 37, pl. iv, fig. 12.

Further citations of "*verreauxi*" will be found under *t. tentorius*, and "*fiski*" under *t. trimeni*.

Common name. Northern Tent-Tortoise (would seem to be the most descriptive).

Illustrations. Excellent figures (lateral and plastral views; nuchal and forelimb) of the type have been furnished by Smith (1839 :pl. viii). Siebenrock (1904c :pls. i-v) supplies good photographs of *verroxii, smithi, fiski* and *boettgeri* (type), and Hewitt (1934 :pls. xvi-xvii) of the types of his numerous subspecies. More recently Müller (1939a :pls. x-xi) has photographed many extremes of this highly variable form.

Types. The type of *verroxii* has been definitely identified by FitzSimons (1937a :260) as a stuffed specimen, now minus eleven shields, in the Royal Scottish Museum at Edinburgh.

As to the type locality of *verroxii*, Power states (1932b :466) that he has systematically searched Sir Andrew Smith's works from which "it appears that he did a great deal of collecting in that part of the country at present occupied by the divisions of Bethulie, Smithfield, and Rouxville." Power concludes that the type "was taken somewhere north of Aliwal North, between the Orange and Caledon Rivers; that is to say, roughly 260 miles east of Niekerk's Hope."

Dr. V. FitzSimons, writing us on 12.v.54, considers Power's suggestion regarding the type locality as reasonable, adding that he has never seen any *verroxii* in the eastern Orange Free State. Mr. C. Jacot-Guillarmod, a keen naturalist whom we also consulted, replied that the few tortoises seen by him in the Orange Free State appeared to be referable to *Homopus.*

Writing on 1.ix.54 from Mamathes, Basutoland, Mr. Jacot-Guillarmod says: "I looked up Andrew Smith's itinerary and find that the type locality of the tortoise cannot be far from here. I should say just north of here round about Levibe, Ficksburg, or even east of here, perhaps along the Phuthiatsana River as he went up this river to its source. This means that he passed within four or five miles of Mamathes."

However, though "the sources of the Orange River" are in Basutoland, where Mr. Jacot-Guillarmod has been residing for the past 36 years, he tells us that during all that time he has never seen a tortoise in the Protectorate. Even the leopard tortoise can no longer be found, and if *verroxii* ever did occur it has presumably been exterminated for tortoises are highly prized by the witch-doctors.

Hewitt (1933b) believes that *verroxii* may be distinguished from *fiski* by the presence of a zone of small scales on the anterior aspect of the front foot immediately above the claws, instead of the large scales which he says continue to the base of the claws in *fiski.* We have been unable to verify whether this key character holds.

In all probability Boulenger (1886b) was induced to describe *fiski* by his overlooking Smith's (1839) mention of the presence of a conical tubercle on the hinder side of the thigh in *verroxii,* and also by the uncertainty as to the latter's type locality (which is possibly much nearer to that of *fiski* than has hitherto been supposed). Boulenger never saw a specimen of *verroxii* and, as recently as April 6, 1954, Mr. J. C. Battersby assures us that there are no representatives of the species in the British Museum, i.e. all their material is referred to *fiski.* When at the British Museum in 1953, one of us (E. E. W.) studied the types of *fiski, seimundi* and *smithi,* and shortly afterwards at Senckenberg the type of *boettgeri*=*oscarboettgeri.* Paratypes of *schonlandi* (M.C.Z. 42222-4) have been available to us also.

Description. Beak weakly or strongly hooked, tricuspid, edge of jaws finely dentate; prefrontal and frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few extremely large (in some instances a single shield is exceptionally enlarged as in *oculifer*), unequal, juxtaposed, subimbricate scutes, forming 2-4 longitudinal and 5-9 transverse series from elbow to outer claw; claws 5; hinder side of thigh with one or more enlarged, conical tubercles;[1] heel with a large spurlike tubercle; claws 4, rarely 5.

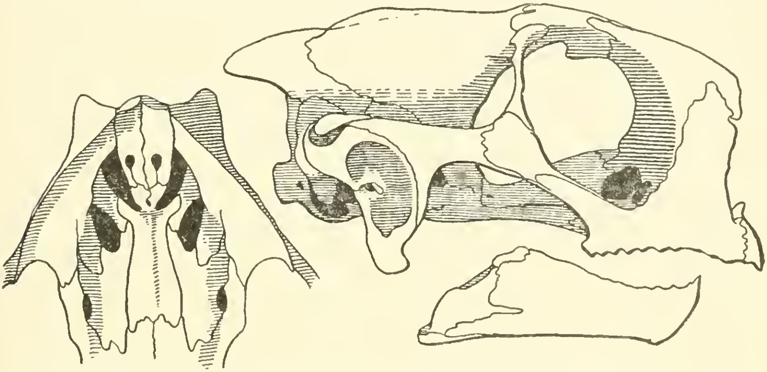

Fig. 32. Skull of *Psammobates t. verroxii* juv. (M.C.Z. 21330). Condylobasal length 15 mm. The youth of the specimen is reflected in the very open sutures.

(S. McDowell del.)

Carapace more or less convex, sides rounded, descending abruptly, very shallowly notched in nuchal region, anterior and posterior margins more or less expanded, sometimes reverted, and not or but slightly serrated; dorsal shields concentrically striated; nuchal usually present, typically broader than long or slightly longer than broad, rarely divided,[2] frequently minute, rarely absent; vertebrals 5, rarely 4[3] or 6,[4] more or less swollen,

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[1] In stating "without" Boulenger (1889a) misread Smith's description.

[2] In type of *depressa* FitzSimons.

[3] *Fide* Power (1933a).

[4] In type of *seimundi* as well as other specimens.

much broader than long, as broad as, broader than, or narrower than, the costals; costals 4, rarely 5,[1] usually not forming an angle with the lateral marginals; marginals 11 or 12; supracaudal undivided, incurved in ♂♂, inclined to spread out like marginals in ♀♀; tail in ♂♂ usually devoid of lateral tubercles, if present, small, in ♀♀ large lateral tubercles present, both sexes without a terminal clawlike tubercle.

Front lobe of plastron usually anteriorly truncate, occasionally somewhat produced,[2] openly notched; gulars paired, rarely subdivided;[3] pectorals more or less narrow where they meet, their anterior border sloping more or less steeply towards the axillary notch; axillaries 2 or 3, rarely 1, one large and the others, if present, small; inguinal moderate to large, sometimes with 1 or 2 supplementary shields, meeting femoral; hind lobe more or less deeply notched posteriorly.

Plastral formula: Abd>h>an>or<g>or=f>or<p. Anal typically longer than g or f; p usually shortest.

Color. Carapace light to brownish yellow, the yellow on each dorsal shield usually subequal in width to the 5 or 6 black rays of which the anterior and posterior pairs on vertebrals and costals meet their fellows to form three series of ocelli. At times the black rays may coalesce so that black predominates; marginals with 1 to 3 black rays. Plastron yellow, sometimes uniform, though normally its median portion is variegated with dark brown.

The plastral pattern in the type of *smithi* approaches that of *tentorius trimeni.* Separation of *smithi* and *boettgeri* from *verroxii* on the grounds that their light rays are yellow (instead of red and yellow as in *verroxii*) appears unjustifiable.

The type ♂ of *seimundi* had a yellowish horn-colored carapace from the centre of whose shields radiated short or interrupted, blackish-brown striae; the plastron was similarly colored with mere traces of the dark radiating striae. The head showed a few dark brown specks, otherwise the soft parts were yellow.

The type ♂ of *H. bergeri*, based on a native *buchu*-box shell, was described as having a carapace that was uniform bright reddish horn-brown except for the bright yellowish areolae.

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[1] In a Cape tortoise, *fide* Siebenrock.

[2] In type of *seimundi*.

[3] *Fide* Power (1932b), whom see for a very detailed study of *verroxii*.

Plastron horn-yellow, its central portion washed with bright reddish brown and a few obscure brownish rays. However, the specimen from Upington, Gordonia, reported on by Siebenrock (1910), had a chestnut brown carapace, each shield edged with darker of varying intensity while the center of the areolae tended to be lighter. Plastron light green, its central portion brownish. Head and limbs gray brown; outer scales on the forelimbs beautifully tinted with light brown. A specimen from Barby (now in the British Museum), which we have seen, corresponds very closely to Siebenrock's description. The Hereroland *bergeri* mentioned by Werner (1910a) had: Carapace red brown, uniform. Plastron yellow. Femoral and anal region brown. Sternfeld (1911b) concluded that *bergeri* was nothing more than a color variant.

In the type ♂ of *depressa* the head is described as being dirty yellow with more or less symmetrical blackish margins, viz. a bar down the front of the snout, a spot on top of the snout, a large spot above each orbit, and a crossbar on the back of the head. For full description of the shell cf. FitzSimons (1938).

Size. The type ♂ of *verroxii* was only 93.1 mm.; the type ♂ of *depressa,* 109 mm., its width 82 mm., breadth 50 mm. Carapace length of largest ♂ (ex Niekerk's Hope), 117.5 mm.; that of the largest ♀ (ex Ukamas), 141 mm., width 102.5 mm., height 74 mm. (*fide* Hewitt:1934)

Power (1933a) supplies data to show that ♂♂ average smaller than ♀♀, which bears out the importance of limiting comparisons to individuals of the same sex. Siebenrock's (1910) suggestion, accepted by Power, that there is a size and habitus difference justifying the separation of *fiski* from *verroxii,* is not supported by the available data.

Breeding. Females collected in April and May held only unripe ova. In October there was a single enlarged ovum besides several smaller ones. In December the oviduct contained a single shelled egg, besides several smaller ova. From this Power (1932b) deduces that a single egg is laid each year, and that this does not hatch until the following spring.

Diet. In the intestines of tortoises from Niekerkshoop one of the Crassulaceae was most frequently present, besides fragments of quartz. Each of these formed the core of a pellet of vegetable matter averaging about 12 x 18 mm. in size; such pellets were surprisingly numerous, no fewer than twenty-six being present in one tortoise (Power:1932b).

Feeds on the *Mesembryanthemum* bushes beneath which these tortoises shelter at Aus (FitzSimons, writing of *boettgeri*: 1935a).

Parasites. Every tortoise in the large series collected at Niekerkshoop by Power (1932b) was infested with spirillum ticks (*Ornithodoros moubata*), especially about the neck where, in some instances, they formed solid masses.

Thread worms of several species referable to the Oxyuridae, were invariably present in the large intestine at its junction with the small intestine.

Habitat. South of the Orange River *verroxii* was found on the flats by Power (1932b), but at Niekerkshoop north of the river *verroxii* was restricted to koppies and *oculifer* to the sandy plains.

Localities. Orange Free State: "near the sources of the Orange River" (for type of *verroxii,* which Power would place here). *Cape Province:* Abiam, Gordonia district; Albany district; Alweynsfontein; Amandelbom Mission, Zak River; Beaufort West; Brandvlei; Britstown; Britstown to Victoria West; Bros Pan; Bros Pan to Wyksvlei; Burghersdorp; Colesberg; Concordia; De Aar; Deelfontein; Gamoep; Gamoep to Alweynsfontein (Alwijnsfontein); Graaf Reinet; *Hanover (U.S.N.M.); Hopetown; Houmoed; Keimoes; Leliefontein (Liliefontein); Little Namaqualand; Marydale; Middleburg; Molopo River — lower; Naauwpoort; Niekerkshoop (Nickerk's Hope); O'okiep; Orange River Station; Philipstown to Petrusville; Plaatjiesfontein near Dwaal; Prieska; Richmond; Richmond to Victoria West; Sea-cow River; Somerset East district; South Gordonia; Springbok (Springbokfontein); Springfield — near; *Steinkopf; Ukamas; Upington; Van Wyksvlei; *Victoria West. *Southwest Africa:* Augustfelde and Plateau Farms, Aus district; Aus (Oas); *Barby, Tiraz Mountains (Brit. Mus.); Bethany; Gibeon; Great Namaqualand; Jakalswater; Karas Mtns.; Keetmanshoop; Keibib; Keimoes; Klein Karas Mtns.; Klein Windhoek; Kubub; Kuibis;; Narudas Sud; Rehoboth.

Range. Possibly southern Orange Free State (for type only), northern Cape Province (from Burghersdorp east to Williston and northwest to O'okiep, northwards through) Southwest Africa (Great Namaqualand to Rehoboth on the Tropic of Capricorn and the solitary 1895 record of Oudemans for Jakalswater near Swakopmund).

We consider erroneous the records of *verroxii* and *smithi* from the Blaauw Mountains, west of the Zoutpansberg range in the northern Transvaal. Siebenrock (1910) himself thought the data was questionable, being so remote from the general range of the species.

Psammobates tentorius trimeni (Boulenger)

1886b. *Testudo trimeni* Boulenger, Proc. Zool. Soc. London, p. 541, col. pl. lvii: Mouth of Orange River, Little Namaqualand, Cape Province.
1889. Boettger, 283.
1889a. Boulenger, 163.
1893a. Boettger, 10.
1898. Sclater, W. L., 97.
1904c. Siebenrock, 320.
1907a. Duerden, 10.
1907c. Duerden, 199.
1909a. Siebenrock, 526.
1910. Siebenrock, 715.
1910a. Werner, 303.
1911d. Sternfeld, 50, fig. 63.
1914a. Hewitt, 247.
1929. Flower, 30.
1934a. Mertens and Müller *in* Rust, 9.
1955a. Mertens (part), 36, pl. iv, fig. 13.
1907b. *Testudo tentoria* var. *fiskii* Duerden (part, not of Boulenger), pl. viii, fig. 11.
1933b. *Chersinella tentoria hexensis* Hewitt, Ann. Natal Mus., 7, p. 286, pl. xv, figs. 39-40: Hex River, Worcester District, Cape Province.
1933b. *Chersinella trimeni* Hewitt, 287, pl. xv, figs. 41-45.
1934. Hewitt, 337.
1935a. FitzSimons, 521.
1937a. *Psammobates trimeni* Hewitt, 791, fig. 1.
1938. FitzSimons, 155.

Common name. Western Tent-Tortoise.

Illustrations. That of Boulenger (1886b) is the best, but those of Duerden (1907b) showing plastral view of alleged "*fiskii*" (error), and Hewitt (1933b) illustrating variations, give a good idea of this race.

Types. The three cotypes in the British Museum have been studied by one of us (E. E. W.); a fourth is preserved in the South African Museum (*fide* Sclater:1898).

Description. Beak scarcely or distinctly hooked, bicuspid, edge of jaws not or but weakly dentate; prefrontal divided longitudinally or broken up; frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few extremely large, unequal, juxtaposed scutes, of which one is often strikingly larger than the others, forming 1-3 longitudinal and 4-6 transverse series from elbow to outer claw; claws 5; hinder side of thigh with or without a never-very-large, flat or subconical tubercle; heel without definite spurlike tubercle; claws 4; tail in ♂♂ devoid of lateral tubercles, which are present in ♀♀, both sexes without a terminal clawlike tubercle.

Carapace convex, sides rounded, shallowly to deeply notched in nuchal region, anterior and posterior margins not expanded, slightly reverted, and moderately serrated;[1] dorsal shields concentrically striated; nuchal moderate, small, minute, or rarely absent; vertebrals 5, more or less convex, typically conical, broader than long, as broad as, or broader than, or narrower than, the costals; costals 4, forming an angle with the lateral marginals, which are convex and consequently separated from the costals by a well-defined longitudinal groove; marginals 11 or 12; supracaudal undivided, incurved in ♂♂, downwardly directed in ♀♀.

Front lobe of plastron anteriorly truncate, openly notched; gulars paired; pectorals moderately broad, their anterior border sloping slightly towards the axillary notch; axillaries 1-2, moderate; inguinal moderate to large, sometimes with 1-2 supplementary shields,[2] meeting femoral; hind lobe deeply notched posteriorly.

Plastral formula: $\text{Abd} > \text{h} > \text{or} = (\text{p, an}) > \text{or} = \text{g}$.

Color. Carapace yellow or orange (occasionally salmon red in life, *fide* Hewitt), the light rays on each dorsal shield narrower than the 4-8 black rays so that black predominates. Plastron yel-

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[1] In which respect we disagree with Duerden (1907c) who considered this species non-serrate.

[2] *Fide* Duerden (1907c); we have also seen them with one such supplementary shield.

low, its central portion occupied by a broad black figure either indented with lighter or variegated with light rays.

Snout yellow with a median black line and similar lateral ones, side of head with a longitudinal suborbital bar terminating in a roundish postorbital spot; crown of head black. Cf. Hewitt (1933b:290) for color in life of soft parts of Bitterfontein specimens, and FitzSimons (1935a) for the juvenile coloring of a Lekkersing tortoise that he assigns to *trimeni*.

Size. Carapace length of largest ♂ (M.C.Z. 33451), 97 mm., breadth 75 mm., height 52 mm. Carapace length of largest ♀ (T.M. 16002), 121 mm., breadth 95 mm., height 67 mm.

Sexual dimorphism. According to Hewitt (1933b:290), supported by our ♂ and ♀, ♂♂ lack the patch of enlarged scales on side of tail which are present in the ♀♀, whose tails — as usual — are shorter.

Hewitt also claims that the foreheads of ♂♂ are more protuberant, and that this is correlated with a broad, downwardly projecting beak that bears a well-developed median, and two lateral, ridges. He asserts that the beak, when pronounced in ♀♀, lacks the sharp ridges. Hewitt also thinks that the lobes of the plastron converge less strongly in ♂♂ and that this results in the gulars and apical distance between the anals being broader than in the ♀♀.

Breeding. An egg, measuring 24.0 x 34.5 mm., was obtained from a ♀ taken near Bitterfontein (Hewitt:1933b).

Habits. During normal summer weather, according to B. Peers (in Hewitt:1933b) Trimen's Tent-Tortoises emerge to feed in the early morning and late afternoon. Upon the approach of unfavorable weather they seek shelter beneath some low-lying bush or euphorbia where they soon bury themselves by excavating the sand, first with the left forefoot, then with the right. Once completely covered they remain dormant until the arrival of cool weather or rain. Following a heavy downpour great numbers of tortoises emerge simultaneously so that many may be captured in a short time. While the rain is falling, according to Peers, whose description, however, is none too clear, the reptile raises its hind legs high so that the grooved shell, aided by the forelimbs, conducts the water to the corners of its mouth where it is eagerly taken in.

Habitat. The sandveld (Peers).

Localities. Cape Province — Little Namaqualand: Anenous — near; Calvinia — near;[1] *Bitterfontein — near; *Lekkersing;[1] Nieuwerust;[1] Orange River Mouth[1] (type locality); *Steinkopf; Van Rhyn's Pass — near, between Van Rhynsdorp and Nieuwhoudtville. *Southwest Africa* — Great Namaqualand: Augustfelde and Plateau Farms, Aus district; Keetmanshoop; 70 km. south of Walfish Bay (W. Triebner coll.).

Range. Extreme western Cape Province (i.e. Little Namaqualand) from Lambert's Bay (extending eastwards into Bushmanland according to Peers,[2] though we are unaware of any records from that area) north to the Orange River, and even occurring north of the river in Great Namaqualand (see discussion p. 310 above).

The record of *trimeni* from Kamelslip on the Nosop River, Bechuanaland, was based on a *buchu*-pouch carapace, i.e. a receptacle for the sweet-scented powder the natives obtain from the *buchu* plant. As this is the only occurrence of *trimeni* in Bechuanaland we reject the record, assuming the shell to have been carried to Kamelslip by its peripatetic owner.

The Clanwilliam and Stellenbosch records mentioned by Siebenrock (1910) as taken from Duerden (1907a), were stated by the latter to be only the home addresses of the donors.

PSAMMOBATES TENTORIUS TENTORIUS (Bell)

1828a.	*Testudo tentoria* Bell, Zool. Jour., 3. p. 420: Africa?
1836.	Bell, text and col. pl. —.
1872b.	Gray, 3, *in* Sowerby and Lear, pl. xiv.
1886b.	Boulenger, 541.
1889.	Boettger, 284.
1889a.	Boulenger, 164.
1892.	Müller, F., 214.
1893.	Trimen, 79.
1897.	Siebenrock, 247, pl. i, fig. 4.
1898.	Sclater, W. L., 97.
1904c.	Siebenrock, 321.
1907a.	Duerden, 10 (a few localities are referable to *t. verroxii*).
1907b.	Duerden, 74, pl. vii, fig. 8; pl. viii, fig. 10.
1907c.	Duerden, 197.

[1] In Transvaal Museum, but seen by us.

[2] Cited by Hewitt (1933b).

1909a. Siebenrock, 527 (some of Duerden's *t. verroxii* localities accepted).
1914a. Hewitt, 247.
1929. Flower, 31.
1934a. Mertens and Müller *in* Rust, 9.
1937a. Flower, 9.
1939a. Müller, L., 129.
1954. Noël-Hume, 76.
1835. *Testudo geometrica* Temminck and Schlegel (part: not of Bell), 73.
1855. *Testudo geometrica* var. *nigriventris* Gray, Cat. Shield Rept., Brit. Mus., p. 8: South Africa.
1870b. *Peltastes tentorius* Gray, 9.
1870c. Gray, 656.
1873b. Gray, 9.
1898. *Testudo verreauxii* Sclater (not of Smith), 96 (Beaufort West).
1933b. *Chersinella tentoria* Hewitt, 265, pl. xiv, figs. 8-9.
1933b. *Chersinella tentoria albanica* Hewitt, Ann. Natal Mus., **7**, p. 266, pl. xiv, figs. 10-15: Mayfair, Albany District, Cape Province.
1933b. *Chersinella tentoria tentorioides* Hewitt, Ann. Natal Mus., **7**, p. 268, pl. xiv, fig. 16: Bowden Hall, Middlebury District, Cape Province.
1933b. *Chersinella tentoria piscatella* Hewitt, Ann. Natal Mus., **7**, p. 269, pl. xiv, figs. 17-18: Little Fish River, Somerset East District, Cape Province.
1933b. *Chersinella tentoria subsulcata* Hewitt, Ann. Natal Mus., **7**, p. 270: Brighton Farm, near Steytlerville, Cape Province.
1934. Hewitt, 336.
1933b. *Chersinella tentoria karuica* Hewitt, Ann. Natal Mus., **7**, p. 272, pl. xiv, figs. 19-24; pl. xv, figs. 25-28: Drogekloof Farm, near Klaarstroom, Prince Albert District, Cape Province.
1934. Hewitt, 336.
1933b. *Chersinella tentoria duerdeni* Hewitt, Ann. Natal Mus., **7**, p. 279, pl. xv, figs. 29-31: Graaf Reinet, Cape Province.
1933b. *Chersinella tentoria lativittata* Hewitt, Ann. Natal Mus., **7**, p. 281, pl. xv, figs. 32-34: Willowmore, Cape Province.
1933b. *Chersinella tentoria karuella* Hewitt, Ann. Natal Mus., **7**, p. 283, pl. xv, figs. 35-38: Uniondale, Cape Province.
1937a. *Psammobates tentoria* Hewitt, pl. x, fig. 5 (skull).
1937e. *Psammobates tentoria albanica* Hewitt, 7, pl. iii, figs. 1-2; pl. xxvii, fig. 9.
1937e. *Psammobates tentoria tentorioides* Hewitt, 8; also as "tent tortoise" skeletal shell, pl. xxviii, fig. 1.
1937e. *Psammobates tentoria piscatella* Hewitt, 8, pl. iii, fig. 3; pl. ivA, figs. 2-3.

1937e. *Psammobates tentoria duerdeni* Hewitt, pl. ii, fig. 3.
1946a. *Psammobates tentoria karruica* (*sic*) FitzSimons, 353.
1950. *Geometric Tortoise* Rose, fig. 206.

Further citations of "*tentoria*," also *tentoria hexensis*, will be found under *t. verroxii* and *t. trimeni*.

Common names. Southern Tent-Tortoise (preferred); South African Starred Tortoise (Noël-Hume:1954); *knoppiesdop* or *knoppiesskilpad* (Afrikaans, *fide* Hewitt:1937e).

Illustrations. Bell's (1836) fine picture of the type will not be available to most workers, who will be grateful to Hewitt (1933b and 1934) for his photographic reproductions of most of the outstanding variants.

Types. The type of *Testudo tentoria* Bell in the Oxford Museum has been examined by E. E. W.

Description. Beak weakly or strongly hooked, bi- or tricuspid; edge of jaws more or less serrate; prefrontal and frontal broken up; upper head shields small, irregular; forelimb anteriorly covered with a few, extremely large, unequal, juxtaposed scutes, forming 2-4 longitudinal and 4-9 transverse series from elbow to outer claw; claws 5; hinder side of thigh with or without 1 or more, large, subconical tubercles; heel without definite spurlike tubercle; claws 4; tail in both sexes devoid of lateral tubercles and without a terminal clawlike tubercle.

Carapace convex, sides rounded, broadly notched in nuchal region, anterior margins slightly expanded, posterior sometimes reverted and slightly serrated; dorsal shields concentrically striated; nuchal occasionally well developed, usually small, minute, or even absent; vertebrals 5, rarely 6 or 7,[1] usually strongly conical[2] and, except for the first, usually broader than long, narrower than the costals; costals 4, occasionally 5, sometimes forming an angle with the lateral marginals; marginals 11-13; supracaudal undivided, incurved in ♂♂, downwardly directed in ♀♀.

Front lobe of plastron anteriorly truncate, openly notched; gulars paired; pectorals very variable, narrow or relatively broad, their anterior border curving or sloping towards the

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[1] *Fide* Hewitt (1933b:271, 275, 277); 7 in U.S.N.M. 16225, seen by E.E.W.

[2] The degree of convexity is highly variable even in tortoises from the same locality, says Duerden (1907c: 189).

axillary notch; axillaries 2 or more, variable in size; inguinal moderate to large, sometimes with 1 or 2 supplementary shields, meeting femoral; hind lobe deeply notched posteriorly.

Plastral formula: Abd>h>or<g>or<an>or<f>p. Pectoral the shortest scute.

Color. Carapace yellow or orange, the light rays on each dorsal shield usually narrower than, though sometimes subequal to or broader than, the 8-14 black rays (8-12 on vertebrals, 12-14 on costals, 3-4 on marginals) so that black frequently predominates. Plastron yellow, sometimes faintly tinged with orange, visible only on the periphery as the central portion is occupied by a broad brown figure.

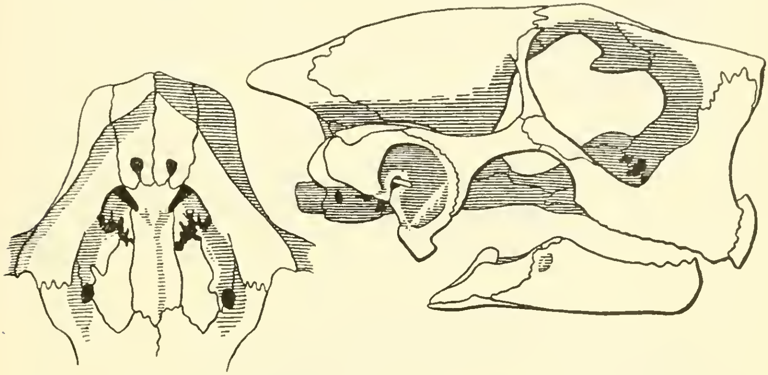

Fig. 33. Skull of *Psammobates t. tentorius* (M.C.Z. 3465). Condylobasal length 24 mm.

(S. McDowell del.)

The tail and adjacent soft skin are red to orange red (*fide* Hewitt :1933b).

Size. Carapace length of the type of *tentorius*, 108 mm. Carapace length of largest ♂ (ex Matjesfontein), 100 mm., breadth 74 mm., height 74 mm. (FitzSimons :1946a). Carapace length of largest ♀ (a paratype of *t. karuella*), 138 mm., breadth 107 mm., height 74 mm. (Hewitt :1933b).

Breeding. In September, 2 or 3 eggs are laid. Two oval eggs of "*albanica*" measured 21.3 x 27 mm. and 23.5 x 31 mm. respectively. Two tortoises that hatched out in May measured

25.4 mm. (given as 1 inch) in length (E. du Toit etc. in Hewitt: 1933b and 1937e).

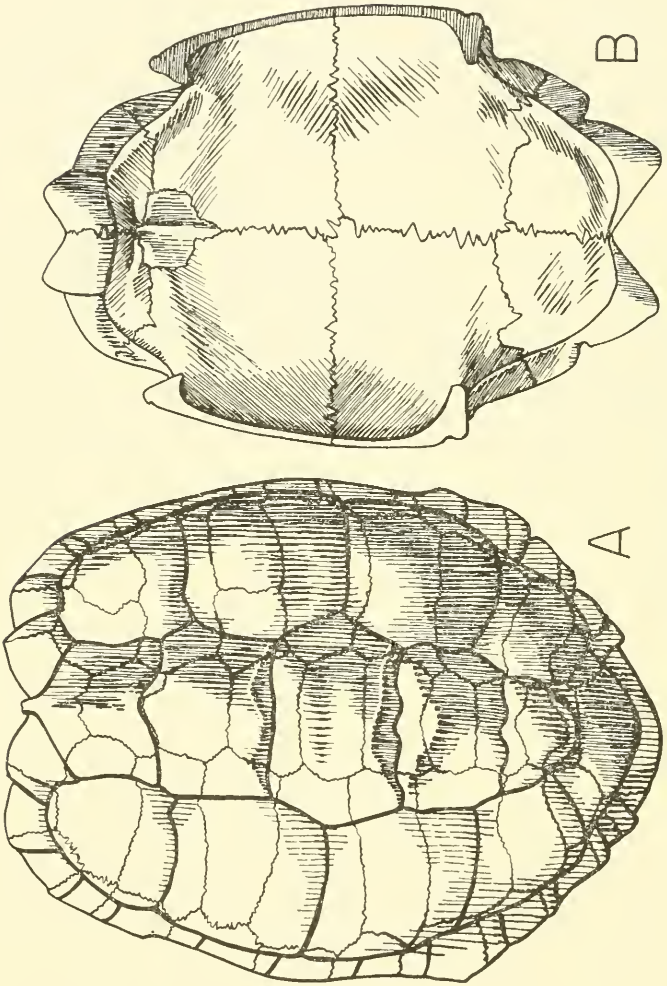

Fig. 34. *Psammobates t. tentorius* (B.M.). *A*, Dorsal view of carapace showing numerous abnormalities; *B*, Internal view of plastron.

(P. Washer del.)

Longevity. Seven years, 5 months, and 6 days for a specimen received at the London Zoo in 1920 (Flower:1937a).

Diet. In a wild state the diet includes *Eragrostis bergiana* (*fide* E. du Toit) lettuce and lucerne in captivity (Hewitt: 1937e).

Enemies. In certain areas ostriches, by devouring the young, have almost exterminated this form (Hewitt:1937e).

Habits. In June not a single tortoise was seen at Drogekloof, though the veld was traversed in every direction daily by Miss I. Z. Oosthuizen; in September — though there had been no rain and the veld was even drier — tortoises were encountered almost every day (Hewitt:1933b).

Tent-Tortoises in captivity develop regular habits, each reptile returning to its favorite corner of the pen after feeding or sunning. Rather more sluggish and timid than other species, the forelimbs, when withdrawn, completely conceal both the head and all surrounding skin (Hewitt:1937e).

Habitat. In the Albany district *tentorius* is found among low bushes in the karroid vegetation on either side of the Great Fish River (Hewitt:1937e).

Localities. Cape Province (but note remarks under Range): Abraham's Kraal, Prince Albert district; *Adendorp; *Beaufort West; Bowdon Hall, Middleburg district; Brandeston Farm, Albany district; Brighton Farm, Steytlerville; Calitzdorp (Calitsdorp); Carlisle Bridge; Dikkop Flats between Grahamstown and Port Elizabeth; Drogelkloof Farm near Klaarstroom; *Fish River near Grahamstown; Graaff Reinet; *Grahamstown; Klipplaat; Koup; Letjesbosch, between Beaufort West and Frazerburg Road; Little Fish River; Matjesfontein; Mayfair, Albany district; Middleton, Carlisle district; Muiskraal; Nelspoort; Oudtshoorn; Prince Albert; Steytlerville; Uniondale; *Upper Karroo; *Warmbad Farm, Uniondale (seen at U.S.N.M.); Welbedacht Farm, Olifants River, Oudtshoorn district; Westondale, Pearston district; Willowmore; Zwartruggens (Swart Ruggens), Aberdeen district.

Range. Southeast Cape Province, mostly south of the 32nd parallel. Typically concentrated in the region from Grahamstown to Uniondale. Apparently intergrading with *Psammobates tentorius verroxii* at Adendorp; Graff Reinet; Middleburgh district (which is north of the 32nd parallel); Nelspoort and Beaufort West. At Matjesfontein and vicinity, intergrading with both *P. t. verroxii* and *P. t. trimeni* may be expected. Erroneously recorded from Mauritius by Gray (1873b).

Genus CHERSINA Gray

1831c. *Chersina* Gray (not of Humphreys: 1797),[1] Syn. Rept., pp. 7, 14, Type: *Testudo angulata* Schweigger (by monotypy).

1929. *Goniochersus* Lindholm, Zool. Anz., **81**, p. 285. Type: *Testudo angulata* Schweigger (by original designation).

1931. *Neotestudo* Hewitt, Ann. Natal Mus., **6**, p. 504. Type: *Testudo angulata* Schweigger (by original designation).

Definition. Skull with triturating surface of maxilla without ridging but a weak ridge on the horny sheath; median premaxillary ridge absent; maxillary not entering roof of palate; anterior palatine foramina moderately large, not concealed; prootic well exposed dorsally; quadrate enclosing stapes in adults; surangular subequal in height to prearticular; neck with second, third or fourth centrum biconvex.

Carapace never hinged; normally the anterior neurals hexagonal; outer side of third costal scute about as long as, or longer than, that of the fourth; submarginal scute absent; suprapygal 1.

Plastron not hinged; gular region greatly thickened and produced; gular shield *single*, much longer than broad.

Distinguishing marks. The only continental African tortoise with a single gular scute.

Range. Union of South Africa (Cape Province only), possibly extending into Southwest Africa.

Fossil record. None.

Remarks. We have separated the peculiar species *angulatus* from the genus *Testudo* on osteological grounds. An external character, the single gular, indeed suffices to set it apart from all the tortoises of continental Africa, but this condition is paralleled by the tortoises of Mauritius and Rodriguez and by the Malagasy species *yniphora*, all of which we refer to the genus *Geochelone*. From the *Geochelone* species with single gulars, *Chersina* differs in the very extensive thickening of the gular region, in which as in some other features it resembles *Kinixys*.

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[1] See footnote 3 on page 218.

Not all of its features are resemblances to *Kinixys,* however, and its true affinities are doubtful.

To illustrate the problem and our method of meeting it we tabulate (Table 6) the characters of *Chersina* and cite for each of them the genera presenting the closest similarity.

TABLE 6

Chersina	Genera showing greatest resemblance	Comment
Maxilla with a very feeble ridge or none	No ridge in *Kinixys, Homopus, Pyxis, Psammobates;* reduced or absent in *Testudo*	An advanced character in which *C.* is intermediate
Quadrate closed behind stapes in adults	*Kinixys, Homopus, Psammobates, Testudo s. str., Malacochersus,* most *Geochelone,* and *Gopherus* and †*Stylemys*	An advanced character achieved in parallel by many genera
Anterior palatine foramina moderate to large	*Testudo*	An advanced character in which *C.* is somewhat intermediate
Anterior marginals elongate	*Kinixys*	A specialized character shared only with *K.*
Neurals variable approaching the octagonal and quadrilateral pattern	*Pyxis, Testudo, Geochelone, Gopherus*	An advanced character which *C.* appears to be approaching independently
Suprapygal single	*Kinixys, Pyxis, Acinixys, Psammobates, Testudo, Malacochersus*	A primitive character shared with emydines
Gular process greatly thickened and extended anteroposteriorly	*Kinixys*	A specialized character shared only with *K.*

From this tabulation it will be seen that except in neural pattern (*Kinixys* is obstinately hexagonal) and in the single gular, *Chersina* is either close to *Kinixys* or more primitive than that genus. If it were to be synonymized with any genus it would seem more reasonable to equate it with *Kinixys* than with *Testudo* or *Geochelone*. But the differences from *Kinixys* seem to us to imply a long separate history, and we are not certain that the relationship to *Kinixys* is as great as emphasis upon two specialized characters would suggest. We prefer therefore to regard this form as a full genus belonging to the series of Ethiopian endemics.

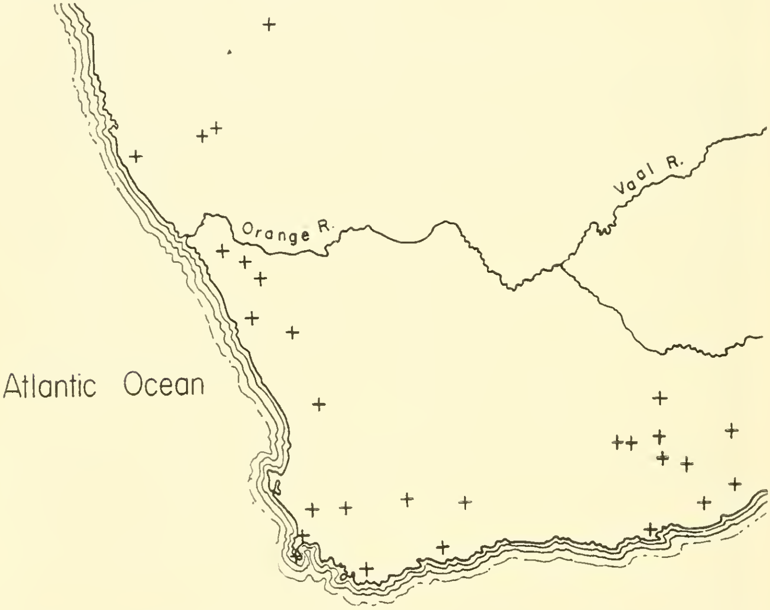

Fig. 35. Distribution of *Chersina angulata* in South Africa.
(P. Washer del.)

The distribution of this tortoise is wholly included within the range of *Psammobates*, possibly within that of *Homopus*.

There appears to be no clearly demarcated geographical variation within *angulata;* as to red on the plastron, see paragraph on *Color* below (p. 348).

Chersina angulata (Schweigger)

1795. *Testudo pusilla* Thunberg, (not Linnaeus, 1758), 3.
1812. *Testudo angulata* Schweigger, Königsberger Arch. Naturwiss. Math., 1, pp. 321, 360, 443: No locality.
1814. Schweigger, 52 (reprint of 1812).
1835. Duméril and Bibron, 130 (not 150).
1835. Temminck and Schlegel (? part *erosa*), 72.
1836. Bell, text and col. pl. —.
1845b. Rüppell, 297.
1857. Jan, 35.
1872b. Gray, 5, *in* Sowerby and Lear, pl. xix.
1889. Boettger, 286.
1889a. Boulenger, 178.
1889. Vaillant, 166, pl. xv, figs. A-B.
1890. Strauch, 57.
1892. Müller, F., 214.
1893a. Boettger, 12.
1898. Jeude, 5.
1898. Johnston, 361.
1898. Sclater, W. L., 97.
1901. Lampe, 194.
1907a. Duerden, 9-10 (only donor's addresses).
1907b. Duerden, 73, pl. vi, fig. 4.
1909a. Siebenrock, 543.
1910a. Werner, 305.
1911d. Sternfeld, 50.
1912b. Werner, 434.
1915. Werner, 331.
1925b. Flower, 932.
1928. Cott, 952.
1929. Flower, 30.
1929. Rose, 188, 225, 231, fig. 125.
1935a. FitzSimons, 519.
1937a. Flower, 9.
1937. Ruckes, 103, pl. x, fig. 4.
1950. Williams, 551.
1812. *Testudo tabulata Africana* Schweigger (not of Hermann), Königsberger Arch. Naturwiss. Math., p. 322: No locality.
1814. Schweigger, 54 (reprint of 1812).
1820. *Chersine pusilla* Merrem (not of Linnaeus: 1758), 38.
1946a. FitzSimons, 354.

1828. *Testudo Bellii* Gray, Spicilegia Zoologica, p. 2, pl. iv, figs. 3-3a: Cape of Good Hope.
1831c. *Chersina angulata* Gray, 15, pls. i-ii.
1831b. Gray, 5.
1844. Gray, 11.
1849. Smith, A., App., 1.
1855. Gray, 12.
1860. Fitzinger, 411.
1862a. Strauch, 23.
1865. Strauch, 36.
1866. Gray (part), 306.
1867a. Steindachner, 4.
1870e. Gray (part), 13.
1873b. Gray, 14.
1873c. Gray, 726, pl. lx, fig. 6.
1873h. Gray, 496.
1885. Smets, 2 (locality erroneous).
1887b. Boettger, 137.
1887a. Müller, F., 296.
1931. *Neotestudo angulata* Hewitt, 504.
1934a. *Goniochersus angulatus* Mertens and Müller *in* Rust, 63.
1955a. Mertens, 34, pl. iii, fig. 14.
1937a. *Chersine angulata* Hewitt, 789, pl. x, fig. 7.
1937e. Hewitt, 6, pl. i, fig. 3; pl. iv, fig. 4; pl. xxvii, fig. 10.
1938. FitzSimons, 153.
1950. Rose, 325, 343, figs. 207-208.
1946. *Testudo* (*Chersine*) *angulata* Cairncross, 396.

Synonymy. Schweigger (1812) took the name *Testudo angulata* from a specimen labeled by Duméril in the Paris Museum; authorship was later claimed by Duméril and Bibron (1835: 130 and 138). *T. tabulata africana* Schweigger (not of Hermann) was also based on a Paris Museum tortoise. Strauch (1862a:67) has explained why *Testudo pusilla* Linnaeus (1758: 199) is not identical with *pusilla* Linnaeus (1766:353). The latter, being preoccupied, cannot be used, as was done by FitzSimons (1946a:354). FitzSimons (1938) suggested that *Chersina* Gray 1831, having been proposed by Humphreys for a gastropod in 1797, is not available, hence his use of *Chersine* Merrem (see however, footnote 3, p. 218).

Common names. Angulated Tortoise (Hewitt:1937e); Bowsprit Tortoise (Flower:1929); bont-skilpad; duine-skilpad;

ploegskaar-skilpad; rooi-skilpad; skaar-skilpad (Afrikaans, all Hewitt:1937e).

Illustrations. There are excellent figures in Gray (1831:pls. i-ii), and Bell (1836), the latter reproduced in Sowerby and Lear (1872:pl. xix).

Description. Beak weakly or strongly hooked, bi- or tricuspid, edge of jaws very weakly serrate; prefrontal divided longitudinally, sometimes separated from the frontal by a small scale; frontal large, or occasionally divided longitudinally,[1] flanked by 4-5 small scales; upper head shields small, irregular; forelimb, more especially anteroventrally, with several rows of moderately large, subequal, juxtaposed or slightly separated scutes forming 2-3 longitudinal and 7-9 transverse series from elbow (on the lower or inner side of which is an isolated large scute) to outer claw; on the upper or outer aspect of the wrist is a semi-bracelet of large scutes; claws 5; hinder side of thigh without large tubercles; heel with one or more enlarged flat scales; tail without terminal clawlike tubercle.

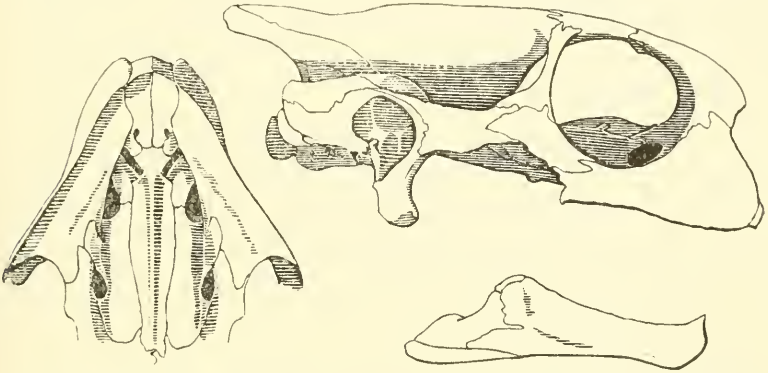

Fig. 36. Skull of *Chersina angulata* (B.M. 67-4-2-152). Condylobasal length 28 mm.

(S. McDowell del.)

Carapace elongate, moderately convex, sides descending abruptly, deeply notched in nuchal region, anterior margins expanded but neither reverted nor serrated, posterior margins not or but moderately expanded, reverted, somewhat sinuate; dorsal

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[1] Divided in a Steinkopf specimen, *fide* Werner (1910a).

shields concentrically striated except in aged specimens, neither swollen nor convex; nuchal narrow, elongate, always small, sometimes absent;[1] vertebrals 5, rarely 6 or 7,[2] flat, the first about as broad as long or longer than broad, the second, third and fourth much broader than long, the fifth broader than long or longer than broad, the third narrower than the third costals; costals 4, rarely 5,[3] usually not forming an angle with the marginals; marginals 11, rarely 10;[4] supracaudal undivided, more or less incurved in ♂ ♂, downwardly directed in ♀ ♀.

Front lobe of plastron always strongly produced, its end truncate or rounded; gular entire;[5] pectorals narrow where they meet, their anterior border sloping steeply towards the axillary notch in adults, less so in young; axillaries 1 or 2 (single in young, double in adults) moderate; inguinal large, meeting femoral; hind lobe deeply notched posteriorly in ♂ ♂, more shallowly in ♀ ♀.

Plastral formula, adults: Abd>g>h>or<an>f>or=p; juveniles: Abd>h>g>an>p>f.

Color. In both juvenile and adult the carapace is pale straw or pale horn to olive, the areola of each vertebral and costal shield usually darker and the periphery broadly margined with black, these borders occasionally interrupted by lighter rays; a broad-based, black, triangular blotch on the sutures between marginals; supracaudal with a median, down-pointing, black triangular mark. Sometimes, however, the pattern may be broken up, indistinct.

Plastron pale straw to yellow; from gular to anals extends a broad, black blotch, uniform, variegated with lighter, or broken up, its borders not sharply defined; lower aspect of lateral marginals yellow, but those posterior to the inguinal tend to display a black blotch at their anterior edge, and there may be a similar spot on one of the anterior marginals.

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[1] Absent in a Richtersveld tortoise (M.C.Z. 42211).

[2] Six in a Great Namaqualand buchu pouch, *fide* Boettger (1889); 7 in a Steinkopf hatchling (M.C.Z. 42210).

[3] Five in a Great Namaqualand buchu pouch, *fide* Boettger (1889).

[4] Ten on right side of a Steinkopf hatchling (M.C.Z. 42210).

[5] Semidivided on the lower surface of an adult ♂ from Penrock, *fide* Hewitt (1931; see also Hewitt :1937a :790). In Rose's figure (1950 :343) the gular is called a "subgular", while the humerals are miscalled "gulars" and the pectorals "humerals."

In life the plastron is said to be reddish by Bell (1836) but the color disappears soon after death. However, Duerden

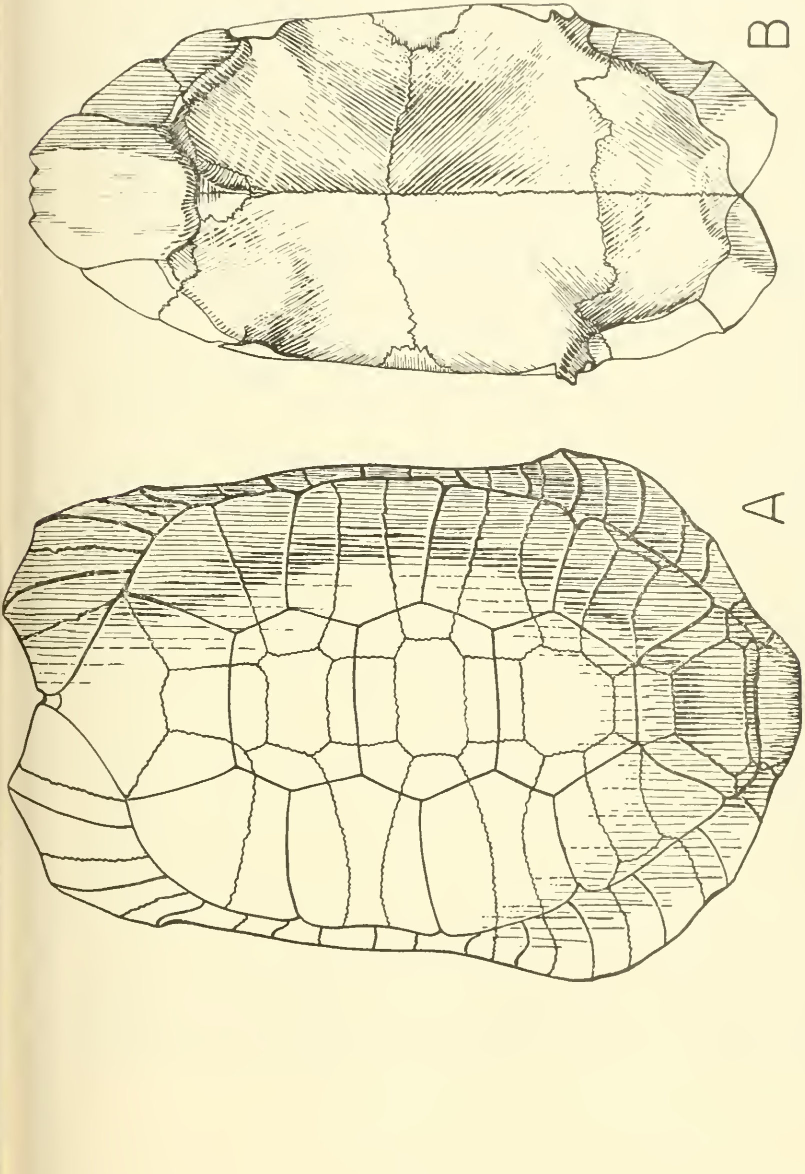

Fig. 37. *Chersina angulata* (M.C.Z. 52250) from South Africa. *A*, Dorsal view of carapace, (x ⅔); *B*, Internal view of plastron, (x ⅔).
(P. Washer del.)

(1907b:74), seemingly suggesting that it is a local characteristic, remarks that *angulata* from the western part of Cape Province possess plastrons having a diffusely reddish ground color. FitzSimons (1935a) states that the sides of the plastron are suffused with reddish in adults, especially so in ♂♂ from Van Rhynsdorp, and later (1938) remarks on the bright rosy red plastrons of Kamieskroon and Klipfontein tortoises.

Snout at tip, and hinder part of head, black; prefrontal and frontal shields yellow (Hewitt:1937e). The coloring of the soft parts as given by Gray (1866:306, etc.) was based on the head and limbs of a *Geoemyda punctularia* associated with the shell of an *angulata* (*fide* Boulenger:1889a:178).

Size. Carapace length of largest ♂, 264 mm., breadth 59 mm. (Hewitt:1937e), length of another ♂ (M.C.Z. 3998), 183 mm., breadth 112 mm., height 80 mm. Carapace length of largest ♀ (T.M. 15996), 163 mm., breadth 104 mm., height 81 mm. (from Soebartsfontein, FitzSimons:1935a); length of a Port Elizabeth ♀ (M.C.Z. 9328) 153 mm., breadth 103 mm., height 68 mm.

Weight. The largest ♂ listed above weighed 5 lbs. (Hewitt: 1937e). See also Cairncross (1946:397) for tabulated increases among hatchlings.

Sexual dimorphism. The rather spadelike projection of the front lobe of the plastron is much more strongly produced in ♂♂ (whose plastron is also somewhat concave in its posterior third) than in ♀♀ (whose tails are noticeably shorter than those of the ♂♂). These sexual differences have been well illustrated in black and white by Vaillant (1889:pl. xv=our Plate 12).

Breeding. In August, at Cape Town, the ♀ digs a nest hole of from 3 to 4 inches in depth; only a single egg is laid (Rose: 1950). However, two eggs (M.C.Z. 21662) were laid on 18.viii. 1925 at the M.C.Z. by a Port Elizabeth tortoise (M.C.Z. 22475). Eggs, though usually oval, are sometimes spherical, rarely pointed at one end. In size they range from 35 x 37 mm. to 34 x 42 mm. (Hewitt:1937e:pl. xxvii, fig. 10).

While the incubation period at Cape Town may range from 12 to 14 months (Rose:1950), Cairncross mentions a 30-grain egg laid on 7.v.40 which, placed in an incubator on 3.viii.40, hatched on 3.xi.40, i.e. in 6 months; however, the hatchling was malformed and died 14.x.41. For growth and weight records of other hatchlings, see Cairncross (1946:397). The hatchling's carapace is flat and strikingly different from the convex shell of the adult (Hewitt:1937e).

Rose managed to protect the egg from rats and other predators by disinterring it and then reburying it at the same depth of soil within a wire basket sunk in the ground and securely covered over by wire netting.

Longevity. Eleven years, nine months in Giza Zoo (Flower: 1925b; 1937a).

Diet. Eats gazanias (A. Rothmann); fond of young beans and regarded as a nuisance by gardeners (Hewitt:1937e); a captive specimen displayed a liking for meat (Rose:1950) but this author's somewhat contradictory statement that true tortoises are "normally strictly vegetarian" should have the second adjective omitted.

Enemies. Unquestionably man. Writing from Mrs. Müller's farm, apparently a day's trek northeast of Cape Town, on September 11, 1773, Thunberg (1795:3) says: "Among the bushes in the sands we frequently saw land-tortoises crawling, and the young ladies in the house had ordered the slaves to bring several of them home of various sizes for our repast. The *Testudo pusilla* was the most common species here, and it was this which was now laid upon the fire for our eating. I slipped into the kitchen on purpose to see the mode of dressing it, and found that the girls were cruel enough to lay the poor animal wide open on the live coals, where, sprawling with its head and feet, it was broiled alive, till at length it burst to pieces with the heat. The eggs, which were in great number, and consisted of yolk only, were the most luscious and desirable part of it."

The 21 young tortoises, with unbroken shells about two inches in diameter, recovered from the stomach of a ♂ Secretary Bird (*Sagittarius serpentarius*) killed on the Cape Flats by Levaillant (1824, Hist. Nat. Oiseaux d'Afrique, 1:70, pl. xxv), were probably referable to *angulata* suggests Rose (1950:344).

Temperament. Males spend much time in sparring with their rivals (Hewitt:1937e). One ♂, by biting the heads of other ♂♂ in the enclosure, induced them to withdraw into their shells, whereupon he would thrust his nose or *plastral projection* beneath their shells and so overturn them. Occasionally he would achieve the same result by butting them head on, then walk away leaving his opponents sprawling on their backs (Rose :1950). Females do not respond readily to a male's advances, in fact they usually endeavor to escape him by running away (Cairncross :1946).

Habitat. The drier coastal and central districts of Cape Province as far eastwards as the Keiskama (Hewitt :1937a). Still occurs on the Cape Flats, but is more often met with on the less-frequented uplands towards Cape Point (Rose :1950).

Localities. Cape Province:[1] Adelaide; *Cape of Good Hope; Cape Flats; Cape Point; Cradock; Dassen Island (introduced); Fish River Valley; Grahamstown; Graaff Reinet; Kamieskroon; Keiskama Valley; Kenkelbosch; Klipfontein; Malmesbury; Matjesfontein; Mortimer; Penrock near Grahamstown; *Port Elizabeth; Queenstown; *Richtersveld; Lekkersing; Rhynheath; Schoombie; Soebatsfontein; *Steinkopf; Stillbay; Van Rhynsdorp; Welbedacht; Worcester; Zoetendahl's Valley. *Southwest Africa:*[2] Bethany (based on buchu pouches collected by Schinz, etc. Boettger: 1887b); Karibib (Shell :Mertens :1955a); Kuibis (shell lacking anterior lobe of plastron, so possibly native preserved. Werner :1915); Orange River mouth (2 live ♀♀, coll. G. May); *Pomona (A.M.N.H., alcoholic); Rietmond near Gibeon (Lampe :1901).

Range. Cape Province west of 28° East longitude, possibly extending northwards into Southwest Africa.

Erroneously recorded from West Africa and Madagascar by Bell (1836); from Natal by Jan (1857); from Matabeleland and Zambezi region by Smets (1885); and the East Indies by Burmeister (not seen).

Genus HOMOPUS Duméril and Bibron

1835. *Homopus* Duméril and Bibron, Erpét. Gén., **2**, p. 145. Type: *Testudo areolata* Thunberg (designation by Fitzinger: 1843: 29).

1835. *Chersobius* Fitzinger, Ann. Wiener Mus., **1**, pp. 108, 112, 122. Type: *Testudo signata* Schoepff (by original designation).

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[1] In an annual report Duerden (1907a) lists *angulata* from 14 donors, whose addresses he gives, but these we omit as there is no way of telling whether the specimens actually came from the places mentioned.

[2] The records from Southwest Africa should be investigated, a statement with which Mertens (1955a) concurs.

1931. *Pseudomopus* Hewitt, Ann. Natal Mus., **6**, pp. 496, 498. Type: *Testudo signata* Schoepff (by original designation).

Definition. Skull with triturating surfaces of maxilla and premaxilla without ridges; maxillary not entering roof of palate; anterior palatine foramina moderate to large, conspicuous; prootic narrowly exposed dorsally; quadrate enclosing stapes; surangular subequal in height to the prearticular; neck with third centrum biconvex.

Carapace never hinged; normally the anterior neurals hexagonal or quadrate; outer side of third costal scute longer than that of fourth; submarginal scute absent; suprapygals 2, the anterior larger, bifurcating posteriorly to embrace the smaller posterior element which is adjacent to, but not crossed by, the sulcus between the fifth vertebral and the supracaudal.

Plastron not hinged; gular region slightly thickened and produced; gular shields paired, usually broader than long.

Range. Union of South Africa (western Orange Free State and Cape Province), possibly extending into Southwest Africa.

Fossil record. None.

Homopus alone of the present day Ethiopian endemic tortoise genera has been alleged to have a fossil record. In 1889 Lydekker (Cat. Foss. Rept. Brit. Mus., part 3, p. 91 seq.) assigned †*Emys comptoni* Bell, of the London Clay Eocene of England, and †*Emys scutella* v. Meyer, from the Oeningen Upper Miocene of Switzerland, to *Homopus*. Bell, as Lydekker points out, when describing †*E. comptoni,* indicated resemblances to *H. areolatus* and *H. signatus* and was probably only deterred from referring the species to *Homopus* by the fact that the London Clay is a marine deposit.

Since Lydekker's time little attention has been paid to these fossils. Hewitt (1937a:792) justly remarked: "It is interesting to note that flattened shells of similar form and size to *Homopus* did occur so long ago in Europe, but the generic identity should be considered very doubtful, as the characters emphasized are quite insufficient."

Fortunately one of us (E.E.W.) has been able to examine material of both of these fossil species — the unique type of †*comptoni* in the British Museum and two specimens of †*scutella* in the Teyler Museum, Haarlem, Holland. The Teyler Museum generously permitted the specimens of †*scutella* to be borrowed and further prepared. Only one side of each had been exposed; skillful preparation by Mr. Arnold Lewis of the Museum of Comparative Zoology has now revealed the other side in each specimen, despite the extreme rottenness of the bone in places.

Whereas superficial examination of this material had seemed to support, or at last did not refute, the assignment to *Homopus*, the more careful study now possible reveals that neither species can be referred to the South African genus. Instead, on totality of characters, both appear referable to *Testudo*.

The type specimen of *comptoni* is defective in various critical areas, and probably could not be placed with certainty were it not that †*scutella*, which it so much resembles, furnishes a guide to its assignment. The two species are considered to be *Testudo* rather than *Homopus* on the following characters:

1. The neural pattern is advanced in both species; already incipiently octagonal *cum* quadrilateral anteriorly in Eocene †*comptoni*, and definitely so in Miocene †*scutella*.
2. There is a single suprapygal, not a larger first suprapygal embracing a second suprapygal as in *Homopus* and *Geochelone*.
3. The gulars of each are slightly longer than broad.
4. The single inguinal scute (in Eocene †*comptoni*) is not in contact with the femoral, i.e. is already more specialized than in *Homopus signatus* or *H. boulengeri*.

By itself none of these features is conclusive or diagnostic, but neither does any of them nor any other character positively support relationship of either species to *Homopus*, while at least the presence of the specialized neural pattern in Miocene *scutella* seems to afford a definite negative. There are no grounds for assignment to any other Ethiopian endemic genus. The single suprapygal is unknown in *Geochelone*, the size of which also renders relationship improbable. On the other hand, all characters are consistent with *Testudo sensu stricto*, which is also geographically probable. While, with some hesitation, we refer these European fossils to *Testudo*, it is with full confidence that we exclude them from the ancestry of *Homopus*. Thus *Homopus*, like all other Ethiopian endemics, is at present quite unknown as a fossil.

Remarks. Despite certain emydine-like features, *Homopus* does not appear to be a primitive genus. Even the seemingly emydine features — relatively depressed shell and transversely developed gulars — are probably as completely secondary as, according to our view, are the unridged maxillae. The anterior neural pattern has departed somewhat from the primitive hexagonal towards a nearly quadrate condition, while the pygal arrangement in *Homopus* is an incipient stage of the advanced pattern. It differs from the typical condition in *Geochelone*,[1] *Gopherus* and †*Stylemys* in that the sulcus between the first vertebral and the supracaudal does not cross the middle of the small second suprapygal; instead it coincides with the suture between suprapygal and pygal.

Hewitt (1931) proposed generically separating *signatus* and *boulengeri* from *Homopus,* under the name of *Pseudomopus,* but later discovered that *Chersobius* Fitzinger (1835) was available. The differences which Hewitt points out are valid, but we do not interpret them as deserving generic recognition. To do so would imply a wider separation and less certainty as to the real affinities of the separated species than, we feel, exists. We regard the species of *Homopus* as forming a single closely-knit series within which are recognizable two species groups: one embracing *signatus* and *boulengeri,* the relatively primitive members of the series, the other comprising the more specialized members — *femoralis* and *areolatus.*

It must be admitted that the skulls of *H. boulengeri* and *areolatus* (Figs. 40, 41) differ appreciably in many ways, but we do not feel that these differences exceed the variation that might be expected within a genus or even within a subgenus. Furthermore, we have not seen skulls of *signatus* or *femoralis* and consequently do not know whether skull structure would group the species in the same way as do external characters such as number of claws and size of inguinals. No very striking skull differences between *signatus* and *boulengeri,* on the one hand, and *femoralis* and *areolatus,* on the other, have been described by Hewitt (1937a), but he mentions differences in skull proportions and other details between *femoralis* and *areolatus.* However, according to him, there does exist in the carpus a species-group difference — the distal carpals of *signatus* and *boulengeri* under-

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[1] All subgenera *except* Eocene †*Hadrianus.*

going fusions, while in *femoralis* and *areolatus* they always remain separate.

So far as known, *H. signatus* and *H. boulengeri* are allopatric, *signatus* mainly occurring in northwest Cape Province with a range closely similar to that of *Psammobates tentorius trimeni,* but apparently penetrating farther inland on the plateau (corresponding to climatic region 3a of Finch and Trewortha: 1943.[1] *H. boulengeri* has its principal range in a long inland zone of southern Cape Province, mostly at elevations between 2000 and 3000 feet (approximately climatic region 4b of Finch and Trewortha).[2]

Recent very surprising evidence (Mertens 1955a, see below p. 362 and p. 365) that both *H. signatus* and *H. boulengeri* occur in southern Southwest Africa complicates this apparently simple picture. The ranges of and interrelationships of the two forms in this area are still obscure, however; this is a problem upon which further work is urgently needed.

The nearest recorded points of approach for the two species are Clanwilliam Mtn. (for *signatus*) and Piquetberg (for *boulengeri*) which are about 50 miles apart. We have not seen either of these specimens and cannot state whether there is any approximation of characters in these neighboring populations. Elsewhere, however, the two forms are so distinct that there seems little ground for.suspecting intergradation. No other member of the genus displays the characteristic freckled pattern of *signatus,* while *boulengeri* appears to be devoid of pattern though very variable as to shade.

Less obvious, though possibly more significant, is the fact that the normal number of marginals in *H. boulengeri* is 12 pairs — unique as a modal condition among testudinids — while *signatus* has the usual 11 pairs.

H. femoralis and *areolatus* are less distinct, but are said to occur together at Halesowen in the Cradock District. This area of sympatry is very limited as compared with the total range of each species. *H. areolatus* is essentially coastal, extending from Cape Town to Alexandria in southern Cape Province, mostly at low elevations and entering higher ones (above 2000 feet) only where it is said to coexist with *femoralis* (for the most part its

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[1] *In* Dudley Stamp: 1953.

[2] Piquetberg itself is at very low elevation (*ca.* 500 ft.) but altitudes up to 3000 ft. from which *boulengeri* may have come, occur in the vicinity.

range coincides with climatic region 5 of Finch and Trewortha). On the other hand, *femoralis* is a creature of the eastern high plateau (roughly climatic region 6 of Finch and Trewortha) mostly occurring at elevations above 3000 feet.

The morphological characters separating these two species are not very striking. They differ in the degree of hooking of the beak, serration of the margin, development of the femoral tubercle, etc., characters which may be entirely valid but which it is easy to imagine being bridged by intermediates. Coloration also differs, but not so impressively as between *signatus* and *boulengeri*.

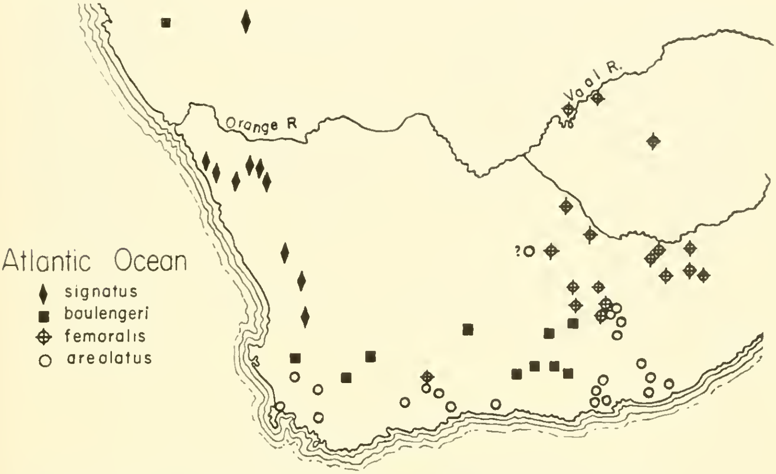

Fig. 38. Distribution of the species of *Homopus* in South Africa. (P. Washer del.)

We have not seen the specimens from Cradock district identified as *areolatus;* it is somewhat astonishing to find *areolatus* invading the highlands at well over 2000 feet, entering an unusual ecology at just the point where its closest relative occurs! We suggest that the alleged coexistence of *femoralis* and *areolatus* in the district be re-investigated. Cradock specimens (seen by one of us) in the British Museum are clearly *femoralis* but lack the serrate margin mentioned by Boulenger in his original description of the type. Thus, though Cradock is the type locality of *femoralis,* it is possible that intergradation between *femoralis* and *areolatus* may occur in the area and just to the south of it.

These same two species — *femoralis* and *areolatus* — have also been reported by FitzSimons (1946a:352-353) as occurring together at Welbedacht Farm, Oudtshoorn district. This locality is over 200 miles from any other from which *femoralis* is known. As the identification, apparently correct, is based on a single individual, the possibility of the tortoise having been transported by human agency is worth consideration.

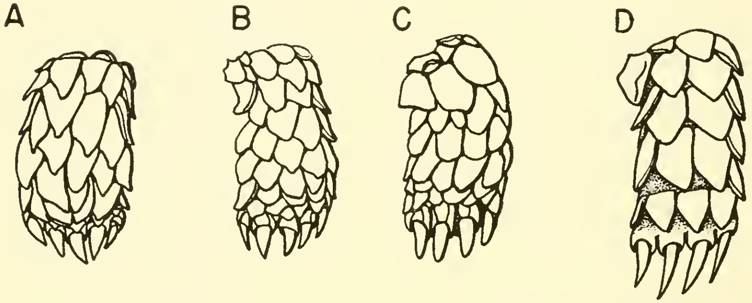

Fig. 39. Forelimb scalation in *Homopus*. *A, H. signatus* (M.C.Z. 21329); *B, H. boulengeri* (M.C.Z. 42231); *C, H. femoralis* (M.C.Z. 17523); *D, H. areolatus* (M.C.Z. 20967).

(P. Washer del.)

Key to the Species of HOMOPUS[1]

1. Forelimb with 5 claws; inguinal shield single, in contact with the femoral shield 2
   Forelimb with 4 claws; inguinal shields 2-4, small or absent, only the innermost in contact with the femoral shield 3
2. Carapace ivory white, yellow or yellowish green, heavily overlaid, spotted or radiated with black; plastron shaded or streaked with brown; posterior margin of carapace in adults usually reverted and serrated; marginals 11-12, usually 11; scutes across forelimb in 5-6 rows. Range:

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[1] For *H. bergeri* see *Psammobates t. verroxii,* not a synonym of *boulengeri* as was once suggested.
For *H. darlingi* and *H. nogueyi* see *Kinixys b. belliana* and *K. b. nogueyi* respectively.

Western Cape Province to southern Southwest Africa ....
signatus (Schoepff) (p. 359)

Carapace light olive green, pale yellow, dark yellowish, reddish or blackish brown, uniform or vertebrals edged with brown or black; plastron yellow, dirty green or dark olive, uniform or mesially brown, or each shield edged with brown; posterior margin of carapace not reverted, and not or but slightly serrated; marginals 11-13, usually 12; scutes across forelimb in 3-5 rows. Range: Karroo Plain of south-central Cape Province, South Africa. Also Southwest Africa (see discussion .... *boulengeri* Duerden (p. 362)

3. Carapace olive or brown, uniform or each shield narrowly edged with black; plastron yellow or greenish, uniform or each shield blackish brown anteriorly; posterior margin of carapace more or less reverted and serrated; beak not or but weakly hooked; usually several small scales above nostril; a pair of prefrontal shields; buttock with a very large conical tubercle; heel with conical spurlike tubercle. Range: Eastern Karroo of Cape Province north to western Orange Free State, South Africa .... *femoralis* Boulenger (p. 365)

Carapace yellowish olive, olive or greenish, each shield reddish brown in the centre, the margins edged with dark brown or black; plastron yellowish, mesially brown, rarely uniform; posterior margin of carapace sometimes reverted and not or but slightly serrated; beak strongly hooked; no small scales above nostril; prefrontal usually single or semidivided posteriorly; buttock without a large conical tubercle, at most a flat and inconspicuous one; heel without a conical spurlike tubercle. Range: Cape Province south of 32° S. latitude, South Africa
.... *areolatus* (Thunberg) (p. 367)

HOMOPUS SIGNATUS (Schoepff)

1782. *Lorica testudinis signatae* Walbaum, Chelonogr. Schildkröten, pp. 71, 120, pl. (which bears an abbreviated form of the name, viz. "Testud. Sign. var."): No locality mentioned.

1792. *Testudo signata* Schoepff, Naturg. Schildkröten, p. 141, pl. xxviii, figs. 2-3; ed. 2, 1801, Hist. Testud., p. 120, pl. xxviii, figs. 2-3). No locality.

1812. Schweigger, 319, 442.
1814. Schweigger, 50.
1831b. Gray, 5.
1831c. Gray, 13.
1836. Bell, text and col. pl.
1865. Strauch, 35.
1872b. Sowerby and Lear, pl. xx (omit text by Gray, cf. *areolatus*).

1802b. *Testudo cafra* Daudin, Hist. Nat. Rept., **2**, p. 291: Kaffraria, Cape Province, South Africa.
1812. Schweigger, 318.
1814. Schweigger, 49.
1820. *Chersine signata* Merrem, 30.
1835. *Homopus*[1] *signatus* Duméril and Bibron, 152.
1849. Smith, A., App., 1.
1870c. Gray, 13 (error).
1872c. Gray (part), 6.
1873b. Gray (part), 15.
1873g. Gray, 320, pl. xii, fig. 1.
1884a. Rochebrune, 15 (in error).
1888d. Boulenger, 136.
1889a. Boulenger, 148.
1890f. Boulenger, 521.
1898. Sclater, W. L., 96.
1905h. Boulenger, 252.
1906c. Duerden, 408.
1907a. Duerden, 10.
1907b. Duerden, 69, fig., pl. vii, figs. 5-6.
1909a. Siebenrock, 514.
1910a. Werner, 299, pl. ix, figs. 13a-b.
1911d. Sternfeld, 48.
1929. Flower, 27.
1955a. Mertens, 34.
1835. *Testudo Chersobius signata* Fitzinger, 122.
1835. *Testudo Chersobius cafra* Fitzinger, 122.
1931. *Pseudomopus signatus* Hewitt, 498.
1934a. Mertens and Müller *in* Rust, 8.
1935. Hewitt, 345.
1935. *Pseudomopus signatus peersi* Hewitt, Rec. Albany Mus., **4**, p. 345, pl. xxxvi: Near Van Rhynsdorp, Klaver District, Cape Province.
1937a. *Chersobius signatus* Hewitt, 791, fig. 3, pl. x, figs. 1-2.
1938. FitzSimons, 155.
1950. FitzSimons, 253.
1950. Rose, 338.

Further citations of "*signatus*" will be found under *Geochelone p. babcocki*, *Psammobates oculifer* and *H. areolatus*.

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[1] *Homopus*, without designated species, was first proposed by Duméril and Bibron in 1834. We have no information as to whether their 1835 volume appeared prior to Fitzinger (1835) in which *Chersobius* was proposed as a subgenus. However, as Fitzinger himself relinquished *Chersobius* in favor of *Homopus* he apparently conceded priority. The matter is discussed by Lindholm (1929:284; footnote 11).

Common Names. Speckled Tortoise (Gray :1844) ; Marked Tortoise (Gray: 1831b) ; Walbaum's Tortoise (Flower :1928).

Illustrations. Walbaum's black and white figures of carapace and plastral views are clearly recognizable, Schoepff's and Bell's colored plates less characteristic.

Description. Beak not or but weakly hooked; prefrontal small, divided longitudinally or broken up; frontal small or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with very large, subequal, juxtaposed, strongly imbricate scutes forming 5-6 longitudinal and 6-7 transverse series from elbow to outer claw; claws 5; hinder side of thigh with a very large conical tubercle; claws 4.

Carapace hardly convex, flattened dorsally, sides sloping, scarcely notched in nuchal region, anterior and posterior margins somewhat expanded, reverted, and more or less strongly serrated; dorsal shields concentrically striated with slightly impressed areolae, not swollen, separated by deep grooves, a vertebral keel in the young; nuchal moderate or small, as broad as or broader than long, sometimes divided;[1] notched anteriorly and occasionally posteriorly; vertebrals 5, occasionally 6 or 7, the first about as long as broad, the third to fifth as broad as or broader than long, the fourth and fifth rather broadly in contact, the third narrower than or equal to the third costal; costals 4, sometimes 5, usually not forming an angle with the marginals; marginals 11-12, usually 11; supracaudal undivided.

Front lobe of plastron anteriorly truncate, projecting somewhat at corners, not or but slightly produced, not or but scarcely notched; gulars paired; pectorals moderate, their anterior border straight; axillary 1, moderate; inguinal 1, small or moderate, in contact with the femoral; hind lobe broadly notched posteriorly.

Plastral formula: Abd>h>an>(g, i, p, f, variable, subequal).

Color. In both juvenile and adult the carapace is ivory white, yellow or yellowish green, heavily overlaid, spotted or radiated with black. Plastron ivory white or yellow, more or less heavily shaded with brown or radiating brown lines. Head and neck yellowish, spotted with black above.

Discussed in detail, and extremes figured by Duerden (1907b).

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[1] Divided in one Steinkopf specimen (M.C.Z. 42218).

Size. Carapace length of largest ♀ (T.M. 22108) 100 mm., breadth 71.5 mm., height 44 mm.

Habitat. Fairly numerous on granite koppies 16 miles from Bitterfontein.

Localities. Cape Province: Bitterfontein; Clanwilliam Mountain; Grootmist; Kaffraria; Kamaggas; Klipfontein; *Little Namaqualand; O'okiep; Springbok (Springbokfontein); *Steinkopf; Van Rhynsdorp. *Southwest Africa:* Keetmanshoop (Ketmanshoop; *fide* Werner :1910a :300).[1]

Range. South Africa — western Cape Province (chiefly in Little Namaqualand), northwards into southern Southwest Africa.

Erroneously reported from Great Namaqualand by Boettger (1893a) through confusion with *Psammobates oculifer,* also from Rehoboth (Fleck :1894; repeated by Sternfeld :1911b); see Mertens (1955a :34). Also in error from Abyssinia and Mauritius (Gray :1844), and Senegambia (Rochebrune :1884a).

HOMOPUS BOULENGERI Duerden

1906c. *Homopus boulengeri* Duerden, Rec. Albany Mus., 1, p. 406, pl. xi, figs. 1, 2 and 5: Willowmore; Aberdeen; and Beaufort West Districts, Cape Province, Union of South Africa.
1907a. Duerden, 10.
1907b. Duerden, 67, fig., pl. vi, fig. 1.
1909a. Siebenrock, 515.
1910. Siebenrock, 697, pls. i and iii.
1955a. Mertens, 33.
1934a. *Pseudomopus boulengeri* Mertens and Müller *in* Rust, 8.
1935. Hewitt, 345.
1946a. FitzSimons, 353.
1950. FitzSimons, 253.
1950. *Chersobius boulengeri* Rose, 338.

Synonymy. Homopus bergeri Lindholm was erroneously synonymized with *H. boulengeri* by Siebenrock (1909a :515); actually it is a synonym of *Psammobates tentorius verroxii.*

Common names. Donner-weer (local name, since it appears after thunderstorms: Hewitt).

Illustrations. Duerden (1906c) supplies rather indistinct

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[1] Mertens (1955a) confirms the presence of this species in Southwest Africa but his specimens are without exact locality.

photos of the plastral and lateral view of a cotype, also figure of head; later (1907b) a dorso-lateral photograph. Siebenrock (1910) also presents dorso-lateral and plastron photos, besides clear pictures of the head, forearm and egg.

Description. Beak not or but moderately or strongly[1] hooked, bicuspid[2] or tricuspid;[1] prefrontal small, divided longitudinally, usually preceded by a small median and two lateral shields of nearly the same size as the prefrontals; frontal broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with extremely large, subequal, juxtaposed, strongly imbricate scutes forming 3-5 longitudinal and 8 transverse series from elbow to outer claw; claws 5; hinder side of thigh with, or rarely without, a large conical tubercle; heel of ♂ surrounded by smaller tubercles but without definite spurlike tubercle; claws 4, rarely 5; tail without terminal clawlike tubercle.

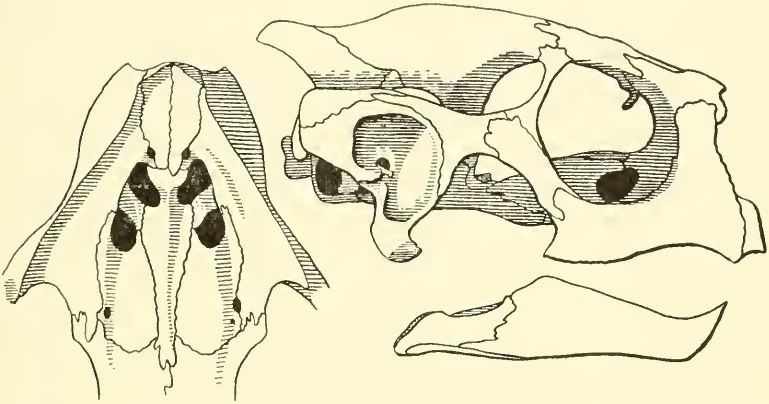

Fig. 40. Skull of *Homopus boulengeri* (A.M.N.H. 7109). Condylobasal length 22 mm.

(S. McDowell del.)

Carapace scarcely convex,* flattened dorsally, sides sloping, scarcely notched in nuchal region, anterior and posterior margins expanded, not or but slightly reverted, not or but slightly ser-

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[1] Strongly *fide* Duerden.

[2] In S.M. 49822 from Plateau Farm, near Aus, Southwest Africa.

rated; dorsal shields concentrically striated, the areolae not impressed,[1] not swollen, separated by deep grooves; nuchal small, as long as or slightly longer than broad; vertebrals 5, broader or much broader than long, as broad as or narrower than the costals, the fourth and fifth rather broadly in contact; costals 4, not forming an angle with the marginals; marginals 11-13, usually 12; supracaudal undivided.

Front lobe of plastron anteriorly truncate, projecting somewhat at corners, not or but slightly produced, not or but slightly notched; gulars paired; pectorals moderate, their anterior border somewhat sloping, widening slightly towards the axillary notch; axillary 1, moderate; inguinal 1, moderate or large, in contact with the femoral; hind lobe broadly notched posteriorly.[2]

Plastral formula: Abd>h>(g, p, f, and an, variable).

Color. Carapace dark reddish or yellowish brown, or light olive green, uniform (in young) or the vertebral shields edged with bright brown or black. Plastron yellow, dirty green or dark olive, uniform or mesially brown, or each shield edged with brown. Jaws brown, head and limbs light olive green. In life the naked parts of skin are said to be bright yellow with minute orange scales.

Size. Carapace length of Duerden's largest cotype 105 mm. Carapace length of largest ♂ (T.M. 19177), 108 mm., breadth 74.5 mm., height 48.5 mm. Carapace length of largest ♀ (T.M. 19838), 110 mm., breadth 80 mm., height 49.5 mm.

Sexual dimorphism. Plastron of ♂♂ deeply concave posteriorly, not in ♀♀; hind lobe of plastron deeply notched in ♂♂, more open in ♀♀ (Duerden).

The relatively small size of the posterior aperture of the ♀ shell opening — 6 mm. long by 15 mm. broad in one specimen — in relation to the large size of the egg, is referred to by Siebenrock (1910) who suggests that during deposition of the egg significant widening of the aperture must take place. This could be achieved by a spontaneous mobility of the posterior lobe of the plastron, which, he says, has been demonstrated to occur in *Pyxis arachnoides* (cf. Siebenrock:1906b) and in *Testudo s. str.*

Breeding. The egg referred to and figured by Siebenrock (*vide*

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[1] Moderately or deeply according to Duerden (1906c:406).

[2] In S.M. 49822 from Plateau Farm, near Aus, Southwest Africa.

supra) measured 22 x 39 mm. The poles were strikingly pointed and it was hard-shelled when removed from the oviduct. As there were no other mature eggs, Siebenrock suggests that only one is produced at a laying.

Localities. Cape Province: Aberdeen district; Beaufort West district; *Cape Province; Hoek-onder-Berg Farm between Montague and Touws River; Matjesfontein; Miller Station, Klipplaats between Aberdeen and Willowmore; Pearston district; Piquetberg; Willowmore; Zwart Ruggens, Aberdeen district. *Southwest Africa:* near Aus.[1]

Range. South Africa — restricted to the Karroo Plain area of south central Cape Province; and apparently Southwest Africa near Aus.[1]

Though its range is not so restricted as Duerden (1906c) assumed, he is apparently correct in saying that no other *Homopus* occurs in its habitat.

HOMOPUS FEMORALIS Boulenger

1888g.	*Homopus femoralis* Boulenger, Proc. Zool. Soc. London, p. 251, pl. xiv: Cradock, Cape Province, Union of South Africa.
1889a.	Boulenger, 147.
1890f.	Boulenger, 521.
1890.	Strauch, 58.
1898.	Johnston, 361 (in error).
1898.	Sclater, W. L., 96.
1906c.	Duerden, 407, pl. xi, fig. 6.
1907a.	Duerden, 10.
1907b.	Duerden, 67, fig., pl. vi, fig. 2, pl. viii, fig. 9.
1909a.	Siebenrock, 514.
1929.	Flower, 27.
1931.	Hewitt, 496, fig. 4a.
1934a.	Mertens and Müller *in* Rust, 8.
1937a.	Hewitt, 788, 791, 795, pl. x, fig. 3.
1937e.	Hewitt, 10, pl. ivA.
1946a.	FitzSimons, 353.
1950.	Rose, 336.

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[1] Mertens (1955a :33) received a living pair (♂, ♀) [one of which we have examined] from Plateau Farm near Aus, Southwest Africa (H. Erni donor). This astonishing record is so far removed from the generally accepted range that we specially asked Dr. Mertens about it. He replied that, though he did not collect them himself, he has every confidence in the collector and, furthermore, that during his trip he heard reports of the occurrence of a strongly-flattened, rock-dwelling tortoise in the southern portion of Southwest Africa.

Common names. Karroo Tortoise or Greater Padloper (Hewitt); Boulenger's Tortoise (Flower); *Padlopertjie* (Afrikaans, A. C. Hoffman *in litt.*).

Illustrations. Boulenger's (1888g) figure of the type is in color.

Description. Beak not or but weakly hooked, tricuspid, edge of jaws serrate; a few small scales above the tubular nostrils; prefrontal large, divided longitudinally; frontal large or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with a few extremely large, subequal, juxtaposed, strongly imbricate, pointed scutes forming 3-4 longitudinal and 7-8 transverse series from elbow to outer claw; claws 4; hinder side of thigh with a very large conical tubercle; heel with large, conical, spurlike tubercles; claws 4; tail without terminal clawlike tubercle.

Carapace somewhat convex, flattened dorsally, sides sloping, not or but scarcely notched in nuchal region, anterior and posterior margins somewhat expanded, more or less reverted, and more or less strongly serrated; dorsal shields concentrically striated with slightly impressed areolae divided by a weak keel, not swollen, convex; nuchal elongate, subtriangular or slightly longer than broad; vertebrals 5, the first as long as or longer than broad, the second to fifth broader than long, the fourth and fifth somewhat narrowly in contact, vertebrals two and three narrower than the costals; costals 4, not forming an angle with the marginals; marginals 11; supracaudal undivided.

Front lobe of plastron anteriorly truncate, not produced, scarcely notched; gulars paired; pectorals very narrow, their anterior border widening abruptly towards the axillary notch; axillary 1; inguinals 2 or 3, the outermost triangular, the others transverse, the innermost in contact with the femoral; hind lobe broadly notched posteriorly.

Plastral formula: $Abd > h > an > or < f > or = g > or = p$. Pectoral is typically the shortest scute.

Color. Carapace olive or brown, pale or dark, with or without a dull red or orange tinge, each shield narrowly edged with black (in young) or uniform (in adult). Plastron yellowish or greenish, each shield blackish brown anteriorly (in young, but sometimes persists), or uniform (adult). The shielded or tuberculate soft parts yellow or pale brownish, the naked areas tinged with salmon or orange. See also discussion in Duerden (1907b: 67).

Size. Carapace length of largest ♂, 133 mm., breadth 102 mm. Carapace length of largest ♀, 157 mm., breadth 121 mm. (both Hewitt:1937c, but no localities mentioned).

Sexual dimorphism. The plastron is flat in both sexes, but the ♂ supracaudal is usually larger and directed downwards.

Breeding. The eggs are oval to nearly spherical, ranging from 25 x 29 mm. to 25 x 33 mm., and quite soft when deposited (Hewitt:1937c:11).

Diet. Bulbine caulescens is a favorite food (P. M. Niven in Hewitt:1937c).

Enemies. See under *areolatus.*

Habitat. Grassveld up to 5,500 feet.

Localities. Cape Province: Aliwal North; Barkly West; Colesberg; Cradock; Dordrecht; Halesowen; Indwe; Lady Grey; Middleburg; New Bethesda; *Philipstown; Sneeuwberg; Stormberg; Warrenton; Welbedacht Farm, Oudtshoorn district;[1] Wodehouse=Dordrecht. *Orange Free State:* Bloemfontein[2] (specimen in Senckenberg Museum seen by E. E. W.).

Range. South Africa — eastern Karroo of Cape Province north to western Orange Free State.

Erroneously reported from British Central Africa by Johnston (1898).

HOMOPUS AREOLATUS (Thunberg)

1787. *Testudo areolata* Thunberg, Kongl. Vetensk, Akad. Handl., **8**, p. 181, fig.: "India" (in error).
1792. Schneider, 267.
1792. Schoepff, 121, pl. xxiii.
1795. Schoepff, 104, pl. xxiii.
1802b. Daudin, 287.
1812. Schweigger, 320, 443 (omit localities).
1814. Schweigger, 51.
1831b. Gray, 5.
1831c. Gray, 13.

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[1] See p. 358 for comments regarding this record.

[2] Dr. A. C. Hoffman, Director of the National Museum in Bloemfontein, sees no reason to question this record as *femoralis* is "very plentiful" and "occurs in practically every district of the Free State." (*in litt.*)

1835. Temminck and Schlegel, 73.
1836. Bell, text and col. pl. —.
1862a. Strauch, 92.
1865. Strauch, 35.
1872b. Gray, 5, *in* Sowerby and Lear, pl. xxi.
1880c. Vaillant, 34, 88.
1887b. Boettger, 140.
1890. Müller, F., 705.
1890. Strauch (part), 58.
1788. *La Vermillon* Lacépède, Hist. nat. Quadrup. ovip. Serpents, 1, p. 166, and *Testudo miniata* in Synopsis Methodica, a table at end of same volume in which binomials are employed: Cape of Good Hope.
1802b. *Testudo pusilla* Daudin (not of Linnaeus), 299.
1804. *Testudo (Africana)* Hermann, Observ. Zool. Animal. Spec., p. 218: No locality.
1820. *Chersine areolata* Merrem, 30.
1829. Gravenhorst, 18.
1820. *Chersine tetradactyla* Merrem, Vers. Syst. Amphib., p. 32: ''India orientali'' (in error).
1831c. *Testudo areolata* var. *pallida* Gray, Synopsis Reptilium, p. 13: South Africa.
1855. Gray, 12.
1835. *Homopus areolatus* Duméril and Bibron, 146.
1844. Gray, 10.
1845b. Rüppell, 297.
1849. Smith, A., App., 1.
1855. Gray, 11.
1857. Jan, 35 (as *Homoeopus*).
1860. Fitzinger, 411.
1867a. Steindachner, 4.
1873b. Gray, 15.
1873c. Gray, 726, pl. lx, fig. 5.
1884a. Rochebrune, 16 (in error).
1885. Smets, 10 (locality erroneous).
1889a. Boulenger, 147.
1890f. Boulenger, 521.
1893a. Boettger, 8.
1895. Oudemans, 321.
1898. Jeude, 5.
1898. Johnston, 361 (in error).
1898. Sclater, W. L., 96.
1903e. Boulenger, 217.
1904b. Tornier, 209, 303, fig. 11.

1906c. Duerden, 407, pl. xi, fig. 4.
1907a. Duerden, 9.
1907b. Duerden, 68, fig. —, pl. vi, fig. 3.
1907j. Boulenger, 482.
1909a. Siebenrock, 513.
1910. Siebenrock, 695.
1925b. Flower, 924.
1928. Cott, 952.
1929. Flower, 26.
1929. Rose, 188, 231, fig. 124.
1931. Hewitt, 496, figs. 4b-4c.
1934a. Mertens and Müller *in* Rust, 8.
1937a. Hewitt, 790, fig. 4, pl. x, fig. 4.
1937e. Hewitt, 9, pl. ii, fig. 4; pl. iv, fig. 2.
1946a. FitzSimons, 352.
1950. Rose, 336, fig. 202.
1950. Williams, 551.
1844. *Homopus signatus* Gray (not of Schoepff), 10.
1855. Gray, 11.
1872c. Gray (part), 6.
1873b. Gray (part), 15.
1872b. *Testudo signatus* Gray (not of Schoepff), 5 (text: *not* pl.).

A further reference to "*Testudo areolata*" will be found under *Kinixys b. belliana.*

Synonymy. Testudo miniata, which Lacépède called "La Vermillon" in allusion to the reddish tinge of its protuberant snout, was first referred to the synonymy of *areolatus* by Bell (1836). *Testudo africana* Hermann is placed in the synonymy of *areolatus* by us on account of its depressed shell, short gulars, and coloration. *Testudo fasciata* Daudin (1802b), heretofore generally regarded as a synonym of *areolatus,* we reject because the type was stated to have had five claws on either forefoot. It is also said to have come from Ceylon.

Common names. Parrot-beaked Tortoise (Hewitt :1937e) would appear preferable to either Areolated Tortoise (Gray :1831b), Thunberg's Tortoise (Flower :1929), or Grooved Tortoise (Rose : 1929), the latter having long been used for *Geochelone sulcata. Padloper* in Afrikaans, on account of their tendency to keep to paths or roads (C. J. Latrobe :1818).

Illustrations. Schoepff's (1792) plates supply dorsal, plastral and lateral views in color. Bell's (1836), reproduced in Sowerby and Lear (1872), show the entire animal, including its plastral aspect, in color.

Description. Beak strongly hooked, tricuspid, edge of jaws anteriorly weakly serrate; no small scales above tubular nostrils; prefrontal large, single or posteriorly semi- or wholly divided longitudinally; frontal moderate or broken up; remaining upper head shields small, irregular; forelimb anteriorly covered with extremely large, subequal, juxtaposed, strongly imbricate, pointed scutes forming 3-4 longitudinal and 6-8 transverse series from elbow to outer claw; claws 4; hinder side of thigh with or without (irrespective of sex) a slightly enlarged, low and inconspicuous tubercle; heel without definite spurlike tubercle; claws 4; tail without terminal clawlike tubercle.

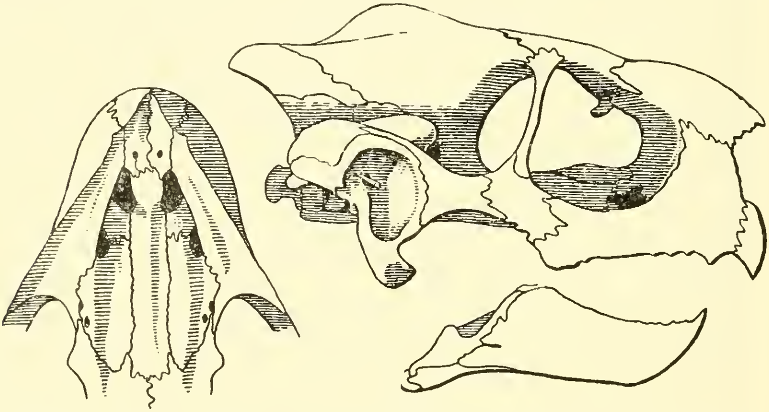

Fig. 41. Skull of *Homopus areolatus* (A.M.N.H. 17792). Condylobasal length 21 mm.

(S. McDowell del.)

Carapace moderately convex, more or less flattened dorsally, sides sloping, scarcely notched in nuchal region, anterior margin not or but slightly expanded, posterior margin not expanded, sometimes reverted, and not or but scarcely serrated; dorsal shields concentrically striated, with impressed areolae sometimes showing a longitudinal keel, more or less swollen, separated by grooves; nuchal variable, elongate, subtriangular or quadrate;

vertebrals 5, rarely 4,[1] 6[2] or 8,[3] scarcely convex, the first and fourth longer than broad or (rarely) as long as broad, the second, third and fifth broader than long, the fourth and fifth only narrowly in contact, the third as broad as, though usually narrower than, the third costal; costals 4, rarely 5,[4] not forming an angle with the marginals; marginals 11, rarely 10, 12[5] or 13; supracaudal undivided, rarely divided.[6]

Front lobe of plastron anteriorly truncate, not produced, not or but scarcely notched; gulars paired, small but broad; pectorals somewhat narrowed, their anterior border steeply sloping and widening abruptly towards the axillary notch; axillaries usually 1 or 2, sometimes 3 or 4, even 5,[7] the inner small, the outer moderate; inguinals 3 or 4, rarely absent,[8] or only the outermost present, outermost triangular, the rest transverse, the innermost in contact with the femoral; hind lobe broadly notched posteriorly.

Plastral formula: Usually Abd>h>an>(g, p, f subequal). F>an in a Grahamstown specimen (M.C.Z. 17524). The femoral suture is always smaller than that of the anal, according to Hewitt (1931:498).

Color. Carapace yellowish olive, olive or greenish, each shield reddish brown in the centre, the margins edged with dark brown or black. Plastron yellowish, mesially brownish, rarely uniform.

According to Siebenrock (1910:697) the ♂♂ are much more lightly colored than the ♀♀, especially the plastrons which in ♂♂ are mostly uniform, while those of the ♀♀ are almost always more or less darkly pigmented; the young of the two sexes are indistinguishable. Duerden (1907b:68) remarks that tortoises from around Cape Town are usually darker than those from eastern Cape Province. For detailed descriptions of the color of live specimens see Bell (1836).

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[1] Four in a specimen mentioned by Oudemans (1895).

[2] Six in a tortoise figured by Schoepff (1792: pl. xxiii), also in one mentioned by Bell (1836).

[3] Eight in a specimen figured by Gottwald (pl. K, fig. 14) *fide* Strauch (1862a).

[4] Five in one mentioned by Bell (1836), and in two of Oudemans (1895).

[5] Twelve in a specimen (U.S.N.M. 131846) without data.

[6] Divided in one of Oudemans' (1895) series from Knysna and Port Elizabeth.

[7] Five occasionally according to Hewitt (1931:499).

[8] Absent in a Knysna tortoise (M.C.Z. 20967) only, but Siebenrock (1910) alleges that they are frequently absent.

Size. Carapace length of largest ♂, presumably from Knysna, 96 mm. (Oudemans:1895); another ♂ (M.C.Z. 21457) from Table Mountain, has a carapace length of 95 mm., breadth 67 mm., height 39.5 mm.

Carapace length of largest ♀, a Grahamstown specimen (Hewitt:1937e), 114 mm., breadth 86 mm.; another Grahamstown ♀ (M.C.Z. 22474), has a carapace length of 107 mm., breadth 82 mm., and height 53 mm.

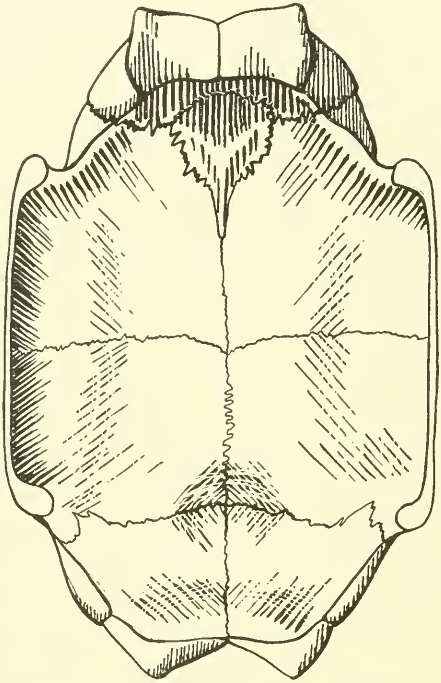

Fig. 42. Internal view of plastron of *Homopus areolatus* (B.M. 64.11.20. 15), x 1.

(P. Washer del.)

Sexual dimorphism. Judging by the material available to us, Siebenrock's (1910:697) conclusion regarding sexual differences in the plastral coloring of adults (*vide supra*) is not quite accurate. We are not in a position to verify other alleged distinctions that he cites. Both Boulenger (1890f) and Oudemans (1895) present charts of secondary sexual characters, the former stating that ♂♂ have larger heads, longer and more pointed snouts, longer mandibular symphyses, and a larger elbow scute. Oudemans failed to note any appreciable sexual difference in size of elbow scute, but concurs as to the validity of the cranial characters cited by Boulenger if restricted to specimens with a carapace length of over 90 mm. Oudemans failed to find the horny terminal tubercle which Boulenger observed on the tail of one of his specimens, but notes that the tails of ♂♂ are somewhat longer. Oudemans comments on the absence of any concavity in the plastrons of his ♂♂; and in our material at most only a very slight central depression is discernible, the plastron being practically flat in both sexes.

Breeding. Nest holes are about 3 inches deep. The eggs, from 2 to 5, possibly averaging 3 at a laying, are elongate ovals ranging from 21 x 27 to 23 x 33 mm. (Hewitt:1937a; pl. xxvii: fig. 8). Incubation takes 7 to 8 months, *fide* Rose (1950:337).

Longevity. Three years, 1 months, 10 days in the London Zoo, but usually die within one year of arrival (Flower:1925b).

Diet. The only information is indirect: it is said not to be destructive in gardens or on farms (Hewitt:1937e).

Parasites. A tick is present on one of the M.C.Z. series.

Enemies. Jackals prey on the young whose shells are easily cracked. One "*Homopus*," together with 23 other reptiles, was recovered from the stomach of a ♀ Secretary Bird (*Sagittarius serpentarius*) shot on the Cape Flats (Stark and Sclatan, Birds of South Africa, **3**:405). Other birds of prey, according to Kolbe as quoted by Lacépède and others, carry them up and drop them on the rocks to break their shells. Crows, on the other hand, turn them over and with their strong beaks attack the softer parts, pecking out the edible portions (Latrobe:1818).

Defense. The head is incompletely protected when it and the forelimbs are withdrawn inside the shell (Hewitt:1937e:10).

Temperament. Readily tamed according to Bell (1836) who found they would take food from one hand while being held in the other. A fairly bold and active tortoise that struggles violently with outstretched head and limbs when picked up (Hewitt:1937e:10).

Habitat. The only *Homopus* species occurring on the Cape Peninsula (Rose:1929). A shade-loving tortoise inhabiting the sour-grass areas from sea-level to the summit of the Zuurberg (Hewitt:1937e:9).

Localities. Cape Province: Albany district; Alexandria district; Bathurst district; Cape Peninsula; Deelfontein;[1] De Wet; *Dunghye Park, Caledon; Garcia; Glen Epstine (as Erskine in Hewitt:1937e), Cradock district; *Grahamstown (including Carlisle Bridge; Mountain Drive and Gunfire Hill); Halesowen; *Kenkelbosch (seen at U.S.N.M.); Knysna; Malmsbury; Mortimer; Oudtshoorn; Pigott Bridge; Port Elizabeth; Simons Bay Mountains; *Table Mountain; *Tootabi near Alicedale; Uitenhage; Welbedacht Farm, Oudtshoorn district; Zuurberg.

Range. Cape Province south of 32° S. lat. (except for Deelfontein record[1]), Union of South Africa.

Erroneously reported from India (Thunberg); Matabeleland and Zambezi region (Smets); British Central Africa (Johnston); Victoria Nyanza (Strauch and Siebenrock); Senegambia (Rochebrune).

Genus KINIXYS Bell

1827. *Kinixys* Bell, Trans. Linn. Soc. London, **15**, p. 398. Type: *castanea* Bell = *Testudo erosa* Schweigger (by original designation).

1835. *Cinothorax* Fitzinger, Ann. Wiener Mus.,**1**, pp. 108, 111, 121. Type: *Kinixys belliana* Gray (designation by Fitzinger: 1843).

1843. *Cinixys* Fitzinger, Syst. Rept., p. 29 (emendation of *Kinixys* Bell).

1873b. *Kinothorax* Gray, Hand-List Shield Rept. Brit. Mus., p. 16 (emendation of *Cinothorax* Fitzinger).

Definition. Skull with triturating surfaces of maxilla and premaxilla without ridges; maxillary not entering roof of palate; anterior palatine foramina large, conspicuous; prootic well exposed dorsally; quadrate enclosing stapes; surangular subequal in height to prearticular; neck with third centrum biconvex.

Carapace of adult movable posteriorly, usually hinged between the fourth and fifth pleurals (costal bones) and seventh and eighth peripherals (marginal bones); outer side of third costal scute shorter than that of fourth; anterior neurals hexa-

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[1] The Deelfontein record requires investigation and verification.

gonal; submarginal scutes present; suprapygals 1 or 2, if 2 typically separated by a straight transverse suture.

Plastron not hinged; gular region greatly thickened and produced; gular shields paired, longer than broad.

Distinguishing marks. The distinctive carapacial hinge sufficiently differentiates adult members of this genus. Young *Kinixys,* prior to development of the hinge, may be recognized by the relationship between third and fourth costal shields as defined above (see Fig. 13), and also by the presence of the submarginal scute, though this may be difficult to see.

Range. Africa from 17° North, south to Bechuanaland and Natal. Madagascar (? introduced).

Fossil record. None.

Remarks. In view of the many remarkable characters distinguishing *Kinixys* — some from all, others from the majority of tortoises — it is not surprising that the genus was separated at an early date and its status never since questioned. However, well differentiated though it is, *Kinixys* is not an isolated genus. Below, we cite special resemblances to single genera among the Ethiopian endemics, while in a previous section we have argued for the phyletic unity of an Ethiopian group that includes *Kinixys.*

Adult members of the genus *Kinixys* are recognizable by the unique hinging of the carapace, but as hinging is ontogenetically a late phenomenon, and one that may sometimes fail to develop both in *Kinixys* and *Testudo* (*vide infra*), it is not fully satisfactory for generic definition. Startling though the hinge of *Kinixys* may be, hinging is a recurrent phenomenon among testudinates, an adaptation to which their solid armor is especially suited. It has occurred once in the Pelomedusidae, once in the Kinosterninae, four times independently in the Emydinae, three times independently in the Testudininae. In many of these instances species with or without hinging are obviously closely related.

The three examples of hinging in the Testudininae all differ, not only from one another, but also from the type of hinging that occurs repeatedly among emydines. In emydines the plastron is hinged between the hyo- and hypoplastron at the junction of pectoral and abdominal scutes. In *Kinixys,* as already mentioned, the hinge is carapacial. In *Pyxis* it occurs far forward on the anterior lobe of the plastron and, as shown by Siebenrock (1906b), tends to involve a break across the entoplastron. In *Testudo,* when present, the hinge is at the base of the posterior lobe where the abdominal scutes contact the femoral, and so involves the hypo- and xiphiplastron. In *Testudo sensu stricto* it may be present in one sex of a species and absent in the other, so that the presence or absence of a hinge cannot be considered as automatically implying generic rank. It is not on account of its hinge that we have retained *Kinixys* as a genus, but because of the complex of characters that indicate a long period of separation and divergence from all related lines.

The hinging of the dorsal shell in *Kinixys* involves the backbone also. The morphology of this peculiar condition has been discussed in some detail by Siebenrock (1907). It is an entirely secondary condition that gradually develops with age. The interdigitating sutures originally present between the seventh and eighth marginals (besides the numerically corresponding peripherals), together with the second and third costal shields (also fourth and fifth pleurals), disappear with maturity as fibrous cartilage intervenes between the now smooth edges of these elements. The hinge first forms peripherally and spreads inward; as a final step the transverse suture between the fourth and fifth neurals is loosened.[1]

There is some evidence that this ontogenetic process occasionally fails to continue to completion. At least, various authors (Müller; Hewitt, etc.) have described apparently mature specimens of *K. b. belliana* in which the dorsal hinge was so poorly developed as to be immovable, or almost so.

Though the hinge is fully formed only in mature members of the genus and is totally absent in hatchlings, a preparatory modification in hatchlings is shown by the shapes of the third and fourth costals: the third being narrowed distally and the fourth correspondingly widened. Furthermore, the fourth costal, contrary to the general rule among turtles, may be substantially greater in area than the third.

This dorsal scute modification appears to be the most constant

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[1] According to Siebenrock (1907) the fifth neural is somewhat displaced, moving forward above the fourth so as to permit of increased mobility. We have been unable to confirm this.

external character by which juvenile *Kinixys* may be recognized. The presence of the so-called "submarginals" of Siebenrock — one or more supernumerary scutes internal to the ventral surface of the second marginal — is also diagnostic of the genus, but these vary much in size and are not always easily visible.

Osteologically, there are various features unconnected with the hinge that make *Kinixys* a specially distinctive genus — though some of these features are shared with one or another related genus. One minor point is the position of the costomarginal sulcus with reference to the pleuroperipheral suture. Whereas in tortoises generally there is complete, or almost complete, congruence between these two landmarks, in *Kinixys* the costomarginal sulcus is, at least on the posterior half of the shell, well down on the peripherals. In this respect *Pyxis* and *Acinixys* are somewhat like *Kinixys,* and the feature is probably an emydine inheritance, as is also the case with the position of the vertebral-supracaudal sulcus on the pygal in *Kinixys* (well down on the pygal in *K. erosa* and *homeana,* higher in *belliana*).

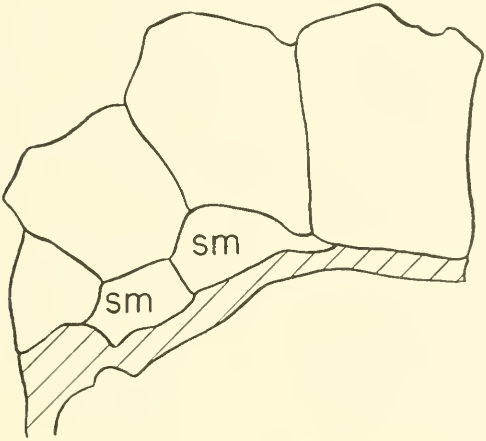

Fig. 43. *Kinixys erosa* (Yale Mus. 5403) (x ⅔). Internal view of left anterior edge of carapace; *sm* = submarginal scale.

(P. Washer del.)

Another peculiarity, shared with *Chersina* however, is the anteroposterior lengthening of the anterior peripherals, the anteroposterior length of the second peripheral being greater than the anteroposterior length of the first pleural. Also rather unusual in a tortoise is the nearly complete absence of differentiation among the pleurals by alternate widening and narrowing.

In *Kinixys* the gular region of the plastron is strikingly modified by hypertrophy of the epiplastral lip. A tendency to develop a thickened epiplastral lip, recessed behind, exists in all tortoises. It is weakest in *Homopus, Malacochersus* and some *Testudo,* such a thickened lip apparently being one of the many testudinate characters displaying parallel development. Its significance is obscure, especially so in the present case in which, as Boulenger (1889a:142) has noticed, the length of the thickened portion may be appreciably more than a fourth of the total length of the plastron. In this respect no other tortoises approach *Kinixys* except *Chersina,* in which the very similar hypertrophy of the epiplastral lip may even exceed the development shown in some *Kinixys* (cf. Figs. 37B and 49).

Among continental African genera the skull of *Kinixys* is distinctive in its pointed snout, as seen from above. This character is discernible in hatchlings and led to further examination and re-identification of the desiccated juvenile from the Rondo Plateau mistakenly assigned to *Malacochersus tornieri* by Loveridge (1942e:248). However a similarly pointed snout is present in *Pyxis* of Madagascar.

According to Hewitt (1937a:791) another characteristic of *Kinixys* is the lack of fusion of the distal carpals. Such fusion is usual in *Geochelone, Testudo* and *Psammobates.* It occurs also in *Homopus signatus* and *boulengeri* but is absent in *H. femoralis* and *areolatus* (*fide* Hewitt:1937a). It is also lacking in two British Museum specimens of *Chersina* examined by one of us (E.E.W.). However, according to Siebenrock (1906b) this is a purely individual character without taxonomic significance. The matter requires re-examining with more adequate material.

Species groups. It has been suggested (for example by Schmidt: 1919) that *belliana* should be removed from *Kinixys,* the type of which is *erosa,* and placed in the genus *Cinothorax* Fitzinger. However, *homeana* so clearly bridges the gap between *erosa* and *belliana* that we can see no advantage in the recognition of *Cinothorax* either as genus or subgenus. This natural grouping is sufficiently indicated in less formal fashion by describing (as much on the ground of ecology as structure) two species groups within the genus, one with the two rain-forest species, *K. erosa* and *K. homeana,* the other with only the savanna form *K. belliana.*

Kinixys belliana, the best known species, occurs over a vast area of African savanna (climatic region 2 of Finch and Trewartha) and borders in a great arc on three sides the range of the other two members of the genus. Both in habitus and coloration it displays great variability. At times these differences are individual, at others they appear to characterize populations, and consequently have resulted in the proposal of numerous species and subspecies. All but one of these we reject as not being sufficiently distinct, either morphologically or geographically. The name *spekii* Gray is an example. One of us (A.L.) has used it on several occasions, but when the species *belliana* was considered as a whole we did not find it possible to retain *spekii,* except in a very

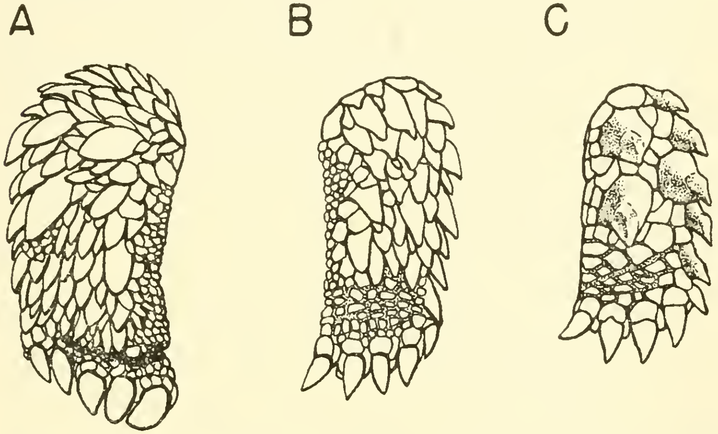

Fig. 44. Forelimb scalation in *Kinixys,* (all x 1). *A, K. b. belliana* (M.C.Z. 41945); *B, K. homeana* (M.C.Z. 38371); *C, K. erosa* (M.C.Z. 22486).

(P. Washer del.)

subjective and geographically meaningless way. A subspecies based on this name would have neither range nor boundaries; it would more easily be applicable to individuals than to populations; it would in fact be a morphological type rather than a geographically differentiated segment of the species. On the available evidence we level this same criticism at the majority of the proposed subspecies of *belliana.*

We are conscious that we may have undervalued some segment (perhaps, for example, *K. spekii,* which was originally described as a full species) of what appears to us, on the available evidence, as one highly variable species. There are obviously characters worthy of study which require better analysis than we have been able to give them. An example is the condition of the postorbital bone. In the material studied by us the postorbital bone may be *absent,* or a *loose* thin bar of bone, or a thin bar of bone *solidly sutured* to the frontal above and the jugal below. However, we have not had material to check in adequate fashion the correla-

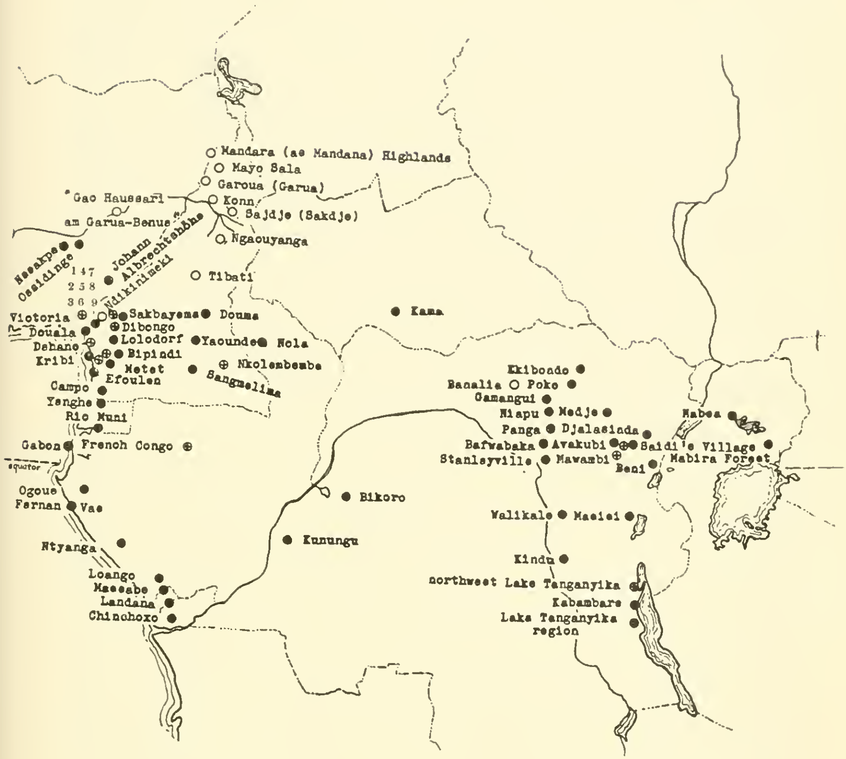

Fig. 45. Locality records of *Kinixys* (exclusive of *K. b. belliana* whose range extends from the Cameroon east and south). Other *erosa* localities encircle Cameroon Mountain, (4), viz. Bonge (1) and Buea (5); with *homeana* recorded from Bibundi (2); Isongo (3); Mpanga (6); Mujuka (7); Mosake (8) and Likomba (9).

(P. Washer del.)

tion of these three conditions with other characters and with geography. We have therefore been conservative in our taxonomic approach. We agree with Hewitt (1931:466) who, while thinking "that a number of allied species and subspecies can be recognized" among what is here called *belliana,* admitted that "the data for sharply defining them are *not yet available.*" (Italics ours.)

The only subspecies of *belliana* that we have retained is *nogueyi* Lataste. It is distinguished by having lost a claw on each forefoot, a condition correlated with a definable range within which it is constant so far as our evidence goes. Though the character of a 4-clawed forefoot is pure in the populations we call *nogueyi,* it crops up occasionally within the range of what we call *b. belliana.* This fact, first noticed in a juvenile from Beira by Boulenger, induced both him and Siebenrock to synonymize *nogueyi.* However, the overwhelming predominance of 5-clawed forefeet throughout the range of *b. belliana* affords ample justification for the retention of *nogueyi* as a western race.

The other ecological species group consists of *K. homeana* and *erosa* which are restricted to the rain forests of West and Central Africa (climatic region 1 of Finch and Trewortha). Morphologically, all three species are readily identifiable, as may be seen by reference to Table 7 on p. 383. As indicated there, *K. homeana* and *erosa,* which occur together in at least a macrogeographic sense, agree in coloration, serration of carapace margin, and in having an elongate and coiled trachea. They differ in a combination of other characters, sufficiently distinct and closely correlated to preclude the possibility that we are dealing with a polymorphic species. In spite of a certain amount of individual variation in single characters, the total differences do hold up in series. *K. homeana* is the rarer of the two, but neither species is well understood biologically and no information is available regarding differences in dietetic or other ecology.

TABLE 7

Characters of the Species of KINIXYS

Kinixys belliana	*Kinixys homeana*	*Kinixys erosa*
Carapace pattern usually radiate, variable	Carapace pattern indistinguishable as between these two species[1]	
Carapace margin neither spinose in young nor serrate in adults	Carapace margin spinose in young and sharply serrate in adults	
Rear end of carapace steeply sloping from *middle* of 5th vertebral	Rear end of carapace overhanging or vertical from *anterior* end of 5th vertebral	Rear end of carapace sloping; if vertical then from *middle* of 5th vertebral
Nuchal scute present, rarely absent	Nuchal scute present, rarely absent	Nuchal scute absent, rarely present
5-9 scutes on forelimb from elbow to outer claw	5-8 scutes on forelimb from elbow to outer claw	3-5 scutes on forelimb from elbow to outer claw
Postorbital bar of skull very thin, elongate, loose or sometimes absent	Postorbital bar of skull moderately thin (thinner and longer than in *erosa*)	Postorbital bar of skull rather short and stout
Habitat in savannas	Habitat in virgin forests	

Key to the Species and Subspecies of KINIXYS

1. Posterior margin of carapace not or but slightly reverted and serrated, never spinose in young; nuchal shield normally present.......... 2
   Posterior margin of carapace more or less strongly reverted and strongly serrated, spinose in young; nuchal shield present or absent........ 3
2. Forelimb with 5 claws (though occasional 4-clawed individuals occur throughout much of the range). Range: Madagascar. Eritrea southwest to Natal, northwest through Bechuanaland and Angola to French Cameroon ....*b. belliana Gray* (p. 384)
   Forelimb with 4 claws (all known specimens have 4). Range: Nigeria west to Senegal ....*b. nogueyi* Lataste (p. 396)
3. Nuchal present, rarely absent; posterior portion of carapace from an-

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[1] For full description, see p. 408 and Pl. 14 *B, C*.

terior part of the fifth vertebral descending abruptly, either vertically or overhanging. Range: Belgian Congo northwest to French Guinea ....*homeana* Bell (p. 400)

Nuchal absent, rarely present; posterior portion of carapace descending gradually, if vertical, then from middle of the fifth vertebral. Range: Uganda and Belgian Congo northwest to Gambia.................... *erosa* Schweigger (p. 404)

KINIXYS BELLIANA BELLIANA Gray

1831c. *Kinixys Belliana* Gray, Synopsis Reptilium, p. 69: No locality ("W. Africa?" was added later by Boulenger, but appears doubtful).
1831b. Gray, 6 (as "*Test.* (*Kinyxis*) *Belliana*").
1835. Duméril and Bibron, 168.
1855. Gray, 13, pl. ii.
1863f. Gray, 196.
1864a. Gray, 169 (reprint of 1863f).
1865. Strauch, 40.
1870e. Gray, 13.
1872c. Gray, 6.
1873b. Gray (part), 16.
1910. Meek, 414.
1919. Schmidt, 406, 600, pl. xi, fig. 2.
1928d. Loveridge, 49.
1929. Flower, 25.
1929h. Loveridge, 14.
1931. Hewitt, 466.
1933. Schmidt, 4.
1934. Pitman, 307.
1936h. Loveridge, 19.
1937a. Flower, 5.
1937f. Loveridge, 495.
1937. Ruckes, 101, pl. x, fig. 8.
1939b. FitzSimons, 18.
1940. Parker, Moreau and Pakenham, 311.
1940a. Scortecci, 126.
1941a. Angel, 151.
1941. Moreau and Pakenham, 109.
1942e. Loveridge, 247.
1943. Scortecci, 270.
1946b. Mertens, 39, 68.
1949. Conant and Hudson, 4.
1950. Rose, 346, figs. 209-210.
1950f. Laurent, R., 133.

1950. Williams, 551.
1951. Monard, 168.
1835. *Cinothorax belliana* Fitzinger, 108.
1843. *Cinixys belliana* Fitzinger, 29.
1849. Smith, A., App., 1.
1854a. Peters, 215.
1866a. Bocage, 40.
1866b. Peters, 887 (*Cinyxis*).
1869a. Peters, 11.
1870. Blanford, 444.
1871b. Sclater, P. L., 544.
1878a. Peters, 202.
1880c. Vaillant, 34, 88.
1882a. Peters, 5.
1886. Vaillant, 137.
1887a. Bocage, 209. (*Cinnixys*).
1887b. Bocage, 86.
1887a. Müller, F., 295 (*Cinyxis*).
1889a. Boulenger, 143.
1890. Strauch (part), 62.
1893a. Boettger, 8.
1893. Trimen, 79.
1894c. Günther, 85 (*Cinyxis*).
1895a. Bocage, 2.
1895. Prato, 19 (*Cynixis*).
1895c. Werner, 127 (*Cininyxis*).
1896a. Bocage, 97.
1896c. Boulenger, 15.
1896. Tornier (part), 2 (*Cinicys*).
1897g. Boulenger, 277.
1897. Tornier, 63.
1898a. Boulenger, 716.
1898. Jeude, 5.
1898. Johnston, 361 (*Cinyxis*).
1898. Sclater, W. L., 96.
1898. Tornier, 282.
1898a. Werner, 203.
1899a. Mocquard, 218 (*Cinyxis*).
1901. Gadow, 365.
1901. Sordelli, 111, figs. 1-2.
1902d. Boulenger, 445 (*Cinyxis*).
1902. Scherer, 253, photo.
1902b. Tornier, 580.

1902e.	Tornier, 665.
1905h.	Boulenger, 252.
1905.	Neumann, 389.
1906b.	Siebenrock, 2, 39, fig. 1.
1907a.	Boulenger, 6.
1907j.	Boulenger, 482, fig. 140.
1907a.	Duerden, 9.
1907.	Siebenrock, 6.
1908.	Chubb, 220.
1908c.	Kammerer, 776.
1908b.	Mocquard, 557.
1908.	Odhner, 2.
1909a.	Chubb, 592.
1909b.	Chubb, 34.
1909a.	Siebenrock (part), 510.
1910.	Müller, L., 622.
1910.	Roux, 100.
1910.	Sternfeld, 4.
1911c.	Boulenger, 162.
1912c.	Sternfeld, 200.
1912b.	Werner, 424.
1913.	Boettger, 345.
1913c.	Nieden, 54.
1913d.	Werner, 40.
1916.	Calabresi, 42.
1916.	Siebenrock, 6.
1917.	Sternfeld, 412.
1919g.	Boulenger, 12 (*Cinyxis*).
1919.	Siebenrock, 276.
1921d.	Loveridge, 50.
1922d.	Loveridge, 523.
1922b.	Procter, 515.
1923g.	Loveridge, 924, 931.
1924b.	Loveridge, 2.
1924a.	Werner, 266.
1927.	Calabresi, 37.
1928.	Cott, 952.
1928b.	Scortecci, 334.
1929.	Rose, 189.
1930a.	Scortecci, 215.
1931.	Monard, 109 (*Cynixis*).
1933m.	Witte, 67.
1937b.	Monard, 146.

1954. Noël-Hume, 72.

1845a. *Kinixys schoensis* Rüppell, Mus. Senckenberg, **3**, p. 226, pl. xvi, figs. 1-3: Shoa, southern Ethiopia.

1845b. Rüppell, 297.

1922a. Mertens, 168 (lists type in Mus. Senckenberg).

1847. *Testudo geometrica* Bianconi (not of Linnaeus), 52, pl. vi, figs. 1-2.

1882a. Peters, 3 (corrects Bianconi's misidentification of *belliana*).

1863b. *Kinixys Spekii* Gray, Ann. Mag. Nat. Hist. (3), **12**, p. 381: Central Africa (i.e. probably northwest Tanganyika Territory).

1870e. Gray, 14.

1931. Hewitt, 469.

1935. Hewitt, 347.

1936j. Loveridge, 218.

1937f. Loveridge, 492, 495.

1943. Scortecci, 270, 282.

1890. *Testudo areolata* Strauch (part; not of Thunberg), 58 (Victoria Nyanza specimen only).

1902b. *Homopus darlingi* Boulenger, Proc. Zool. Soc. London, **2**, p. 15, pl. iv: Salisbury District, Mashonaland, Southern Rhodesia.

1906. Duerden, 408, pl. xi, fig. 3.

1907. Duerden, 68, fig.

1920c. *Testudo Loveridgii* Boulenger (part: the small specimen without locality was erroneously attributed to *loveridgii*), p. 264.

1920. *Hinged Land Tortoise* Carpenter, 186 (Lake Victoria).

1927c. *Cinixys lobatsiana* Power, Trans. Roy. Soc. S. Africa, **14**, p. 410, pls. xix-xx: Lobatsi, Bechuanaland Protectorate.

1931. Power, 46, 49, figs. 1-2.

1931. *Kinixys belliana zombensis* Hewitt, Ann. Natal Mus., **6**, p. 469, fig. 1c, pl. xxxviii, fig. 4: Zomba, Nyasaland.

1934a. Mertens and Müller *in* Rust, 8.

1935. Hewitt, pl. xxxiv, fig. 1 (not mentioned in text).

1931. *Kinixys belliana zuluensis* Hewitt, Ann. Natal Mus., **6**, p. 471, figs. 1a-1b, pl. xxxviii, figs. 1-3, 5-10: Richard's Bay, Zululand.

1934a. Mertens and Müller *in* Rust, 8.

1935. Hewitt, 350, pl. xxxv, figs. 1-2.

1931. *Kinixys australis* Hewitt, Ann. Natal Mus., **6**, p. 477, pl. xxxvi, figs. 4-6: White River, eastern Transvaal.

1931. *Kinixys darlingi* Hewitt, 481.

1934a. Mertens and Müller *in* Rust, 8.

1934. Pitman, 307.

1931. *Kinixys jordani* Hewitt, Ann. Natal Mus., **6**, p. 481, pl. xxxvii, figs. 7-9 (not figs. 1-3 as stated): Isoka, Northern Rhodesia.

1934. Pitman, 307.

1931. *Kinixys youngi* Hewitt, Ann. Natal Mus., **6**, p. 486, fig. 1d, pl. xxxvii, figs. 4-5: Shore of Lake Nyasa below Livingstonia, Nyasaland.
1934a. Mertens and Müller *in* Rust, 8.
1949. Moyle, 582.
1931. *Kinixys lobatsiana* Hewitt, 488, figs. 1e-1f and 2, pl. xxxvii, figs. 6-7.
1934a. Mertens and Müller *in* Rust, 8.
1932. *Kinixys australis mababiensis* FitzSimons, Ann. Transvaal Mus., 15, p. 37: Tsotsoroga Pan, Mababe Flats, Bechuanaland Protectorate.
1934a. Mertens and Müller *in* Rust, 8.
1935b. FitzSimons, 302, pl. x, figs. 1-3.
1934a. *Kinixys australis australis* Mertens and Müller *in* Rust, 8.
1934a. *Kinixys belliana belliana* Mertens and Müller *in* Rust, 8.
1937b. Mertens, 5.
1938e. Mertens, 430.
1952. Witte, 12.
1953e. Loveridge, 158.
1953h. Loveridge, 140.
1953. Witte, 15, pl. iv, fig. 1.
1955b. Mertens, 52.
1934a. *Kinixys belliana spekei* Mertens and Müller *in* Rust, 8.
1935. *Kinixys natalensis* Hewitt, Rec. Albany Mus., **4**, p. 353, pl. xxxv, figs. 3-4: Jameson's Drift, Tugela River Valley, Natal.
1937a. *Kinixys zuluensis* Hewitt, 791, fig. 5 (of foot).
1942e. *Malacochersus tornieri* Loveridge (not of Siebenrock), 248 (misdet., juvenile found dead, crushed and dried).
1946. *Kinixys zombensis* Mitchell, 19.

Further citations of *Kinixys*, or *Cinixys, belliana* will be found under *K. b. nogueyi*.

Common names. Bell's Eastern Hinged-Tortoise; *doba* (at Tete:Peters); *enfudu* (Ganda:Carpenter); *fudi* (Pokomo:Loveridge); *furgobi* (Gogo:Loveridge); *furu* (Cewa:Mitchell); *imbati* (at Ngangela:Monard); *kakafula* (eastern Angola:Laurent); *Kamba* (Manganja & Sena:Mitchell); *kobi* (Mwera: Loveridge); *nambi* (Makonde and Mawiha:Loveridge); *ngongo* (Yao:Loveridge; Mitchell); *nguru* (Sagella and Taita:Loveridge); *ufutu* (Matabele:Chubb); *umbeo* (in Benguela:Bocage).

Description. Beak not or but weakly to moderately hooked, uni- or tricuspid; edge of jaws not serrate; prefrontal large, entire, semidivided or divided longitudinally, rarely broken up; frontal large (occasionally divided longitudinally), moderate or broken up; upper head shields small, irregular; forelimb anteriorly covered with a few or many, large, unequal, scattered or juxtaposed, strongly imbricate or non-imbricate, more or less pointed (subcircular or pointed in young, subacute in adults) scutes which on anterior edge form a longitudinal series of 5-9 from elbow to outer claw; claws 5, rarely 4 [1]; hinder side of thigh without enlarged tubercles; heel with or without well-defined spurlike tubercles; claws 4, rarely 3 [2]; tail terminating in a more or less distinct horny tubercle that is sometimes much larger in ♂ ♂.

Carapace moderately convex or markedly flattened dorsally, sides sloping, scarely or not (though sometimes deeply [3]) notched in nuchal region; anterior margin not or but slightly expanded, not or but slightly reverted, not spinose in young, posterior margin not expanded, not or but slightly reverted, not or but slightly (occasionally moderately[4]) serrated, not spinose in young, rear

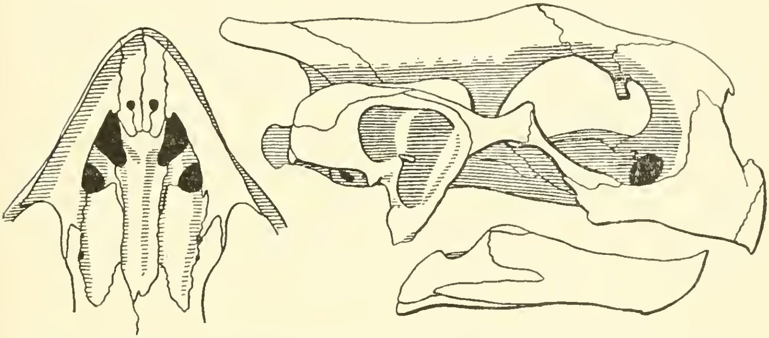

Fig. 46. Skull of *Kinixys b. belliana* (A.M.N.H. 10029). Condylobasal length 37 mm.

(S. McDowell del.)

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[1] Four in 2 out of 23 tortoises from Uele region of Congo, a third had 4 on one forefoot and 5 on the other (Schmidt:1919:407); four in 3 (M.C.Z. 40011, 40013, 40017) out of 8 Kenya specimens, and four on both forefeet of 1 (M.C.Z. 44451) of 8 Southern Rhodesia tortoises examined by us. This Rhodesian tortoise is unusual in that it is the fourth claw that is lacking; four in a juvenile only of a series of at least 6 from Beira (Boulenger: 1907j: 482 and Hewitt: 1935: 353). The missing claw on each forefoot is represented by a light-colored, rounded tubercle (Battersby in letter of 15.xii.54). All 14 Tanganyika and all 24 Nyasaland specimens in the M.C.Z. have the normal five claws of *b. belliana*.

[2] Three in a Belgian Congo tortoise mentioned by Schmidt (1919: 407).

[3] Deeply notched in an Mtimbuka juvenile (M.C.Z. 50328) as the nuchal is absent.

[4] Moderately serrated in type of *lobatsiana* Power (1927c:pls. xix-xx).

end in young sloping more or less steeply, in adults even more so; dorsal shields concentrically striated, the striations more or less reduced by wear in aged specimens, not or only sometimes swollen,[1] not convex; nuchal usually elongate, though as broad as, or much broader than, long in very young, occasionally divided, minute[2] or absent;[3] vertebrals 5, rarely 4,[4] 6 or 7,[5] not or but slightly convex, first broader than long in young, broader than long, as broad as long, or longer than broad in adults; second to fifth as broad as, or broader than, long; second broader, subequal to, or narrower than, fifth in young, narrower in adults; fifth flat in young, more or less convex in adults; costals 4, rarely 3[6] or 5,[7] usually not forming an angle with the marginals; marginals 9-12,[8] usually 11; supracaudal undivided, rarely divided,[9] with or without a tendency to be incurved in ♂ ♂, otherwise not or but slightly reverted in both sexes.

Front lobe of plastron anteriorly truncate, very thick, not or but slightly or moderately projecting beyond the anterior border of the carapace, not bifid, not or very openly notched; gulars paired; pectorals[10] moderate, their anterior borders straight or widening more or less gradually towards the axillary notch; axillaries 2-4, the innermost small, inconspicuous or absent, the outermost more or less concealed; inguinal 1,[11] large, in contact

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[1] Strongly swollen, with deep gutters between the shields, in 3 Mafia Island tortoises (*fide* Siebenrock : 1906b : 2).

[2] Divided in a juvenile (U.S.N.M. 41699). When rudimentary it may result in the marginals meeting either before or behind it (Strauch : 1890).

[3] Absent in an Mtimbuka juvenile (M.C.Z. 50328) and in one of a Beira series (Hewitt : 1931).

[4] Four in a carapace from Moroni figured by Sordelli (1901 :111) with consequent elongation of the third vertebral, etc.

[5] Six or seven in an Ujiji and some Mtimbuka adults (M.C.Z. 48001 ; 50318 ; 50323).

[6] Three on right side of a Garamba ♀ (A.M.N.H. 10047) where the missing costal is replaced by an extended vertebral that is in contact with the marginals.

[7] Five in an Mtimbuka ♂ (M.C.Z. 50318).

[8] Nine on left, ten on right of Moroni carapace (Sordelli :1901) ; ten on right, eleven on left in a Sandown ♀ (Hewitt) ; twelve on left side of an Ithanga juvenile (M.C.Z. 8158(and twelve in an Mtimbuka ♀ (M.C.Z. 50323) with the hinge between marginals 8 and 9 instead of between 7 and 8, the normal arrangement ; twelve in an Ujiji ♂ (M.C.Z. 48001) whose hinge is between marginals 7 and 8 ; in an Angolan tortoise the hinge was between 6 and 7 (*fide* Bocage : 1866a), as also in a Natal specimen mentioned by Hewitt (1935).

[9] Divided in a Mussera tortoise (*fide* P. L. Sclater :1871b) ; also in several from Natal, made cotypes of *natalensis* (Hewitt : 1935).

[10] Pectoral on right side of a Cheren ♂ is fused with the corresponding abdominal shield (Scortecci : 1928b) ; pectorals fail to meet in an Uele tortoise (A.M.N.H. 10031) mentioned by Schmidt (1919 : 407).

[11] Absent in a Natal tortoise (*fide* Hewitt :1935 :353).

with the femoral; hind lobe very short, truncate, not or but slightly notched posteriorly.

Plastral formula: Abh>, h>(g, p, f, an, all extremely variable).

Color. Carapace straw-colored, yellowish brown, olivaceous brown or reddish brown; in young uniform, or the areolae deep brown surrounded by a zone of yellow which may extend to the margins of each shield or be interrupted by fine black radiations from the darker areolae or be entirely replaced by black edging. The juvenile coloring may persist in adults, though usually with the modification that the black edging of the shields is irregularly or symmetrically broken up by yellow pigment, or only the black areolae of the juvenile pattern persists, in which event it is frequently interrupted by a median, longitudinal, yellow streak. In a few individuals, chiefly ♂♂, the coloring may be uniform.

Plastron horn color, uniform or smudged with black, the latter sometimes in the form of radiations from around the areolae.

The literature teems with descriptions of deviations of the above, for the coloring of *belliana* is extremely variable — due in part to the normal zonary pattern of the young being replaced by the secondary or radiate arrangement found in adults, in part because ♂♂ tend towards uniformity while ♀♀ are apt to be darker.

Size. Carapace length of largest ♂ (M.C.Z. 18151) from Turiani, 193 mm., breadth 125 mm., height 83 mm.; carapace length of largest ♀ (M.C.Z. 50321) from Mtimbuka, 207 mm., breadth 135 mm., height 88 mm. Possibly the smallest, from Uliya, length 50 mm., breadth 46 mm., height 25 mm. (All three collected by Loveridge.)

That the *belliana* of open savanna have higher shells, while the more depressed *spekii* type live in rocky terrain, where they may seek shelter beneath boulders, was suggested by Loveridge (1923g:924) who, both then and later (1936j:1942e:1953e), furnished tabulated measurements. In 1942 he reluctantly returned *spekii* to the synonymy in the absence of evidence that the low-vaulted form, which predominates in certain localities like Mtimbuka, has any zoogeographical significance. With this decision we concur after careful reappraisal of all available material and data.

Sexual dimorphism. In addition to a certain amount of sexual dichromatism among adult *belliana,* as indicated above, the most promising aids to determining sex are:

Plastron usually somewhat concave along the median axis; anal shields forming an almost straight edge posteriorly; tail very long, normally terminating in a large horny tubercle .... ♂
Plastron flat; anal shields forming an incurved edge posteriorly; tail short, normally terminating in a very small horny tubercle .... ♀

The caudal tubercle is not always so well-developed in males as to be the infallible guide to sex supposed by Sternfeld (1917: 412).

Breeding. On October 10, at Lumbo, a 207 mm. ♀ held a mass of ovules ranging from pea-sized to 28 mm. in diameter; of the latter there were about 15 (Loveridge:1921d).

In May, 2 oval eggs were present in one tortoise, and 3 each in two other Mafia Island ♀♀ (Siebenrock:1906b:fig. 1), their dimensions correlated with those of the parent, for the eggs of a 168 mm. tortoise measured 41 x 33 mm., those of a 192 mm. reptile 45 x 36 mm.

Longevity. Nine years and 9 months (Conant and Hudson: 1949); 9 years, 3 months, 28 days (Flower:1937a).

Diet. Frequently seen feeding on fallen bananas and mangoes; two were observed eating sugar cane in a plantation during a downpour (Scherer:1902). Four found feeding on fungi at Lobatsi (Power:1927c); fungi (Mitchell:1946); take pawpaw readily (Loveridge:1928). Though plenty of grass was present in the enclosure, Loveridge (1923g:925) found one of these tortoises eating hard Indian corn; a single kernel would be taken up and dropped five or six times before being swallowed. Another *Kinixys,* munching something at the time, was found nosing a large yellow carpenter bee (*Xylocopa nigrita*) of whose hind legs one was missing. Though the tortoise was seen to return again and again to the bee, it never actually bit it. The insect, which had only recently died, had probably fallen from a beam above. A ♂, feeding in bright sunshine beside the Voi road, made off with surprising agility when approached (Loveridge:1936j: 220).

Parasites. Ticks (*Amblyomma nuttalli*)[1] have been recorded from many localities (Loveridge). Nematodes are commonly found in the intestines of Congo tortoises (Lang, *in* Schmidt: 1919).

Enemies. In Angola the natives esteem these tortoises as food (Anchieta, *in* Bocage:1895a). In Faradje district of the Belgian Congo, following the grass fires of February and March, the Azande and Logo organize tortoise-hunts. The reptiles are located by the natives' dogs, and the animals unearthed by the iron-shod butts of spears. The rear portion of the carapace is readily separated at the hinge and the meat removed for stewing. The stomach and cloaca are usually rejected but the rest of the reptile, including nematodes which are thought to add to the flavor, are dropped in the cooking pot. These tribesmen of the northeast Congo apparently prefer tortoises to chicken, and fancy them more than the semi-aquatic terrapin (Pelomedusidae) which have a strong musky odor (Lang, *in* Schmidt:1919:410).

Apart from man, *Kinixys* appears to have few enemies. However, Lang records finding the shell of a recently eaten one whose carapace and plastron were marked by the teeth of a leopard the tracks of which were plainly visible. In East Africa tortoises may sometimes be found wandering about with shells that have been bitten by hyenas or other carnivores, the scars completely healed. The empty shell of one specimen (M.C.Z. 18153) is studded with tooth marks and the bone re-ossified where an extensive piece has been broken right off.

A *Kinixys* with carapace fractured and bleeding, as if dropped from a height by some bird of prey, was found by Carpenter (1920:186).

Defense. When picked up, a Bell's Box-Tortoise may snap its beak and struggle wildly, so that its captor is liable to be scratched by the flailing forelimbs or wet by the pungent cloacal fluid that is discharged. Another individual may emit a hiss as it withdraws its head within the sheltering carapace, completing its concealment by bringing forward and folding the heavily armored forelimbs. Simultaneously, air is expelled from the lungs as the rear portion of the carapace comes down to enclose the hind limbs and tail (Lang, *in* Schmidt:1919).

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[1] Early records of *A. marmoreum* were based on ticks that have been re-examined by Dr. J. C. Bequaert and found to be *nuttalli.*

Aestivation. At the commencement of the dry season (December to May) in the Uele, by burrowing among the roots of trees, into termitaria, or a few inches below ground, *Kinixys* usually escapes the devastating grassfires, remaining quiescent until aroused by the onset of the rains (Lang, *in* Schmidt:1919:410).

Habits. In the coastal belt of the Congo, where it inhabits low granite hills, *Kinixys* appears only in the hot rainy season (October to May) remaining underground during the cold weather according to the natives (Sclater:1871b:544). Fairly common in the savanna of the northeast Uele where they find shelter and food in the dense undergrowth of the moister areas bordering swamps and shallow watercourses. During the rainy season they wander further afield so that the natives have difficulty in locating them in their dry-season haunts. At the beginning of the rains (June) three of the tortoises were found in a shallow pool, overgrown with vegetation. One, released near a river, walked to the edge of the steep bank and unhesitatingly dropped into the water where, though powerless against the strong current, it appeared at ease (Lang, *loc. cit.*). Found beneath bushes and in thickets along the river banks of Eritrea (Blanford:1870). In Tanganyika commonly encountered during the rainy season in damp areas of the savanna (*fide* Böhm), also in a papyrus swamp according to Stuhlmann (Tornier:1896). Plentiful at Broken Hill during rains (Pitman:1934). J. M. McCallum (*in* Hewitt: 1935:494) reports on the readiness with which "*lobatsiana*" will enter water. A 75 mm. juvenile was found in a termitarium at Entendweni, Zululand (Odhner:1908).

Though members of this genus are said to usually walk on the claws of their forefeet, *lobatsiana* places "the palms on the ground at every step and can remain standing on the palms, the carapace being raised a little from the ground" *fide* Hewitt (1931:500;footnote).

In captivity these tortoises thrive best when kept under humid conditions at high temperatures *fide* Kammerer (1908b:770). Instead of taking advantage of the shelters provided for them at Kilosa, seven *K. b. belliana* were apt to stay out at night, particularly when raining, spending the entire night in efforts to escape from their enclosure (Loveridge *in* Procter:1922b:523, where its habits are contrasted with those of *Malacochersus*).

Localities. Sudan: Khartoum; Liranga; Moroni; Talodi, Nuba Mountain Province; Sudan (as "Sandom" [1]); *Torit. *Eritrea:* Anseba Valley; Asmara; Cheren. *Ethiopia:* El Direre, Tertale; Errer (Erer) River near Harar; Shoa (Schoa). *British Somaliland:* Berbera. *Somalia:* "Adden Cabola"[2] (? Caboba); "Badditu to Dime"; Webi River in Ennia-Gallaland. *Uganda:* Busu Hill; Busu (Bussu) near Jinja; Masindi; Mount Elgon. *Kenya Colony:* Athi Plains; *Golbanti; *Ithanga Hills; *Kibwezi; Kitui; Moyale; Mtito Andei; Nairobi; Taru; Tereale (Pozzi-); *Voi; Yatta Plains. *Tanganyika Territory:* Amboni near Tanga; Bubu near Kondoa; Bukome; "Central Africa" (for type of *spekii*); Dodoma; Godegode; Ikikuyu; Kakoma; Korogwe (Kerogwe); Kigoma; Kilimanjaro Mtn.; *Kilosa; *Kiponda to Mitungu; Kiserawe; *Kitaya; Kongonda near Dodoma; Lake Rutamba; Lake Tanganyika; Lake Victoria; Longido West; Mafia Id.; Maji ya Chumvi; Mbulu near Arusha; *Mikindani; Mkata River; Mkomasi River; Morogoro; Mugango. 24 km. S. W. Musoma; Myombo; *Nchingidi, Rondo Plateau; Ngoga; Nyangesi, Usukuma; Pangani River bank; Pwaga; *Simbo near Tabora; Tamborale (Muana Tomboloo); Tanga; *Turiani; *Ujiji; Uliya. *Zanzibar Island:* Mafia Id.; *Zanzibar (Müller: 1887a; Strauch :1890; etc.). *Mozambique:* Amatongas; Beira; Boror; Caia; Charre; Chitau; Gauca; Inhambane; Lumbo; Mesuril; Sena; Tete. *Nyasaland:* Angoniland; Chibotela; Chikwawa; Chiromo; Chitala River; *Cholo Mtn.; Fort Johnston; Lake Shirwa (Chilwa); Lakeshore below Livingstonia; Likangala; Monkey Bay; *Mpimbi near Zomba; *Mtimbuka; Port Herald; Zomba. *Northern Rhodesia:* Broken Hill; *Isoka; Petauke. *Southern Rhodesia:* *Birchenough Bridge; *Bulawayo; Changadzi River; Essevale; *Hot Springs; Marandellas to Umtali; Mazoe; Salisbury district; Sandown; *Selinda Mtn. and valley at its foot; Shangani River. *Bechuanaland Protectorate:* Lobatsi; Tsotsoroga Pan, Mababe Flats. *Transvaal:* Glentig near Nylstrom; Naauwpoort; White River. *Natal:* Dimani's Stream; Entondweni (Entendweni); Impanza near Greytown; Jameson's Drift; Manaba; Matubatuba; Natambana; Richard's Bay; Tugela River and Valley; Umfolosi Station. *Angola:* Caconda;

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[1] In Boulenger (1889a), correction confirmed by J. C. Battersby (15.xii.1954).

[2] In Calabresi (1916), reporting on the Stefani and Paoli material with many misspellings.

Capangombe; Caquindo (Kakindo); Chitau (C.M.) Cubal; Cubango (Kuvangu); Duque de Bragança; Ebanga; Galanga; Gauca (C.M.) Lui River, Muata-Yamvo region; Lunda; Mbale River; Muita; Osi; Quissange; Vila da Ponte. *Belgian Congo:* Abimva; Avakubi; Bowa River; Cape Tembwe; Dika; Faradje; Ganza; Garamba; Kabambaie; Kabulumba; Kansenia; ''Kanzluze''; *Kapiri; Kasonga to Uvira; Kaswabilenga; Kateke; *Lukafu; Lukonzolwa; Mahagi Port; Manda; Masombwe; Mpala; Mulungwe River; Musosa; Musserra; Niangara; Northwest shore of Lake Tanganyika; Uele region. *French Cameroon:* Meiganga; Yoko (5 claws present on forefeet of both).

Madagascar: Ambanja (two alive: Angel :1941a :151); Ambassuara (Peters :1873c :792); Nosy (Nossi) Bé (Boettger :1889: 295).

Range. Eritrea southwest to Natal, northwest through Bechuanaland and Angola to French Cameroon where it meets with the western race. Also Madagascar. (The possibility of its having been introduced here should not be overlooked. But for Angel's recent record from northern Madagascar, we might have questioned its occurrence, half a century having elapsed since the indefinite records of Müller, Strauch and others.)

Kinixys belliana nogueyi (Lataste)

1844. *Kinixys belliana* Gray, part, not of Gray 1831, p. 12.
1855. Gray (part), 13, pl. ii.
1873b. Gray (part), 16.
1884a. Rochebrune, 16.
1857. *Cinixys Belliana* Jan (not of Gray 1831), 35.
1890. Strauch (part), 62.
1893c. Matschie, 208.
1896a. Bocage, 74.
1901c. Tornier, 66.
1906i. Boulenger, 197 (as *Cinyxis*).
1906b. Siebenrock, 3.
1907j. Boulenger, 482.
1907. Siebenrock, 6.
1909. Gendre, cvi.
1921a. Chabanaud, 461.
1921b. Chabanaud, 522.
1937. Andersson, 3.

1886. *Homopus Nogueyi* Lataste, Le Naturaliste (2), **8**, p. 286: Medina (as Médine), Upper Senegal.
1889a. Boulenger, 148.
1901c. Tornier, 67.
1906c. Duerden, 408.
1888a. *Cinixys Dorri* Lataste, Le Naturaliste (2), **10**, pp. 164, 226, fig. 1: Bakel, Upper Senegal.
1903b. *Cinixys nogueyi* Siebenrock, 185, 442.
1931. *Kinixys nogueyi* Hewitt, 468.
1934a. *Kinixys belliana nogueyi* Mertens and Müller *in* Rust, 8.
1952a. Loveridge, 231.
1955. Cansdale, 89, 103.

Common names. Bell's Western Hinged-Tortoise. *Nkounou* (in Senegal: Rochebrune).

History. The species was named for M. Gustave Noguey of the Linnaean Society of Bordeaux. Siebenrock (1903b) was the first to detect Lataste's error in assigning *nogueyi* to the genus *Homopus;* he also re-examined the eleven Togo tortoises referred to *belliana* by Tornier (1901e) and found that all had 4 claws on the forelimbs. Boulenger (1906i) questioned Siebenrock's action in making *nogueyi* a full species, pointing out that in some West African examples radiating black streaks *are* present, while the gular/anal proportions do not differentiate *nogueyi* from *belliana.* Boulenger regarded *nogueyi* as a 4-clawed variety of *belliana.* Later (1907j) he reported a young *belliana* from Beira, Mozambique, as having only 4 claws (though the adults from the same locality had 5), so concluded that *nogueyi* was inseparable. Loveridge (1952a), after studying five 4-clawed tortoises from Togo and Dahomey, regarded it as a West African race and defined the range.

Description. Beak weakly to moderately hooked, uni- or bicuspid, edge of jaws not serrate; prefrontal divided longitudinally; frontal large or small, occasionally divided longitudinally; upper head shields small, irregular; forelimb anteriorly covered with a few, large, unequal, scattered or juxtaposed, strongly imbricate, subcircular or subacute scutes which on the anterior edge form a longitudinal series of 6-7 from elbow to outer claw; claws 4; hinder side of thigh without enlarged tubercles; heel without, or with a trace of an enlarged tubercle; claws 4.

Carapace moderately convex, flattened dorsally, sides sloping in young, descending abruptly in adult, not or but openly notched in nuchal region; anterior margin somewhat expanded and not or but slightly reverted, not serrated, not spinose in young; posterior margin not expanded, not or but slightly reverted, not serrated, not spinose in young; rear end in young sloping gradually, in adults vertically from the middle of the fifth vertebral; dorsal shields concentrically striated (the striations more or less reduced by wear in aged specimens), neither swollen nor convex.

Nuchal about as long as broad in young, elongate in adults; vertebrals 5,[1] without median keel (except in young which may show the barest trace), not convex, first broader than long in young, longer than broad in adults, second to fifth broader than long, second as broad as fifth in young, narrower in adults, fifth flat in hatchlings, somewhat convex in adults; costals 4, not forming an angle with the marginals; marginals 11-12 [2]; supracaudal undivided, more or less reverted; tail terminating in a horny tubercle.

Front lobe of plastron very thick, not or but slightly projecting beyond the anterior border of the carapace, not or but scarcely notched; gulars paired; pectorals moderate, their anterior border widening gradually towards the axillary notch; axillaries 3, the innermost small, the outermost more or less concealed; inguinal large, in contact with the femoral; hind lobe very short, truncate, not notched posteriorly.

Plastral formula: Abd>h>g>or=or<f>p>or<an.

Color. Carapace light olive green or reddish brown, uniform, or each dorsal shield with yellowish green areolae and bordered with black, which may be interrupted at the angles. Plastron yellow, or greenish yellow, more or less marked by black or reddish brown.

Size. Carapace length of a ♂ (I.F.A.N. 2052) from Bassila, 148 mm., carapace length of largest Togo tortoise, unsexed, in Berlin Museum, 220 mm.; largest ♀ (I.F.A.N. 2052 also) from Bassila, 152 mm.; of the type ♀ (B. M.) from Medina, 135 mm., breadth 99 mm., height 60 mm. Carapace length of a juv. (M.C.Z. 51755) from Tohoun, 48 mm.

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[1] A relatively small azygous shield split off from left side of fifth vertebral in a Kabala ♂ (M.C.Z. 54118).

[2] Twelve on left side only of Kabala ♂ (M.C.Z. 54118).

Diet. Lataste, finding much debris of Coleoptera as well as vegetable matter in the intestines of the ♀ cotype, cites this as evidence of the reptile being insectivorous as well as vegetarian.

Enemies. Ornaments are made from the emptied shell (Cansdale:1955). Loveridge (1952a), noting that the claws and soles of each foot of a Tohoun tortoise appear to have been sliced off with a sharp knife, suggests it may have been done by an African who was afraid of being scratched.

Aestivation. Burrows into the ground during the dry season according to native reports (Cansdale:1955).

Localities. French Cameroon: Garoua (Garua); Konn; Mandara (as Mandana) Highlands (shell only, so race questionable); Mayo Sala; Ndikinimeki; Ngaouyanga; Sajdje (Sakdje); Tibati.[1] *Nigeria:* Gando (Gandu); "Gao Haussari am Garua-Benue"[2]; Lagos. *Dahomey:* *Bassila; Porto Novo.[3] *Togo:* Adele (as Bismarckburg); Lome; Misahöhe (see Höhe); Tohoun (or Tohou). *Gold Coast:* Kintampo; Somanya, Krobo (M.C. Lesage). *Sierra Leone:* *Kabala, Koinadugu district; Musaia.[4] *French Guinea:* Beyla; Forecariah; Kankan; Labe, Fouta-Djalon. *Portuguese Guinea:* Bolama. *Gambia:* MacCarthy Island. *French Sudan:* Diafarabe; Pama, Gourma district (as Pama-Gurma in Tornier:1901c). *Senegal:* Bakel; Kaolack; Medina; Sindia, 50 km. from Dakar (A. Villiers).

Range. French Cameroon west to Senegal.

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[1] We are indebted to Dr. V. Aellen and Mons. W. Lanz for examining the specimens from six of these localities in French Cameroon and ascertaining that the forefeet bore 4 claws in every one of the eight tortoises involved.

[2] Apparently this refers to some Gao in the Haussa country of northern Nigeria west of Garoua on the Benue River in French Cameroon, in an effort to distinguish it from the well known Gao on the Niger River. Passare was the collector, states Tornier (1901c: 67).

[3] Specimens from Porto Novo; Lome; Forecariah; Kankan; Diafarabe and Kaolack, all have forefeet bearing 4 claws, writes A. Villiers (11.ii.55, etc.) in whose care they are at I.F.A.N., Dakar, Senegal.

[4] A limbless 58 mm. shell, originally said to have measured 64 mm., so shrinkage during drying may account for the surprisingly abrupt, *homeana*-like declivity of the carapace posteriorly. Collected in northern Sierra Leone in 1948 by T. S. Jones. Now in the British Museum and seen by us.

Kinixys homeana Bell

1827. *Kinixys Homeana* Bell, Trans. Linn. Soc. London, **15**, p. 400, pl. xvii, fig. 2: West Africa (The statement that the types came from Sierra Leone, was later amended by Boulenger (1889a: 143) to Cape Coast, Ashanti, i.e. Gold Coast. Both Bell and Boulenger give Lt. M. C. Friend as the collector.)
1831b. Gray, 6.
1831c. Gray, 15.
1835. Duméril and Bibron, 161, pl. xiv, figs. 2-2a.
1844. Gray, 11.
1845. Wyman, 38.
1850. Berthold, 423, pls. xliii-xlv.
1855. Gray, 13.
1863f. Gray, 170 (reprint of 1863f).
1864a. Gray, 197.
1865. Strauch, 38.
1870e. Gray, 14.
1873b. Gray, 17.
1884a. Rochebrune, 17.
1919. Schmidt, 403, 598.
1929. Flower, 25.
1930a. Barbour and Loveridge, 770.
1934a. Mertens and Müller *in* Rust, 8.
1937c. Loveridge, 269.
1937. Ruckes, 101.
1938b. Mertens, 33.
1941e. Loveridge, 115.
1950. Williams, 551.
1951. Monard, 168.
1955. Cansdale, 89, 103, fig. H5.
1856a. *Cinixys Homeana* Duméril, 372.
1860. Duméril, 162.
1875a. Peters, 196.
1887a. Müller, F., 295.
1889a. Boulenger, 143.
1890. Strauch, 61.
1893c. Matschie, 208.
1897. Sjöstedt, 6.
1898a. Werner, 203.
1899. Siebenrock, 566, pl. i, figs. 1-2.
1900b. Boulenger, 447.
1901. Gadow, 364.
1901b. Tornier, 61.

1902c.	Tornier, 665.
1906a.	Mocquard, 479.
1909a.	Siebenrock, 510.
1910.	Müller, L., 622.
1910.	Sternfeld, 5, fig. 7.
1911.	Lampe, 145.
1911a.	Masi, 35.
1912c.	Sternfeld, 200.
1916.	Siebenrock, 5.
1917.	Sternfeld, 412.
1919.	Siebenrock, 276.
1921a.	Chabanaud, 461.
1921b.	Chabanaud, 522.
1954.	Noël-Hume, 74.

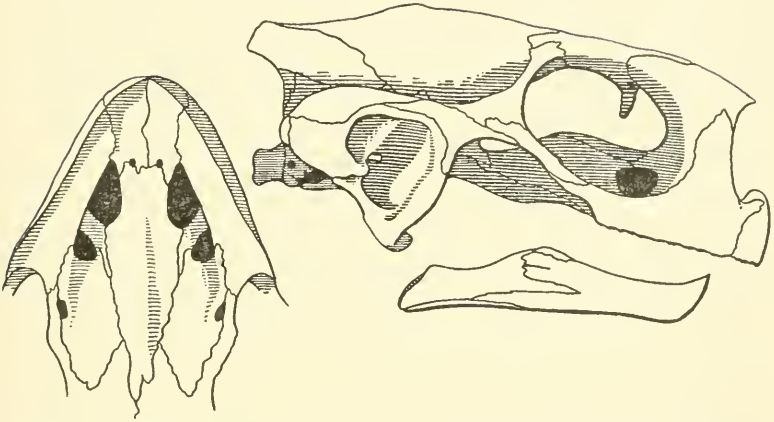

Fig. 47. Skull of *Kinixys homeana* (A.M.N.H. 43306). Condylobasal length 41 mm.

(S. McDowell del.)

Common name. Home's Hinged-Tortoise (Gray).

Illustrations. Bell's (1827) finely executed drawing consists of a lateral view of the shell in black and white to show its abruptly descending rear end in striking contrast to that of *erosa* (as *castanea*) on the same plate. Duméril and Bibron (1835) furnish a colored figure (also lateral), together with a line drawing of the plastral scutes.

Description. Beak moderately to strongly hooked, unicuspid;

edge of jaws not dentate; prefrontal divided longitudinally; frontal large, small, or broken up; upper head shields small, irregular; forelimb anteriorly covered with a few scattered, large, unequal, strongly imbricate, more or less pointed scutes which on the anterior edge form a longitudinal series of 5 to 8 from elbow to outer claw; claws 5; hinder side of thigh without enlarged tubercles; heel with or without a spurlike tubercle; claws 4; tail terminating in a small, somewhat clawlike tubercle that is larger in ♂♂.

Carapace flattened dorsally, sides sloping, not or but openly notched in nuchal region, anterior margin strongly expanded and not or but slightly reverted, spinose in young, posterior margin not expanded, more or less strongly reverted and strongly serrated, spinose in young, rear end in young sloping gradually, in adults vertically from the anterior part of the fifth vertebral; dorsal shields concentrically striated though sometimes scarcely distinguishable, through wear, in aged specimens, neither swollen nor convex (except the fifth vertebral); nuchal elongate, very rarely absent[1]; vertebrals 5, with a slight median keel, first broader than long in young, as long as, or longer than, broad in adults, second to fifth broader than long, the third broader than the third costal; costals 4, rarely 5[2] or 7,[3] not or but rarely forming an angle with the marginals; marginals 11, rarely 12,[3] the anterior much longer than the posterior ones; supracaudal undivided, rarely divided,[4] more or less strongly reverted in both sexes.

Front lobe of plastron very thick, not or but slightly projecting beyond the anterior border of the carapace, openly notched; gulars paired; axillaries 2-4, the innermost, if present, small, the outermost more or less concealed; inguinal large, in contact with the femoral; hind lobe very short, rounded, truncate, notched posteriorly.

Plastral formula: Abd > h > (g, p, f, an, very variable), f or an shortest.

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[1] Absent in one Zorzor tortoise (U.S.N.M. 109698) confirming Loveridge (1941e: 115), and in an Oda specimen (C.N.H.M. 53630) studied by E. E. Williams.

[2] Five on left side only of a Nkolembembe tortoise (Sternfeld :1917).

[3] Five on right, 7 on left, of a Zorzor specimen (U.S.N.M. 109698) which has 12 marginals on left side only (Loveridge : 1941e).

[4] Divided in a juvenile from Gabon (Duméril :1860).

Color. Essentially similar to that of *K. erosa,* which see.

Size. Carapace length of largest ♂ (U.S.N.M. 10962), from Zorzor, 200 mm., *not* exceeded by a Mujuka ♂ (S.M. 156) of 210 mm. mentioned by Mertens (1938b:33) as it was apparently measured over the curve. Carapace length of largest ♀ (U.S. N.M. 109685), also from Zorzor, 210 mm. (*fide* Loveridge:1941e: 115). The holotype was said to be 190 mm. long, 132 mm. broad, and 85 mm. in height.

Sexual dimorphism. As in *erosa.* The length of the gular suture in relation to the length of the plastron, was found by Loveridge (1941e:115) to have some significance in seven tortoises from Zorzor. It might not hold good for larger series.

Localities. Belgian Congo: Mawambi (Mavambi); northwest of Lake Tanganyika (Siebenrock:1916); near Saidi's Village (Loveridge:1937e). *French Equatorial Africa:* French Congo. *Rio Muni:* Yenghe (Jengwe, Cameroon). *French Cameroon:* Bipindi; Dehane; Dibongo near Edea; Kribi; Nkolembembe (Nkoubembe); Nkoolong (C.M.); *Sakbayeme. *British Cameroon:* Bibundi; Bonge, Meme River; Isongo; Johann Albrechtshöhe; Likomba; Mapanja; Mosake; Mujuka; Victoria. *Nigeria:* Bonny (Boni); *Ifon, Ondo district (M.C.Z.). *Gold Coast:* Abetifi; Ada (C.N.H.M.); Ashanti; Cape Coast Castle. *Ivory Coast:* Adiopodoume (V. Aellen); *Liberia:* *Cape Palmas; *Lenga, Farmington River; Zorzor.

Range. Belgian Congo northwest to French Guinea, or at least Liberia.

Wyman (1845:38) received a shell from the Cape Verde Islands, presumably a human importation. Senegal and Gambia (Rochebrune:1884a) are similarly rejected pending confirmation. The Mawambi record (Sternfeld:1912c), being based on a head and limbs, was questioned by Schmidt (1919:403). However, later records from the Belgian Congo (Siebenrock:1916; Loveridge:1937c) validate the presence of *homeana* in this general region, so we have tentatively allowed the Mawambi record to stand.

We emphatically reject the alleged occurrence at Kiu, Ukamba, Kenya Colony of such a rain-forest species as *homeana.* Siebenrock (1916:5) evidently entertained doubts for he made enquiries of Lampe respecting it and was assured that the specimen in question had been presented to the Wiesbaden Museum by a missionary who had personally picked it up at Kiu about 1912. Dr. F. Neubar, Director of Wiesbaden Museum, informs us (7.i.55) that no reference to such a specimen can be found in their catalogue, and also that much of their material was lost in a fire.

In the absence of the specimen, speculation seems idle for many alternative explanations are possible. The simplest is to assume a transposition of specimens in the museum; such things have been known to occur! Again there may have been a mistake as to the provenance of that particular specimen on the part of the collector, who may have previously been stationed at some mission in West Africa. It might be pointed out that in 1912 there were no dining cars on the trains plying between Lake Victoria and Mombasa, so that it was customary to disembark all passengers at Kiu (alt. 4861 feet) for meals at the station restaurant. Thus the possibility of the young tortoise having escaped from the custody of some passenger, homeward bound from the eastern Congo, should not be overlooked.

K. homeana does occur in the extreme eastern Congo; *erosa,* continues eastward, though sparsely, in Uganda. The two agree in the serrated nature of the posterior edge of their carapaces so it is barely possible that Siebenrock might have confused them, though this is unlikely as he (*loc. cit.*) cites the differing scutellation of their respective forearms — 4 or 5 for *erosa,* 5 to 8 in the case of *homeana.* In this respect *homeana* approaches *belliana*, which has 5 to 9 scales on the forearm, and *belliana* is a relatively common reptile in Ukamba. A misidentification with *belliana* would be likely only if the carapace of the Kiu juvenile seemed abnormally serrate to Siebenrock.

K. homeana has been erroneously recorded as occurring in Guadeloupe and Demara, South America, by Gray (1831c), followed by Duméril and Bibron (1835).

KINIXYS EROSA (Schweigger)

1802. *Testudo Denticulata* Shaw (not of Linnaeus), **3**, p. 59, pl. xiii.

1812. *Testudo erosa* Schweigger, Königsberger Arch. Naturwiss. Math., 1, p. 321: "America septentrionali (Shaw)."

1814. Schweigger, 52 (reprint of 1812).
1826. *Testudo Schöpfii* Fitzinger, Neue Classif, Rept., p. 44: No locality (*nom. nov.*).
1836. Fitzinger, 121.
1827. *Kinixys castanea* Bell, Trans. Linn. Soc. London, **15:** p. 398, pl. xvii, fig. 1: Africa.
1831c. *Kinixys*[1] *erosa* Gray, 16.
1835. Duméril and Bibron, 165.
1844. Gray, 12.
1851. Duméril and Duméril, 6.
1855. Gray, 13.
1856a. Duméril, 372.
1857. Jan, 35.
1859. Cope, 294.
1860. Duméril, 162.
1862a. Strauch, 24.
1863f. Gray, 197.
1864a. Gray, 170 (reprint of 1863f).
1865. Strauch, 39.
1866a. Bocage, 40.
1870e. Gray, 14.
1873b. Gray, 17.
1873h. Gray, 320, pl. xii, fig. 2.
1874. Reichenow, 298.
1875a. Peters, 196.
1877c. Peters, 611.
1880c. Vaillant, 34, 88.
1882a. Müller, F., 165.
1882. Pechuël-Loesche, 278.
1884a. Rochebrune, 17 (ignored).
1884b. Sauvage, 200.
1886. Vaillant, 137.
1887a. Müller, F., 295.
1888a. Boettger, 12.
1889a. Boulenger, 141, figs. 40-41.
1890. Büttikofer, 436, 478.
1890. Strauch, 61.
1893a. Boettger, 8.
1893c. Matschie, 208.
1895a. Bocage, 1.
1895c. Werner, 127 (*Cininyxis*).
1897. Sjöstedt, 6.

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[1] Variously misspelled *Kinyxis, Cinyxis* and *Cinixys* in a few of the citations following.

1898.	Jeude, 5.
1898a.	Werner, 203.
1900.	Boulenger, 447.
1901.	Gadow, 364, fig. 82.
1902c.	Tornier, 664.
1905.	Barbier, 84, pl. iii.
1905f.	Boulenger, 183.
1906i.	Boulenger, 197.
1906.	Johnston, 820, 833.
1906a.	Mocquard, 479.
1907.	Johnson, 11, 68, photo.
1907.	Siebenrock, 2, fig. —, pl. i.
1908c.	Kammerer, 775, fig. 15.
1909a.	Siebenrock, 509.
1910.	Sternfeld, 4, fig. 6.
1911.	Lampe, 145.
1912b.	Werner, 424, fig.
1916.	Siebenrock, 4, figs. 1-2.
1917.	Sternfeld, 408, 411.
1919g.	Boulenger, 11.
1919.	Schmidt, 403, 598, pl. xi, fig. 1, map 3.
1919.	Siebenrock, 275.
1920.	Werner, 424, fig. —.
1929.	Flower, 25.
1929h.	Loveridge, 14.
1930a.	Barbour and Loveridge, 770.
1933.	Hamerton, 455.
1933m.	Witte, 67.
1934a.	Mertens and Müller *in* Rust, 8.
1937c.	Loveridge, 269.
1937f.	Loveridge, 502.
1937b.	Monard, 145.
1937.	Ruckes, 101, pl. x, fig. 7.
1941.	Witte, 106.
1941e.	Loveridge, 115.
1942b.	Pitman, 214.
1949.	Conant and Hudson, 4.
1949.	Moyle, 582.
1950.	Williams, 551.
1951.	Monard, 168.
1952.	Aurelio Bassilio, photo facing p. 97 (as *Cinisis*).
1953.	Witte, 15.
1954d.	Laurent, 296.

1954. Noël-Hume, 73, pl. v.
1955. Cansdale, 89, 103.
1839. *Kinixis denticulata* Hallowell (not of Linnaeus), 161-169, pls. viii-ix.

Common names. Schweigger's Hinged-Tortoise (Flower); *mbulutobe* (on Loango Coast:Pechuël-Loesche).

Illustrations. Both Shaw (1802) and Bell (1827) provide good drawings of the shell of this distinctive species; more recently Siebenrock (1907) figures the entire tortoise, and excellent photographs from life appear in Johnson (1907), Schmidt (1919) and Noël-Hume (1954).

Description. Beak weakly to strongly hooked, unicuspid; edge of jaws not dentate; prefrontal divided longitudinally; frontal large or broken up; upper head shields small, irregular; forelimb anteriorly covered with a few scattered, extremely large, unequal, imbricate or non-imbricate, more or less pointed scutes which on the anterior edge form a longitudinal series of 4 to 5 from elbow to outer claw; claws 5; hinder side of thigh without enlarged tubercles; heel usually without any spurlike tubercle, if present situated low on the heel; claws 4; tail terminating in a horny, clawlike tubercle that is much larger in ♂♂.

Carapace flattened dorsally, sides sloping, not or but scarcely to moderately notched in nuchal region, anterior margin strongly expanded and slightly to strongly reverted, spinose in young, posterior margin not expanded, more or less strongly reverted and strongly serrated, spinose in young, rear end in young sloping gradually, in adults more steeply, if vertical only from the middle of the fifth vertebral; dorsal shields concentrically striated, neither swollen nor convex (except as noted below); nuchal absent or rarely present, elongate,[1] occasionally developed on the underside only [2]; vertebrals 5, first broader than long in young, broader than long, as broad as long, or longer than broad in adults, second to fifth broader than long, second broader or subequal to fifth in young, narrower in adults, fifth flat in hatchlings, more or less convex in adults, broader than the costals; costals 4, rarely 3,[3] not or but rarely forming an angle with the

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[1] Present in a Nola tortoise (M.C.Z. 44285).

[2] In a Sangmelima specimen (Siebenrock: 1916).

[3] Three in a Landana tortoise whose missing costal was replaced by broadened fourth and fifth vertebrals (Strauch: 1890).

marginals; marginals 11, rarely 12,[1] the anterior much longer than the posterior ones; supracaudal undivided, more or less reverted in both sexes.

Front lobe of plastron very thick, projecting beyond the anterior border of the carapace, openly or deeply notched, bifid; gulars paired; axillaries 3-4, the innermost small, the one or two outermost more or less concealed; inguinal large, in contact with the femoral; hind lobe very short, truncate, not or very broadly notched posteriorly.

Plastral formula: Abd>h>(g, p, f, an, all extremely variable).

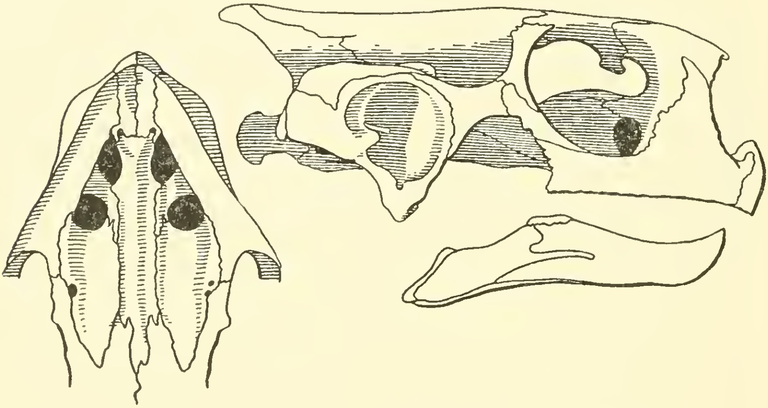

Fig. 48. Skull of *Kinixys erosa* (A.M.N.H. 69727). Condylobasal length 53 mm.

(S. McDowell del.)

For description of a pathological individual, cf. Tornier (1902c).

Color. Carapace of hatchlings pale brown, nearly uniform, darkening with age until almost black while the centers of the shields remain somewhat lighter; in older juveniles and all adults irregularly stellate patches of light yellow appear on the outer margins of the costals, also in smaller areas on the vertebrals, upper portions of the costals and the anteriormost and posteriormost marginals.

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[1] Twelve on left side of a Sakbayeme specimen (M.C.Z. 34014).

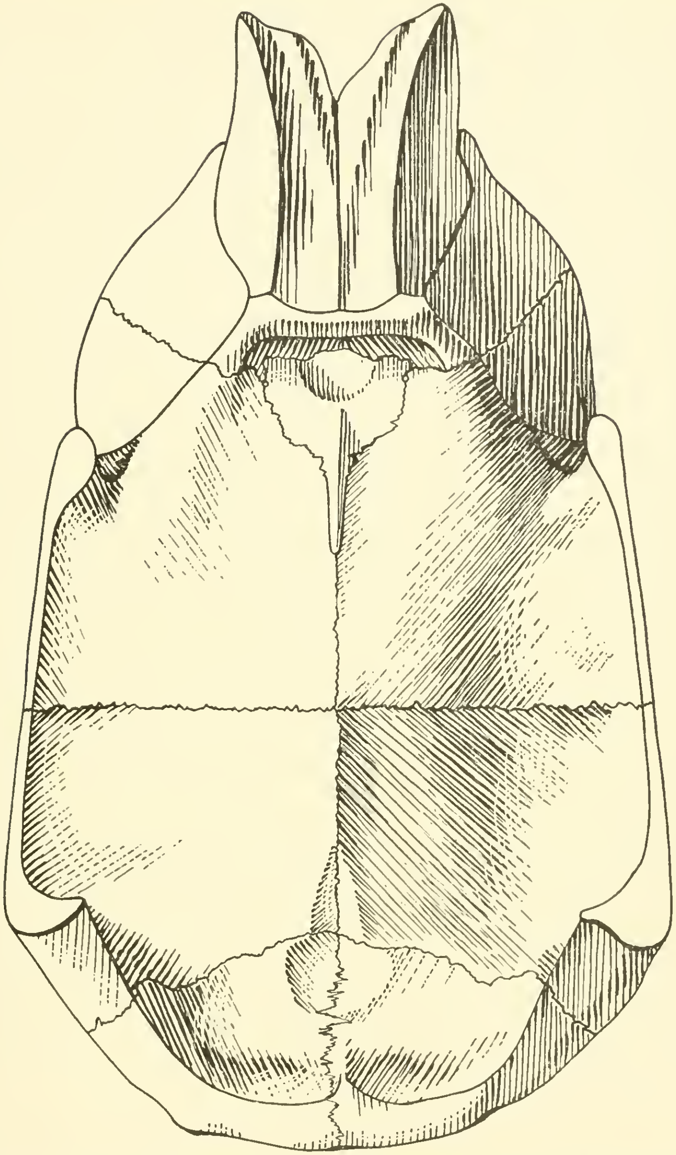

Fig. 49. Internal view of plastron of *Kinixys erosa* (Yale Mus. 4586).
(P. Washer del.)

Plastron yellow, more frequently retained on the gulars than on the remaining shields whose centers are brown or black, sometimes so extensive as to reduce the yellow to narrow lines along the sutures or occasionally a midplastral yellow zone.

Size. Carapace length of largest ♂ (A.M.N.H. 10023), from Banalia, 323 mm., breadth 236 mm., height 122 mm. (Schmidt). Carapace length of largest ♀ (M.C.Z. 52169), from Inferri Chiefdom, 260 mm., breadth 172 mm., height 106 mm.

Sexual dimorphism. The plastron of older ♂♂ is more or less concave, their tails considerably longer than those of ♀♀.

Breeding. Herbert Lang was told by the Congolese that *erosa* deposits its eggs in sandy ground and covers the site with leaves. One of four eggs laid by a captive tortoise measured 31 x 36 x 40 mm. (Schmidt:1919:406).

Longevity. Three years and five months in Philadelphia Zoo (Conant and Hudson:1949).

Diet. Apparently omnivorous. In captivity one ate apples, pears, sweet potatoes and meat — both raw and cooked (Hallowell:1839). Possibly Büttikofer (1890:436) is repeating native stories when he states that *erosa* eats insects and snails.

Hamerton (1933:455) records a captive tortoise dying of faecal concretions.

Enemies. Eaten by Liberians (Büttikofer) and by Gold Coast natives (Cansdale[1]); also by the inhabitants of the Loango Coast, who convert the shells into ornamental receptacles (Pechuël-Loesche:1882). Eaten also by the Congolese who employ dogs to track the tortoises whose odor betrays them (Lang *in* Schmidt).

Habits. In Liberia *erosa* frequents the shady banks of rivers (Büttikofer). On the Loango Coast Pechuël-Loesche (1882) was informed by the natives that these tortoises actually live in the brooks and rivers, exclusive of tidal estuaries, and bury in the mud. Despite their unwebbed feet they swim well, and captive *erosa* dived to obtain their food in a rather deep basin of water. These aquatic habits, continues Werner (1920), were confirmed by Ussher who informed him that his captive specimen remained in water for as much as a month.

The oft-repeated statement that these tortoises are slow and lethargic, says Kammerer (1908c), is due to captive specimens

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[1] In letter of 30.xi.1954.

being subjected to uncongenial conditions such as too little moisture or too low temperatures.

The best account is given by Lang (*in* Schmidt:1919:405), who states that *erosa* "is fond of marshy sites. During the day it hides beneath logs, roots, and heaps of dead and living vegetation, sometimes completely covering itself with debris. The projecting forked gular portion of the plastron and the slightly upturned edges of the carapace are very useful in this task; the head is partly retracted, and the feet then push and wedge until the turtle is hidden from view."

Localities. Uganda: Mabira Forest; Nabea. *Cabinda:* Chinchoxo; Landana. *Belgian Congo:* *Avakubi; Bafwabaka, "Bafwasikuli"[1]; Banalia; Beni; Bikoro; Djalasinda; Duma, Ubangi; Ekibondo; Gamangui; Kabambare; *Kindu (Kindo:U.S.N.M.); Koloka; Kunungu; Lake Tanganyika region; "Lissimu"[1]; Masisi in Parc National Albert; Medje (Madie); Niapu; Panga; Poko; *Saidi's Village; Stanleyville; Walikale. *French Equatorial Africa:* Fernan Vaz (Fernand Vas); Gabon; Kama (Camma); Loango; Massabe (Massaba; Massabi); *Nola; *Ntyanga (? Nyanga, or Ntchonga Lake), French Congo (U.S.N.M.); Ogoue (Ogobai). *Rio Muni:* Rio Muni. *French Cameroon:* *Bipindi (C.M.); Campo (or Kampo); Douala; *Efoulen (Efulen); *Kribi; *Lolodorf (C.M.); *Metet (C.M.); Ndikinimeki; *Sakbayeme; *Sangmelima (C.M.); Yaounde (Jaunde). *British Cameroon:* Bonge, Meme River; Buea; Cameroon Mtn.; Johann Albrechtshöhe; Nssakpe; Ossidinge. *Gold Coast:* Aburi; Ankobra (Ancober) River; Ashanti. *Ivory Coast:* Adiopodoume; Yapo Nord (both V.Aellen). *Liberia:* *Bonuta (Bonutah); *Cape Palmas; *Cuttington College, Suacoco; *Harbel; *Lenga, Farmington River; Mesurado River; *Paiata (Peahtah); St. Paul River; *Zorzor. *Sierra Leone:* Barri Chiefdom; *Imferri Chiefdom; *northeast Sierra Leone. *Gambia.* (B.M. 43.2.29.1 and ♂ shell).

Range. Uganda and Belgian Congo northwest to Gambia.

Senegal (Rochebrune) is rejected pending confirmation. Erroneously recorded from North America (Shaw), Guadeloupe (Duméril and Bibron), and Mozambique (Gray).

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[1] In Stanleyville district; a Christy locality (Boulenger: 1919g).

Family TRIONYCHIDAE

1828b. *Trionychidae* Bell, Zool. Jour., **3**, p. 515.

Definition. Cryptodirous testudinates of fully aquatic habit. Horny shields except for obscure rudiments absent, represented by naked skin.

Skull without nasal bones; prefrontals always in contact dorsally, usually with descending processes that are well separated when present; temporal region deeply emarginate posteriorly; parietal never meeting squamosal; postorbital sometimes reduced; quadrate surrounding stapes; post-otic antrum well developed; parietal with well developed descending processes; upper jaw without ridges on its triturating surfaces; vomer usually present, if present short, *not* separating the palatines; mandible with well developed coronoid bone.

Neck vertebrae without a biconvex centrum, all opisthocoelous except the eighth which is doubly convex in front but united to the centrum of the first dorsal only by ligament; entire coracoid blade broad and saber-shaped; tuberosities of humerus widely separated; trochanteric fossa of femur widely open; phalanges with condyles; claws 3.

Carapace not directly united to plastron; carapace not hinged, but plastron with some flexibility between anterior elements; pleural bones always forming a solid disk, but peripheral bones absent (possibly represented by a few ossifications in one genus); nuchal overlapping, or overlapped by, the first pleural, without typical costiform processes or attachment surface for eighth cervical; neural bones hexagonal, mostly short-sided behind, variable in number; pygals absent; plastron with some development of fontanelles; entoplastron absent, mimicked by a separated posterior portion of the epiplastra.

Range. North America; Africa; Asia.

Fossil record. First known from the Lower Cretaceous of Asia (with a possibly ancestral type — *Sinaspideretes* Young and Chow, 1953, Acta Scientia Sinica **2**:226-227, pl. 6 — in the Upper Jurassic or Wealden of the same region). A good record in North America since the Cretaceous; in Europe from Paleocene to Pleistocene. Known in Africa since the Lower Miocene.

Remarks. The trionychids or "soft-shelled turtles"[1] have

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[1] A misnomer that has frequently caused misconceptions. Actually in these turtles the carapacial disk is at least as solidly ossified as in other testudinates: only the fleshy margins are soft, except in *Lissemys*, which retains peripherals.

often been separated as one of the major groups within the turtles, coordinate in rank with the Pleurodira, with the marine turtles, and with the land and freshwater forms of more normal or primitive habitus. There are many characters to support such a separation. The peculiar plastron with its callosities and the unique modification of the anterior elements (Williams and McDowell:1952); the skull with its peculiar intermaxillary foramen; the singular fragmented basal plate of the hyoid; the amazing connection of cervical column and dorsal vertebrae (by zygapophyses only); the sickle-shaped scapula; the unique hyperphalangy of the digits; the remarkable penis; the absence of a urogenital sinus, etc., are a formidable complex of features, by any one of which a trionychid may be recognized.

A full analysis of the Trionychidae, setting up phyletic lines and considering carefully both fossil and Recent forms, has not yet been attempted. Yet there are indications such an analysis is less difficult than reputed. It is true that the herpetologist dealing only with externals, is perplexed by the lack of characters he can utilize, and is further disturbed by ontogenetic change (as in the shape and number of the plastral callosities), as well as by individual variation (as in the breadth of the maxillary triturating surfaces). In these turtles, however, even more than in others, it is necessary to go below the surface and, for example, use osteological characters. Consequently for every species we offer two descriptions, one of externals, including color, and a second dealing with its osteological characteristics.

When the osteology is taken into account the African species are remarkably distinct. We have not carried through a study of the osteological characters of the extra-African species, but preliminary explorations by one of us, and by previous workers, convince us of its practicality. Siebenrock (1902b), for example, has demonstrated the usefulness of plastral characters. He presents a key to the living trionychids based entirely on the plastron, also an atlas of plastral bone conformation. Both atlas and key are still very useful. In his key Siebenrock did not emphasize the number or shape of the callosities — very wisely, for it is the latter that (because of individual and age variation) are most likely to make use of his atlas difficult and deceptive. On the contrary, if attention is paid to the shapes and processes of the underlying bones, the characters employed by Siebenrock successfully separate all but the most closely related species. All the African species are clearly separable by their plastral characters.

The skulls of trionychids, to mention another area of osteological study that has proved rewarding in the African species, have not been exploited sufficiently. More attention has been paid to general shape and to the varying breadth of the maxillary triturating surfaces than to suture patterns and details of morphology which promise to be much more useful.

TABLE 8

Characters of the two sections of the Trionychidae

GROUP I	GROUP II
Trionyx; Pelochelys; Chitra.	*Lissemys; Cyclanorbis; Cycloderma.*
Plastron without cutaneous femoral valves.	Plastron with cutaneous femoral valves under which the hind limb may be concealed.
Sculpture characteristically of anastomosing ridges.	Sculpture more often tuberculate.
Nuchal bone without conspicuous ventral ridges, its posterior margin overlying the first pleural (costal bone).	Nuchal bone with a conspicuous ventral ridge on each side extending posterolaterally to underlie the first pleural (costal bone).
Hyo- and hypoplastra distinct.	Hyo- and hypoplastra fused.
Xiphiplastron gripping lateral prong of posteromedial process of hypoplastron.	Xiphiplastron gripping middle prong of the three prongs of the posteromedial process of hypoplastron.
Posterior border of pterygoids without an ascending process that makes sutural contact with the opisthotic.	Posterior border of pterygoids with an ascending process forming a suture with the opisthotic and greatly restricting the fenestra postotica.

Relationships and Grouping of the Living Trionychids

Since no thorough analysis of all living trionychids has been carried out, any discussion of relationships must necessarily be tentative. Nevertheless, it seems advisable to attempt to place the African species in their proper perspective within the family. Our approach is a conservative one. African trionychids, and the family as a whole, fall into two very distinct major groups which have often been separated as distinct subfamilies. The division, very clear-cut, is based on a conspicuous external character and several internal ones, as set out in Table 8.[1]

As Group I contains only a single African representative — *Trionyx triunguis* — it would be out of place here to discuss its subdivisions in detail. Our purpose is merely to indicate the probable position of *triunguis* in our *tentative* arrangement of the group, which may be subdivided as follows:

Subgroup 1. Relatively unspecialized species primarily Oriental in distribution, primitively with a dorsal pattern of large ocelli.

- A. Those with a preneural.
  1. *Trionyx hurum*
  2. *T. leithii*
  3. *T. nigricans*
  4. *T. gangeticus*
- B. Those with no preneural and with a mandibular symphysial ridge.
  5. *T. formosus*
  6. *T. cartilagineus*
- C. Those with no preneural but without a symphysial ridge.
  7. *T. subplanus*

Subgroup 2. Species with highly modified skulls, primarily Oriental in distribution.

1. *Pelochelys bibronii*
2. *Chitra indica*

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[1] Siebenrock (1907; 25 footnote) invites attention to a partial restriction of the fenestra postotica in *Dogania* (= *Trionyx*) *subplana* and *Trionyx sinensis* by a *descending* process of the opisthotic. This condition, which we have verified for *Trionyx subplanus*, differs strikingly from the condition in *Lissemys*, etc., in which the pterygoid forms an *ascending* process. However, in some *Trionyx triunguis* (see p. 429 and Fig. 54) the pterygoids may send up an ascending process like that of *Lissemys*, but in this case it fails to make contact with the opisthotic.

Subgroup 3. Relatively unspecialized species primarily extra-Oriental in distribution, primitively without a dorsal pattern of large ocelli.

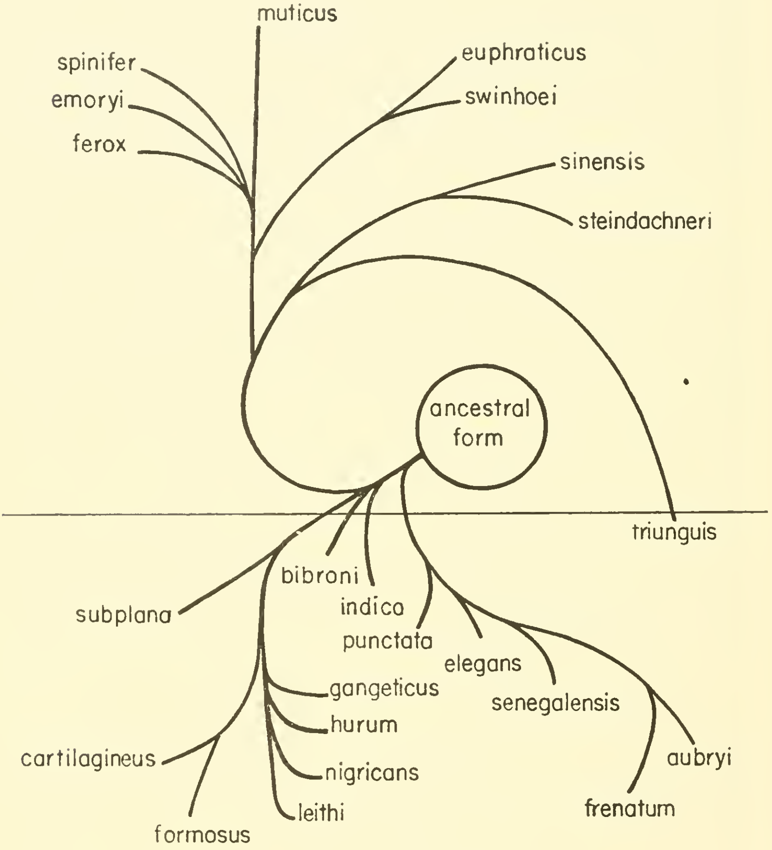

Fig. 50. Dendrogram of trionychid species relationships. The purely hypothetical horizontal line divides those species which may have evolved north of the ancient Tethys sea from those which may have evolved south of it.

(P. Washer del.)

A. Those whose 8th pleurals are typically not reduced.
    1. *Trionyx triunguis*
    2. *T. sinensis*
    3. *T. steindachneri*
B. Those whose 8th pleurals are typically partially reduced.
    3. *T. euphraticus*
    4. *T. swinhoei*
C. Those whose 8th pleurals are typically much reduced or absent.
    5. *T. ferox*
    6. *T. emoryi*
    7. *T. spinifer*
    8. *T. muticus*

This conception of the most probable relationships within the Trionychidae is presented as a dendrogram (see Fig. 50).

Trionyx triunguis, as indicated on the dendrogram, is phyletically quite remote from the other African trionychids. It and they represent two invasions of Africa. Curiously, however, so far as the available fossil record indicates, the two invasions may have been simultaneous. Both groups are clearly represented in the Lower Miocene, which offers the first record of trionychids in Africa.

An overall view of the characters of African trionychids is given in the following table.

In Group II there is, in addition to the two African genera, one Indian genus — *Lissemys. Lissemys,* while clearly a member of the group, seems not to be very closely related to *Cyclanorbis* or *Cycloderma.* From both, as well as from all other trionychids, it differs in the possession of peripheral ossifications (usually regarded as non-homologous with the peripherals of other turtles).

The African members of Group II appear to form a series of their own. Each species has its individual specialization and yet appears to form part of a sequence which, beginning with the most primitive form, is as follows: *Cyclanorbis elegans, C. senegalensis, Cycloderma frenatum, C. aubryi.* Alone of the African series, *Cyclanorbis elegans* retains prefrontal connection with the vomer (primitively present in all turtles; lost, except in this series, only in *Chitra* and the suborder Pleuro-

TABLE 9
Characters of the African Species of Trionychidae

triunguis	*elegans*	*senegalensis*	*frenatum*	*aubryi*
premaxillary bone small but distinct	premaxillary bone small but distinct	as in *elegans*	premaxillary bone apparently absent, at most scalelike	as in *frenatum*
distance from tip of premaxillary to orbit much greater than long diameter of the orbit	distance from tip of premaxillary to orbit less than the long diameter of the orbit	distance from tip of premaxillary to orbit greater than the long diameter of the orbit	distance from tip of premaxillary to orbit subequal to long diameter of the orbit	as in *frenatum*
height of orbit somewhat greater than the interorbital width	height of orbit about twice the interorbital width	as in *elegans*	as in *elegans*	height of orbit about one and one third the interorbital width
prefrontal bones meet the vomer	prefrontal bones meet the vomer	prefrontal bones not meeting vomer	as in *senegalensis*	as in *senegalensis*
intermaxillary foramen large, ovoid	intermaxillary foramen absent	intermaxillary foramen small, narrowed anteriorly	as in *senegalensis*	as in *senegalensis*
prechoanal part of vomer concealed by union of maxillary medial processes	prechoanal part of vomer concealed by union of maxillary medial processes	vomer exposed throughout its entire length or concealed	as in *elegans*	as in *elegans*
jugal enters orbit	jugal enters orbit	as in *elegans*	as in *elegans*	jugal excluded
jugal separated from or only narrowly in contact with parietal	jugal *narrowly* in contact with the parietal	as in *elegans*	jugal *broadly* in contact with the parietal	as in *frenatum*
neurals 8;	neurals 6-8 +	neurals 1-5 +	neurals 7-8 +	neurals 7-8 +
no preneural	preneural	preneural	preneural	preneural
callosities in adults 4-5.	callosities in adults 2-4	callosities in adults 7-9 or more	callosities in adults 7	as in *frenatum*
sometimes an azygous callosity in gular region	never any callosities in gular region	supernumerary callosities in gular region	callosities on preplastra and fused epiplastra	as in *frenatum*
xiphiplastral callosities always present	xiphiplastral callosities weak or absent	as in *elegans*	xiphiplastral callosities strongly developed	as in *frenatum*
xiphiplastra long, triangular	xiphiplastra posteriorly pointed	xiphiplastra posteriorly broad and notched	as in *senegalensis*	as in *senegalensis*
color of hatchling: head profusely spotted with lighter; throat spotted and vermiculated;	*color of hatchling:* head profusely spotted with yellow; throat vermiculated;	*color of hatchling:* head vaguely mottled; throat immaculate;	*color of hatchling:* head grayish with 5 lines; throat nearly immaculate;	*color of hatchling:* head light brown with 5 lines; throat indistinctly flecked;
carapace olive to dark brown, uniform or much speckled;	carapace green with irregular yellow blotches;	carapace gray-brown vaguely mottled;	carapace gray or green, nearly uniform;	carapace light brownish with a chocolate brown vertebral stripe;
plastron white, immaculate or with dusky vermiculations anteriorly	plastron spotted with yellow to periphery	plastron with a brownish blotch in centre, periphery immaculate	plastron whitish with small black blotches	plastron with two broad V-shaped, chocolate-brown markings, a small one on gular region, a larger one from axillae to tail
size of disk to 950 mm.	size of disk to 440 mm.	size of disk to 350 mm.	size of disk to 470 mm.	size of disk to 330 mm.

dira).[1] *C. senegalensis* lacks the vomer-prefrontal connection but, as in *elegans,* has a narrow postorbital bar. This bar is tremendously broadened in both species of *Cycloderma,* resulting in extensive contact between parietal and jugal, though in primitive fashion *C. frenatum* still retains the jugal entering the orbit. In *C. aubryi* the jugal is excluded from the orbit, thus completing the series of cranial modifications by one that is unique in the family.

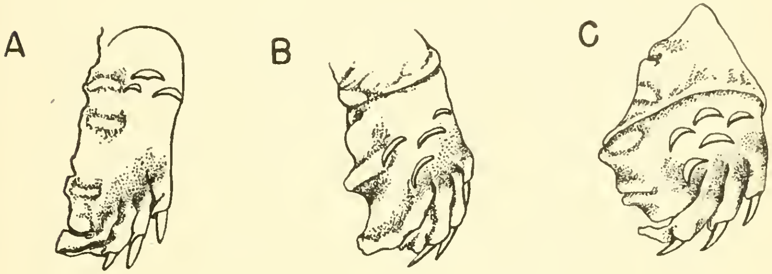

Fig. 51. Forefoot scalation in certain trionychids. *A, Trionyx triunguis* (M.C.Z. 16509); *B, Cyclanorbis elegans* (B.M.); *C, Cyclanorbis senegalensis* (Z.M.U.).

(P. Washer del.)

Key to the Trionychidae of Africa

1. Femoral flaps absent; nuchal somewhat overlapping second rib; hyo- and hypoplastra separate; lateral prong of posteromedial process of hypoplastron gripped by xiphiplastron; pterygoids not joining opisthotic; fenestra postotica not or not much restricted; head spotted. Range: Egypt and Eritrea south to Lake Rudolf, southwest to Lake Albert and Angola, northwest to Senegal......*Trionyx triunguis* Forskål (p. 3)

   Femoral flaps present; nuchal not overlapping second rib, more or less projecting under second pleural; hyo- and hypoplastra fused; middle prong of posteromedial process of hyo-hypoplastron gripped by xiphiplastron; pterygoids joining opisthotic, greatly restricting fenestra postotica 2

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[1] In trionychids the connection is mostly formed by ascending processes of the vomer meeting the prefrontals. In primitive turtles and in many modern forms (e.g. marine turtles), the prefrontal and vomer share about equally in this peculiar bony strut. In testudinids the connection is almost entirely formed from the prefrontals.

2. Head spotted or partly vermiculated, at least in young; postorbital arch narrower than diameter of orbit; preplastra long, angular; no trace of a xiphiplastral commissure .... 3 (*Cyclanorbis* Gray)[1]

   Head striped, at least in young; postorbital arch wider than diameter of orbit; preplastra short, straight; a xiphiplastral commissure present .... 4 (*Cycloderma* Peters)

3. Carapace of hatchlings with large yellow blotches; plastral area with a large dark central blotch profusely spotted with yellow, at least anteriorly; no trace of gular callosities at any age; xiphiplastra pointed posteriorly; prefrontal bones meeting vomer. Range: Sudan; Nigeria; Togo ....*Cyclanorbis elegans* Gray (p. 438)

   Carapace of hatchlings with small black spots; central plastral area more or less blotched with dark; gular callosities, 4 or more in adults, present even in the halfgrown; xiphiplastra broad and notched posteriorly; prefrontal bones not meeting vomer. Range: Sudan west through French Cameroon to Senegal .... *C. senagalensis* (Duméril and Bibron) (p. 443)

4. Carapace of hatchlings orange or orange brown with a narrow black vertebral line anteriorly; jugal bone excluded from orbit; in adults the azygous callosity is subcircular, large; hyo-hypoplastral callosities in contact with xiphiplastral callosities by long straight sutures. Range: Portuguese, French, and adjacent rivers of western Belgian Congo ....*Cycloderma aubryi* (Duméril) (p. 453)

   Carapace of hatchlings pale gray or leaden[2] without a vertebral streak; jugal bone enters orbit; in adults the azygous callosity is crescentic, subcrescentic or semilunar, and smallest of all the callosities; hyo-hypoplastral callosities separated from, or in contact with the xiphiplastral callosities by only a short suture. Range: Tanganyika Territory (Rovuma River and Lake Nyasa) southwest through Nyasaland (Lake Nyasa and Shire River) to Mozambique (Zambezi River and affluents) ....*C. frenatum* Peters (p. 459)

Genus TRIONYX Geoffroy

1809a. *Trionyx* Geoffroy, Ann. Mus. Hist. Nat. (Paris), **14**, p. 1. Type by original designation: *Trionyx aegyptiacus* = *Testudo triunguis* Forskål.

1830. *Aspidonectes* Wagler, Natür. Syst. Amphib., p. 134. Type by Stejneger's designation: *Trionyx aegyptiacus* Geoffroy = *Testudo triunguis* Forskål.

1835. *Gymnopus* Duméril and Bibron, Erpét. Gén., **2**, p. 472. New name for *Aspidonectes* Wagler.

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[1] A single juvenile specimen from the northwest shore of Lake Tanganyika will not key out even generically on the characters here used and may be a new form. See page 450.

[2] Green in Zambezi turtles according to Peters (1822a, pl. 1).

1835. *Platypeltis* Fitzinger, Ann. Wiener Mus., 1, pp. 109, 120, 127. Type by Fitzinger's 1843 designation: *Testudo ferox* Schneider.

1835. *Pelodiscus* Fitzinger, Ann. Wiener Mus., 1, pp. 110, 120, 127. Type by Fitzinger's 1843 designation: *Trionyx sinensis* Wiegmann.

1835. *Amyda* Fitzinger, Ann. Wiener Mus., 1, pp. 110, 120, 127. Type by original designation: *Trionyx subplanus* Geoffroy.

1843. *Potamochelys* Fitzinger, Syst. Rept., p. 30. Type by original designation: *Trionyx javanicus* Wiegmann = *Testudo cartilaginea* Boddaert.

1844. *Tyrse* Gray, Cat. Tortoises Brit. Mus., p. 47. Type by tautonomy: *Trionyx niloticus* Gray = *Testudo triunguis* Forskål.

1844. *Dogania* Gray, Cat. Tortoises Brit. Mus., p. 49. Type by monotypy: *Trionyx subplanus* Geoffroy.

1864c. *Rafetus* Gray, Proc. Zool. Soc. London, p. 81. Type by monotypy: *Testudo euphratica* Daudin.

1864c. *Aspilus* Gray, Proc. Zool. Soc. London, p. 83. Type by original designation: *Trionyx cariniferus* Gray = *Testudo cartilaginea* Boddaert.

1869c. *Landemania* Gray, Proc. Zool. Soc. London, p. 215. Type by monotypy: *L. irrorata* Gray = *Trionyx sinensis* Wiegmann.

1869c. *Fordia* Gray, Proc. Zool. Soc. London, p. 219. Type by monotypy: *F. africana* Gray = *Testudo triunguis* Forskål.

1869c. *Callinia* Gray, Proc. Zool. Soc. London, p. 221. Type by Stejneger's designation: *Trionyx spinifer* Lesueur.

1872. *Nilssonia* Gray, Ann. Mag. Nat. Hist. (4), **10**, p. 332. Type by monotypy: *Trionyx formosus* Gray.

1873. *Isola* Gray, Proc. Zool. Soc. London, p. 51, fig. 2. Type by monotypy: *Trionyx peguensis* Gray = *Trionyx formosus* Gray.

1873. *Ida* Gray, Proc. Zool. Soc. London, p. 55, fig. 7. Type by monotypy: *Trionyx ornata* Gray = *Testudo cartilaginea* Boddaert.

1873. *Oscaria* Gray, Ann. Mag. Nat. Hist. (4), **12**, p. 157. Type by monotypy: *O. swinhoei* Gray.

1880. *Yuen* Heude, Mém. Hist. Nat. Emp. Chinois, 1, p. 18. Type *fide* Stejneger: *Y. leprosus* Heude = *Oscaria swinhoei* Gray.

1880. *Psilognathus* Heude, Mém. Hist. Nat. Emp. Chinois, 1, p. 24, pl. ii. Type by monotypy: *P. laevis* Heude = *Trionyx sinensis* Weigmann.

1880. *Temnognathus* Heude, Mém. Hist. Nat. Emp. Chinois, 1, p. 25, pl. iii. Type by monotypy: *T. mordax* Heude = *Trionyx sinensis* Wiegmann.

1880. *Gomphopelta* Heude, Mém. Hist. Nat. Emp. Chinois, 1, p. 27, pl. iv. Type by monotypy: *G. officinalis* Heude = *Trionyx sinensis* Wiegmann.

1880. *Coelognathus* Heude (not of Hessling: 1852), Mém. Hist. Nat. Emp. Chinois, **1**, p. 29, pl. v. Type by monotypy: *C. novemcostatus* Heude = *Trionyx sinensis* Wiegmann.

1880. *Tortisternum* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 31, pl. vi. Type by monotypy: *T. novemcostatum* Heude = *Trionyx sinensis* Wiegmann.

1880. *Ceramopelta* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 33, pl. vii. Type by monotypy: *C. latirostris* Heude = *Trionyx sinensis* Wiegmann.

1880. *Coptopelta* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 34, pl. viii. Type by monotypy: *C. septemcostata* Heude = *Trionyx sinensis* Wiegmann.

1880. *Cinctisternum* Heude, Mém. Hist. Nat. Emp. Chinois, **1**, p. 36, pl. ix. Type by monotypy: *C. bicinctum* Heude = *Trionyx sinensis* Wiegmann.

1903. *Aspideretes* Hay, Proc. Amer. Philos. Soc., **42**, p. 274. Type by original designation: *Trionyx gangeticus* Cuvier.

1944. *Euamyda* Stejneger, Bull. Mus. Comp. Zool., **94**, p. 9. New name for *Amyda mutica* Agassiz.

Synonymy. The listing of *Amyda* Schweigger MS in the synonymy of his *Trionyx* by Geoffroy-Saint-Hilaire (1809a:15), neither constitutes the proposal of a new name nor validates it. Nor is *Amyda* validated by its brief mention by Oken (1816: Lehrbuch der Naturgeschichte, Teil 3, Abt. 2, 348). The first acceptable usage would appear to be that of Fitzinger (1835: 120) as listed above, and the first explicit designation of a type species that by Fitzinger (1843:30) — *Amyda subplana.* Since we regard *subplanus* as a species of *Trionyx,* the necessity of substituting *Amyda* Fitzinger, 1836, for the currently used *Dogania* Gray, 1844, does not arise.

In regard to the type of *Trionyx* Geoffroy, we concur with Schmidt (1953, Checklist of North American Amphibians and Reptiles, p. 108) in believing that Geoffroy, when citing *T. aegyptiacus* as giving an *exact idea* of the habitus and generic characters of *Trionyx,* was consciously and with full intent designating the type of that genus. Admittedly the word ''type'' was not used by Geoffroy, but we must point out that no species except the genotype can give an *exact idea* of the habitus and generic characters of a genus, and that this is the sole function and meaning of a genotype. Furthermore, we invite attention to evidence that Geoffroy's words were accepted as a type designation by at least one of his contemporaries. Bory de Saint Vincent (1828, Résumé d'Erpétologie ou d'Histoire naturelle des Reptiles [Paris], p. 77) has this to say: "C'est au célèbre professeur Geoffroy de Saint-Hilaire que l'on doit l'établissement de ce genre [*Trionyx*] dont le type fut une très singulière tortue du Nil que nous avons fait représenter dans notre planche 6ᵉ."

Definition. Cutaneous femoral flaps absent.

Skull without maxillary ridging; intermaxillary foramen moderate to large; prefrontal always with connection to vomer; jugal not or but scarcely in contact with parietal; postorbital arch narrower than diameter of orbit; pterygoids never joining opisthotic; fenestra postotica unrestricted.

Carapace without prenuchal bone, without peripheral ossifications; nuchal bone not notched laterally, no raised ventrolateral processes, its lateral margin tending to overlie the second rib; between the first pleurals are 1 or 2 neurals; neurals 7 to 9; pleurals 7 or 8 pairs, the last one or two in contact medially.

Plastron with preplastra long and angular; hyo- and hypoplastra separate, the latter's posteromedial process with a prong that is inserted between the two anterior prongs of the adjacent xiphiplastron; callosities variable.

Range. North America; Africa; Asia.

Fossil record. A good record since the Cretaceous. First reported in Africa from the Lower Miocene of Kenya; first recorded in North Africa from the Pliocene; present in the western portion of North Africa in the Pleistocene.

TRIONYX TRIUNGUIS (Forskål)

1775. *Testudo triunguis* Forskål, Descr. Anim. Avium. Amphib., p. ix: Nile River.
1789. Gmelin, 1039.
1792. Schneider, 280.
1809a. *Trionyx aegyptiacus* Geoffroy, Ann. Mus. Hist. Nat. (Paris), **14**, p. 12, pls. i-ii: Nile River, Egypt.
1809b. Geoffroy, 368 (proof of priority over 1809a unobtainable).
1812. Schweigger (part), 286, 328, 364.
1814. Schweigger (part) (reprint of 1812), 16.
1820. Goldfuss, 179.

1820. Merrem, 20.
1824. Mohring (on osteology: not seen).
1827a. Geoffroy, 115, pl. i, figs. 1-1′.
1828. Bory de Saint Vincent, 77.
1829. Bory de Saint Vincent, 2, pl. vi.
1829. Guérin, 6, pl. i, fig. 7 (as *Tryonix*).
1835. Rüppell, 3, footnote.
1856a. Duméril, 377.
1856. Lichtenstein and Martens, 1.
1857. Jan, 36.
1860. Duméril, 168, footnote.
1862b. Peters, 271.
1862a. Strauch, 175.
1865. Strauch, 126.
1870a. Steindachner, 326.
1874. Reichenow, 298.
1877. Bruhl, pl. xxxiii, figs. 9, 13; pl. xxxiv, figs. 7, 10.
1880. Boettger, 208.
1880. Bruhl, pl. lxix, figs. 5-6 (skull).
1880b. Vaillant, 797.
1880c. Vaillant, 54, pl. xxx, fig. 14.
1887. Lortet, 24.
1897. Sjöstedt, 33.
1905. Barbier, 96.
1831c. *Trionyx Niloticus* "Shaw", Gray, Syn. Rept., p. 46: Nile River.
1831b. Gray, 18.
1835. Temminck and Schlegel, 31.
1845b. Rüppell, 298.
1855. Gray, 68.
1867. Baker, 44, 203, 374 (as *Trionis*).
1882a. Müller, F., 164.
1882. Pechuël-Loesche, 277.
1929. Worthington, 123.
1835. *Gymnopus aegyptiacus* Duméril and Bibron, 484.
1851. Duméril and Duméril, 22.
1851. Guichenot, 190.
1867a. Bocage, 218.
1884a. Rochebrune, 31, pl. iii, figs. 1-2.
1884b. Sauvage, 200.
1837. *Trionyx labiatus* Bell, Monog. Testudinata, text to col. pls. — (= xviii-xx): Sierra Leone.
1872b. Gray, p. 11, *in* Sowerby and Lear pls. lii-liv.
1843. *Aspidonectes Aegyptiacus* Fitzinger, 30.

1855. Fitzinger, 252.
1844. *Trionyx Mortoni* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, p. 120: Africa.
1844. *Tyrse nilotica* Gray, 48.
1864c. Gray, 88.
1870e. Gray, 108.
1872c. Gray, 27.
1873b. Gray, 84.
1873g. Gray, 470.
1859. *Aspidonectes aspilus* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 295: Ovenga and Rembo Rivers, Fernan Vaz (as Fernando Vas), Gabon.
1869c. *Fordia africana* Gray, Proc. Zool. Soc. London, p. 219: Nile River at Khartoum, Anglo-Egyptian Sudan.
1869b. Gray, 191.
1870. Gray, 100 (reprint of 1869c).
1873. Gray, 43, figs. 1a-1d.
1873b. Gray, 77.
1875a. *Trionyx triunguis* Peters, 196.
1876a. Peters, 117.
1877c. Peters, 611.
1882. Pechuël-Loesche, 277.
1889a. Boulenger, 254.
1889. Hesse, 261.
1890. Büttikofer, 437, 478.
1890. Strauch, 113.
1893a. Boettger, 16.
1893c. Matschie, 208.
1895a. Bocage, 7.
1896. Anderson, 95.
1896c. Boulenger, 17.
1897g. Boulenger, 277.
1897b. Mocquard, 5.
1897. Sjöstedt, 7.
1898. Anderson, 32, col. pl. iii.
1898. Jeude, 10.
1898a. Werner, 204.
1900b. Boulenger, 447.
1901. Gadow, 410.
1901c. Tornier, 68.
1902b. Siebenrock, 826, fig. 8.
1902c. Tornier, 665.

1902a. Werner, 348.
1904. Andersson, 9.
1906. Johnston, 820, 833.
1906a. Mocquard, 481.
1906a. Siebenrock, 827.
1908. Johnston, 929 (generic name only).
1908. Werner, 1826.
1909b. Pellegrin, 413.
1909a. Siebenrock, 600.
1910. Müller, L., 623.
1910. Sternfeld, 7, fig. 16.
1911a. Masi, 37.
1917. Sternfeld, 417.
1923g. Loveridge, 933.
1924b. Loveridge, 3.
1925b. Flower, 935.
1926a. Mertens, 152.
1927. Calabresi, 38.
1928b. Scortecci, 336.
1928b. Witte, 49.
1929. Flower, 51.
1929. Hummel, 376.
1930a. Scortecci, 216.
1932a. Parker, 229.
1933. Flower, 753.
1933m. Witte, 68.
1933. Worthington, 38, 189 (as *Trionix*).
1937a. Flower, 16, 37.
1937f. Loveridge, 489, 495, 503.
1943. Scortecci, 270, 283.
1948c. Cansdale, 71 (as *Trionyx* only).
1948. Deraniyagala, 29.
1950. Williams, 552.
1953. Durrell, 253, fig.
1884a. *Gymnopus aspilus* Rochebrune, 32.
1893. *Pelodiscus triunguis* Baur, 220.
1899. *Leathery tortoises* Ansorge, 289.
1919. *Amyda triunguis* Schmidt, 598, 601.
1930a. Barbour and Loveridge, 770.
1934a. Mertens and Müller *in* Rust, 12.
1940c. Mertens, 236, figs.1-5.
1955. Cansdale, 93, 104, fig. H6.
1948. *Trionyx triunguis rudolfianus* Deraniyagala, Spolia Zeylanica, **25**,

part 2, p. 30, fig. 5, pl. xii, fig. c: Ferguson's Gulf, Lake Rudolf, Kenya Colony.

1955. *Amyda triunguis triunguis* Hellmich, 11, 12, 15 (of reprint).

Synonymy. The young soft-shelled turtle, allegedly from the Gabon River, described by Strauch (1890:113, pl. iii, figs. 3-4) as *Trionyx vertebralis,* later proved to be a juvenile *Trionyx subplanus* Geoffroy, according to Siebenrock (1909:606).

Common names. Nile Soft-shelled Turtle (Flower:1929); Soft-shelled River-Turtle (Cansdale); *abibi* (Alua and Gang of West Nile:Pitman MS.); *abu geda* (Arabic on White Nile:Werner); *bekoom* (Liberia:R. P. Currie); *ger* (Alva and Gang for any aquatic turtle: Pitman MS); *gondo* (in Catumbela: Anchieta); *kunda* (Banziri: Johnston); *navingo* (Bagungu of Bunyoro: Pitman MS.); *neko* (Sango: Johnston); *terseh, tirse* or *tyrse* (Arabic: *fide* Anderson, Forskål and Geoffroy respectively; also *cirsé* or *thirsé: fide* Burton); *um diraga* (riverine Arabs: Flower).

Illustrations. Bell's fine colored plates (1837) of this species (as *labiatus*) are reproduced in Sowerby and Lear (1872:pls. lii-liv); equally good are the colored figures in Anderson (1898:pl. iii), reproduced in black and white as our Plate 15.

Description. Proboscis projecting, the distance from its tip to the orbit longer than orbital diameter in both young and adults; nostril with a papilla-like process projecting laterally from the median wall; forelimb with 3 sharp-edged, crescentic skin-folds on its anterior surface and two weal-like skin-thickenings (absent in young) on outer aspect; hind foot with another sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail very short, pointed, not projecting beyond the posterior leathery margin of the carapace.

Carapace of young with an indistinct keel and covered with tubercles arranged in more or less wavy longitudinal lines; carapace[1] of adults smoother in life but showing, when dried, the underlying bony sculpture; leathery margin relatively extensive, posteriorly extending well beyond tail.

Plastron of young smooth, without callosities, which are late in developing (not visible in a specimen [M.C.Z. 53573] with a carapacial length of 217 mm.); in adults absent on preplastra

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[1] A kyphotic shell from the mouth of the Catumbela River is mentioned by Mertens (1926a), more fully with illustrations (1940c).

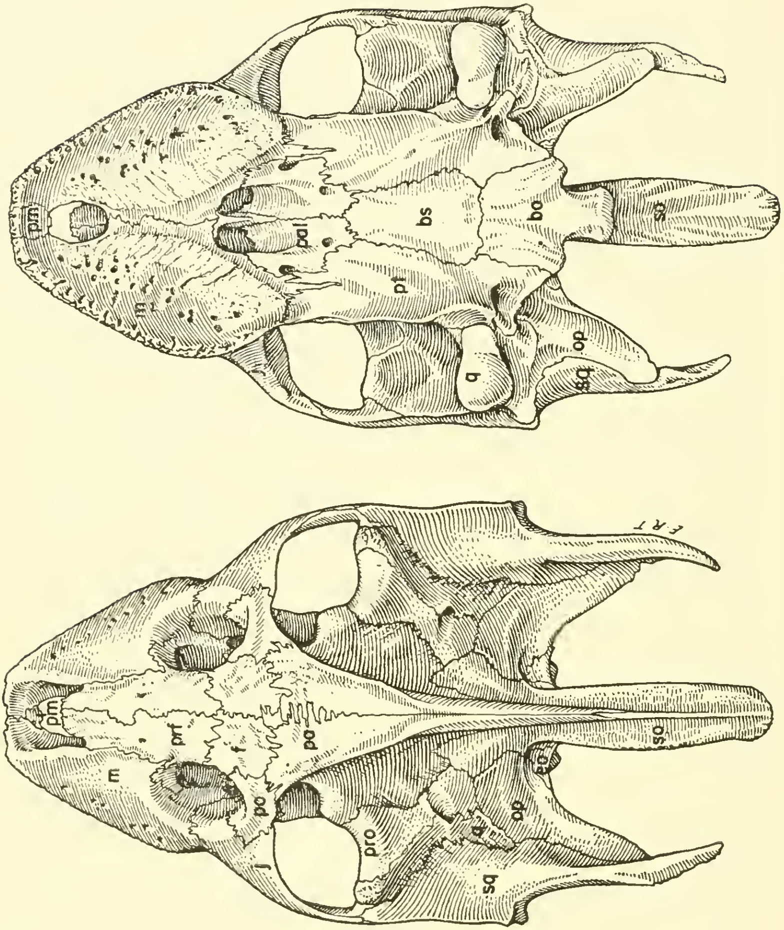

Fig. 52. Skull of *Trionyx triunguis* (B.M. 1947.3.6.12). x ⅔. *Bo* = basioccipital; *bs* = basisphenoid; *eo* = exoccipital; *f* = frontal; *j* = jugal; *m* = maxillary; *op* = opisthotic; *pa* = parietal; *pal* = palatine; *pm* = premaxillary; *po* = postorbital; *prf* = prefrontal; *pro* = prootic; *pt* = pterygoid; *q* = quadrate; *so* = supraoccipital; *sq* = squamosal.

(E. R. Turlington del.)

and the fused epiplastra, present on both hyo- and hypoplastra and on xiphiplastra; anterior edges of the hypoplastral callosities relatively straight; hypoplastral and xiphiplastral callosities not in contact; xiphiplastral callosities not in contact medially; no caudal or femoral flaps but a pronounced crural-caudal skinfold.

Osteological description. Skull. Distance between tip of premaxilla and orbit much greater than the long diameter of orbit; height of orbit greater than the interorbital width, which is subequal to the width of naris; premaxilla single, not separating maxillae underneath the naris, anteriorly bordering a large, ovoid, intermaxillary foramen that is laterally and posteriorly bordered by the maxillae, which are in contact medially for a distance greater than the length of the foramen; vomer stout, in contact with descending processes of the prefrontals, its interchoanal portion relatively short; choanae narrowed, narrower than the least distance between the maxillary triturating surfaces and not bordered by them; postorbital arch not half as wide as the long diameter of orbit; jugal not or but rarely meeting parietal, and then but narrowly; orbit entered by jugal which may, or may not, meet squamosal; squamosal crests thin, sharp, and curving medially; pterygoids sometimes approaching[1] but never meeting opisthotic, not restricting postotic fenestra; mandible without symphysial ridge, its symphysial width equalling or exceeding the long diameter of the orbit.

Carapace. Carapacial bones coarsely pitted and vermiculated; no prenuchal bone; nuchal bone not notched laterally, overlying the second rib; between the first pleurals a single neural; neurals 8; pleurals 8 pairs, the eighth (and sometimes the seventh) wholly or partially in contact medially.

Plastron. Preplastra widely separated, the anterior branch short, about half as long as the posterior; epiplastra fused, forming an acute or right angle; hyo- and hypoplastra distinct, the anteromedial process of the latter with 3 to 5 prongs, medial process broad with several prongs, both medial and posteromedial processes usually united to form an extensive dentate margin;

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[1] The pterygoid sends up a triangular, tongue-like process which almost meets the opisthotic in a Lobito Bay turtle (A.M.N.H. 50724) and a second specimen (A.M.N.H. 36599) from "Africa." In another Lobito Bay turtle (A.M.N.H. 50723), as well as in B.M. and M.C.Z. material, this process does not exist.

xiphiplastra very long, triangular, medioanterially united by 2 or 3 prongs inserted into 3 or 4 notches, a long oval fontanelle intervenes in front of the posterior portions which are also in contact.

Callosities 4 (hyo-hypoplastral and xiphiplastral pairs) or 5 (an additional azygous element on the fused epiplastra), sculptured like the carapace, well developed but never completely covering the bones.

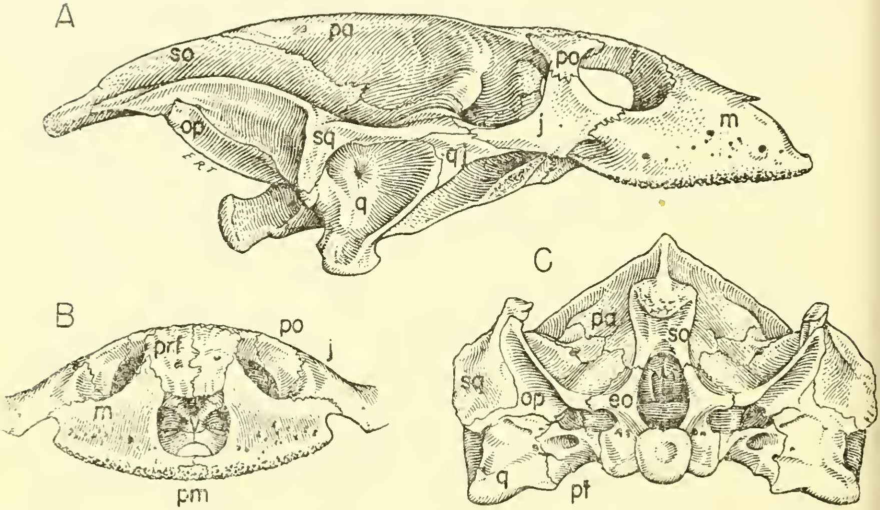

Fig. 53. Skull of *Trionyx triunguis* (B.M. 1947.3.6.12) x ⅔. Letter symbols as in Figure 52 except *v* = vomer. *A*, Lateral view; *B*, anterior view; *C*, posterior view.

(E. R. Turlington del.)

Color. Carapace olive, dark olive, olive brown or dark brown, uniform or profusely speckled with dark-margined, white (yellow) spots, often well-marked in young, obscure or obsolete in adults; fleshy disk very narrowly edged with yellowish.

Plastral area white or creamy white, immaculate or with coarse, dusky vermiculations anteriorly; fleshy underside of disk dark, laterally with large, dark-bordered, light spots tending to become much smaller posteriorly, also edged with yellowish, either narrowly or presenting a scalloped appearance.

Head and limbs above dark, profusely spotted with lighter; throat of young dark with larger spots and vermiculations, of adults immaculate white or yellow; limbs below lighter, uniform, spotted, or vaguely vermiculate.

Size. Over-all measurements are discarded on account of the extensile neck. It is not clear whether Anderson (1898), when stating that this turtle "attains to a metre in length," was referring to over-all or carapace length. Carapace length of largest [1] 950 mm., from Gaboon River (A.H.A. Duméril:1860:169); another with a length of 800 mm. was taken in Lake Albert (Witte:1928b); a third was 780 mm., breadth 570 mm., from Lake Fisherman (Büttikofer:1890); a Nile specimen of 680 mm., breadth 540 mm., was caught near Duem (Siebenrock:1906a).

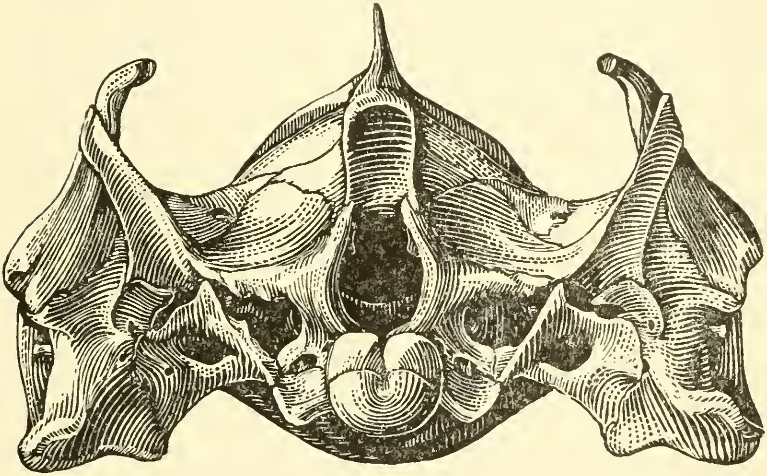

Fig. 54. Skull of *Trionyx triunguis* (A.M.N.H. 36599). Occipital view to show the occasional presence of pterygoid ascending processes.
(S. McDowell del.)

A ♂ from Khartoum measured 630 mm., a ♀ from Giza 700 mm. (Flower:1933).

Weight. Largest of sixteen turtles taken in Lake Albert by Worthington (1929) weighed 80 lbs. (as 37 kilos.). The 950 mm.

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[1] If this is Duméril's meaning when he says: "sa longeur totale est de 1 m, 33 : le bouclier seul a 0 m, 95."

triunguis from the Gaboon weighed 65 lbs. (as 29.7 kilos.), yet the 780 mm. specimen from Lake Fisherman was 75 lbs. Possibly Baker (1867:44), who estimated the weight of one that he hooked (but which escaped before being landed) as "at least 100 lbs." is the source of Worthington's mentioning this weight (1933), but we do not know the basis for that of Mocquard (1906a), who puts the weight of this species as about "100 kilograms," i.e. 220 lbs.!!

Breeding. On March 13, 1928, a ♀ from Butiaba held 27 eggs with shells, measuring rather more than an inch in diameter; there were possibly 100 more about half that size developing in the ovary (Worthington:1929). During April, in Egypt, from 50 to 60 eggs are laid in a sandbank where they are hatched by the solar heat (Anderson:1898). On July 10, 1825, Rüppell observed a *triunguis* on an island in the Nile. The reptile was gently scraping the sand on the upper part of a steep bank. There, three inches below the surface, she deposited 29 spherical eggs, each having a diameter of about 1¼ inches (as 16 lines). The eggs were removed to the ship where, after only two hours, a single young one broke through the shell and began immediately to swim in a basin of water (Rüppell:1835:3).

Longevity. Twenty-five and a half years; another, still alive on 16.ix.36, had been in the London Zoo for 22 years, 1 month, 17 days (Flower:1937a).

Diet. Stomachs of the soft-shelled turtles captured by Rüppell (1835) held nothing but vegetable matter, viz. fragments of dates, gherkins and pumpkins. The reptiles came ashore at night in search of such food, according to local fishermen, who averred they would not take meat bait. This was confirmed by Rüppell's experience, for none took his meat bait but two were hooked when bread-dough was used. The stomachs of two turtles taken in Liberia contained many palm nuts; these Büttikofer (1890) thought they must procure on shore. Anderson (1898:33) thinks it highly improbable that "so thoroughly an aquatic animal as *Trionyx* should leave the water in search of food," and with Flower (1933), apparently regards Arab statements as to *triunguis* digging up and devouring crocodile eggs or hatchlings, as unproven. The allegation that they eat hatchling crocodiles dates back at least to Goldfuss (1820).

Anderson (1898) states that shellfish and fish appear to form their staple food, and these are eaten under water. Worthington (1929) agrees that mollusks and fish, both living and rotting, constitute their principal food, but from one he recovered scraps of goatskin and feet, from another ten large dragonfly nymphs.

Flower (1933), when feeding captive *triunguis* on live bolti fish (*Tilapia*), observed that if a turtle seized a fish in its jaws that was too large to be swallowed whole, it impaled the fish on its foreclaws, tore off the head, and employed its forefeet in finishing the meal. One captive ate ham (Hesse:1889); more unfortunate was the type of *labiatus* which refused all food and died after three weeks (Bell:1837).

Enemies. Being regarded as a delicacy, the Nile Soft-shelled Turtle has been hunted for hundreds, possibly thousands of years, yet a few manage to survive in Egypt. In the Sudan certain natives specialize in the capture of these reptiles when they come ashore to lay their eggs (Flower:1933). References in the literature reveal that the species is preyed upon by Africans in many parts of its range. In the Gold Coast they are sometimes taken in cane fish traps, or the larger turtles are hooked by bottom fishers (Cansdale:1948c).

Durrell (1953) reports that the flesh, when stewed, was "most palatable," tasting "like a rich and slightly oily veal." Baker (1867:374), who removed upwards of a hundred eggs from one of the turtles he hooked, regarded the flavor of resulting omelettes as "rather strong."

Near Kasenyi, Lake Albert, Africans do not eat *triunguis* — possibly for superstitious reasons — and allegedly release any turtles that become entangled in their nets, as P. Janseens informed Dr. J. P. Chapin (*fide* label of vii.1937 on A.M.N.H. 60263).

By stretching the untanned skin of a fish over a turtle carapace, Africans convert it into a guitar (Baker:1867:203). Anderson (1898:33:footnote) quotes Prospero Alpini as saying, in 1735, that the larger carapaces were utilized for making shields, and adds that the practice still persisted in Nubia.

Defense. Sir Samuel Baker (1867:44) relates how, using a strip of glistening perch on a stout hook fitted to treble-twisted wire, he caught an enormous turtle "at least 100 lbs. weight."

However, when his Arab assistant drew the reptile, struggling and snapping, close to the steep bank, its jaws cut through the triple brass wire as with shears.

Durrell (1953) states that the jaws of a decapitated turtle snapped on, and splintered, a piece of wood. Hesse (1889) writes of one snapping at his fingers. According to Bell (1837) the movable and extended coriaceous margin of the carapace enabled the type of *labiatus* to conceal itself in very shallow mud in much the same manner as would a flounder or plaice.

Temperament. Vicious and always ready to bite (Cansdale: 1948c).

Habits. Soft-shelled Turtles run extremely fast when taken out of the water, according to Baker (1867:374) who landed three. A ♀ in the Giza Zoological Gardens frequently travelled from one pond to another. To do so she had to climb a metre-high, vertical fence of wire netting and, after gaining the top, flop down on the farther side (Flower:1933). A very small turtle surprised Worthington (1933:38) by climbing from a bucket. He describes them as wallowing in the crater lakes of an island in Lake Rudolf, where he landed a fifty-pounder accidentally hooked by one of its feet. When occasion demands, however, these turtles can swim fast in their chosen element (Hesse:1889).

Habitat. Ponds, lakes and rivers, but Auguste Duméril (1860: 168:footnote) records a *triunguis* with a carapace length of 950 mm., and weighing 29.7 kilograms, as having been taken in the ocean about 3 or 4 km. from the mouth of the Gaboon River. The collector did not believe such an able swimmer as *Trionyx* could have been carried so far by the river in flood.

However, Flower (1933:754) believes that when the Nile is in spate these turtles are carried into the Mediterranean along with the carcasses of cattle and donkeys, and so up the Palestine coast by the powerful inshore current.

Localities. Egypt:[1] Embaba district, Giza Province; Ezbet Semeda Saleh, Fayum Province; Kom Ombo, Aswan Province; Nile near Cairo; Philae; Wadi Halfa. *Sudan:* *Atbara village (U.S.N.M.); Berber Province; Blue Nile; Delladilla, deep in Base; Dongola; Duem; Halfa Province; Khartoum; Kulgeila,

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[1] For discussion of questionable records, see Flower (1933).

Dongola Province; Roseires (Rosairos in B.M.), Blue Nile; Sennar; Shandi; *Sul River; Upper Nile (1873). *Eritrea:* Asmara; Setit River (Fiume). *Ethiopia:* (as Abyssinie:1851) Lake Tana (Zana). *Somalia:* Ganana; Lugh. *Uganda:* Butiaba, Lake Albert. *Kenya Colony:* Ferguson's Gulf, Lake Rudolf; Kaliokwell River Mouth, Lake Rudolf. *Angola:* Benguela; Cuanza; *Cunga; Catumbela; Loanda; *Lobito Bay (A.M.N.H.). *Cabinda:* Chinchoxo. *Belgian Congo:* *Congo River at Lukolela (A.M.N.H.); *Lake Albert at Kasenyi (A.M.N.H.); Mahagi Port; Mayombe (Mayumbe). *French Equatorial Africa:* Bilchem; Fernan Vaz (Fernand Vas); *Gabon River; Kuilu River below Bumina; Lambarene; Loango Coast; Ogoue (Ogowe); Ovenga River; Rembo River. *French Cameroon:* Dibongo, near Edea; Lake Ossa; *Sakbayeme. *British Cameroon:* Bonge, Meme River; Lake Soden; Ossidinge. *Togo:* Kete Krachi (Kratje). *Gold Coast:* Accra; Birrim, tributary of Pra River. *Liberia:* Fisherman Lake; Grand Bassam (G. Massam); *Saint John River near Gbanga; Saint Paul River near Muhlenberg Mission, Mt. Coffee. *Sierra Leone:* *Wanje River near Gbap; *near Kale; *near Subu. *Portuguese Guinea:* Bissao (Bissau). *Gambia. Senegal:* Dagana (1870). *French West Africa:* Bilchem on Niger-chad frontier.

Range. Egypt and Eritrea south to Lake Rudolf, southwest to Lake Albert and Angola, northwest to Senegal. Accidental along Palestine coast of Asia Minor (cf. Flower:1933).

Erroneously included in the fauna of Lake Victoria by Loveridge (1924b) on the basis of alleged remains in the Miocene deposits of Karungu Bay, Lake Victoria, for, as pointed out by Worthington (1929) no living *triunguis* has been taken above the Murchison Falls, White Nile.

Werner (1924a:269), unaware of any record for *triunguis* above Duem on the White Nile, suggests that it occurs only in the lower and middle reaches of that river, besides the entire length of the Blue Nile. Werner makes no mention of its presence in Lakes Albert and Rudolf, and thinks that in the Upper Nile, Sobat River, and Bahr el Ghazal, *Trionyx* is replaced by *Cyclanorbis*.

Genus CYCLANORBIS Gray

1854. *Cyclanorbis* Gray, Proc. Zool. Soc. London, 1852, p. 135. Type: *petersii* Gray (by monotypy) = *senegalensis* (Duméril and Bibron).

1856. *Cyclanosteus* Gray, Proc. Zool. Soc. London, 1855, p. 201. Type: *petersii* Gray (designation by Günther 1865, in Zool. Rec. for 1864).

1865e. *Tetrathyra* Gray, Proc. Zool. Soc. London, p. 323. Type: *petersii* Gray (by monotypy).

1870e. *Baikiea* Gray (not *Baikia* Gray: 1865), Suppl. Cat. Shield Rept., Part 1, p. 114. Type: *elegans* Gray (by monotypy).

Definition. Cutaneous femoral flaps present, permitting concealment of the hind limbs.

Skull without maxillary ridging; intermaxillary foramen small or absent; prefrontals with or without connection with the vomer; jugal narrowly in contact with parietal; postorbital arch narrower than diameter of orbit; pterygoids joining opisthotic, greatly restricting fenestra postotica.

Carapace with prenuchal bone present or absent, without peripheral ossifications; nuchal bone not notched laterally, ventrally with raised posterolateral processes which tend to underlie the first pleurals, between which are two neurals; neural number variable; pleurals 8 pairs, one to all meeting medially.

Plastron with preplastra long and angular; hyo- and hypoplastra fused, their posteromedial process with 3 prongs between which are inserted the 2 anterior prongs of the adjacent xiphiplastron; callosities variable in number, present or absent on gulars.

Range. Southern Sudan west to Senegal.

Fossil record. No fossils certainly identifiable; however, see under *Cycloderma.* The fragment reported by Dacqué (1912: Geol. Pal. Abhandl.:14:322) is at present indeterminable, as Siebenrock suggested when consulted by Dacqué.

Remarks. Both in skull and shell, as a glance at the table on p. 418 will show, the two species of *Cyclanorbis* are strikingly different. These differences, however, reflect the relative primitiveness of *elegans* and relative specialization of *senegalensis*, but the two are still closer to one another than to any other African trionychids. Nevertheless, should it ever seem desirable to separate them generically, the name *Baikiea* Gray is available for *elegans* while the type of *Cyclanorbis* is *senegalensis.*

C. senegalensis offers no problems at the species level, though ontogenetic changes in the callosities induced Gray to propose names which he very soon synonymized. On the other hand, our identification of *oligotylus* with *elegans* clarifies a muddle of names that began in 1864 when Gray described and figured a skull from Gambia as being possibly that of an adult *senegalensis.* Later Gray associated this skull and similar ones with the mottled juveniles which he described as *Baikiea elegans.* This action was reversed by Boulenger (1889a:272) who returned the skulls to *senegalensis,* restricting *elegans* to the two young cotypes described by Gray. In consequence, Siebenrock (1902b:810), accepting Boulenger's verdict without seeing the British Museum skulls, described a new species *oligotylus,* based on an adult shell.

The persistence of this confusion till the present, is largely attributable to the absence of an adequate ontogenetic series. While there is still no such series of this species, more material is now available and the situation in the freshwaters of north central Africa appears to be as follows:

In this region, so far as is known, there are *only two* kinds of juvenile trionychids with femoral flaps. The two are readily distinguished by color and pattern. One of these is clearly *elegans,* the other is definitely *senegalensis.*

So far as known, there are *only two* kinds of adult cyclanorbide shells from this region. They differ in maximum size, number of neurals [1] (and correspondingly in the number of pleurals in contact), the extreme development of callosities in one versus their great reduction in the other. One corresponds to Siebenrock's description of *oligotylus,* the other is definitely *senegalensis.*

Similarly there are *only two* kinds of adult cyclanorbide skulls known from this region. The larger are clearly referable to *oligotylus* but are also identical with the large skulls which

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[1] We consider that size in conjunction with the neural number is a good guide for the separation of the two species. Thus Werner's Mongalla collections reported on by Siebenrock (1906a) and Werner (1924a) separate readily into two series — all the large shells having 6 or more neurals, all the smaller ones 5 or less. Neural number does not increase during ontogeny.

formed part of Gray's concept of *elegans;* the smaller are definitely *senegalensis.*

At each age level there is therefore good evidence for the existence of *only two* cyclanorbide turtles in north central Africa. This has become increasingly clear over the years and the newer collections have been identified on this basis. Thus for some time the British Museum has been labeling its strongly mottled cyclanorbide juveniles *oligotylus,* correctly assuming that they were juveniles of the large adults they had also received. It is only because no comparison with the juvenile cotypes of *elegans* was made that the identity of *oligotylus* and *elegans* has remained so long undiscovered.

CYCLANORBIS ELEGANS (Gray)

1864c. *Cyclanosteus senegalensis* (adult ?), Gray (part: omit figs. 16-18 only), 97, figs. 19-21.
1865d. *Tetrathyra baikii* Gray (part: omit shell), 205.
1865e. Gray (part: omit shell), 324 (reprint of 1865d).
1869c. *Baikica elegans* Gray, Proc. Zool. Soc. London, p. 222, pl. xv, fig. 2: Africa (West ?).
1870e. Gray (part: omit *C. senegalensis* var. *callosa*), 114, fig. 39.
1873. Gray, 69.
1873b. Gray, 86.
1889a. *Cyclanorbis elegans* Boulenger, 272.
1909a. Siebenrock, 594.
1919. Schmidt, 601.
1934a. Mertens and Müller *in* Rust, 12.
1889a. *Cyclanorbis senegalensis* Boulenger (part: not of D. and B.), 272 (cotypes r, s, t of *Baikica elegans*).
1897. Siebenrock, 248, pl. ii, fig. 5; pl. iv, fig. 20.
1901c. Tornier, 68 (material lost, but agrees with *elegans* with possible exception of Jendi specimen).
1902b. *Cyclanorbis oligotylus* Siebenrock, Sitzb. Akad. Wiss. Wien, 111, pp. 810, 842, fig. 17: Nubia (Upper Nile?).
1905a. Siebenrock, 465, fig. 2.
1906a. Siebenrock, 838, fig. 8.
1908. Werner, 169.
1909a. Siebenrock, 594.
1912b. Werner, 493.
1919. Schmidt, 601.
1924a. Werner, 269.
1934a. Mertens and Müller *in* Rust, 12.

Synonymy. Further citations of "*baikii* (part)" will be found under *Cyclanorbis senegalensis.*

Common name. Nubian Soft-shelled Turtle.

Description of hatchling.[1] Proboscis projecting, the distance from its tip to the orbit (not eye) greater than the orbital diameter; upper lips meeting in front to form a flat arch; nostril with a papilla-like process projecting from the median wall; forefoot with 4, sharp-edged crescentic skinfolds on its upper surface, another indistinct weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe: tail rudimentary, not projecting beyond the posterior rim of the carapace.

Carapace of hatchling with a moderate vertebral keel and numerous, raised, rather wavy, longitudinal lines comprised of small individual tubercles anteriorly converging towards a strongly tubercular nuchal area; leathery margin posteriorly smooth, not extensive, scarcely extending beyond the tail.

Plastron of hatchling smooth, without callosities, femoral (but no caudal) flaps permit concealment of hind limbs.

Osteological description. Skull. Distance between tip of premaxilla and orbit greater than the long diameter of orbit; height of orbit about one and one-third to one and one-half times the interorbital width, which is less than the width of naris; premaxilla single, not separating maxillae underneath the naris; behind the premaxilla the maxillary triturating surfaces meet, their inward extensions closing or partly closing over the intermaxillary foramen; behind the triturating surfaces more dorsal flanges of the maxillae meet mesially ventral to the vomer for a distance greater or less than the palatal length of the premaxilla; vomer slender, in contact with the prefrontals, its interchoanal portion moderately long; choanae only slightly narrowed by inward extensions of the triturating surfaces of the maxillae; postorbital arch somewhat more than half the long diameter of the orbit; orbit entered by jugal, which is narrowly in contact with the parietal; squamosal crests long, sharp, straight or incurved; pterygoids meeting opisthotic, greatly restricting postotic fenestra; mandible without symphysial ridge, its ventral symphysial width less than the diameter of the orbit.

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[1] Based on a Khartoum specimen (B.M. 1909.3.25.3).

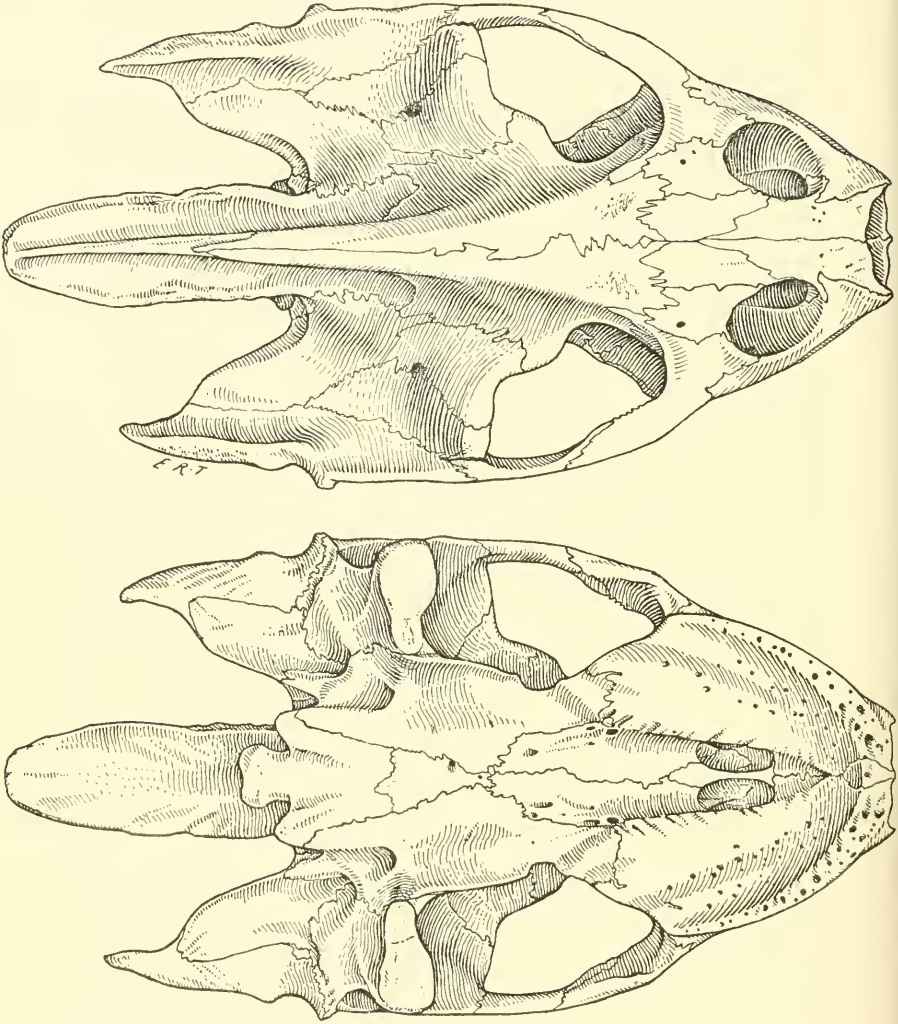

Fig. 55. Skull of *Cyclanorbis elegans* (Cotype. B.M. 65.5.9.22 = 1947. 3.6.28), x ⅔. Dorsal and ventral views.

(E. R. Turlington del.)

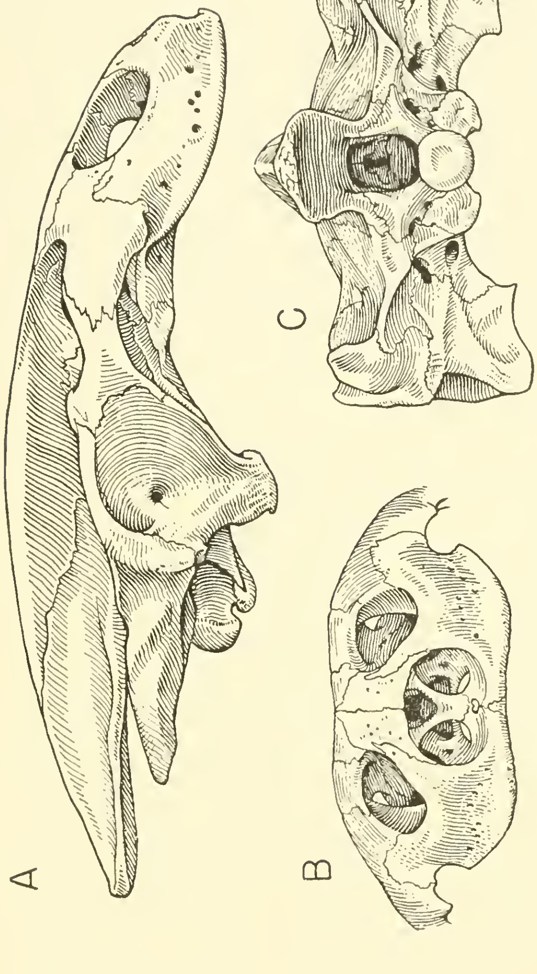

Fig. 56. Skull of *Cyclanorbis elegans* (Cotype. B.M. 65.5.9.22 = 1947. 3.6.28), x ⅔. *A*, Lateral view; *B*, anterior view; *C*, posterior view. (E. R. Turlington del.)

Carapace. Carapacial bones distinctly granulated; no prenuchal bone; nuchal bone not notched laterally but with multiple digitations underlying to a small extent the first pleurals, between which are two neurals; neurals 8 or 9, forming a continuous series, or the last two separated; pleurals 8 pairs, the eighth in contact medially.

Plastron. Preplastra widely separated, the anterior branch long, longer than the posterior; epiplastra fused, forming an acute angle; hyo- and hypoplastra fused, their anterior border straight or somewhat concave, *not* convex, posterior border of this compound bone very deeply excavated, anteromedial process with indistinct prongs; medial process short, only slightly projecting, posteromedial process with only 3 prongs between which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra rodlike, anteriorly broader, nowhere in contact though converging posteriorly, neither notched nor broad but pointed posteriorly.

Callosities 2 or 4, sculptured like the carapace; usually 2 on the hyo-hyoplastra only, covering most of these bones but widely separated medially; occasionally small callosities on the xiphiplastra.

Color. Carapace of hatchling [1] dark olive brown with large irregular blotches of yellow, the periphery sometimes with a few, scattered, somewhat smaller, roundish, yellow spots. Carapace of adults light brown to olive green, the periphery spotted and vermiculated with light green.

Plastron of hatchling yellowish, its central area dark, profusely spotted with lighter, not, or only sometimes, extending to the periphery; fleshy underside of disk edged or spotted with yellow. Plastron of adults dirty yellow, obscurely blotched with darker.

Head and neck of hatchling gray brown above, anteriorly spotted with lighter, posteriorly darker and unspotted; chin and throat anteriorly vermiculated; neck below, yellow, immaculate; limbs uniform or mottled with yellow. Head of adults above dark brown with light green vermiculations; temporal region olive green; neck lighter, speckled and spotted with yellow; throat and neck below, uniformly yellow.

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[1] Checked by a Khartoum specimen (B.M. 1909.3.25.3) with carapace length of 67 mm., and breadth of 50 mm.

Size. Carapace length, including fleshy margin, of *oligotylus* type, 605 mm., its breadth 465 mm., its height 150 mm.; disk of same specimen 440 mm., breadth 400 mm.; exceeded by a dorsal disk from Mongalla with a length of 490 mm. (Siebenrock:1906).

Enemies. At Mongalla, on the Bahr el Jebel, thirteen *Cyclanorbis* carapaces, representing both species, were purchased by Werner, but he could not get the Bari tribesmen to part with an entire turtle. Even the plastron and fleshy margins were sought after for culinary purposes (Siebenrock:1906).

Localities. Sudan: Bahr el Jebel at Mongalla; Nubia; Sobat River at Khor Attar; Upper Sobat at Nasser; White Nile at Khartoum and at *Tonga. *French Equatorial Africa:* Schari River near Fort Archambault (V.M.). *Nigeria:* Niger River at Lohata, Kabba Province. *Togo:* Kete Krachi (Kratje); Mango (Mangu); Yendi (Jendi).

Range. Sudan; Nigeria; Togo.

CYCLANORBIS SENEGALENSIS (Duméril and Bibron)

1835. *Cryptopus Senegalensis* Duméril and Bibron, Erpét, Gén., **2**, p. 504: Senegal.

1851. Duméril and Duméril, 23.

1844. *Emyda senegalensis* Gray, 47.

1855. Gray, 64.

1860e. Gray, 316.

1854. *Cyclanorbis Petersii* Gray, Proc. Zool. Soc. London, 1852, p. 135: Gambia River, Gambia.

1855. Gray, 69.

1855. *Cyclanosteus Petersii* Gray, 64, pl. xxix.

1860e. Gray, 315.

1860. *Cycloderma senegalense* Duméril, 168.

1865. Strauch, 131.

1862a. *Cycloderma Petersii* Strauch, 56.

1864c. *Cyclanosteus senegalensis* Gray (part: omit figs. 19-21), 95, figs. 16-18.

1870d. Gray, 717, pl. xliii.

1872c. Gray, 27.

1873. Gray, 70.

1873b. Gray, 87.

1884a. Rochebrune (ignored).

1865d. *Tetrathyra baikii* Gray (part: omit young and skulls), Ann. Mag. Nat. Hist. (3), **16**, p. 205, fig. —: ? Niger River, West Africa.

1865e. Gray, 324, fig. — (reprint of 1865d).
1873. Gray, 70.
1873b. Gray, 86.
1884a. Rochebrune, 35 (ignored).
1865f. *Cyclanosteus senegalensis* var. *equilifera* Gray, Proc. Zool. Soc. London, p. 423, fig. 2: Niger River, West Africa.
1870e. Gray, 113, fig. a.
1865f. *Cyclanosteus senegalensis* var. *normalis* Gray, Proc. Zool. Soc. London, p. 423: Niger River, West Africa.
1865f. *Cyclanosteus senegalensis* var. *callosa* Gray, Proc. Zool. Soc. London, p. 423, fig. 1: Niger River, West Africa.
1870e. Gray, 113, fig. 38.
1884a. *Tetrathyra vaillantii* Rochebrune, Faune Senegambie, Reptiles, p. 36, pl. iv, figs. 1-2: Senegal (localities unreliable).
1889a. *Cyclanorbis senegalensis* Boulenger (part: omit *Baikiea elegans* cotypes), 271.
1898. Siebenrock, 425.
1899. Siebenrock, 566.
1900. Flower, 967.
1902b. Siebenrock, 839, fig. 16.
1905a. Siebenrock, 467.
1906a. Siebenrock, 835, fig. 7.
1908. Werner (1907), 1826, 1924.
1909a. Siebenrock, 594.
1910. Müller, L., 624.
1910. Sternfeld, 8.
1912b. Werner, 493.
1913. Siebenrock, 43, fig. 22.
1917. Sternfeld, 416.
1919. Schmidt, 601.
1924a. Werner, 269.
1925. Flower, 935.
1929. Flower, 54.
1934a. Mertens and Müller *in* Rust, 12.
1937. Andersson, 3.
1937a. Flower, 16.

Further citations of "*senegalensis*" and "*baikii* (part)" will be found under *Cyclanorbis elegans*.

Common names. Senegal Soft-shelled Turtle (Flower:1929); African Bungoma (Gray:1844).

Illustrations. Dorsal, ventral and lateral views of the shell are furnished by Gray (1855:pl.xxix), also the skull and jaws

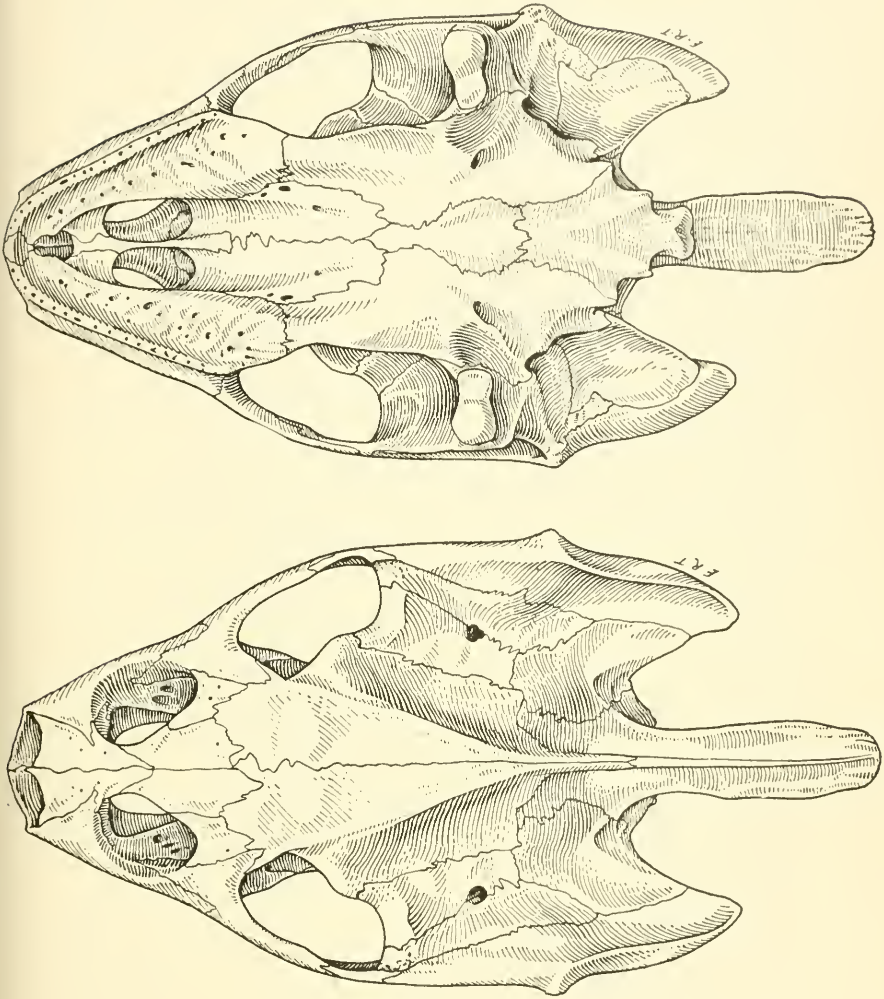

Fig. 57. Skull of *Cyclanorbis senegalensis* (B.M. 65.5.9.20), x ⅔. Dorsal and ventral views.

(E. R. Turlington del.)

(Gray:1864c:figs.16-18), while Siebenrock supplies dorsal (1913b:fig.22) and ventral (1902b:fig.16) views of the plastron.

Description of hatchlings and young.[1] Proboscis projecting, the distance from its tip to the orbit (not eye) shorter than, subequal to, or greater than the orbital diameter; nostril with papilla-like process projecting upwards from its infra-median corner; upper lips meeting in front to form a flat arch; forefoot with 5 or 6, sharp-edged, crescentic skinfolds on its upper surface (see Fig. 51*C*), another indistinct weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary, not projecting beyond the posterior rim of the carapace.

Carapace of young with a moderate vertebral keel and numerous, raised, rather wavy, longitudinal lines comprised of small individual tubercles anteriorly converging toward a strongly tubercular nuchal area, leathery margin posteriorly smooth, not extensive, scarcely extending beyond the tail.

Plastron of young, smooth, without callosities; femoral and caudal flaps permit concealment of hind limbs and (probably) tail.

Osteological description. Skull. Distance between tip of premaxilla and orbit greater than the long diameter of orbit; height of orbit about twice the interorbital width, which is less than the width of naris; premaxilla single, not separating maxillae underneath the naris; inward extensions of the maxillary triturating surfaces anteriorly narrowing the small intermaxillary foramen, almost excluding the premaxillae from its medio-anterior margin, elsewhere bordering the foramen (except sometimes medioposteriorly where the maxillae may be separated by the vomer, which then also separates them behind the foramen); length of the foramen subequal to its distance from the anterior choanal margins; vomer slender, without ascending processes to prefrontals; its interchoanal portion moderately long; choanae bordered by the triturating surfaces, postorbital arch about equal to half the long diameter of the orbit; orbit broadly entered by jugal, which is in contact with the parietal; squamosal crests short and blunt; pterygoids meeting opisthotic, greatly restricting postotic fenes-

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[1] Based on two Maccarthy Id. hatchlings (B.M. 1901.7.16.26-27), a hatchling and two young from Togo (in the Berlin Museum), and seven specimens from the Schari River near Fort Archambault, French West Africa.

tra; mandible without symphysial ridge, its symphysial width less than the long diameter of the orbit.

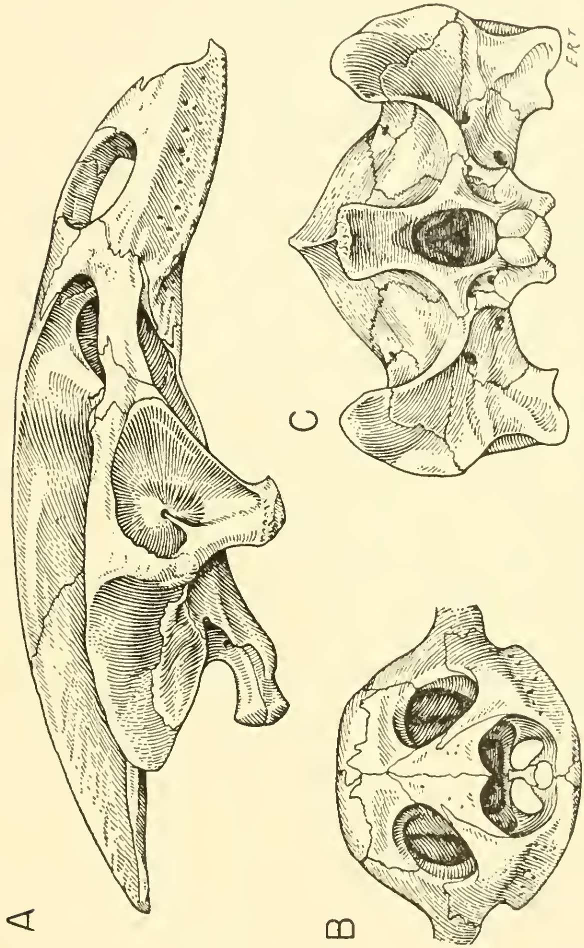

Fig. 58. Skull of *Cyclanorbis senegalensis* (B.M. 65.5.9.20), x $\frac{4}{3}$. *A*, lateral view; *B*, anterior view; *C*, posterior view.

(E. R. Turlington del.)

Carapace. Carapacial bones rather finely granulated and vermiculated; a prenuchal bone in adults; nuchal bone not notched laterally, extending slightly below the first pleurals, between which are two neurals; neurals variable in number, not forming a continuous series; pleurals 8 pairs, a variable number in contact medially.

Plastron. Preplastra widely separated, the anterior branch longer than the posterior; epiplastra fused, forming an acute angle, their pointed posterior prong inserted in a deep notch which separates the rounded inner margin from the strongly convex anterior border of the fused hyo- and hypoplastra; posterior border of this compound bone very deeply excavated, the anteromedial process with several almost juxtaposed prongs, the medial process very short, scarcely projecting beyond the rim, the posteromedial process with only 3 prongs between which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra oblong, slightly wider at their anterior and posterior ends, with 1 or 2 notches posteriorly, converging posteriorly but nowhere in contact.

Callosities 7 to 9, sculptured like the carapace, extremely developed in adults except on the xiphiplastra where they may be absent, even in adults; regularly present anteriorly, but not overlying any bones, are two small, subquadrilateral callosities in contact medially; posteriorly these are in contact with the preplastral callosities, which are large oblique ovals in contact medially; fitting between the latter posteriorly is the forwardly directed apex of the fused epiplastra bearing a large triangular callosity; in this general anterior region additional callosities are sometimes present (*fide* Gray:1865d); hyo-hypoplastral callosities, covering almost the entire surfaces of these bones, nearly meet medially; xiphiplastral callosities poorly developed or absent.

Pointing out that the callosities increase in number and size with age, but that their development appears to proceed more slowly in the Nile than in West African rivers, Siebenrock (1906) states that the hypoplastral callosity changes in shape as it develops. This is borne out by the B.M. and Vienna material examined by E.E.W.

Thus while fully adult *senegalensis* have the hyo-hypoplastral callosity strongly convex anteriorly, as described above, in younger specimens the anterior edge of this element is straight — as in adult *elegans*. From the Schari River series in Vienna Museum it would appear that the anterior convexity occurs in specimens with a carapace length between 210 and 220 mm. But while the anterior convexity of the hyo-hypoplastral callosity is not developed in *senegalensis* with carapace lengths of 200 mm. or under, there is a greater development of all the callosities in all *senegalensis* (except hatchlings and near hatchlings) than there is in *elegans*. Thus, while callosities are already well indicated on a Schari River *senegalensis* with a carapace length of 128 mm., there is still no trace of them on a Schari River *elegans* of 170 mm.

In Schari River *senegalensis* the first traces of preplastral callosities appear in specimens with a carapace length of 128 mm., and these have become quite large in those with a carapace length approaching or exceeding 200 mm. In *elegans*, so far as is known, preplastral callosities are never developed. This fact, together with the more retarded condition of the hyo-hypoplastral callosity in *elegans* as compared with *senegalensis* of the same size, and differences in coloration, should always permit separation of young *elegans* from halfgrown *senegalensis*.

Color. Carapace of hatchling grayish or brownish, sparsely punctate with black and indistinctly mottled with lighter, most clearly around the posterior periphery which may be edged with lighter. Plastron yellowish or cream colored, centrally quite heavily blotched with darker. Head, neck and limbs gray or brownish, finely spotted with white or indistinctly vermiculate with lighter; throat, and neck below, whitish (based on five specimens seen by us, viz. three hatchlings from Maccarthy Id. and Togo, also two young from Togo).

Carapace of adult blackish olive, the periphery narrowly edged with white; plastron pure white or yellowish, clouded with brown. Head above, olive or blackish, sparsely punctate with lighter, sides of head indistinctly vermiculated with dusky (Gray :1870d :pl. xliii, not text).

Carapace of adult light brown, its fleshy margin dark brown, immaculate. Plastron yellow. Head and neck above, olive green; below, yellow (*fide* Siebenrock :1905a).

Size. Length of dorsal disk of a hatchling (Berlin Mus. 26687) from Kundja Konkomba, Togo, *ca.* 46 mm.; of a gravid ♀ from Duem, 225 mm. (Siebenrock:1906a); length of largest disk, 350 mm. (Boulenger:1889a).

Breeding. On April 12th, at Duem, 6 hard-shelled, almost spherical eggs measuring 36 mm. in diameter, were removed from a ♀ whose cloaca was so flaccid that Werner thought she must have been captured while laying (Siebenrock:1906a).

Longevity. Ten years, 2 days, and still living in London Zoo at the time of the report (Flower:1929).

Enemies. These turtles are hunted by the Bari tribesmen of the Bahr el Jebel who utilize the carapacial disks as basins, and esteem the fleshy margins for their food value (Werner; cited by Siebenrock:1906a).

Defense. When these turtles are molested they withdraw their heads and forelimbs, enclosing them by raising the anterior plastral lobe to meet the carapacial margin; the hind limbs are similarly withdrawn beneath the protecting femoral flaps (Sternfeld:1917).

Habits. During the Gambian rainy season young *senegalensis* move into the marshes where four were captured. Africans place these turtles in their wells, possibly to keep them free of putrifying matter as Anderson (1937) suggests.

Localities. Sudan: Bahr el Zeraf; White Nile at Duem, and north to Renk, and at Tonga. *French Equatorial Africa:* *Gabon (skull in M.C.Z.); *Schari River near Fort Archambault (V.M.). *French Cameroon:* Lake Tchad (also as Chad and Tsade). *Togo:* Kundja Konkomba; Mango (Mangu). *Nigeria:* Lagos; Niger River at Lohata, Kabba Province. *Gambia:* Gambia River; Maccarthy Island. *Senegal:* (Type locality).

Range. Sudan west through French Cameroon and Gabon to Senegal.

"CYCLANORBIS" sp.

By the courtesy of Dr. Eiselt of the Naturhistorisches Museum, Vienna, we have been able to examine the soft-shell-turtle hatchling said by Werner (1924a:270) to have come from the northwest shore of Lake Tanganyika. This specimen, as noted on p. 420, will not key out even generically on the characters used by us. In having the distance from tip of the proboscis to the orbit greater than the orbital diameter (in so young a specimen), it resembles *Cyclanorbis* rather than *Cycloderma.* In possessing a caudal flap as well as femoral flaps it resembles *Cyclanorbis senegalensis* or the species of *Cycloderma.* In coloration, being without spots or vermiculations on head, neck, carapace or plastron, it differs from all other African soft-shells examined by us. This hatchling may be a local variant of *senegalensis,* but at present no soft-shell turtle is known from Lake Tanganyika. It may well represent a new form, but we consider it undesirable to erect a new name on the basis of a single hatchling of somewhat indefinite origin.

Description of hatchling (V.M. 14826) from northwest shore of Lake Tanganyika. Proboscis projecting, the distance from its tip to the orbit greater than orbital diameter; nostril with papilla-like process projecting upwards from the inframedian corner; forefoot with 4, sharp-edged, crescentic skinfolds on its upper surface, another indistinct weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary, not projecting beyond the posterior rim of the carapace.

Carapace with a moderate vertebral keel and numerous raised, wavy, longitudinal lines comprised of small tubercles anteriorly converging toward a tubercular nuchal area; leathery margin posteriorly smooth, not extensive, scarcely extending beyond the tail.

Plastron smooth, without callosities; femoral and caudal flaps permit concealment of hind limbs and (probably) of tail.

Color. Carapace uniform olive (olive green *fide* Werner). Plastron uniform yellowish white. Head and neck above, gray-brown (gray-green: Werner) without spots, lines or vermiculations; throat and neck below, yellowish white.

Size. Length of dorsal disk (V.M. 14826) 70 mm.; breadth 60 mm. (as given by Werner).

Genus CYCLODERMA Peters

1854a. *Cycloderma* Peters, Monatsb. Akad. Wiss. Berlin, p. 216. Type: *Cycloderma frenatum* Peters.

1859. *Heptathyra* Cope, Proc. Acad. Nat. Sci. Philadelphia, p. 294. Type: *Cryptopus aubryi* A. Duméril.

1856. *Cryptopodus* Duméril, Revue Mag. Zool. (2), 8, p. 374. Lapsus for *Cryptopus* Duméril and Bibron, 1835.

1860a. *Aspidochelys* Gray, Proc. Zool. Soc. London, p. 6. Type: *A. livingstonii* Gray = *frenatum* Peters.

Definition. Cutaneous femoral flaps present, permitting concealment of the hind limbs.

Skull without maxillary ridging; intermaxillary foramen small; postfrontals not meeting vomer; jugal broadly in contact with parietal; postorbital arch wider than diameter or orbit; pterygoids joining opisthotic, greatly restricting fenestra postotica.

Carapace without prenuchal bone, without peripheral ossifications; nuchal bone notched laterally, ventrally with raised posterolateral processes which tend to underlie the first pleurals, between which are two neurals, rarely one; neurals 8 or 9, rarely 7, pleurals 8 pairs, the seventh and eighth, or eighth only, in contact medially.

Plastron with preplastra short and straight; hyo- and hypoplastra fused, their posteromedial process with three prongs between which are inserted the two anterior prongs of the adjacent xiphiplastron; callosities in adults 7, always present on gulars.

Range. East (Tanganyika Territory south to Mozambique) and West (Portuguese, Belgian and French Congo) Africa.

Fossil record. First reported in the Lower Miocene of Kenya; also known from the Pleistocene of Lake Rudolf. Although these remains are certainly cyclanorbide, the generic identification is uncertain; they may be referable to *Cyclanorbis.*

Remarks. The unity of the genus *Cycloderma* is clearer than that of *Cyclanorbis.* Discrimination of the two species is also very easy. There is, however, the possibility of a taxonomic problem within the species *frenatum.* The original Zambezi series were described by Peters as being dark green in general color, as also shown on his plate. Our material[1] from Lake Nyasa and the Ruvuma River, however, consists of pale gray to leaden hatchlings and pale to dark olive adults. Other minor differences are noted in the color description below (p. 464).

[1] Twenty-one juveniles and 11 adults (Loveridge coll.).

There may be also a parallel osteological difference. The skulls[1] of all our *frenatum* from Lake Nyasa and the Ruvuma lack a vomer, for which, in fact, there is no evident place of attachment. On the other hand, a vomer, though very narrow and much reduced, is shown in Peters' figure of a Zambezi skull. The vomer is present in a Zambezi specimen (B.M.) as well as another skull (Senck. Mus.), unfortunately without locality, seen by one of us (E. E. W.).

Thus the possibility of constant color and skull differences between the nominate population of the Zambezi, and those from further north needs to be investigated. Should these differences hold good, the more northerly populations will merit subspecific distinction.

No suspicion of geographical differentiation attaches to *aubryi*, but in this case there is an interesting biological problem. The pattern of *aubryi* is very distinctive, indeed unique among trionychids. On the head and nape is a chocolate brown vertebral streak which is continued on to at least the anterior third of the rather light brownish disk. Curiously enough, in the same West African rain-forest region inhabited by *C. aubryi*, a very similar pattern is present in two species of the pleurodiran genus *Pelusios*. The juveniles of both *P. gabonensis* and *niger* have similarly light brown carapaces with a black vetebral stripe which, in *gabonensis*, is continued on to the head. While in *C. aubryi* the pattern persists throughout life, in *P. niger* it occurs only in the hatchling stage, and has an intermediate duration in *P. gabonensis*. The significance of this apparent mimicry is quite unknown.

CYCLODERMA AUBRYI (Duméril)

1856a. *Cryptopodus Aubryi* Duméril, Revue Mag. Zool., (2), 8. p. 374, pl. xx: Gabon, French Congo.
1859. *Heptathyra aubryi* Cope, 294.
1864c. Gray (part), 93, figs.
1870e. Gray, 93.
1884a. Rochebrune (in error), 28, pl. ii, figs. 1-2.
1860. *Cycloderma aubryi* Duméril, 166.
1875a. Peters, 196.
1876a. Peters, 117, pl. —, figs. 1-2.

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[1] Seven skulls (Loveridge coll.).

1877c.	Peters, 611.
1880b.	Vaillant, 797.
1880c.	Vaillant, 53, pl. xxx, fig. 13.
1889a.	Boulenger, 267.
1895a.	Bocage, 8.
1896.	Günther, 263.
1897.	Sjöstedt, 33.
1898a.	Werner, 204.
1900b.	Boulenger, 447.
1902b.	Siebenrock, 836, fig. 14.
1902c.	Tornier, 665.
1906i.	Boulenger, 197.
1906a.	Mocquard, 480.
1909a.	Siebenrock, 593.
1910.	Sternfeld, 8, fig. 15.
1917.	Sternfeld, 415.
1919.	Schmidt, 598.
1929.	Flower, 53.
1933m.	Witte, 68.
1934a.	Mertens and Müller *in* Rust, 12.
1950.	Williams, 552.
1953a.	Laurent, R., 21, 26.
1953.	Witte, 21.
1864c.	*Heptathyra frenata* Gray (part), 94.
1873b.	Gray (part), 76.

Common name. Aubry's Soft-shelled Turtle (Flower:1929).

Illustrations. The black and white drawings on plate xx of Duméril's original description (1856a), copied here as our Plate 18 (top), clearly show the principal characteristics.

Description. Proboscis projecting, the distance from its tip to the orbit (not eye) shorter than or subequal to (in young), or longer than (in adults), the orbital diameter; nostril without papilla-like process projecting from its infra-median corner; upper lips meeting in front to form a more or less pointed arch; forefoot with 6 or 7 sharp-edged, crescentic skin-folds on its upper surface, another weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary,[1] not projecting beyond the posterior leathery rim of the carapace.

Carapace of young with a moderate vertebral keel and numerous tubercles, those in center not arranged in longitudinal lines,

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[1] Possibly slightly longer in ♂♂ than in ♀♀.

the lateral ones showing a tendency to such arrangement; carapace of adults smooth in life, at least centrally, but showing, when dried, the underlying bony sculpture; the disk with a distinct nuchal excavation, less convex, shorter and rounder than in *frenatum;* leathery margin not extensive, posteriorly scarcely extending beyond tail.

Plastron of hatchlings smooth, without callosities; in young (90 mm., M.C.Z. 4300) callosities present on preplastra, *on the fused epiplastra,* hyo-hypoplastra and xiphiplastra; at this age the anterior edges of the hyo-hypoplastral callosities are almost straight, later becoming strongly convex anterolaterally; in adults the azygous callosity is subcircular, large; hyo-hypoplastral callosities in contact with xiphiplastral callosities by long straight sutures; femoral and caudal flaps permit concealment of hind limbs and tail.

Osteological description.[1] Skull. Distance between tip of premaxilla and orbit greater than long diameter of orbit; height of orbit about one-third greater than the interorbital width, which is somewhat less than the width of naris; premaxilla apparently absent; intermaxillary foramen small, pear-shaped with apex directed forwards; both in front and behind this foramen the maxillae in contact medially, the posterior medial suture much longer than the foramen; vomer slender without ascending processes to prefrontals, its interchoanal portion relatively elongate; choanae restricted anteriorly by inward expansion of the triturating surfaces, expanding abruptly posteriorly; postorbital arch much wider than the long diameter of orbit; orbit not entered by jugal, which is excluded by broad contact of postorbital and maxilla but is broadly in contact with parietal; squamosal crests long, sharp, incurved; pterygoids meeting opisthotic, greatly restricting postotic fenestra; mandible without symphysial ridge, its ventral symphysial width much less than diameter of orbit.

Carapace. Carapacial bones finely granulated and vermiculated; no prenuchal bone; nuchal bone notched laterally, underlying the first pleurals, between which are two neurals; neurals 8 or 9, forming a continuous series; pleurals 8 pairs, the eighth in contact medially.

Plastron. Preplastra (no information); epiplastra fused, forming an obtuse angle, their pointed posterior prong inserted

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[1] Based on B.M. 63.6.13.5 only.

in a deep notch which separates the rounded inner margin from the strongly convex outer margin of the fused hyo- and hypoplastra; the posterior border of this compound bone very deeply excavated, its anteromedial process with 2-3 juxtaposed prongs.

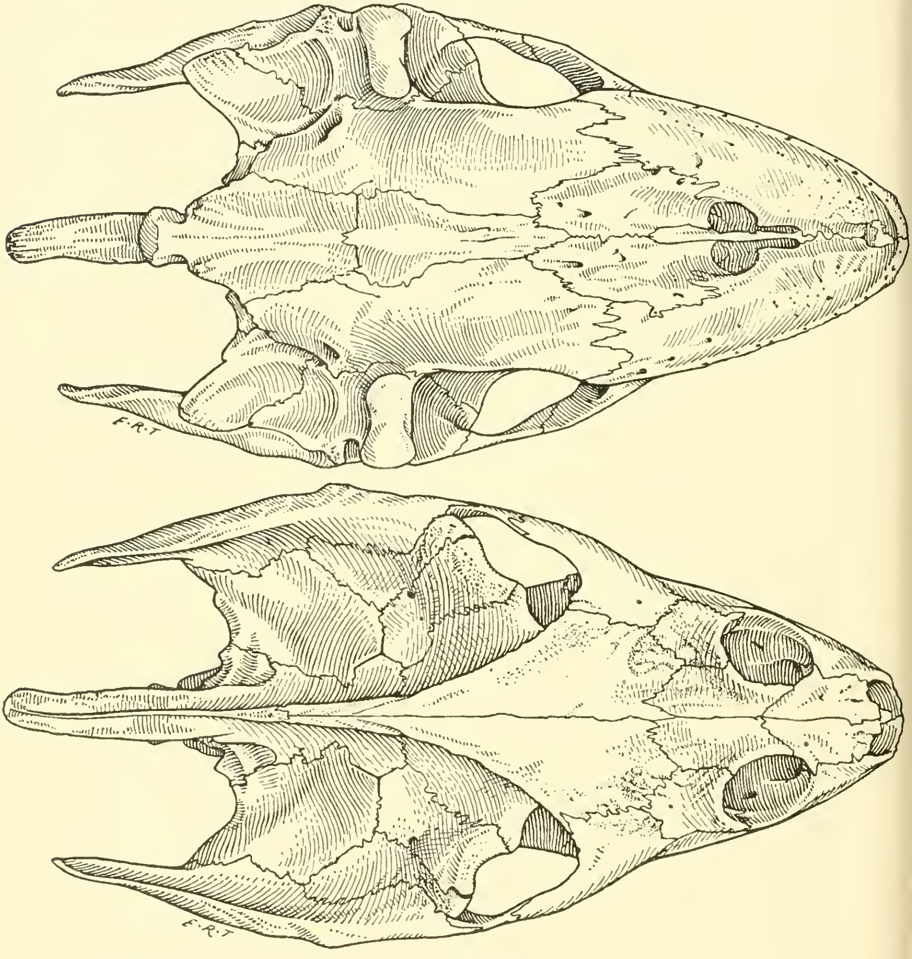

Fig. 59. Skull of *Cycloderma aubryi* (B.M. 63.6.13.5), x 5/6. Dorsal and ventral views.

(E. R. Turlington del.)

the medial process very short, *not* projecting beyond the rim, the posteromedial process with 3-4 prongs, between the lateral three of which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra rather wide with 3 prongs posteriorly, in contact medially by a prong of one fitting into a notch on the other.

Callosities 7, sculptured like the carapace, extremely developed in adults, covering most of the plastral area; preplastral callosities large, nearly half-moon-shaped, in contact medially by a long straight suture; fused epiplastra bearing a large, almost round, azygous callosity; hyo-hypoplastral callosities large, covering most of the surfaces of these bones and almost meeting medially, meeting in an oblique straight line the large trapezoidal xiphiplastral callosity; xiphiplastral callosities in contact medially over their entire length.

Color. Carapace of young dull orange to yellow brown with a few scattered brown or black specks or blotches and a chocolate brown line on the anterior third of the vertebral keel.

Plastron mostly yellow, anteriorly a broad chocolate brown, more or less V-shaped marking whose truncate arms are directed posteriorly; from the axillae the arms of another, but much larger, black, V-shaped figure converge posteriorly to cover the femoral and caudal flaps; under aspect of the fleshy margin yellow.

Head above, yellow brown with five almost hairlike (sometimes converging anteriorly) longitudinal lines, a median one beginning on the crown extends down the neck (in line with the one on the carapace), two arise in the interocular region and terminate on the occiput, each of the remaining pair commence at the nostril and, passing through the eye, continue along the side of the neck; chin and throat whitish indistinctly flecked with darker; limbs largely dark chocolate brown, each bearing a large yellow patch.

Size. Carapace length *over curve* of the Gabon type, 455 mm., the disk alone *over curve* 330 mm., its breadth 310 mm. (*fide* Duméril:1856a); head and neck together 280 mm. A Fernan Vaz turtle with head and neck of exactly the same length (11″) is said by Cope (1859) to have a total length of 760 mm. (2′ 6″). Carapace length of an Eala specimen (M.C.Z. 43000) is 90 mm., breadth 80 mm.; both measurements being taken in a straight line. Carapace length of a Lake "Ogemwe" (? Azinguo) hatchling (B.M. 1908.5.25.3), 55 mm., breadth 44 mm.

Habitat. Included in the rain forest fauna by Schmidt (1919).

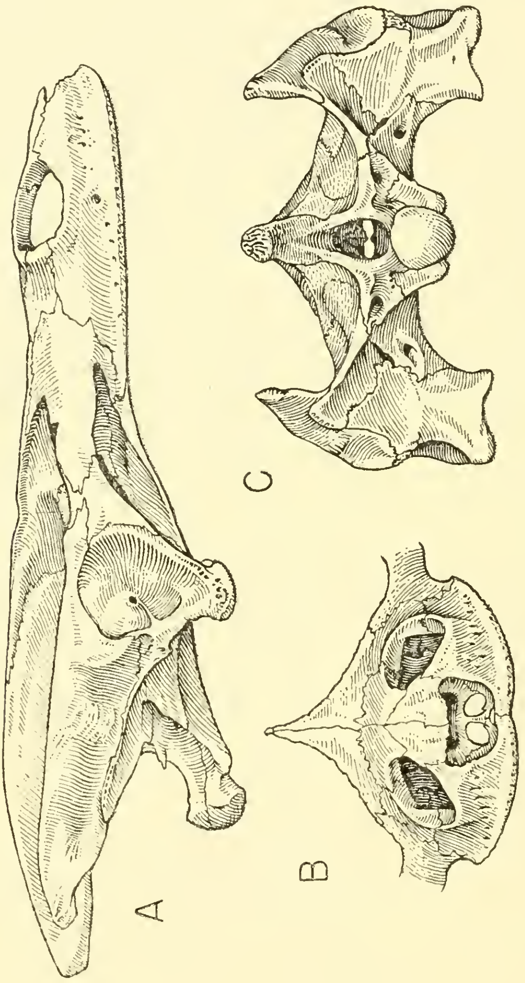

Fig. 60. Skull of *Cycloderma aubryi* (B.M. 63.6.13.5), x $\frac{5}{6}$. A, Lateral view; *B*, anterior view; *C*, posterior view.

(E. R. Turlington del.)

Localities. Cabinda: Chinchoxo. *Belgian Congo:* *Eala, Flandria, (i.e. Bokele), Equateur Province; *Tumba, Lake Loondo (B.M.). We concur with de Witte (1953) that the "Katanga: 1898" specimen is a very questionable record. *French Equatorial Africa:* Fernan Vaz (Fernando Vas); Gabon; *Lake "Ogemwe" (B.M.) (?Azinguo); Lambarene (Limbareni); Ogoue (Ogowai); Oubangui (Ubangi) River near Libengue (Libenge).

We know of no specimen actually taken in the Cameroons. Its alleged presence there dates from a list by Sjöstedt (1897) who failed to collect it. Subsequently cited in the lists of Werner (1898a) and Sternfeld (1910), but without material.

Range. Portuguese, Belgian (western) and French Congo.

CYCLODERMA FRENATUM Peters

1854a. *Cycloderma frenatum* Peters, Monatsb. Akad. Wiss. Berlin, p. 216: Zambezi River, Mozambique.
1882a. Peters, 14, pls. i-iiia.
1889a. Boulenger, 265.
1894a. Günther (1893), 618.
1896a. Bocage, 97.
1897. Johnston (also 1898 ed.), 356, 361.
1900b. Tornier, 583.
1902b. Siebenrock, 834, fig. 13.
1902b. Tornier, 580.
1909a. Siebenrock, 592.
1913c. Nieden, 64.
1929. Lindholm, 291.
1934a. Mertens and Müller *in* Rust, 12.
1934. Pitman, 307.
1937f. Loveridge, 489, 495.
1942e. Loveridge, 251.
1946. Mitchell, 21.
1950. Rose, 330, figs. 198-199.
1950. Williams, 552.
1953e. Loveridge, 160.
1855. *Cyclanosteus frenatus* Gray, 64 (ex Peters MS).
1860a. *Aspidochelys livingstonii* Gray, Proc. Zool. Soc. London, p. 6, pl. xxii, figs. 1-2: Tributaries of the Zambezi River, Mozambique.
1860f. Gray, p. 430.
1864e. *Heptathyra livingstonii* Gray, 94.
1864e. *Heptathyra frenata* Gray (part), 94.

1870e.	Gray, 93.
1873b.	Gray (part), 76.
1884a.	Rochebrune (in error), 30.

Synonymy. Further citations of "*frenata*" will be found under *Cycloderma aubryi,* with which this species was confused by Gray (1864c). *Aspidochelys livingstonii* was supposed to be generically distinct because of certain characters of the callosities; when Gray realized these developed with age he himself (1870e) synonymized *livingstonii* with *frenatum.*

Common names. Zambezi Soft-shelled Turtle (English); Zambezi Mud-Turtle (Loveridge); "*cassi* or *ncassi*" (at Sena and Tete: Peters, but see below); *kalibungu* (Sena: Mitchell); *litetamera* (Yao: Loveridge); *mbulundwe* (Yao: Mitchell); *nahi* (Makonde: Loveridge); *nkhasi* (Manganja and Cewa: Mitchell).

Illustrations. Peters (1882a) furnishes fine colored drawings (pl. i, copied as our black and white Plate 18 [bottom]), of dorsal and ventral aspects of what is presumably a ♂; also a figure (pl. iiia) showing plastral marbling in the ♀; skulls, skeleton, etc. (pls. ii-iii).

Description. Proboscis projecting, the distance from its tip to the orbit equal to (in young), or longer than (in adults) the orbital diameter; nostril with papilla-like process projecting upwards from its inframedian corner; upper lips meeting in front to form a flat arch; forefoot with 4 or 5 sharp-edged, crescentic skin-folds on its upper surface, another weal-like thickening on outer aspect; hind foot with a sharp-edged crescentic fold under the heel posterior to the base of the fifth toe; tail rudimentary,[1] not projecting beyond the posterior leathery rim of the carapace.

Carapace of young with a moderate vertebral keel and numerous, raised, rather wavy, longitudinal lines; carapace of adults smooth in life, at least centrally, but showing, when dried, the underlying bony sculpture; the disk is less excavated anteriorly than in *aubryi,* besides being more convex, longer and narrower; leathery margin not extensive posteriorly, scarcely extending beyond tail.

Plastron of hatchling smooth, without callosities (in the young these first appear as small pairs on the preplastra, hyo-hypoplastra and xiphiplastra, while the last to develop is the azygous

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[1] Cf. *Sexual dimorphism* below.

element on the fused epiplastra) ; femoral and caudal flaps permit concealment of hind limbs and tail.

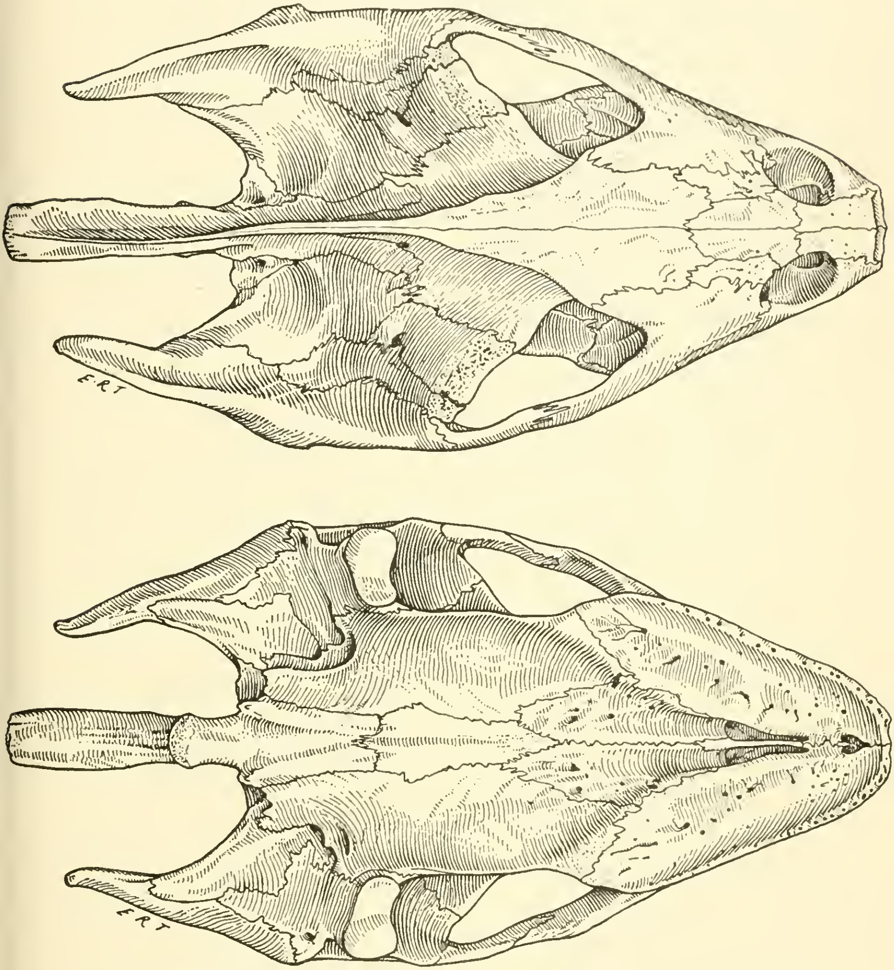

Fig. 61. Skull of *Cycloderma frenatum* (B.M. 84.2.4.1), (Zambezi specimen), x ⅔. Dorsal and ventral views.

(E. R. Turlington del.)

Osteological description. Skull of adult.[1] Distance between tip of premaxilla and orbit subequal to long diameter of orbit; height of orbit about twice the interorbital width, which is less than the width of naris; premaxilla apparently absent (rudimentary, *fide* Peters in Zambezi specimens); intermaxillary foramen small, heart- or pear-shaped with apex directed forwards; both in front and behind this foramen the maxillae in contact medially, the posterior medial suture longer than the foramen; vomer very slender, without ascending processes to the prefrontals, its interchoanal portion relatively elongate, or vomer absent; internal choanae narrowed anteriorly by inward expansion of the triturating surfaces, expanding gradually posteriorly; postorbital arch much wider than the long diameter of orbit; orbit entered by jugal, which is broadly in contact with parietal; squamosal crests long, sharp, incurved; pterygoids meeting opisthotic, greatly restricting postotic fenestra; mandible without symphysial ridge, its symphysial width less than the long diameter of the orbit.

Carapace. Carapacial bones finely granulated and vermiculated; no prenuchal bone; nuchal bone notched laterally, underlying the first pleurals, between which are two neurals, rarely one;[2] neurals 8 or 9, rarely 7,[2] usually forming a continuous series; pleurals 8 pairs, the seventh and eighth, or eighth only in contact medially.

Plastron. Preplastra widely separated, only the anterior branch present; epiplastra fused, forming an acute angle, their pointed posterior prong inserted in a notch which separates the rounded inner margin from the strongly convex anterior border of the fused hyo- and hypoplastra; posterior border of this compound bone very deeply excavated; the anteromedial process with 3 prongs, the medial process typically very short and, as a rule, scarcely projecting beyond the rim; the posteromedial process with only 3 prongs between which are inserted the 2 anterior prongs of the xiphiplastron; xiphiplastra short and

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[1] The skull, with condylobasal length of 31 mm., of a juvenile skeleton (A.M.N.H. 56479) from Lake Nyasa, Nyasaland, shows striking differences in the proportions to those of the adults described above. For example, the distance between tip of premaxilla and orbit is very much *shorter* than the long diameter of the orbit. Presumably similar discrepancies due to ontogenetic change would have been noticed in other African trionychids had skeletal preparations of their young been available.

[2] One only between the first pair of pleurals, and only 7 neurals in one (M.C.Z. 48032) of a series of seven from the Rovuma River.

broad with 3 or 4 notches posteriorly, on the posterior half of each notch a short process joining a similar process on the other element.

Callosities 7, sculptured like the carapace, very well developed

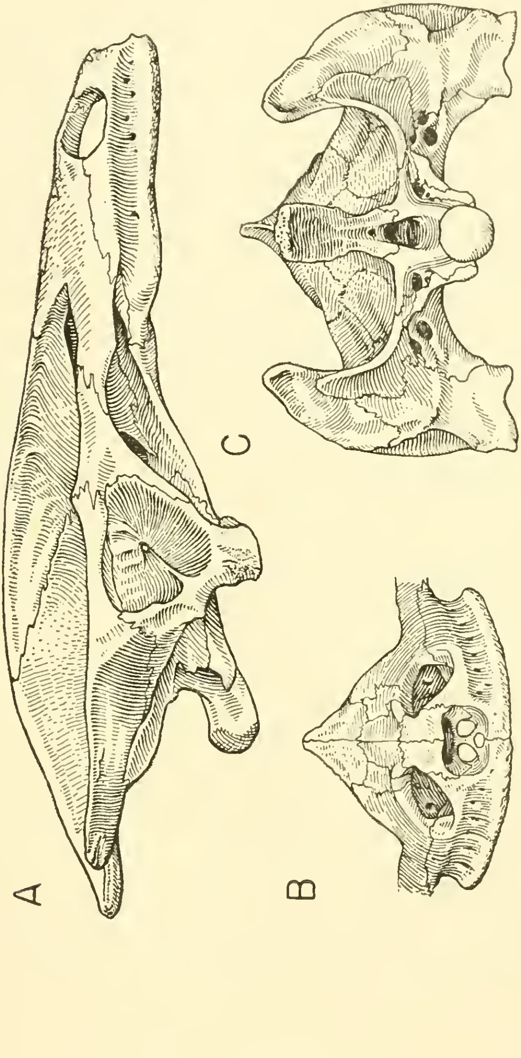

Fig. 62. Skull of *Cycloderma frenatum* (B.M. 84.2.4.1), (Zambezi specimen), x ⅔. *A*, Lateral view; *B*, anterior view; *C*, posterior view. (E. R. Turlington del.)

in adults; preplastral callosities large oblique ovals, in contact medially; fused epiplastra bearing a small, crescentic to semilunar callosity, smallest of any and last to develop; hyo-hypoplastral callosities covering most of the surfaces of these bones but widely separated medially; hyo-hypoplastral callosities separated from, or in contact with the xiphiplastral callosities by only a short suture; xiphiplastral callosities large oblique ovals, in contact medially.

Color. Carapace in Lake Nyasa hatchlings ranges from pale green to leaden, the periphery usually edged with white; carapace of adults pale to dark olive, uniform or with a trace of blotching. Zambezi turtles would appear to differ somewhat, for Peters (1882a) describes young specimens as green and adults as dark green, uniform, or with interrupted black bands and scattered white spots.

Plastron of Lake Nyasa hatchlings was often almost white, more usually an irregular black blotch was present in the umbilical region, an elongate, oblique blotch near each forelimb, a rounder one anterior to each hind limb, and a smaller sixth spot in the anal region. Plastron of adult ♀♀ is china white to flesh-pink almost obscured by pearly gray reticulations. These reticulations are sometimes absent in what may be ♂♂. For example, the subject of Peters' colored plate (1882a, pl. i), possibly a Zambezi ♂, is shown as having a cream-colored plastron extensively infuscated with dusky blotches.

The head and neck in Lake Nyasa hatchlings were gray with a dark, light-edged, interorbital crossbar, five similar, but wavy and sometimes broken, longitudinal lines from near occiput to base of the long neck; throat and underside of neck pure white, uniform or showing some dusky streaks. Head and neck of adults very dark olive, the dark longitudinal lines of the young turtle obsolete or, more usually, absent. Peters (1882a), writing of Zambezi turtles, states that the head and neck in both age groups display numerous white dots. Feet gray above, lighter below.

Size. Carapace length *over curve* of a Zambezi ♂, 560 mm., the disk alone *over curve* 470 mm., its breadth 420 mm. (*fide* Peters:1882a, whose figures do not quite tally, for he gives the total length as 970 mm., though head and neck together are only

340 mm., the tail, which would not project beyond the carapacial margin, 65 mm.).

Overall carapace length (*in a straight line*) of three Nyasa ♀♀ averaged about 560 mm., breadth 418 mm. The head and neck of one (M.C.Z. 50357) measures 420 mm.; breadth of head 100 mm. Disk length of largest gravid Rovuma ♀ (M.C.Z. 48030) 390 mm., its width (also without leathery margin) 310 mm. (Loveridge:1942e and 1953e).

Overall carapace lengths of 31 Nyasa hatchlings were from 40 to 48 mm., their breadths 30 to 36 mm. Peters mentions a Zambezi hatchling of 45 mm.

Weight. Weight of largest Zambezi ♂ between 28 to 30 lbs. (as 13-14 kilos., Peters:1882a); that of largest Rovuma ♀, 25 lbs. (Loveridge:1942e).

Sexual dimorphism. Possibly the sexes of adults, though not of young, may be told by the fact that the tail of the ♂ is visible in ventral view (cf. Peters:1882a:pl. i), while that of the ♀ is concealed beneath the caudal flap (*ibid.*, pl. iiia, fig. 1). We are unable to confirm Peters' statement that the carapace is narrower in ♂♂ than in ♀♀ (the relative proportions said to be 1:1⅓ and 1:1¼) or that the union between carapace and plastron is longer in ♂♂ than in ♀♀.

Breeding. On January 11th, at Tete, a hatchling with umbilical scar was found by Peters (1882a). Between December 24th and early February, at Fort Johnston, nine hatchlings were taken by B. L. Mitchell (letter of 10.iv.47). On February 7th, at Mtimbuka, natives brought in three clutches of eggs numbering 15, 16 and 19, respectively. On February 10th, 19th and 28th, three ♀♀ were captured when coming ashore to lay. All three held spherical, hard-shelled eggs ranging from 33 to 35 mm. in diameter. One ♀ laid 3 eggs before being killed, 19 more were present in her oviducts, and many shell-less ova of various sizes were present in the ovaries. On February 7th, the fourth day after a heavy downpour that terminated about eight months drought (but did not inaugurate the rains as was hoped), a young turtle, its carapace caked in mud, was found. Twenty other hatchlings were collected during the three weeks following (Loveridge:1953e). On March 27th and 28th, at Kitaya, two ♀♀ held 17 and 19 hard-shelled eggs ranging from 31 to 32 mm. in diameter; in addition one turtle held 55 small ova in various stages of development. (Loveridge:1942e).

Diet. The powerful, all-pervading, fishy odour of Kitaya turtles led Loveridge (1942e) to suggest that these reptiles subsist largely on fish in the Rovuma River. Mitchell found that captive hatchlings from Lake Nyasa eagerly took fine strips of fish or meat from his fingers. However, he concluded (1946:21) that feral adults subsist principally on aquatic snails and mussels. At Mtimbuka the former were *Lanistes ellipticus* and *L. sordidus;* the clams proved to be *Mutela alata* and *simpsoni,* with a robust cockle-like shell (*Caelatura nyassensis*) particularly abundant (Loveridge:1953e).

These large mussels embed themselves vertically in the mud or sandy bottom of lakes and ponds, and considerable effort is required to dig them out. For the purpose, *Cycloderma* must use the powerful claws on its forefeet. Usually the shells are crushed and swallowed, though occasionally undamaged valves have been defecated by freshly captured turtles (Mitchell: 1946).

Parasites. Leaches were present on turtles at Kitaya and Mtimbuka; two removed from the neck of a Lake Nyasa ♀ (M.C.Z. 50357) were of the family Glossiphonidae, possibly *Placobdella jaegerskioeldi.*

Enemies. In 1926 Dr. J. O. Shircore observed two small rufous otters running around a dessicating puddle about 100 yards from the right bank of the Kilombero River, Mahenge District. The object of their interest appeared to be a soft-shelled turtle that had withdrawn within its defenses. At least this was its position when he reached the spot after shooting one of the otters. Subsequently, Dr. Shircore sent a photo of turtle and otter to one of us (Loveridge:1942e).

On February 11th, 1949, Loveridge saw scores of eggshells on the village middens around Mtimbuka. A Yao, whose home was only about ten miles north of Mtimbuka, accepted turtle eggs gladly, but the more sophisticated members of the staff scorned the idea of eating them. Loveridge, himself, ate 18, finding them quite edible though not as palatable as fowl's eggs. It is when coming ashore to lay that these turtles fall an easy prey to Africans; consequently ♂♂ are rare in collections (Loveridge: 1953e).

Defense. Though presumably, when molested, *Cycloderma* is capable of inflicting a severe bite with its strong crushing jaws, instead it withdraws both head and forelimbs within the fleshy margins of its shell, the hind limbs beneath dermal flaps, thus completely closing the plastron before and behind. When picked up, however, a *Cycloderma* is occasionally difficult to handle, for vigorous kicking of the clawed feet, which can reach any part of the shell's edge, may displace the captor's hands (Mitchell: 1946).

Temperament. In stating that *Cycloderma* "are very fierce," Johnston (1897) was apparently attributing to them the well-merited reputation of *Trionyx.* Actually these turtles are timid and inoffensive, withdrawing their heads and limbs within the protection of the shell at the slightest disturbance. When all is quiet, the head is protruded with the utmost caution by very gradual stages and withdrawn precipitately to the accompaniment of a kind of snort at the least sound or movement in their vicinity (Loveridge:1942e:252, which consult for a concrete example of such timidity). This inoffensiveness is confirmed by Mitchell (1946).

Habits. Surprisingly active according to Peters (1882a), both in the water and on land where, using their forefeet and snout, they quickly burrow into soft mud in an effort to hide. One of these turtles, with head held well above the surface, paddled swiftly past Loveridge (1942e) as he was wading thigh-deep in a lake. When twenty feet away the reptile dived and was seen no more.

Mitchell (1946) states that during the daytime two captive turtles, that he kept in a pond at Salima, remained for long periods with their nostrils protruding from the water. They did not rise to the surface between 4.00 P.M. and 8.30 A.M. and remained on the bottom during cold weather. He suggests that at such times they obtain oxygen by means of the mass of blood vessels on the unpigmented ventral surface in the vicinity of the flaps. Their only attempts at escape were made at night during rainy weather, or after the water in their pond had been changed. One turtle that got away was recaptured a fortnight later; though without water during this time the reptile was apparently none the worse.

In January, when Loveridge (1953e) endeavoured to secure topotypic *frenatum* near Tete, local native fishermen asserted that these turtles would not be seen until the rains, already two months overdue, broke.

Habitat. Rivers, lakes and stagnant ponds.

Localities. Tanganyika Territory: Kilombero River, Mahenge District (sight record by Shircore; photo seen by A.L.); Lake Nyasa at Manda (as Wiedhafen); *Rovuma River at Kitaya. *Mozambique:* Lake Inhalutanda near Tete; Licuare River, tributary of the Zambezi; *Zambezi River near Tete. *Nyasaland.* *Chowe; *Lake Nyasa at Mtimbuka and at Fort Johnston[1]; Lake Shirwa (Chilwa) (''said to occur'': Mitchell); Upper Shire; Lower Shire (''said to occur, but rare'': Mitchell). *?Northern Rhodesia:* chelonian remains near Munyamadzi River, Luangwa Valley, Mpika District (*fide* Pitman).

The erroneous recording by Tornier (1900b) of Fülleborn's specimen as from ''Wiedhafen, Victoria Nyassa,'' resulted in later authors adding Victoria Nyanza or Lake Victoria to the range.

Range. Southern Tanganyika west and south through Nyasaland and possibly Northern Rhodesia to Mozambique (Zambezi River).

Gray's records (1864c: 1873b) for Gabon were due to confusion with *aubryi.*

MARINE TURTLES

General Remarks

The treatment being given to the marine turtles of the families CHELONIIDAE and DERMOCHELYIDAE, differs substantially from that accorded to the other Cryptodira of Africa. While African to the extent that, without exception, they land on the continent or its offshore islands to deposit their eggs, the group is so cosmopolitan that any revisionary study of them should be undertaken on a worldwide rather than a regional basis. This, lacking adequate material, we have not attempted.

The literature dealing with African records, to which — with

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[1] We presume that this is also the correct locality for a British Museum specimen labeled "Zomba." Zomba, where Sir Harry Johnston lived, was presumably only the dispatching point of the donor.

few exceptions — we have restricted our citations, is scanty in the extreme. Though there are good reasons to suppose that turtles are by no means rare in the waters surrounding the African continent, yet for extensive areas there are curious gaps in the record. Such hiatuses are presumably due to the failure of travellers to collect and preserve such admittedly cumbersome reptiles.

In the following account, therefore, we present no figures, no analyses of the species, no fossil history, and relatively little general discussion or comment on habits, as we were averse to drawing on extra-territorial sources.

In conformity with this treatment, and in the absence of the necessary material, we have refrained from discussing the alleged Atlantic and Pacific races of the green turtle, hawksbill, loggerhead and leatherback. In all these instances we have listed only the species name and, following it as synonyms, the putative subspecies. Only in the case of the much more distinct *Lepidochelys* races have we registered a decision. We have omitted, as not germane to our area, the problem of the status of *Chelonia depressa* Garman.

For those who desire more complete discussions of the Recent marine turtles, we recommend Deraniyagala (1939) and Carr (1952). The fossil marine turtles are currently being studied by Dr. Rainer Zangerl, to whose publications those interested must be referred.

Incidence of occurrence of the various species on the Senegal coast has been furnished by Cadenat (1949:17) but the figures also reflect edibility or marketable value, suggesting that selection practiced by local fishermen may have influenced the results.

TABLE 10

Marine turtles caught on the Senegal Coast.

Species	Total Individuals Captured	Incidence
Chelonia mydas	256	86.48%
Eretmochelys imbricata	23	7.77%
Caretta and *Lepidochelys*	10	3.39%
Dermochelys coriacea	7	2.36%

Nomenclature. On several occasions Deraniyagala (e.g. 1943) has asserted, though not formally proposed, that on grounds of priority the names of the loggerhead turtles require to be totally altered from present usage, *Caretta* being the correct name of the forms currently called *Lepidochelys,* and *Thalassochelys* the correct name of those now called *Caretta.* The use of the name *Thalassochelys* would involve little hardship since this name is classic, having been applied to both loggerheads by Boulenger (1889a) in the catalogue that all discreet students of this order still faithfully consult. However, an exchange of names such as would be required by the use of *Caretta* for the olive-green loggerheads, rather than for the red-brown forms, is a perversion of nomenclature to be avoided at almost any cost. We therefore venture to comment upon Deraniyagala's reason for proposing the change. He calls attention to the fact that Linnaeus' species *Testudo caretta* was a composite. He believes that the first unambiguous use of the Linnaean name is that of Schoepff (1792), who presents several figures under this name. From the scalation shown in these figures, Deraniyagala deduces that Schoepff was in effect restricting *Testudo caretta* to the form now known as Kemp's Loggerhead.

However, Schoepff's figures appear in editions both with and without colored plates. There are at the Museum of Comparative Zoology four copies of Schoepff, two without and two with colored plates. In the latter editions, apparently not examined by Deraniyagala, the figures of *Testudo caretta* are colored a very fine red-brown, in shade and texture a splendid representation of the red-brown loggerhead. Thus, accepting Deraniyagala's interpretation of the scalation at face value, the color of these plates seems to demonstrate that Schoepff's concept of *Testudo caretta* was, like that of Linnaeus, a composite one.

We have not concerned ourselves with Deraniyagala's reasoning in other regards, nor have we pursued the matter further. We merely wish to protest against the spirit of antiquarian and wholly bibliographic research which leads to these proposals for name changes. We point out that such researches (e.g. in the case of *Trionyx*) almost invariably lead to confusion and instability, insoluble except by the plenary powers of the International Commission. This is the more certain since antiquarian researches will rarely be complete and thus will leave us for all future time at the mercy of the chance discovery of some rare and (nomenclature apart) worthless book.

We deprecate also the forcing of text or figures of the oldest writers into modern standards of precision. As everyone is aware, the figures of the older naturalists were as often as not composite and (with praiseworthy exceptions) rarely accurate, while not infrequently descriptions are unrecognizable beyond the order. The most exhaustive discussion and analysis of such figures and texts can never carry conviction or produce agreement.

In the present case the Copenhagen rules may prevent in fact, as they certainly prohibit in spirit, the changing of these long-accepted names.

Key to the Marine Turtles Breeding in Africa

1\. Upper jaw conspicuously bicuspid at symphysis; upper shell covered with smooth skin (or *small* scales in juveniles) overlying a mosaic of small bones and showing 7 prominent longitudinal ridges; limbs clawless....
Dermochelys coriacea (Linnaeus) (p. 499).

Upper jaw not bicuspid; upper shell covered with large horny shields overlying large bony plates, and ridges 0 to 3; limbs with 1 or 2 claws 2

2\. Upper shell with 4 pairs of costal shields of which the foremost pair is never the smallest and is separated from the nuchal shield........ 3

Upper shell with 5 or more pairs of costal shields of which the foremost pair is the smallest and normally in contact with the nuchal shield.. 4

3\. Snout not compressed; 2 prefrontal shields on head; shields of upper shell not overlapping (except in very young turtles); usually a single claw on each limb ....*Chelonia mydas* (Linnaeus) (p. 474)

Snout compressed; 4 prefrontal shields on head; shields of upper shell strongly overlapping (except in very young or very old turtles); usually 2 claws on each limb ....
Eretmochelys imbricata (Linnaeus) (p. 485)

4\. Upper shell normally with only 5 pairs of coastal shields; bridge on either side of lower shell with 3 enlarged inframarginal shields without pores; color of adults and young predominantly reddish brown..............
Caretta caretta (Linnaeus) (p. 490)

Upper shell normally with 6 to 9 (rarely 4 or 5) pairs of costal shields; bridge on either side of lower shell with 4 enlarged inframarginal shields, each with or without a pore; color of adults predominantly olive, of young olivaceous black ....
Lepidochelys olivacea olivacea (Eschscholtz) (p. 495)

Family CHELONIIDAE

1882. *Cheloniidae* Cope, Proc. American Philos. Soc., **22**, p. 143.

Definition. Cryptodirous testudinates adapted to marine life. Horny shields normally present; costal scutes 4 or 5 pairs; marginals, exclusive of the nuchal and supracaudals, 11 or 12 pairs; inframarginal series complete; additional axillary shields also present; plastron with 6 pairs of scutes and one unpaired scute; an intergular commonly present.

Skull without nasal bones; prefrontals always in contact dorsally, always with descending processes that are moderately separated inferiorly; temporal region posteriorly very little emarginate; parietal meeting squamosal; no bones tending to be reduced; quadrate never enclosing stapes; postotic antrum absent; parietals with reduced descending processes; upper jaw with or without ridges on its triturating surfaces; vomer always present, separating palatines; mandible with coronoid bone.

Neck vertebrae with only one biconvex centrum, usually the fourth, typically a plane joint between the sixth and seventh centra, the eighth centrum concave in front, doubly or not; coracoids with their median borders moderately expanded; humerus of a specialized marine type with deltopectoral crest far down the shaft; trochanteric fossa of femur reduced by union of the trochanters; phalanges without condyles; claws 1 or 2.

Carapace heart-shaped, united to plastron only by ligament; neither carapace nor plastron hinged; pleural bones somewhat reduced and often peripheral fenestrae persisting till late in life; nuchal without costiform processes but with a ventral attachment area for the eighth cervical; neural bones hexagonal, short-sided in front, variable in number; pygals 3; plastron never cruciform but with some development of fontanelles; entoplastron always present, more or less lance-shaped.

Range. Tropical, subtropical and — as an occasional visitor — temperate oceans.

Genus CHELONIA Brongniart

1800. *Chelonia* Brongniart[1] (part), Bull. Soc. Philom. Paris, **2**, p. 89.

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[1] In 1801 this name was used by Sonnini and Latreille (Hist. Nat. Rept., 1, p. 22) but they correctly attributed it to Brongniart, whose article we have examined.

"Ce sont les tortues de mer." Type: *Testudo mydas* Linnaeus (designation by Fitzinger: 1843).

1837. *Chelona* Burmeister, Handbuch Naturg., **2**, Abt. Zool., p. 731. Type: *T. mydas* Linnaeus (by monotypy).

1838. *Mydas* Cocteau (not of Fabricius: 1799), Rept. in De la Sagra, Hist. Fis. Pol. Nat. Cuba **4**, p. 22. Type: *T. mydas* Linnaeus (by tautonomy).

1843. *Mydasea* Gervais, Dict. Hist. Nat., **3**, p. 457. Type: *T. mydas* Linnaeus (by monotypy).

1845. *Euchelonia* Tschudi, Fauna Peruana, p. 22. Type: *T. mydas* Linnaeus (by monotypy).

1848. *Megemys* Gistel, Naturg. Thier., p. viii. *Nomen novum* for *Chelonia*.

1858. *Euchelys* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 447. Type: *E. macropus* Girard = *T. mydas* Linnaeus (by monotypy).

1862a. *Chelone* Strauch, Mém. Acad. Imp. Sci. St. Petersbourg, (7), **5**, No. 7, p. 59. Type: *Testudo viridis* Schneider = *T. mydas* Linnaeus (by original designation).

Definition. Head with 1 pair of prefrontal shields; postoculars 3-4; claws 1.

Skull with triturating surface of maxilla ridged, the ridge rising to a dentate projection at suture with the premaxillae; premaxillae in contact with vomer which separates the maxillae; maxilla with vertical ribbing on inner surface of its cutting edge; descending processes of prefrontals in contact with vomer and palatines; a blunt ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view concealed by the extensive secondary palate; pterygoids flat posteriorly; frontal usually entering orbit; crista pretemporalis reduced; mandibular symphysis short; the somewhat serrate labial margin (the horny sheath is sharply serrate) rising to a sharp point at the symphysis; the lingual margin surmounted by a wider blunt ridge rising to a higher point at the symphysis, the two points united by a sharp symphysial ridge.

Carapace with persistent lateral fontanelles; neurals 9-11, usually hexagonal, short-sided in front; peripherals 11 pairs, the tenth pair not in contact with the ribs; nuchal shield not in contact with first costals; costals typically 4 pairs.

Plastron with a large intergular shield; inframarginals 4 pairs, without pores.

Range. Tropical, subtropical and — as an occasional visitor — temperate oceans.

CHELONIA MYDAS (Linnaeus)[1]

1758. *Testudo Mydas* Linnaeus, Syst. Nat., ed. 10, 1, p. 197: Ascension Island.
1802b. Daudin, 10, pl. xvi, fig. 1.
1860. Tristram, 405.
1782. *Testudo* (*macropus*), Walbaum, Chelongr. Schildkröten, p. 112: No locality.
1783. *Testudo Viridis* Schneider, Natur. Schildkröten, p. 299: No locality.
1787. *Testudo japonica* Thunberg, Vetensk. Acad. Handl., **8**, p. 178, pl. vii, fig. 1: Japan.
1788. *La Tortue Franche* Lacépède, Hist. Nat. Quad. ovip. Serpens, 1, p. 54; and *Testudo marina* (seu *vulgaris*) in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Torrid Zone.
1788. *La Tortue écaille-verte* Lacépède, Hist. Nat. Quad. ovip. Serpens, 1, p. 92; and *Testudo viridis-squamosa* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Amazon River, Brazil.
1802b. *Testudo cepediana* Daudin, Hist. Nat. Rept., **2**, p. 50, pl. xvii, fig. 1: No locality.
1812. *Chelonia virgata* (Duméril) Schweigger, Königsberger Arch. Naturwiss. Math., pp. 291, 411: Seas of the Torrid Zone.
1814. Schweigger, 21.
1835. Duméril and Bibron, 541.
1849. Smith, A., App., 2.
1855. Gray, 74.
1873b. Gray, 93.
1820. *Caretta esculenta* Merrem, Vers. Syst. Amphib., p. 18: Atlantic Ocean.
1820. *Caretta nasicornis* Merrem, Vers. Syst. Amphib., p. 18: Ocean near America.
1820. *Caretta Thunbergii* Merrem, Vers. Syst. Amphib., p. 19: Japan.
1829. *Chelonia maculosa* Cuvier, Règne Animal, ed. 2, **2**, p. 13: No locality.
1829. *Chelonia lachrymata* Cuvier, Règne Animal, ed. 2, **2**, p. 13: No locality.
1834. *Chelonia bicarinata* Lesson, in Bélanger, Voy. Indes-Orient., Zool., p. 301: Atlantic Ocean.
1835. *Chelonia Marmorata* Duméril and Bibron, Erpét. Gén., **2**, p. 546, pl. xxiii, fig. 1: Ascension Island.
1844. *Chelonia viridis* Gray, 54.
1855. Gray, 75.

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[1] For the most part this bibliography is restricted to synonyms, together with citations dealing with African material. Nomenclatorial changes such as *Chelone*, *Chelonia*, *midas* and *mydas* call for careful checking.

1875. Melliss, 99.

1858. *Chelonia formosa* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 456, pl. xxxi, figs. 1-4: Fiji Islands.

1858. *Chelonia tenuis* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 459, pl. xxxi, fig. 8: Honden Island, Paumotu Group, Tahiti and Eimeo; Rosa Island.

1865. *Chelone viridis* Strauch, 141.

1885a. Boettger, 172 (as marine turtle, later identified as *viridis*).

1885. Greeff (1884), 49. footnote.

1888a. Boettger, 174.

1890. Büttikofer, **1**, 302.

1866a. *Chelonia midas* Bocage, 41.

1890. Büttikofer, **1**, 266, 269.

1868. *Chelonia Agassizii* Bocourt, Ann. Sci. Nat. Zool. (Paris), (5), **10**, p. 122: Nagulate River mouth, Guatemala.

1872. *Chelonia mydas* Sowerby and Lear, pls. lix-lx.

1878. Reichenow, p. 92.

1882. Pechuël-Loesche, 277.

1882a. Peters, 18.

1906a. Mocquard, 481.

1909a. Siebenrock, 545.

1912b. Werner, 454.

1929. Flower, 38.

1933. Flower, 750.

1936j. Loveridge, 221.

1937a. Flower, 13.

1937e. Hewitt, 15.

1937f. Loveridge, 488.

1949. Cadenat, 16, figs. 1-3, 10, 14, 15a.

1949. Villiers, 165.

1950. Rose, 327.

1950. Williams, 552.

1873b. *Mydas viridis* Gray, 95.

1884a. Rochebrune, 40.

1880. *Chelonia depressa* Garman (part at least), Bull. Mus. Comp. Zool., **6**, p. 124: East Indies juv. (N. Australian adult may be distinct. Also following Fry (1913), we omit *Natator tessellatus* McCulloch, 1908, from Port Darwin, N. Australia, from the synonymy).

1887. *Chelonia lata* Philippi, Zool. Garten, **28**, p. 84: near Valparaiso, Chile.

1889a. *Chelone mydas* Boulenger, 180.

1890. Büttikofer, **2**, 438, 478.

1893a. Boettger, 12.

1895a. Bocage, 6.

1896a. Bocage, 74, 98.
1896. Lönnberg, 11, 12 (on Linnaeus' type).
1901. Gadow, 381.
1901. Steindachner, 326.
1903a. Bocage, 52.
1903a. Boulenger, 92 (footnote), 96.
1906. Johnston, 819, 833, fig. 311.
1906b. Siebenrock, 39.
1908. Sordelli, 17.
1911d. Sternfeld, 51.
1913. Boettger, 318, 330, 332, 335.
1915. Rawitz, 657, pl. xlviii, figs. 59-61.
1923g. Loveridge, 930, 933.
1924b. Loveridge, 3.
1925b. Flower, 932.
1927. Calabresi, 37.
1938. Cozzolino, 241, graphs.
1947. Irvine, 309.
1955. Cansdale, 95, 104.
1925b. *Chelone virgata* Flower, 932.
1931. *Chelone midas* Ingrams, 429.
1934a. *Chelonia mydas mydas* Mertens and Müller *in* Rust, 10.
1934a. *Chelonia mydas japonica* Mertens and Müller *in* Rust, 10.

Common names. Green Turtle; Edible Turtle (English); *anjwa* or *apuhulu* (Nzima of Gold Coast:Irvine); *apuhuru* (Fante of Gold Coast:Irvine); *assa* (Cape Delgado:Peters); *hala* (Ga of Gold Coast:Irvine); *itataruca* (Mozambique Id.: Peters); *kassa* (Swahili:Ingrams); *klo* (Ewe at Keta:Irvine); *nruvi* (Mozambique Id.:Peters); *taza* (Bajun of Lamu:*fide* "Ngamba," 1932: The Field:159:421).

Illustrations. The finest colored plates of this turtle, dorsal and ventral views, are those in Sowerby and Lear (1872:pls. lix-lx).

Description.[1] Snout short; beak not hooked, without cusps; edge of jaws apparently smooth; prefrontals elongate, a single pair; frontal azygous, small; frontoparietal large; parietals 2; supraocular rather large; postoculars 4; supratemporals 2; forelimb with moderately enlarged scales along anterior edge, behind them several rows of scales, posterior edge with a series of en-

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[1] Based exclusively on a single specimen from Lamu Island (M.C.Z. 40019) and one from Madagascar (M.C.Z. 16866).

larged scales; each fore- and hindlimb with 1 claw;[1] tail short.

Carapace ovate, subtectiform (juv.) or smooth (adult), nuchal region truncate, margin serrate posteriorly; dorsal shields juxtaposed; nuchal broader than long, not in contact with first costals, not in contact with second marginals; vertebrals 5, first much the broadest, much broader than long, the rest as broad as, or broader than long, or II to IV longer than broad; costals 4, fourth smallest; marginals 11 pairs; supracaudal divided.

Plastron anteriorly subtruncate, no obvious lateral keels; plastral shields juxtaposed; intergular moderate; brachials 2 or 3 with some smaller scales extending anteriorly; inframarginals 4, without pores; inguinal small; interanal minute or absent.

Color. Carapace of young olive to dark brown; plastron white or yellow. Crown and sides of head dark, throat yellowish; limbs above olive to brown margined with white or yellow, below pure white or yellow with a large dark blotch, or blotches, or almost entirely dark.

Carapace of adult essentially similar to that of young, but with radiating lines or marbling; plastron yellow, immaculate. Head dark above, but on the sides the shields are more conspicuously edged with yellow.

The foregoing color description of the species is general as our African material is so scanty. For more detailed descriptions consult Deraniyagala (1939:228-230) or Carr (1952:348-349).

Size and Weight. Three juveniles, each about 5 inches (.127 meter) in length and weighing a lb. (.45 kilo), when received at the London Zoological Gardens in July-August, 1924, developed in the course of about 9 years and 4 months to 50 lbs. (22..68 kilos) each on November 8, 1933 (Flower:1937a).

Büttikofer (1890:**1**:260) mentions a Robertsport specimen as being 1 meter long by 75 cm. broad. The largest individuals from Europa Island were from 3¼ to 4 feet in length with weights up to 999 lbs. (450 kilos), *fide* Siebenrock (1906b). This is considerably in excess of the average adult weight of 336 lbs. mentioned by Gadow (1901:381).

Sexual dimorphism. Males have much the longer tails according to Voeltzkow (*in* Boettger:1913).

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[1] Two claws are present on both fore- and hindlimbs of very young specimens, at which stage they correspond to *Euchelys macropus* Girard, as noted by Peters (1882a) and also observed by Deraniyagala (1939 : 224).

Breeding. On the West African coast the laying season is from September to January (Gadow:1901:382). More specifically on Rolas and San Thomé Islands it is from December to January (Greef:1885). Where the warm waters of the Gulf of Guinea break on the beaches of the northern Loango Coast, Green Turtles emerge to lay, at the beginning of the November rains. They are scarcer on the southern shores of Loango which are washed by the colder Atlantic currents.

That breeding takes place off the South African coast is adduced by Hewitt (1937e) from the occurrence of an occasional hatchling with a carapace length of 50 mm. and umbilical scar still unhealed.

In Aldabra Island lagoon the ♂♂ fight desperately with each other during the breeding season, the natives told Voeltzkow (*in* Boettger:1913), but at Europa Island they usually remain outside the reef, rarely visit the bay, and never come ashore. At low tide during the period — December 4th to 20th — of Voeltzkow's visit, one might observe the ♀♀ as black patches against the white sand of the lagoon. As night fell they began coming ashore in considerable numbers. From his vantage point on the ship Voeltzkow observed seven emerge at the same time. He notes that the turtles made numerous trial excavations without laying, and describes at some length the technique they employed. He frequently found eggs, sometimes an entire laying, decomposed, apparently as a result of heavy rain and too much moisture. This led him to conclude that Europa Id. was by no means an ideal breeding site for these reptiles. The mortality among laying ♀♀ was high for their corpses were encountered along the beach and among the dunes, as many as five being met with in the course of one walk. On Aldabra, said the natives, the ♀♀ disappear after reaching a certain age and are covered with barnacles when they return to the island for laying. This is chiefly between May and December when, at intervals of six weeks, a Green Turtle will come ashore three times, on each occasion laying as many as 125 eggs. Voeltzkow's full account should be compared with that of Cozzolino, synopsized below, as they differ in details. Probably the most detailed account of a Green Turtle laying in Africa is that of Cozzolino (1938) whose observations were made on a small island 10° S off the Somali coast. Gravid ♀♀ appeared offshore cruising to and fro with their heads above the surface as if selecting a suitable spot to land. Landing takes place chiefly during the waxing, rarely during the waning, of the moon. On emerging from the water, leaving a characteristic imprint on the sand, each turtle makes for the more elevated portions of the beach beyond the reach of the highest tides.

As soon as the turtle reaches a suitable spot she promptly starts excavating, the sickle-shaped forelimbs alternating with the hind limbs. The former fling the sand aside, the latter throw it backwards. In a very short time the extent of the oval-shaped excavation begins to be apparent, and within twenty minutes is carried to a depth of about two feet ("60 cm."), the turtle disappearing from sight. She betrays her presence, however, by emitting a loud puffing sound that is audible to anyone with normal hearing for a distance of sixty yards (50 meters).

At this juncture a second operation commences. The sand being relatively loose at this depth, the tail tip is used to move it over a small area corresponding to the cloacal orifice.[1] Then the hind flipper, being turned inwards to form a scoop, is employed to lift out the displaced sand until a second cavity is excavated to a depth of about fifteen inches (35-40 cm.) with a diameter of from ten to twelve inches (25-30 cm.).

On completion of this second operation the turtle brings her hind limbs together to form an arc-shaped covering extending from the posterior margin of the carapace to the rim of the hole. Into the hole one or two eggs at a time are then dropped at irregular intervals of a second or two's duration. With the aid of a flashlight, which in no way disturbed the turtle, Cozzolino was able to watch the process and counted a total of 163 eggs. As soon as the full complement was laid the turtle quickly filled in the smaller, then the larger, hole with sand and briskly returned to the sea.

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[1] It seems to us the turtle's action may have been misinterpreted and that the cloacal orifice was being moved about as urine was being discharged in order to bind the sand in preparation for its removal.

Cozzolino thinks that as many as 600 eggs may be laid by a single turtle during one month, basing his belief on the fact that more than 1000 eggs were present in the ovaries of the specimens he dissected. He also thinks that a ♀, though remaining in the vicinity where she first laid, never deposited subsequent batches of eggs in the immediate vicinity of the first site. He measured some of the spheroid eggs whose diameters ranged from 42-46 mm.,[1] their weights from 45-65 grams. For the first 48 hours after deposition the chalky white shells remained soft so that an egg might be dropped from a height of three feet or so without breaking. Under normal temperature conditions dehydration sets in after 48 hours, the shell shrivels and becomes brittle and the shape of the egg changes.

Incubation takes from 30 to 34 days, at which time the hatchlings struggle to the surface, sometimes taking an oblique course from the nest. This Cozzolino discovered after surrounding a nest-site with fishing net at a distance of 20 inches (50 cm.) and the turtlets appeared outside the net, usually on the seaward side. Thereafter he set his nets at a distance of 27½ inches (70 cm.) and captured about 153 hatchlings from each of three nests.

Hatching takes place at night and the young turtlets instinctively orient themselves and make for the sea. Many never reach it, however, for in crossing the beaches they are attacked by famished crustaceans. Survivors of the massacre which do reach the ocean are then preyed upon by other predators.

Longevity. Fifteen years for a Pacific Green Turtle in New York Aquarium, but only six years for an Atlantic specimen (Flower:1925b).

Enemies. On Aldabra Island hatchling turtles are preyed upon by Gray Herons (*Ardea cinerea cinerea*) and Frigate Birds (*Fregata minor aldabrensis*); sharks swallow young turtles entire and attack larger ones by biting off their flippers. Natives harpooned the adults when asleep or sunning in lagoons or along the shallower stretches of the coastline. About 3000 were annually taken at the time of Voeltzkow's visit — 1903-1905 (cf. Boettger:1913).

As only about 500 of these could be sent to Mahé, owing to the scarcity of shipping, the remainder were processed locally. The flesh, cut into strips and salted, was sun-dried for export to

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[1] 35 mm. for a Liberian egg measured by Büttikofer (1890).

the Seychelles where workers favored it as an article of diet. The fat was cooked for shipment to France where it enjoyed a reputation as a remedy for chest diseases.

On Juan de Nova Island the natives have a curious way of dealing with the discarded portions of the turtles they kill. On the sloping dunes one sees a great many scaffoldings a yard or more in height, strengthened by cross sticks and the whole securely bound together by fiber. Behind the scaffolding a small bank is constructed. In front of the scaffolding an area of from one to two meters square is marked off and covered with the twigs of *Pemphis ocidula.* Upon these twigs are laid the turtle plastra; the carapaces, each overlapping the one in front, are arranged in long rows to the right and left while from the scaffolding hang the heads of the turtles. No such scaffolding was seen on Madagascar where the Sakalava Fody merely impale the discarded heads on stakes.

On Ascension Id., according to D. Krümmel (Werner:1912b), Green Turtles are captured and held in lagoons connected with the ocean. By May, when the season ends, there may be several hundred. The meat appears twice weekly in the Commandant's mess, and one or more turtles are presented to each visiting warship.

The use of sucker fish (*Remora remora*) to capture turtles has long been practiced on the coast of East Africa from Mombasa to Natal. The earliest references appear to be those of Andrew Sparrman who, on his return from Natal, briefly described (1787)[1] how the natives, having attached one cord to the fish's head and another around the tail, released the *remora* in the sea in the vicinity of a turtle. As soon as the fish attached itself to a turtle, both fish and reptile were drawn to the boat where the reptile could be seized or harpooned. Sparrman wrote that turtles were hunted in similar fashion on the coasts of Madagascar.

During a voyage from the Cape to Ethiopia, Henry Salt stopped at Mesuril (as Masuril), a village in Mozambique harbour. There, on September 9, 1809, he was presented with a large example of *Echeneis naucrates* which the Bishop of Mesuril

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[1] For all *Remora* references see the extensive bibliography by E. W. Gudger, 1919, American Nat., **53**, pp. 520-525.

informed him would attach itself to the plastron of a turtle with such tenacity that the reptile rarely got away.

In 1829 Philibert Commerson's more detailed description of the method employed at Mozambique was published by Lacépède. Commerson states that a ring, small enough not to slip over the caudal fin, is placed about the tail of a *remora;* to the ring is attached a long cord. After this preparation the fish is placed in a receptacle, containing salt water, in the bottom of the fisherman's boat. Sail is set and the craft headed towards an area where turtles are likely to be basking on the surface. Aroused by the approaching boat, however, the lightly sleeping reptiles seek safety in diving.

It is at this juncture that the *remora* is released, and sufficient cord paid out to enable the fish to reach the turtle. Commerson states that it is only after the fish has made futile attempts to escape that it seeks shelter beneath the turtle to whose plastron it adheres by means of a sucker on its head and nape, thus enabling its employers to pull the turtle to the boat.

When returning from Pemba Island to Zanzibar, Frederic Holmwood[1] (1884) observed several fish dart out from beneath the steam launch, on which he was travelling, whenever garbage was thrown overboard. These *chazo,* as the boatmen called the fish, after feeding, returned and attached themselves to the bottom and sides of the launch. All Holmwood's efforts to pull one off by force failed, but a Zanzibari readily detached it by drawing the fish sideways. Later, Holmwood discovered that the local fishermen were accustomed to employ these *remora,* ranging in length from 2 to 4½ feet and in weight from 2 to 8 lbs., in catching turtles. He was informed that sharks and even large crocodiles were captured by this means in Malagasy waters. Between trips, the *remora* are kept in canoe-like dug-out logs stored in the huts of the fishermen who periodically change the water.

The rings worn by the fish were attached in various ways, though generally welded to a simple iron band. In some instances the band had been worn for so many years that it had become imbedded in a thick fleshy formation. One *chazo* had an extensive wound where the ring had been torn off. This fish,

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[1] Holmwood, 1884, "On the Employment of the *Remora* by Native Fishermen on the East Coast of Africa." Proc. Zool. Soc. London, pp. 411-413, figs. 1-2.

said its owner, had caught the two turtles which were lying in his canoe and then affixed itself to a shark. It continued to hold on until all the spare line had been paid out and the ring torn off. The injured fish had then left the shark and returned to the boat, a by no means unusual occurrence so Holmwood was told.

Photographs of turtle hunting by means of *remora* are shown in the film ''West of Zanzibar'' (1954). However, the technique is not confined to East Africa, being practiced by fishermen in Chinese and Australian waters as well as in the West Indies.

In the belief that citrus leaves mitigate the pungent odor of boiling turtle flesh, it is customary in the Gold Coast to place leaves and meat together in the cooking pot. The eggs too are considered a great delicacy by the Gold Coast people. After first boiling them in sea-water the shells are perforated to drain off their watery contents, leaving the yolks. These are then baked and eaten, the taste being compared to rich cake (Irvine :1947).

Man is unquestionably the worst enemy of the Green Turtle, famous for soup though its carapace is of no commercial value. With natives everywhere hunting these turtles for their flesh and fat, besides searching for their eggs which are also highly esteemed as food, the extermination of this reptile would appear to be only a matter of time. Further information regarding their exploitation in other parts of the world will be found in Gadow (1901 :382), Deraniyagala (1939 :320) and Carr (1952: 353-357).

Temperament. The placidity with which a Green Turtle ignores inspection, making no attempt to bite even when touched, is commented on by Voeltzkow (*in* Boettger :1913).

Habits. Two captive Mozambique Green Turtles emitted croaking (''qakenden'') sounds, says Peters (1882a).

Habitat. Green Turtles frequent the submarine ''prairies à Posidonies ou Cymodocées'' off the coast of Senegal, and where these occur near the shore, as at Joal, the proportion of *mydas* taken is considerable. In such areas they are captured at all seasons, though no systematic hunting takes place, being either harpooned or taken when they venture ashore during the egg-laying season (Cadenat :1949 :22).

Localities. Egypt: Port Said. *Somalia:* Mogadiscio (Mogadish). *Socotra Island:* Abd el Kuri Id.; Shadwan Id. *Kenya Colony:* *Lamu Id; *Mombasa Id. (B.M.). *Tanganyika Territory:* *Dar es Salaam; Tanga. *Zanzibar Island. Mozambique:* Europa Id.; Juan de Nova Id.; Mozambique Id.; Querimba Id. *Cape Province:* Bird Id.; Cape of Good Hope; East London; Kei River mouth; Kleinemonde. *Ascension Island. Angola:* off Loanda. *Cabinda:* Chinchoxo. *Belgian Congo:* Banana at mouth of Congo River. *French Equatorial Africa:* Loango Coast. *São Thomé Island. Principe Island. Rolas Island. Gold Coast. Liberia:* Monrovia; Robertsport. *Portuguese Guinea. Senegal:* Banc d'Arguin (Argain); Hann; Joal; Mbour; other localities of questionable authenticity are listed by Rochebrune (1884a). *Cape Verde Islands:* São Vicente (Saint Vincent) Id. *Canary Islands:* Teneriffa Id.

Range. All African coasts, Indian and Atlantic oceans and — as an accidental visitor — the temperate seas.

Genus ERETMOCHELYS Fitzinger

1828. *Caretta* Ritgen (not of Rafinesque: 1814), Nova Acta Acad. Leop.-Carol., **14**, p. 270. Type: *Testudo imbricata* Linnaeus (by monotypy).

1843. *Eretmochelys* Fitzinger, Syst. Rept., p. 30. Type: *T. imbricata* Linnaeus (by original designation).

1868. *Herpysmostes* Gistel, Die Lurche Europa, p. 145. Type: *T. imbricata* Linnaeus (*fide* Mertens, 1936, Senckenbergiana, **18**, p. 75).

1873j. *Onychochelys* Gray, Proc. Zool. Soc. London, p. 397, figs. 1-2. Type: *O. kraussi* Gray = *T. imbricata* Linnaeus (by monotypy).

Definition. Head with 2 pairs of prefrontal shields; postoculars 3; claws 2.

Skull with triturating surface of maxilla ridged, the ridge strongest anteriorly, extending somewhat on to the premaxillae; premaxillae in contact with vomer which separates the maxillae; maxillae without vertical ribbing on inner surface of its cutting edge; descending processes of prefrontals in contact with vomer only; a blunt and rather low ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view not concealed by the moderate secondary palate; pterygoids deeply concave posteriorly; frontal entering orbit; crista praetemporalis strong; mandibular symphysis pointed, concave, as long as broad; labial margin sharp, straight, not rising to a point at the symphysis; lingual margin lower than the labial, without ridge; no symphysial ridge.

Carapace without lateral fontanelles in fully adult individuals; neurals 9-11, usually hexagonal, short-sided in front; peripherals 11 pairs, the ninth pair not in contact with the ribs; nuchal shield not in contact with first costals; costals typically 4 pairs.

Plastron with a large intergular shield; inframarginals 4 pairs, without pores.

Range. Tropical, subtropical and — as an occasional visitor — temperate oceans.

ERETMOCHELYS IMBRICATA (Linnaeus)

1766. *Testudo imbricata* Linnaeus, Syst. Nat., ed. 12, **1**, p. 350: American and Asiatic Seas.
1834. *Chelonia pseudo-mydas* Lesson, *in* Bélanger, Voy. Indies-Orient., Zool., p. 299: Atlantic Ocean.
1834. *Chelonia pseudo-caretta* Lesson, *in* Bélanger, Voy. Indies-Orient., Zool., p. 302: Atlantic Ocean.
1835. *Caretta Bissa* Rüppell, Neue Wirbelth. Fauna Abyss., Amphib., p. 4, pl. ii: Red Sea.
1922a. Mertens, 168 (lists type, as syn. of *imbricata*).
1835. *Chelonia imbricata* Temminck and Schlegel, p. 13, pl. v.
1872. Sowerby and Lear, pls. lvii-lviii.
1875. Melliss, 99.
1882a. Peters, 17.
1890. Büttikofer, **2**, 438, 478.
1896a. Bocage, 98.
1906a. Mocquard, 481.
1909a. Siebenrock, 547.
1913c. Nieden, 55.
1921d. Loveridge, 51.
1849. *Caretta imbricata* A. Smith, App., 2.
1873b. Gray, 92.
1884a. Rochebrune, 39.
1857. *Eretmochelys squamata* Agassiz, Contr. Nat. Hist. U. S., **1**, p. 382: Indian and Pacific Oceans.
1858. *Caretta squamosa* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 442, pl. xxx, figs. 1-7: Sulu Seas and Indian Ocean.

1858. *Caretta rostrata* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 446, pl. xxx, figs. 8-13: Fiji Islands.
1873j. *Onychochelys kraussi* Gray, Proc. Zool. Soc. London, p. 398, figs. 1-2: Atlantic Ocean off French Guiana.
1885. *Chelone imbricata* Greef (1884), 49, footnote.
1889a. Boulenger, 183.
1893a. Boettger, 12.
1896. Tornier, 3.
1897. Tornier, 63.
1898. Sclater, W. L., 97.
1898. Tornier, 283.
1900b. Tornier, 582.
1901. Gadow, 385.
1901. Steindachner, 326.
1903a. Boulenger, 92, 96.
1906i. Boulenger, 197.
1906. Johnston, 819, 833.
1910. Sternfeld, 5, fig. 10.
1911d. Sternfeld, 51.
1914. Fuchs, 1914, pp. 1-325, figs. 1-182, pls. i-vi.
1923g. Loveridge, 933.
1924b. Loveridge, 3 (as *impricata*)
1925b. Flower, 932.
1929. Rose, 184.
1930a. Scortecci, 215.
1931. Ingrams, 429.
1937b. Angel, 1696.
1955. Cansdale, 96, 104.
1929. *Eretmochelys imbricata* Flower, 39.
1929. Lindholm, 287.
1933. Flower, 750.
1933h. Loveridge, 207.
1937a. Flower, 13.
1937e. Hewitt, 16, pl. ivB.
1937f. Loveridge, 488.
1947. Irvine, 311.
1949. Cadenat, 16.
1949. Villiers, 165.
1950. Rose, 327.
1950. Williams, 552.
1952. Williams and McDowell, pl. i, fig. 4.
1934a. *Eretmochelys imbricata imbricata* Mertens and Müller *in* Rust, 10.
1934a. *Eretmochelys imbricata squamosa* Mertens and Müller *in* Rust, 10.

Common names. Hawksbill Turtle (English); *anyite* (Ewe: Irvine); *apuhuru* (Fante: Irvine); *ayikplonto* (Ga: Irvine); *baga* for ♀, *bissa* for ♂ (Arabic in Red Sea: Rüppell); *hala-apatadzi* (Ga: Irvine, *q. v.* for other Gold Coast names); *ingappa* (Mozambique: Peters); *ngamba* (Cape Delgado Island: Peters; Zanzibar: Ingrams).

Illustrations. A reasonably good colored plate will be found in Rüppell (1835), and very fine ones of a subadult in Sowerby and Lear (1872b: pls. lvii-lviii).

Description. (Based exclusively on six African and Malagasy specimens in the Museum of Comparative Zoology).

Snout elongate, compressed; beak drawn out but not hooked, without cusps; edge of jaws apparently smooth; prefrontals not elongate, in 2 pairs; frontal azygous, small, rarely[1] fused with frontoparietal; frontoparietal large, entire or semidivided anteriorly; parietals 2, transverse in juveniles, somewhat elongate in adults; a small interparietal sometimes present; supraocular rather large; postoculars 3, rarely[2] 4; supratemporals 2 or 3, one sometimes fused with a temporal; forelimb with moderately enlarged scales along anterior edge, behind them several rows of scales, posterior edge with a series of enlarged scales; both fore- and hind limbs with 2 claws; tail short.

Carapace ovate, subtectiform in adults, with 3 interrupted keels in young but only a trace of the lateral ones persisting in adults, nuchal region truncate, margin weakly serrate in young, strongly in adults; dorsal shields juxtaposed in hatchling, imbricate in adults, juxtaposed in aged individuals; nuchal broader than long, not in contact with first costals, not in contact with second marginals; vertebrals 5, exposed portion of each broader than long at all ages, the first no broader than the others in young, broader than the others in adults; costals 4, fourth smallest; marginals 11 pairs; supracaudal divided.

Plastron anteriorly rounded, 2 prominent lateral keels; plastral shields of adult more or less imbricate; intergular moderate; brachials 2 or 3 with some smaller scales extending anteriorly; inframarginals 4, without pores; inguinal small; interanal minute or absent.

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[1] Fused in a Zanzibar specimen (M.C.Z. 1141) and a Malagasy turtle (M.C.Z. 16867).

[2] Four in a Zanzibar specimen (M.C.Z. 1141).

Color. Carapace of young light brown flecked with darker, or black blotched with lighter; plastron substantially similar. Head and limbs light brown to black, more or less uniform.

Carapace of adult horn to reddish brown heavily marbled or streaked with black; plastron yellow, the posterior portion of each shield blotched with black. Head and limbs dark above, but on the sides and below yellow heavily blotched with black.

The foregoing color description is based solely on our African and Malagasy material.

Size. Carapace length of largest in the Paris Museum 740 mm.; surpassed by one of Rüppell's "*bissa*" which was 765 mm., by 690 mm. broad; the lectotype was only 750 mm., by 635 mm. broad; the record is apparently 850 mm. (B.M.).

Breeding. On Rolas and São Thomé Island the ♀♀ come ashore to lay from December to February (Greef:1885). In the Red Sea region they lay from February to March; after laying, the ♀♀ regularly return to the site, according to Rüppell (1835).

Longevity. Fifteen years, 7 months, 28 days, and still alive about 1937 (Flower:1937a). The alleged record of 32 years, quoted by Gadow (1901:386), has been traced to Tennant (1861:294), who quoted Bennett (1843:275) who followed it back to 1826 and 1794 (Flower:1925b, where full references to preceding citations will be found).

Enemies. In Liberia it is eaten by the Africans but not by Europeans (Johnston:1906). The plates of the ♂♂ are thinner than those of the ♀♀, and consequently are of less value commercially (Rüppell:1835). Between 700 and 800 kilograms of high grade tortoise-shell was annually taken from the Hawksbill Turtles in the vicinity of Cape Delgrado (Peters:1882a). As much as 8 lbs. of shell may be removed from a single large specimen (Gadow:1901). Great numbers of stripped carapaces were observed around the natives' huts on Abd el Kuri Island by H. O. Forbes, who remarks that though it still occurs off the coast of Socotra Island it is not nearly so common as it was eighteen centuries ago when it was an article of trade much sought after by merchants from Arabia (Boulenger:1903a).

Temperament. In marked contrast to the Green Turtle, the Hawksbill bites so freely that Malagasy fishermen carry in their boats a piece of wood which they hold out to a harpooned turtle. Once the reptile has seized the proffered wood it does not readily let go. If this procedure is not followed, so the men told Voeltzkow (*in* Boettger:1913), the turtle is apt to bite on their frail craft when being hauled aboard, and may inflict considerable damage.

Localities. Egypt: Saint John Id.; Red Sea coasts from Zebejir to Zukur. *Eritrea:* Massaua. *Socotra Island:* Abd el Kuri Id.; Socotra Id. *Kenya Colony:* Frere Town; *Mombasa Id. *Tanganyika Territory:* Dar es Salaam; Lindi; Tanga. *Zanzibar Island:* *Zanzibar. *Mozambique:* Cape Delgado; Mozambique Id.; Querimba Id. near Ibo. *Cape Province:* False Bay; Simonstown Beach; Table Bay. *Ascension Island:* *(M.C.Z. 4095). *French Equatorial Africa:* Gabon Coast (P.M.). *São Thomé Island. Principe Island:* Rolas Id. (only). *French Cameroon:* Longuy (Longji). *Gold Coast:* *Tenia (B.M.). *Liberia:* Angel River. *Sierra Leone:* *Bonthé, Bonthé district. *Senegal:* Banc d'Arguin (Argain); Joal (Joalles); other localities of questionable authenticity are listed by Rochebrune (1884a). *Cape Verde Islands:* Fogo Id.

Range. East, South and West coasts of Africa, Indian and Atlantic oceans and — as an accidental visitor — the temperate seas.

Genus CARETTA Rafinesque

1814. *Caretta* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66. Type: *C. nasuta* Rafinesque = *Testudo caretta* Linnaeus (by monotypy).

1835. *Thalassochelys* Fitzinger, Ann. Wiener Mus., **1**, pp. 110, 121, 128. Type: *T. caouana* Fitzinger = *T. caretta* Linnaeus (designation by Fitzinger, 1843).

1838. *Caouana* Cocteau, Rept. in De la Sagra, Hist. Fis. Pol. Nat. Cuba, **4**, p. 31. Type: *T. cephalo* Schneider = *T. caretta* Linnaeus (by monotypy).

1843. *Halichelys* Fitzinger, Syst. Rept., p. 30. Type: *H. atra* Fitzinger = *T. caretta* Linnaeus (by original designation).

1873j. *Cephalochelys* Gray, Proc. Zool. Soc. London, p. 408. Type: *C. oceanica* Gray = *T. caretta* Linnaeus (by monotypy).

1873j. *Eremonia Gray*, Proc. Zool. Soc. London, p. 408. Type: *E. elongata* Gray = *T. caretta* Linnaeus (by monotypy).

Definition. Head with 2 pairs of prefrontal shields; postoculars 3; claws 2.

Skull with triturating surface of maxilla *not* ridged; premaxillae not reached by vomer which does not separate the maxillae; maxilla without vertical ribbing or a sharp cutting edge, its whole surface sloping dorsomedially as part of a large crushing surface; descending processes of prefrontals in contact with vomer and palatines; a blunt ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view concealed by the extensive secondary palate; pterygoids deeply concave posteriorly; frontal excluded from orbit; crista praetemporalis strong; mandibular symphysis rounded, concave, longer than broad; neither labial nor margins raised as cutting edges; no symphysial ridge.

Carapace without lateral fontanelles in adults; neurals 7-11, occasionally some separated, typically hexagonal, short-sided in front; peripherals 12-13 pairs, the ninth or tenth pair not in contact with the ribs; nuchal usually in contact with first costals: costals typically 5 pairs.

Plastron without, or with only a very small, intergular shield; inframarginals 3 pairs, without pores.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

CARETTA CARETTA (Linnaeus)

1758. *Testudo Caretta* Linnaeus, Syst. Nat., ed. 10, **1**, p. 197: Islands off America.

1783. *Testudo Cephalo* Schneider, Naturg. Schildkröten, p. 303: No locality.

1788. *La Caouane* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, p. 95; and *Testudo caouana* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Jamaica, British West Indies (restricted).

1788. *La Tortue nasicorne* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, p. 103; and *Testudo nasicornis* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: America.

1814. *Caretta nasuta* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66: Sicily (*fide* Lindholm: 1929).

1820. *Caretta atra* Merrem, Vers. Syst. Amphib., p. 17: Ascension Island.

1833. *Chelonia pelasgorum* Valenciennes, pl. vi, *in* Bory de Saint Vincent, Expéd. sci. de Morée, Zool.: Modon, etc., Mediterranean Sea.

1844. *Caouana elongata* Gray, Cat. Tortoises Brit. Mus., p. 53: No locality.
1858. *Thalassochelys corticata* Girard, U. S. Explor. Exped. 1838-1842, Herp., p. 431, pl. xxix: Madeira Islands.
1894. Oliver, 100.
1896b. Oliver, 118.
1862a. *Chelonia corticata* Strauch, 19.
1903. Mayet, 9.
1873j. *Cephalochelys oceanica* Gray, Proc. Zool. Soc. London, p. 408: ? Mexico.
1884a. *Caouana caretta* Rochebrune, 38.
1887. *Thalassiochelys tarapacona* (*sic*) Philippi, Zool. Garten, **28**, p. 85: Iquique, Chile (identified by subsequent description. See Philippi, 1899).
1889a. *Thalassochelys caretta* Boulenger (part), 184.
1891c. Steindachner, 305, 306.
1893a. Boettger (part), 13.
1895a. Bocage, 6.
1896a. Bocage, 66.
1898. Jeude, 11.
1898. Sclater, W. L., 97.
1901. Gadow (part), 326, 387, figs. 69, 84 (diagrams based on a misconception involving young of one species, adults of another).
1902. Bocage, 208.
1903a. Boulenger, 96.
1906a. Mocquard, 481.
1912a. Pellegrin, 256.
1923g. Loveridge, 933.
1924b. Loveridge, 3.
1925. Flower, 932.
1926c. Pellegrin, 49.
1929. Rose, 184, fig. 122.
1932d. Witte, 57.
1899. *Thalassochelys tarapacana* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 731 (validating redescription).
1899. *Chelonia Caouana* Doumergue, 253.
1909a. *Caretta caretta* Siebenrock, 549.
1911d. Sternfeld, 52, fig. 64.
1912b. Werner, 465.
1929. Flower, 39.
1929. Lindholm, 287.
1933. Flower, 751.
1934. Mosauer, 52.

1937b. Angel, 1696.

1937a. Flower, 14, 37.

1937e. Hewitt, 15, pl. ivB.

1949. Cadenat, 17, figs. 4, 5, 7-12, 15b, 16a.

1949. Villiers, 165.

1950. Rose, 327, fig. 127.

1950. Williams, 552.

1930. *Caretta* [*caretta* inferred] Babcock (part), 95.

1933. *Caretta gigas* Deraniyagala, Ceylon Jour. Sci., Sect. B, **18**, p. 66, figs. 4-6, pl. v: Gulf of Mannar, Ceylon.

1934a. *Caretta caretta caretta* Mertens and Müller *in* Rust, 10.

1935. *Tortue caret* Witte, 94.

1939. *Caretta caretta gigas* Deraniyagala, 162.

Common names. Red-brown Loggerhead (English); *fahroun el barr* (in Tunisia:Mosauer); *nduvi* (at Lindi:Loveridge MS).

Description.[1] Snout relatively short, not compressed; beak distinctly hooked, unicuspid; edge of jaws apparently smooth; prefrontals not elongate, in 2 pairs with an additional central pair; frontal azygous, small, longer than broad; frontoparietal large, as broad as long, semidivided posteriorly; parietals not elongate, broken up; supraocular moderately large; postoculars 3; supratemporals in 3 pairs; forelimb with moderately enlarged scales along anterior edge, behind them numerous small scales, posterior edge with a series of distinctly enlarged scales; both fore- and hind limbs with 2 claws; tail moderately short.

Carapace ovate, tectiform, with a strong interrupted vertebral keel and nearly obsolescent lateral keels (in the young Madeira specimen); nuchal region truncate, margin somewhat serrate; dorsal shields juxtaposed; nuchal broader than long, in contact with first costals on right side, excluded on left; vertebrals 6, first smallest;[2] costals 5, first smallest; marginals 13 pairs; supracaudal divided.

Plastron anteriorly rounded, 4 strong, obtuse, interrupted, lateral keels; plastral shields juxtaposed; intergular present, small; brachials 3 with some smaller scales extending anteriorly; inframarginals 3, without pores; inguinal absent; interanal absent.

Color. Carapace reddish brown,[3] points of keels and marginals

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[1] Based on the almost foot-long, Madeiran type of *T. corticata* Girard (U.S.N.M. 7778) examined by E. E. W.

[2] The normal first vertebral in the type of *corticata* (U.S.N.M. 7778) is asymmetrically divided.

[3] In the now dried type of *corticata* more uniformly reddish than described by Girard.

lighter; plastron whitish yellow to yellowish brown. Head scales reddish centrally, narrowly margined with yellow; eyelids conspicuously black (*fide* Doumergue); neck yellowish; throat yellowish brown; limbs above, reddish brown, below, yellowish brown.

Size and Weight. In the almost complete absence of African material we offer the following remarks.

The carapace of a Florida loggerhead at hatching had a length of about 48 mm., a breadth of 35 mm., and a weight of about 20 grams. When four-and-a-half years old this turtle weighed 81½ lbs. (37 kilos.) and its carapace measured about 2 feet (630 mm.) in length, and 1 foot, 11 inches (590 mm.) in breadth. Its rate of growth was much more rapid than that of three other loggerheads reared under almost similar conditions. Yet all three revealed that these turtles attain to maturity much more rapidly than was generally supposed (Parker:1939).

Carapace length of a hatchling (M.C.Z. 4017) from Key West, Florida, 49 mm., breadth 41 mm., length of forelimb from axilla to tip, 35 mm.; the carapace length being contained in that of the forelimb .71 per cent.

Carapace length of a young turtle (M.C.Z. 28202) from Bermuda, 83 mm., breadth 72 mm., length of forelimb from axilla to tip 65 mm.; the carapace length being contained in that of the forelimb .79 per cent.

Carapaces rarely exceed 700 mm. in length at Oran (*fide* Doumergue:1899). Carapace lengths of adults from Hann and Joal, Senegal, were 1040 and 1080 mm., respectively (Cadenat: 1949:19).

Carapace length *over the curve* of the largest known "*gigas*" ♂, from China (*fide* Fang:1934 *in* Deraniyagala: 1939), 940 mm.; largest "*gigas*" ♀ from Moratuva, Ceylon 960 mm. (*fide* Deraniyagala:1939:183).

Longevity. Possibly 33 years in the Vasco da Gama Aquarium in Lisbon, where several lived from 1898 until 1931, when they succumbed during a spell of exceptionally hot weather (*fide* Dr. Rodrigo Boto, who so informed Flower:1937a). Another loggerhead, whose age when received at the Berlin Zoological Gardens in September, 1913, was estimated at 2 years, was still alive on September 19, 1936. Consequently the animal was at least 23, possibly 25, years old.

Diet. In spring, loggerheads appear within the narrow sandbar on the west coast of Lanzarote Island in order to feed on the abundant mussels (*Gari depressa,* recorded as *Psammobia vespertina,* and *Venus verrucosa*) which occur there (Steindachner: 1891c).

Enemies. The flesh of the caouanne is good to eat, according to Doumergue (1899).

Localities. French Morocco: Mogador. *Algeria:* Oran. *Tunisia:* Bizerte; Gabes; Sfax market; Tunis. *Egypt:* Alexandria; Brullos; Damietta; Port Said. *Socotra Island:* Abd el Kuri Id.; Bandar Saleh. *Kenya Colony* (Loveridge:1923g). *Mozambique:* *Inhambane (U.S.N.M.). *Cape Province:* Kalk Bay; Muizenberg; Peddie Coast. *Southwest Africa. Ascension Island. Belgian Congo:* Banana. *French Equatorial Africa:* Gabon. *Ivory Coast:* San Pedro. *Senegal:* Fadiouth; Hann; Joal. *Rio de Oro* (*fide* Carr:1952:383, but Cameroons may be included on basis of *Lepidochelys,* which see). *Cape Verde Islands:* Sal Id. near São Vicente Id. *Canary Islands:* Lanzarote Id.; Teneriffa Id. *Madeira Islands:* Madeira Id.

Range. All African coasts, Indian and Atlantic oceans, the Mediterranean and — as an accidental visitor — the temperate seas.

Genus LEPIDOCHELYS Fitzinger

1843. *Lepidochelys* Fitzinger, Syst. Rept., p. 30. Type: *Chelonia olivacea* Eschscholtz (by original designation).

1880. *Colpochelys* Garman, Bull. Mus. Comp. Zool., **6**, p. 124. Type: *kempi* Garman (by monotypy).

Definition. Head with 2 pairs of prefrontal shields; postoculars 3-4; claws 2-3 (though adults sometimes have only 1).

Skull with triturating surface of maxilla ridged, the ridge subequal in height throughout, not extending on to the premaxillae; premaxillae in contact with vomer which separates the maxillae; maxilla without vertical ribbing on inner surface of its cutting edge; descending processes of prefrontals in contact with vomer only; no obvious ridge on vomer and palatines at the anterior margin of the internal choanae; choanae in ventral view not concealed by the moderate secondary palate; pterygoids deeply concave posteriorly; frontal entering orbit; crista praetemporalis strong; mandibular symphysis pointed, about as long as broad; labial and lingual margins slightly raised into cutting edges; a more or less distinct symphysial ridge.

Carapace without lateral fontanelles in adults; neurals 12-15, some quadrate, others hexagonal, short-sided in front; peripherals usually 12-13 pairs, the tenth pair not in contact with the ribs; nuchal shield usually in contact with first costals; costals 5 or more pairs.

Plastron without, or with only a very small, intergular shield; inframarginals 4 pairs, each with a pore near its posterior edge.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

LEPIDOCHELYS OLIVACEA OLIVACEA (Eschscholtz)

1820. ?*Chelonia multiscutata* Kuhl, Beitr. Zool. Anat., p. 78: No locality.
1829. *Chelonia olivacea* Eschscholtz, Zool. Atlas, p. 3, pl. iii: Manila Bay, Philippine Islands, China Sea.
1860. Duméril, 170.
1835. *Chelonia Dussumierii* Duméril and Bibron, Erpét. Gén., **2**, p. 557, pl. xxiv, figs. 1-1a: China Sea and Malabar Coast.
1835. *Caretta olivacea* Rüppell, 7, pl. iii.
1839. Parker, 129.
1949. Cadenat, 17, 23, figs. 6, 16b.
1844. *Caouana Rüppellii* Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 53: ? India (*nomen nudum*).
1849. *Caouana dessumierii* (*sic*) A. Smith, App., 2.
1857. *Chelonia polyaspis* Bleeker, Nat. Tijdshr. Ned. Indies, **14**, p. 239: Batavia, Java.
1884a. *Caouana olivacea* Rochebrune, 38.
1888a. *Thalassochelys olivacea* Boettger, 18.
1889a. *Chelonia dubia* Bleeker (*nomen nudum*) in Boulenger, Cat. Chelon. Rhyncho. Crocod. Brit. Mus., p. 186: Borneo.
1899. *Thalassochelys controversa* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 732: No locality.
1900b. *Thalassochelys caretta* Tornier (not of Linnaeus), 582.
1902c. Tornier, 665 (head lost, but hatchlings studied by us).
1910. Sternfeld, 5 (based on the 1902c material just mentioned).
1913c. Nieden, 55.
1930a. Scortecci, 215.
1908. *Caretta remivaga* Hay, Proc. U. S. Nat. Mus., **34**, p. 194, pl. x, figs. 1-3, pl. xi, fig. 5: Ventosa Bay, Gulf of Tehuantepec, Mexico.

1934a. *Caretta caretta olivacea* Mertens and Müller *in* Rust, 10.
1937f. Loveridge, 488.
1943. *Lepidochelys olivacea olivacea* Deraniyagala, 81, 92, figs. 1, 3a, 5a, 6a.

Common names. Olive Loggerhead (English); *bage* (in Eritrea:Rüppell).

Illustrations. A clear and detailed drawing of the dorsal view, together with a lateral view of the head and plastron from below, is furnished by Rüppell (1835).

Description.[1] Snout relatively short, not compressed; beak scarcely or slightly hooked, not or but slightly bicuspid (tricuspid in Rüppell's figure); edge of jaws apparently smooth; prefrontals not elongate, in 2 pairs;[2] frontal azygous, small, as broad as, or broader than, long (in hatchlings), longer than broad (in adult); frontoparietal large, broader than long, semi- or wholly divided; parietals transverse (in hatchlings), elongate (in adult), or somewhat broken up (in either); supraocular moderately large; postoculars 3-4; supratemporals broken up; forelimb with moderately enlarged scales along its anterior edge, behind them several rows of scales, posterior edge with a series of distinctly enlarged scales; both fore- and hind limbs with 2 claws, though on the former scarcely distinguishable; tail short.

Carapace ovate, hardly tectiform, with a weak, interrupted, vertebral keel, in hatchlings similar lateral keels are also present, nuchal region truncate, margin scarcely serrate; dorsal shields juxtaposed; nuchal broader than long, normally[3] in contact with the first costals, not in contact with second marginals; vertebrals 5-7, in hatchlings all broader than long except the last which is usually longer than broad, in adults I is somewhat broader than long, II-VI as long as, or longer than, broad, VII much the broadest; costals[4] 6 or 7,[5] first smallest; marginals 12 pairs;

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[1] Based on five hatchlings from the Cameroon (Berlin Mus. 15513), three hatchlings from the Gabon (Paris Mus. 41.58) and Rüppell's (1835) figures and description of a Massaua specimen. Checked on nine hatchlings from Ceylon; India; New Britain and Mexico, but their deviations are not included in this description.

[2] The second pair of frontals are fused with the supraocular on one or both sides in three of the five Cameroon hatchlings.

[3] Nuchal separated from first costal by a marginal in one Cameroon hatchling.

[4] Of the five Cameroon hatchlings two have 5 costals on both sides; one has 5 on the right, 6 on the left; two have 6 on both sides. The series, obviously from one nest, must be regarded as intergrades between *L. o. olivacea* (Eschscholtz) and *L. o. kempi* (Garman). Incomplete supernumerary costals, split off from the larger complete ones, occur in the Gabon hatchlings; we have not included these incomplete scutes in the costal count.

[5] Seven in a Senegal specimen (Cadenat:1949).

supracaudal divided.

Plastron anteriorly rounded, 2 obtuse, interrupted, lateral keels; plastral shields juxtaposed; intergular small, rarely divided [1] or absent; brachials 2-3 with some subequal or smaller shields extending anteriorly; inframarginals 4, each with or without a small pore posteriorly; inguinals minute or absent; interanal minute or absent.

Color. Carapace of hatchlings (from Gabon) uniformly olivaceous black, or (in Cameroon intermediates) wholly black; plastron, head and limbs suffused with brown.

Carapace of adult (from Massaua, Rüppell :1835) olive green; plastron sulphur yellow. Head, neck and foot above, olive green; below sulphur yellow. Iris dark brown, eyeball blue-gray.

Size. Carapace lengths and breadths of five hatchlings from Cameroon (Berlin Mus.) range from 42 x 38 to 44 x 40 mm., those of three hatchlings from Gabon (Paris Mus.), 49 x 45, 50 x 44 and 50 x 45 mm., respectively. This will give some idea of the variation in length to breadth ratio in hatchlings that almost certainly came from only two broods. Rüppell's Massaua turtle was said to be 630 mm. in length as well as breadth. Carapace lengths of specimens from Ngaparo and Joal, Senegal, were 660 and 690 mm. respectively (Cadenat :1949), while the possible maximum length for an adult may be 790 mm.; breadth 680 mm. (*fide* Deraniyagala :1939).

Breeding. In May on the Eritrean coast (Rüppell :1835).

Localities. Egypt? Eritrea: Massaua. *Socotra Island. Tanganyika Territory:* Lindi. *Cape Province:* Table Bay. *Belgian Congo:* Banana; Moanda (Royal Museum of the Belgian Congo, *fide* Carr *in litt.*). *French Equatorial Africa:* Gabon Coast, *British Cameroon:* *Victoria (intermediates *olivacea* × *kempi*). *Gold Coast:* *Tenia (B.M.). *Ivory Coast:* (Paris Mus.). *Senegal:* Goree Id.; Guet N'Dar; Hann, Joal; Ngaparo.

Range. East, South and West coasts of Africa, Indian and Pacific Oceans, also — as an accidental visitor — the temperate seas.

From the Azores we have seen a young *L. o. kempi* (Monaco Mus. 2660), taken by the Prince of Monaco in 1913, while hatch-

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[1] Divided on a Cameroon (Berlin Mus.) and on a Gold Coast hatchling (Brit. Mus.) seen by us.

lings from the Cameroons (Z.M.U. 15513) must be considered intermediates between the two races (see footnote to p. 497).

Family DERMOCHELYIDAE

1902. *Dermochelyidae* Wieland, Amer. Jour. Sci., (4), **14**, p. 107.

Definition. Cryptodirous testudinates adapted to a marine life. Horny shields present in young, replaced in adults by smooth skin.

Skull without nasal bones; prefrontals in contact dorsally, with descending processes that are moderately separated; temporal region hardly emarginate posteriorly; parietal meeting squamosal; postorbital very large; no bones tending to be reduced; quadrate not enclosing stapes; postotic antrum absent; parietals without descending processes; upper jaw without ridges on its triturating surface; vomer present, separating palatines; mandible without a coronoid bone.

Neck vertebrae with only one biconvex centrum — the fourth, typically an articular connection between the sixth and seventh centra, the eighth centrum concave in front, doubly or not; coracoids with their median borders not expanded; humerus of an exaggerated marine type with deltopectoral crest very far down the shaft; trochanteric fossa of femur reduced by union of the trochanters; phalanges without condyles; claws absent.

Carapace with epithecal component very strongly developed, represented by a mosaic of small bones; thecal carapace and plastron greatly reduced, not directly united; neither carapace nor plastron hinged; pleural bones reduced to the endochondral ribs, separated by wide fenestrae; peripherals absent; nuchal a butterfly-shaped bone with a ventral attachment surface for the eighth vertebra; neural bones absent, represented only by the neural arches of the vertebrae; pygals absent; plastron reduced to a narrow ring of bones surrounding a great fontanelle; entoplastron absent.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

Genus DERMOCHELYS Blainville

1816. *Dermochelys* Blainville,[1] Bull. Soc. Philom. Paris, p. "111" (misprint = 119). Type: *Testudo coriacea* Linnaeus (by monotypy in Cuvier: 1829).

1820. *Sphargis* Merrem, Vers. Syst. Amphib., p. 19. Type: *T. coriacea* Linnaeus (by monotypy).

1822. *Coriudo* Fleming, Phil. Zool., **2**, p. 271. Type: *T. coriacea* Linnaeus (by monotypy).

1828. *Seytina* Wagler, Isis von Oken, p. 861. (Substitute name for *Sphargis* Merrem.)

1830. *Dermatochelys* Wagler, Natur. Syst. Amphib., p. 133. (Emendation for *Dermochelys*.)

1832. *Chelyra* Rafinesque, Atlantic Jour., **1**, p. 64. Type: *T. coriacea* Linnaeus (by monotypy).

Definition. Similar to that given under DERMOCHELYIDAE, the family being monotypic.

Range. Tropical, subtropical and — as an accidental visitor — temperate oceans.

DERMOCHELYS CORIACEA (Linnaeus)

1766. *Testudo coriacea* Linnaeus, Syst. Nat., ed. 12, **1**, p. 350: Mediterranean Sea.

1789. Poiet, 283.

1802b. Daudin, 62, pl. xviii, fig. 1.

1771. *Testudo arcuata* Catesby, Nat. Hist. Carolina, **2**, p. 40: Coasts of Carolina and Florida (by inference).

1788. *Le Luth* Lacépède, Hist. Nat. Quad. ovip. Serpens, **1**, p. 111; and *Testudo lyra* in Synopsis Methodica, a table (in which binomials are used) at end of same volume: Barbary Coast.

1792. *Testudo tuberculata* Schoepff, Hist. Testud., p. 144: No locality.[2]

1814. *Chelonia lutaria* Rafinesque, Specchio Sci. (Palermo), **2**, No. 9, p. 66: Sicily (*fide* Lindholm: 1929).

1820. *Sphargis mercuralis* Merrem, Vers. Syst. Amphib., p. 19: Mediterranean Sea and Atlantic Ocean.

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[1] In the same year *Dermochelys* was also proposed by Blainville in Jour. Phys. Chim. Hist. nat. (Paris), **83**, p. 259. We cannot say which publication had priority, but it is the Bulletin that is currently cited by herpetologists. In neither paper was *any* species mentioned. However, *coriacea* Linnaeus was the only included species assigned to *Dermochelis* (*sic*) by Cuvier (1829, Regné Animal, ed. 2, **2**, p. 14) and this has been accepted as the type by the "Official List of Generic Names in Zoology."

[2] Attributed by Schoepff to Pennant, 1771, Philos. Trans. Royal Soc. London, **61**, p. 271 (*not* 275), pl. x, figs. 4-5, but Pennant merely provides an English name — Tuberculated Tortoise — to a specimen which he thinks may be *Testudo coriacea* Linnaeus. In Schoepff's 1801 ed. *tuberculata* appears on p. 123.

1835. Temminck and Schlegel, 6, pls. i-iii.
1849. Smith, A., App., 2.
1829. *Dermochelis Atlantica* Lesueur, in Cuvier, Regné Animal, **2**, p. 14, footnote: No locality (*nomen nudum*).
1830. *Dermatochelys porcata* Wagler, Natür. Syst. Amphib., pl. i, figs. 1-23: No locality (uses *coriacea* in text, p. 133).
1862a. *Sphargis coriacea* Strauch, 19.
1872. Gervais, p. 199, pls. v-ix.
1873b. Gray, 96.
1884a. Rochebrune, 40.
1894. Oliver, 101.
1896. Doumergue, 477.
1896b. Oliver, 118.
1899. Doumergue, 255.
1933. Heldt, 1-40, figs. 1-17.
1949. Cadenat, 16, fig. 13.
1844. *Sphargis coriacea* var. *Schlegelii* Garman, U.S. Nat. Mus. Bull., **25**, pp. 295, 303: Tropical Pacific and Indian Oceans.
1889a. *Dermochelys coriacea* Boulenger, 10.
1890. Büttikofer, **1**, 266; **2**, 437, 478, fig.
1893c. Matschie, 208.
1899. Sclater, 96.
1901c. Tornier, 66.
1906a. Mocquard, 483.
1909a. Siebenrock, 553.
1911b. Sternfeld, 52.
1925b. Flower, 918.
1929. Lindholm, 287.
1929. Rose, 184.
1933. Flower, 752.
1937e. Hewitt, 16, pl. ivB.
1937f. Loveridge, 488.
1947. Irvine, 312.
1949. Villiers, 165, fig.
1950. Rose, 327.
1950. Williams, 552.
1955. Cansdale, 97, 104.
1899. *Sphargis angusta* Philippi, Anales Univ. Chile (Santiago), No. 104, p. 730, pl. i: Tocopilla, Chile.
1901. *Dermatochelys coriacea* Gadow, 325, 333, fig. 73.
1906. *Dermochelis coriacea* Johnston, 819, 833.
1934a. *Dermochelys coriacea coriacea* Mertens and Müller *in* Rust, 10.
1934a. *Dermochelys coriacea schlegeli* Mertens and Müller *in* Rust 10.

Common names. Leatherback; Leathery Turtle; Luth or Trunk Turtle (English); *bosange* (Ga:Irvine, whom see for other Gold Coast names); *noa* (Swahili at Lindi:Loveridge MS).

Illustrations. Those of Temminck and Schlegel (1835:pls. i-iii) are quite good.

Description. (Based exclusively on a juvenile (M.C.Z. 21055) from the Guinea Coast, West Africa.)

Snout moderate; beak deeply notched in middle, strikingly bicuspid; edge of jaws denticulate; prefrontals in 2 pairs, of which the posterior pair may be broken up; frontal broken up; frontoparietal large; parietals, supraocular, postoculars, and supratemporals broken up; forelimb with slightly enlarged scales along anterior edge, behind them many rows of smaller scales, posterior edge without noticeably enlarged scales; both fore- and hind limbs clawless; tail short.

Carapace a mosaic of small polygonal plates, 7 longitudinal rows of which are enlarged to form conspicuous ridges, ovate, slightly arched, posteriorly prolonged into a caudal point.

Plastron also a mosaic of polygonal plates, 5 longitudinal rows, of which the median is double, forming conspicuous keels, anteriorly truncate, posteriorly pointed.

Color. Of juvenile from Guinea coast. Carapace and plastron black, each keel tipped with yellow; crown and sides of head dark, throat yellowish; limbs black narrowly edged with yellow.

Of adult from Gulf of Gabes. Above, blackish brown, the black ground color of the neck and fleshy parts sometimes washed with rose and finely spotted with whitish yellow; sides yellowish gray; the brownish black limbs show patches of white at their articulations. Below, the limbs are spotted with whitish yellow. Plastron grayish black flecked with white and yellowish spots (Heldt:1933:13).

Size and Weight. Overall length of juvenile (ex Guinea coast), from tip of snout to terminal tip of carapace, 95 mm.; carapace length approximately 65 mm.; breadth 43 mm.; length of forelimb from axilla to tip 58 mm.

A ♀ killed at Mahfa River mouth was 6 feet long, and 4 feet broad, with an estimated weight of 400 kg. (Büttikofer, 1890: 1:268).

A Luth taken in 1885 on the beach of the Bay of Arzew, measured over 8 feet (2½ metres) long, and 6½ feet (2 metres) broad, according to M. Bouty, Comptroller of Mines, who examined it (Doumergue:1896).

A slightly smaller one taken in the Gulf of Gabes on September 11, 1930, had an *estimated* weight of 650 kg., but this may be exaggerated according to Heldt (1933:9), who should be consulted for measurements of this specimen and more detailed ones of another taken in the Gulf of Gabes on May 27, 1933. Maximum weight has been given as 681.82 kg. (1,500 lbs.) (cf. Deraniyagala, 1939:100).

Breeding. Besides many hundreds of smaller ova, one Luth held 750 eggs with diameters ranging from 10-50 mm., but even the largest were still immature (Heldt:1933). Lays on the Barbary coast (Daudin:1802b). On November 24 and 27 respectively, two Luths came ashore at the mouth of the Mahfa River, Liberia. Hundreds of partially and fully developed eggs were present in the turtle examined by Büttikofer (1890:1:260).

Longevity. Three weeks in New York Aquarium (Flower: 1925).

Parasites. Trematodes (*Astrorchis renicapite* Leidy) of the family Pronocephalidae were present in the intestines of a Gulf of Gabes Luth. Parasites determined by R. P. Dollfus (Heldt: 1933:33).

Companions. A Luth from the Gulf of Gabes was accompanied by about 40 Sucking-fish (*Remora remora*) and 100 Pilot-fish (*Echeneis ductor*) says Heldt (1933: 9 and 31).

Enemies. The flesh, though tough, oily, and an unappetizing red, tasted better than it looked. The abundant green fat was so nearly fluid that it partially melted in Büttikofer's hand. The eggs, though not without an oily taste, were considerably more palatable than the flesh (Büttikofer, 1890:1:268). See also Heldt (1933:35). On the Gold Coast the flesh and eggs are eaten only by the Kru people (Irvine:1947).

Localities. Algeria: Golfe d'Arzeu (Baia d'Arzew). *Tunisia:* Gabes Gulf; Hafacha near Tarf il Ma; Monastir; Sidi Daoud, Cap Bon. *Egypt:* Alexandria market. *East Africa:* Seychelles (no coastal record known to us). *Cape Province:* Algoa Bay; Cape of Good Hope; Table Bay. *Southwest Africa. French*

Equatorial Africa: Gabon. *Togo:* Sebbe (Sebe; Zebe). *Gold Coast:* Tenia (B.M.). *Liberia:* Mahfa River mouth near Robertsport. *French Guinea?:* *"Guinea Coast." *Senegal:* Hann; Rufisque.

Range. All African coasts, Indian and Atlantic Oceans, the Mediterranean and — as an accidental visitor — the temperate seas.

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INDEX TO ALL SCIENTIFIC NAMES[1]

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[1] Misprints such as *Cinicys*, *Cininixys*, *Homoeopus*, *Tistudo*, etc., are not included. The pagination of a valid name's main discussion is indicated by boldface type. All synonyms are indexed. Pages on which illustrations and maps occur are cited in italics after the other page references.

PLATES

PLATE 1

Geochelone sulcata. (From Sowerby and Lear.)

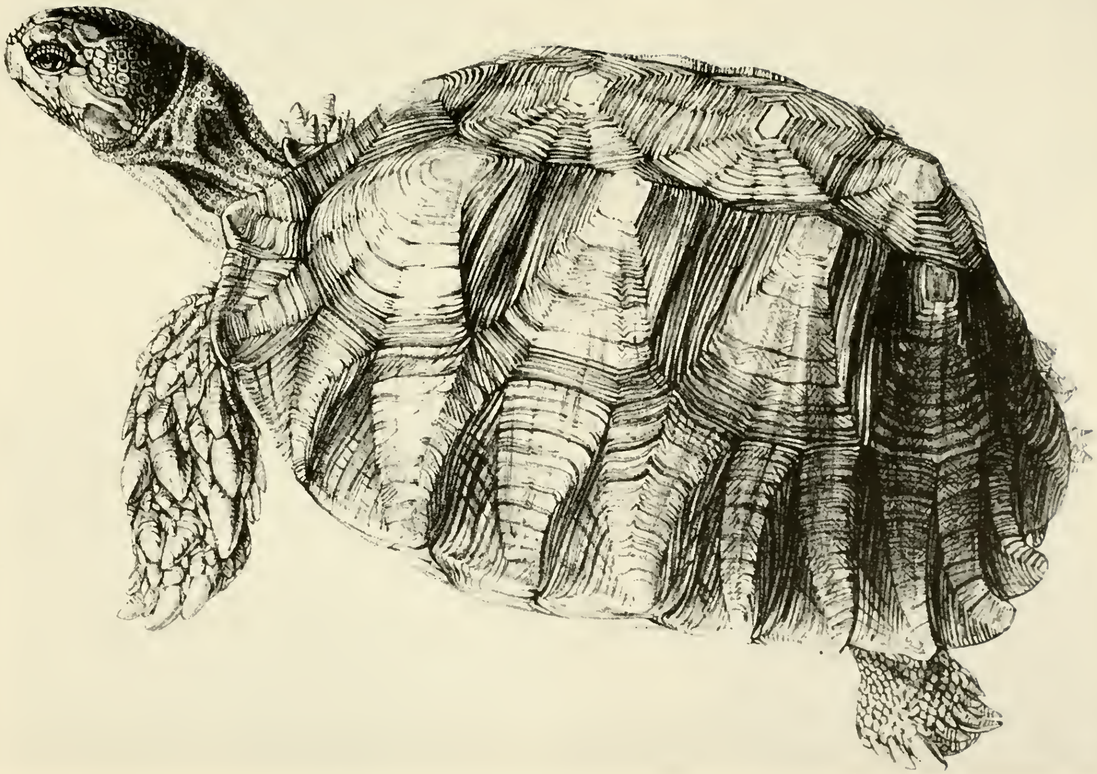

PLATE 1

PLATE 2

Geochelone pardalis subspecies

A. *G. p. pardalis* juv. (M.C.Z. 22473) ex Aroab, Southwest Africa.

B. *G. p. babcocki* juv. (M.C.Z. 40005) ex Mt. Mbololo, Kenya Colony.

C. *G. p. pardalis* adult (M.C.Z. 16713) ex Kolmanskop, Southwest Africa.

D. *G. p. babcocki* adult (M.C.Z. 18156) ex Arusha, Tanganyika Territory.

(Frank White, photographer.)

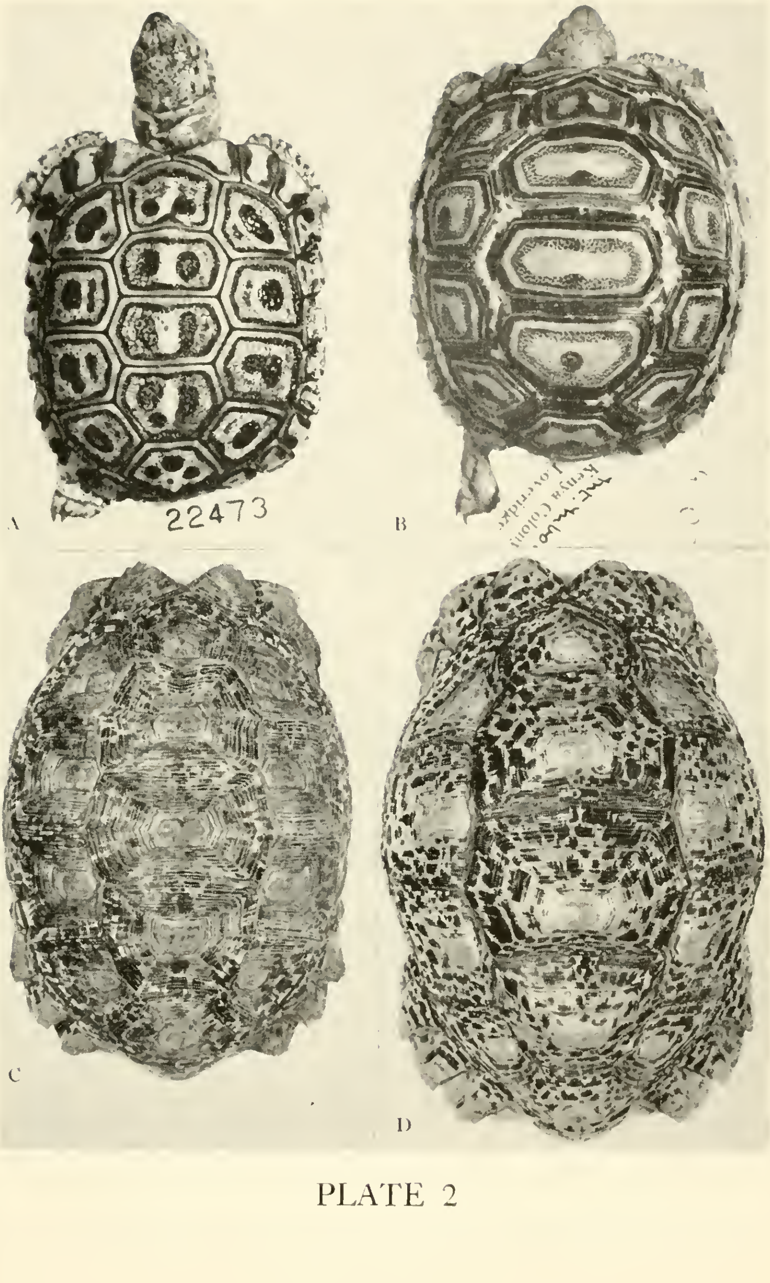

PLATE 2

PLATE 3

Testudo graeca graeca

Adult (M.C.Z. 29909) ex Mamora Forest, Rabat, Morocco. Dorsal and ventral views.

(Frank White, photographer.)

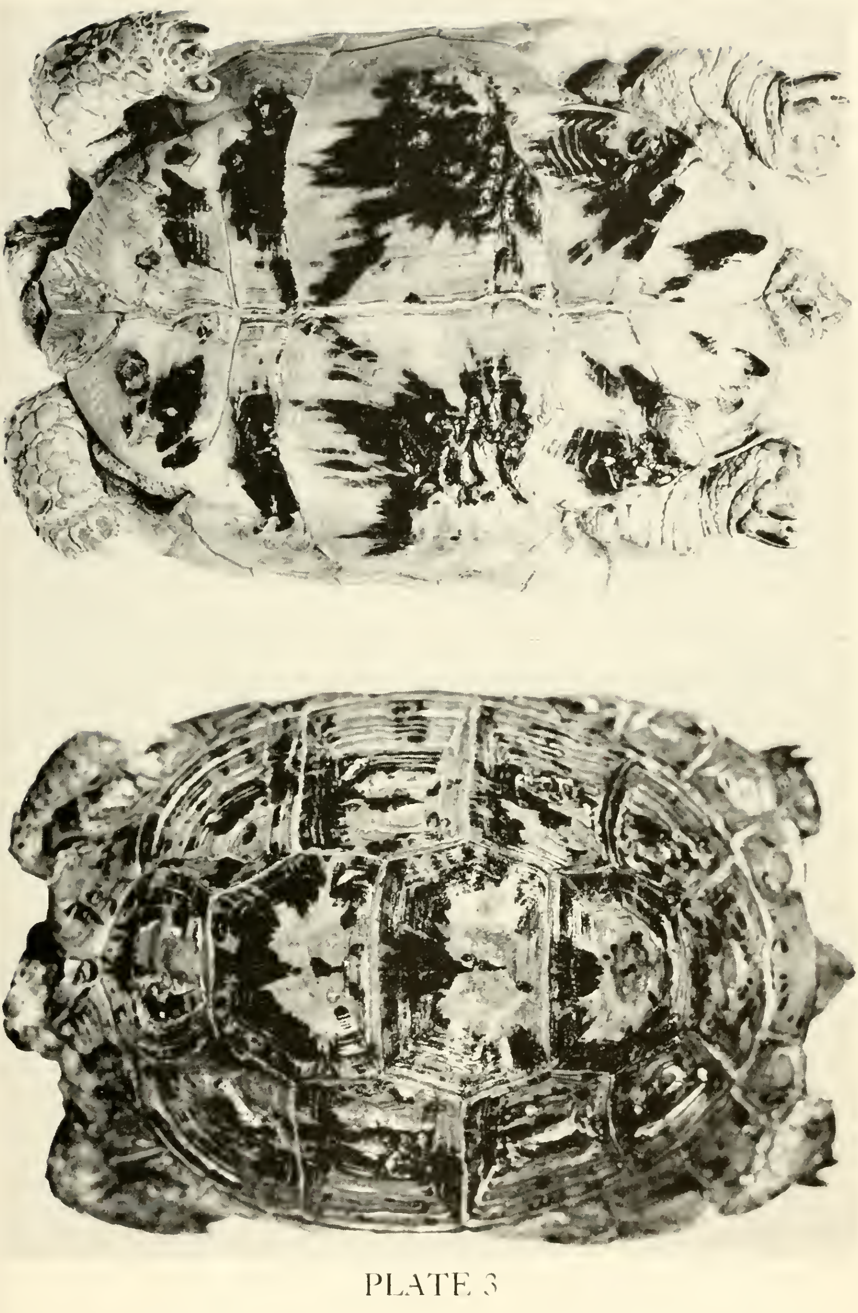

PLATE 3

PLATE 4

Testudo kleinmanni

Adult (M.C.Z. 54044) ex Salum, Western Desert, Egypt. Dorsal and ventral views.

(Frank White, photographer.)

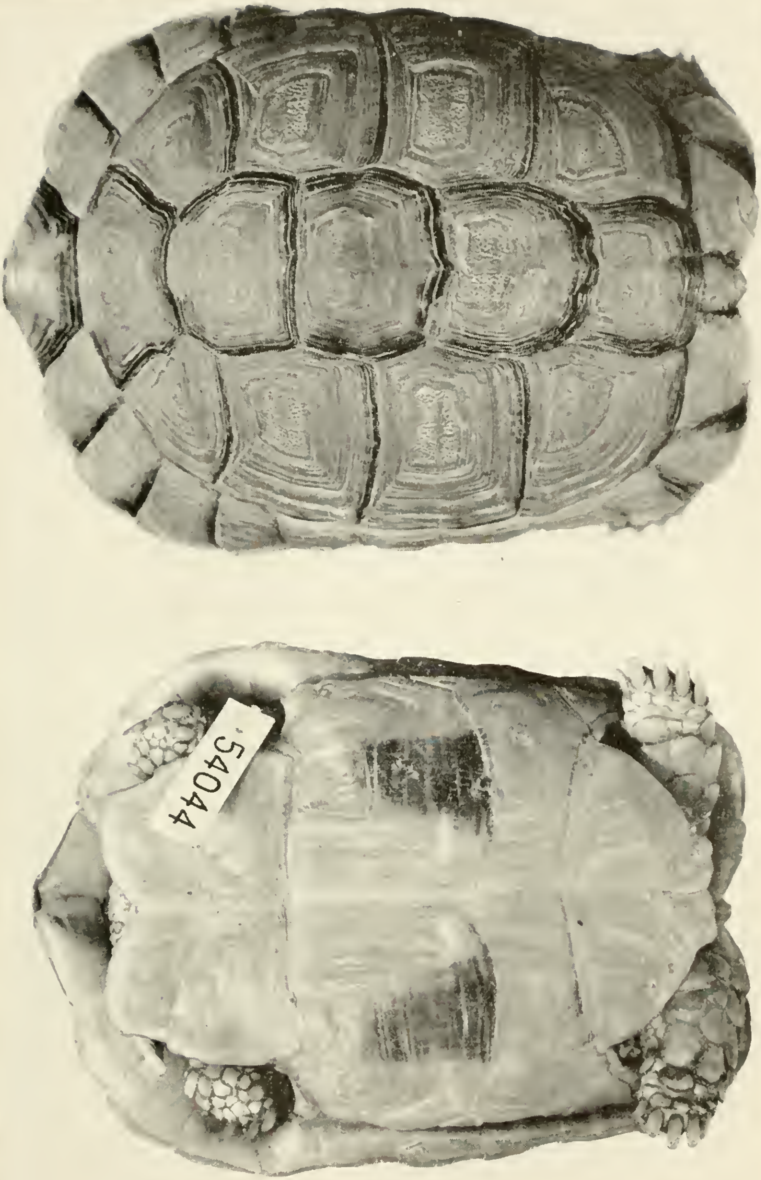

PLATE 4

PLATE 5

Malacochersus tornieri

Adult (M.C.Z. 30004) ex Mangasini, Usandawi, Tanganyika. Dorsal and ventral views.

(Frank White, photographer.)

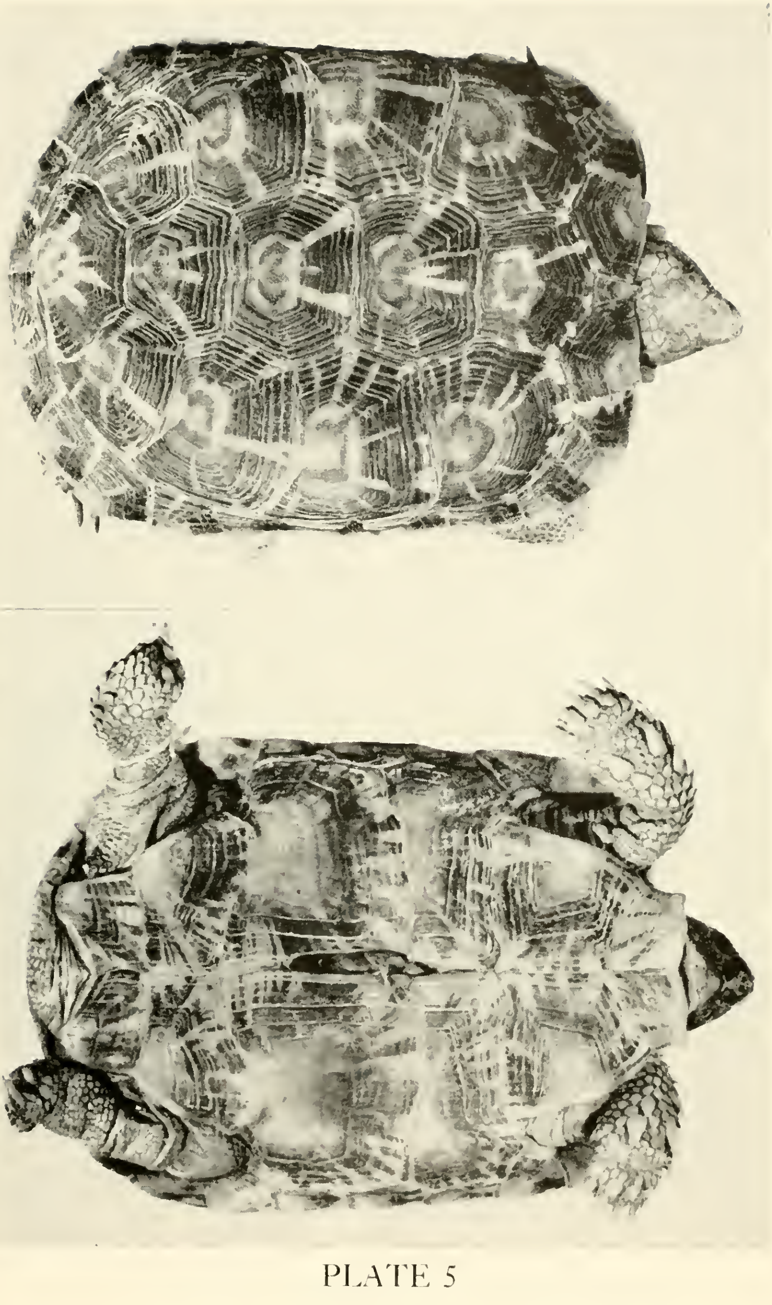

PLATE 5

PLATE 6

Malacochersus tornieri

Juvenile (Holotype of *procterae*, B.M. 1923.10.9.102 now 1946.1.22.59) ex Ikikuyu, south of Gulwe, Tanganyika.

B, C. Dorsal and ventral views; A. head and limbs enlarged.

(Courtesy of British Museum. Peter Green, photographer.)

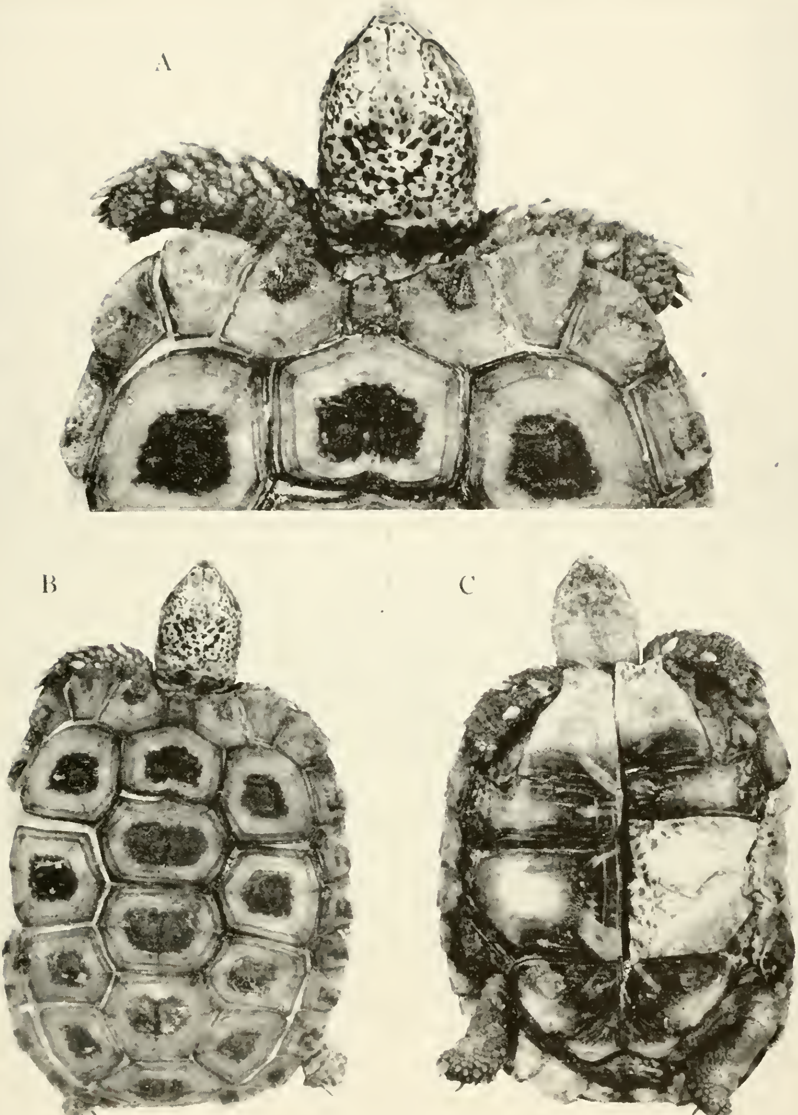

PLATE 6

PLATE 7

Psammobates oculifer

Adult (Type of *semiserrata*) ex ''between Latakoo and the Tropic of Capricorn.''

a, a. Nuchal shield and forelimb of *oculifer,* compared with

b, b. nuchal shield and forelimb of *geometricus.*

(From Andrew Smith.)

PLATE 7

PLATE 8

Psammobates geometricus

A, B. Juv. (*luteola* phase) (P.M.) ex ''Cap''.
(Frank White, photographer.)

C, D. Adult (B.M.) ex South Africa.
(Courtesy of British Museum. Peter Green, photographer.)

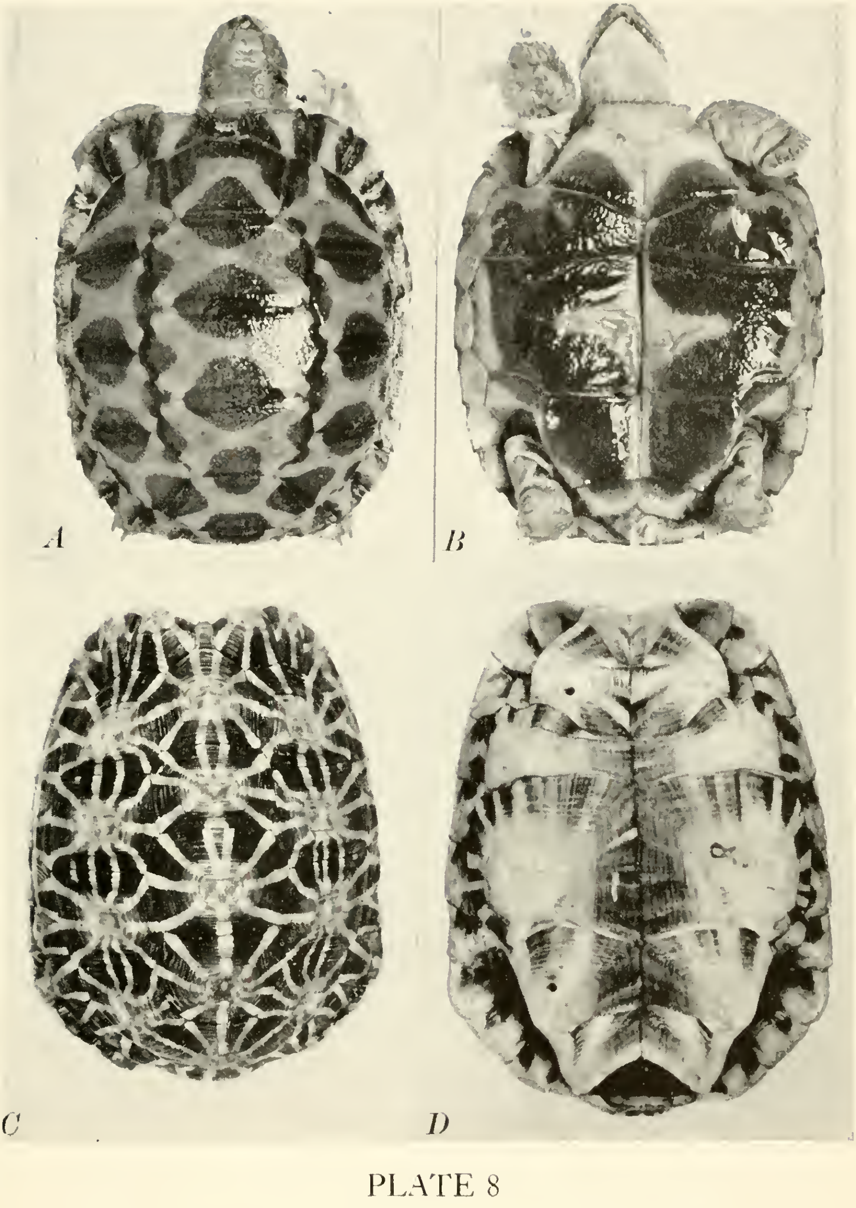

PLATE 8

PLATE 9

Psammobates tentorius verroxii

Adult (Type of *verroxii*) ex "near the sources of the Garriep or Orange River."

(From Andrew Smith.)

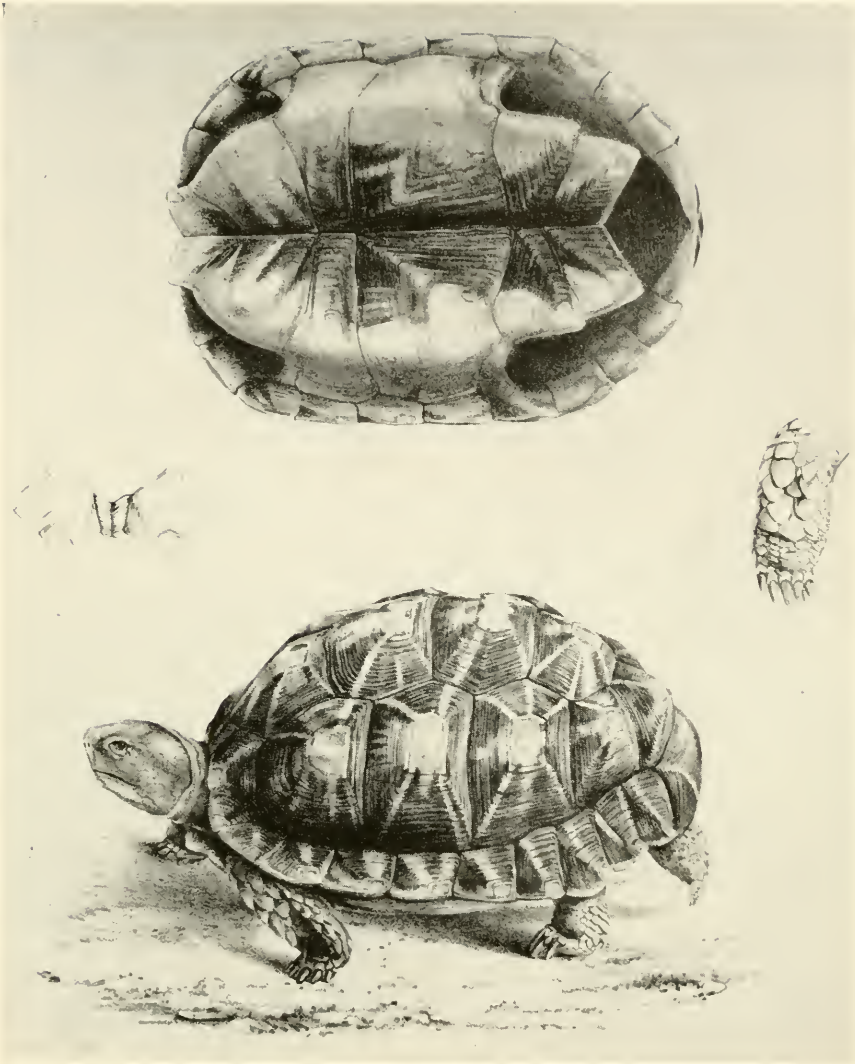

PLATE 9

PLATE 10

Psammobates tentorius subspecies: dorsal patterns.

A. *P. t. verroxii* Adult (Paratype of *schonlandi*. M.C.Z. 42222) ex Steinkopf, L. Namaqualand.

B. *P. t. verroxii* Adult (color form *bergeri* in B.M.) ex Barby, Tiraz Mtns., Southwest Africa.

C. *P. t. tentorius* Adult (typical pattern. M.C.Z.) ex ''South Africa.''

D. *P. t. tentorius* Adult (aberrant. M.C.Z. 46604) ex ''South Africa.''

(Frank White, photographer.)

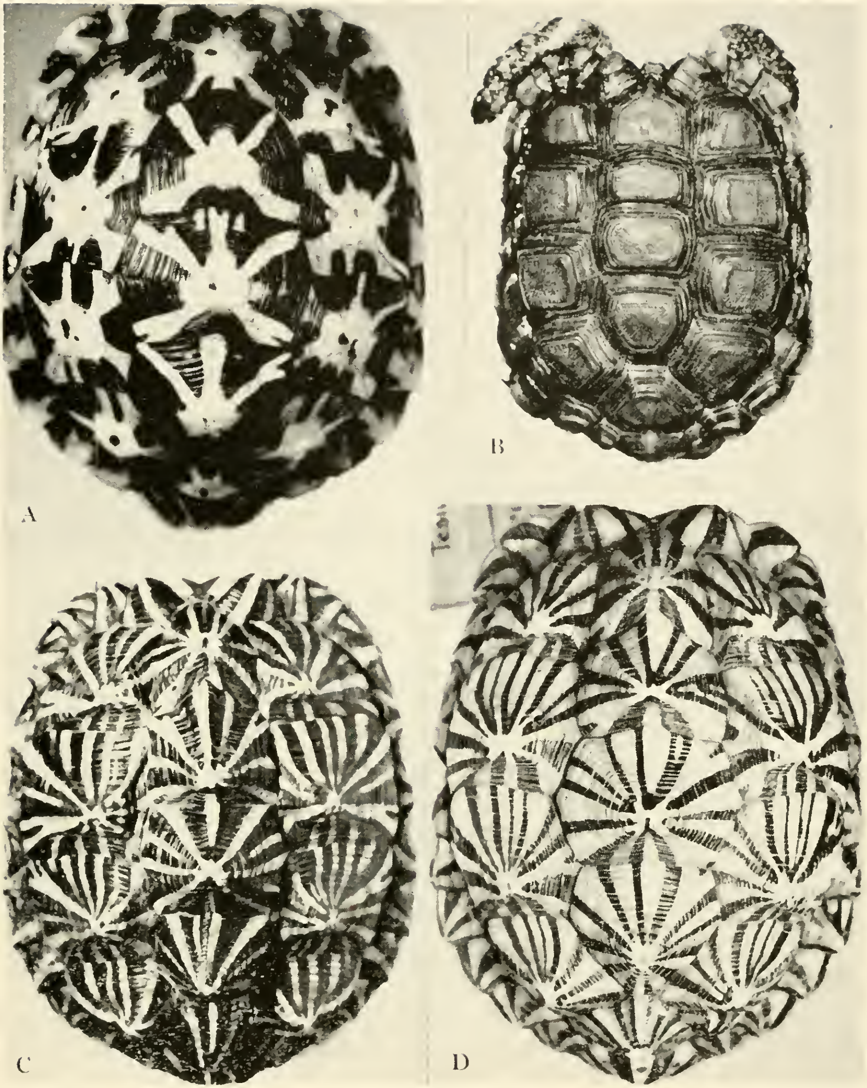

PLATE 10

PLATE 11

Psammobates tentorius tentorius

Plastral patterns of nine Transvaal Museum specimens from Matjesfontein, Cape Province.

A. T.M. 19537. B. T.M. 19650. C. T.M. 19497.
D. T.M. 19496. E. T.M. 19649. F. T.M. 19536.
G. T.M. 19480. H. T.M. 19479. I. T.M. 19495.

(Frank White, photographer.)

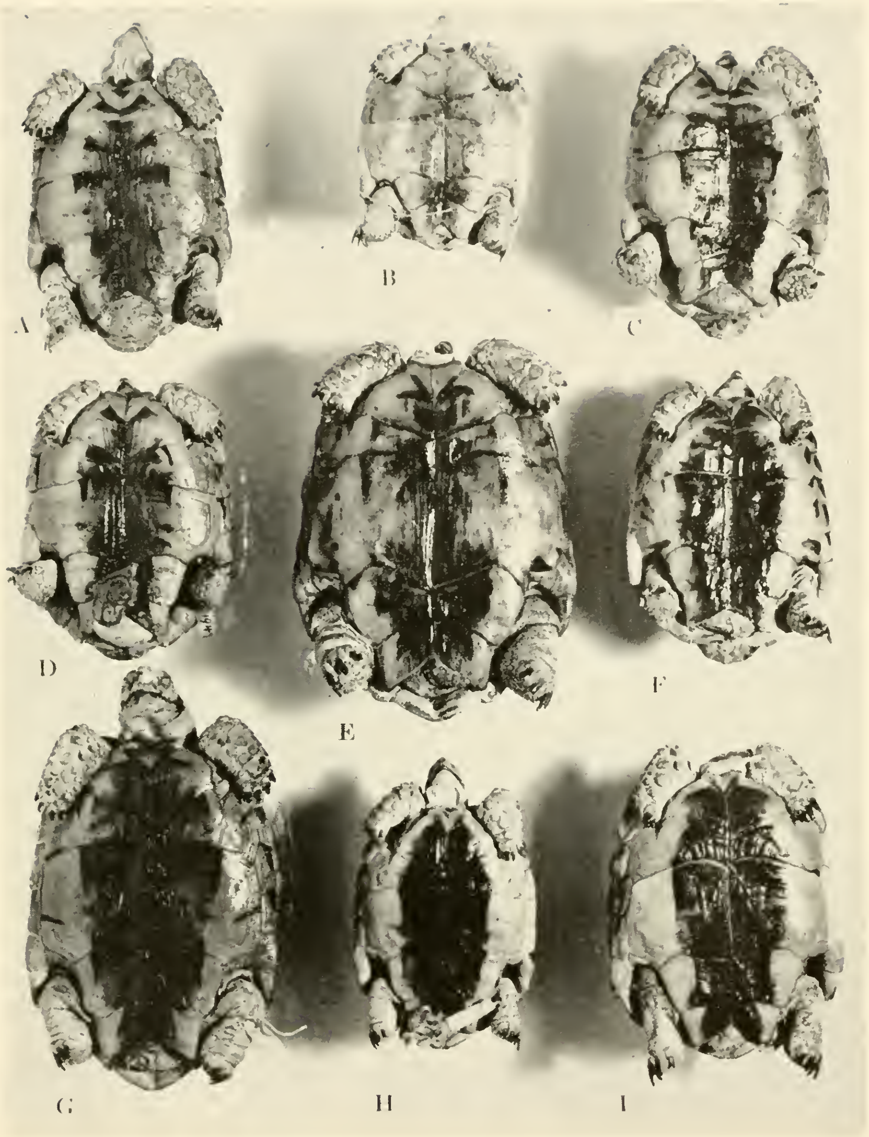

PLATE 11

PLATE 12

Chersina angulata ♂ and ♀

A. Dorsal view of strongly projecting gular in ♂.
A′. Plastral aspect of same.
B. Dorsal view of moderately projecting gular in ♀.
B′. Plastral aspect of same.

(From Vaillant.)

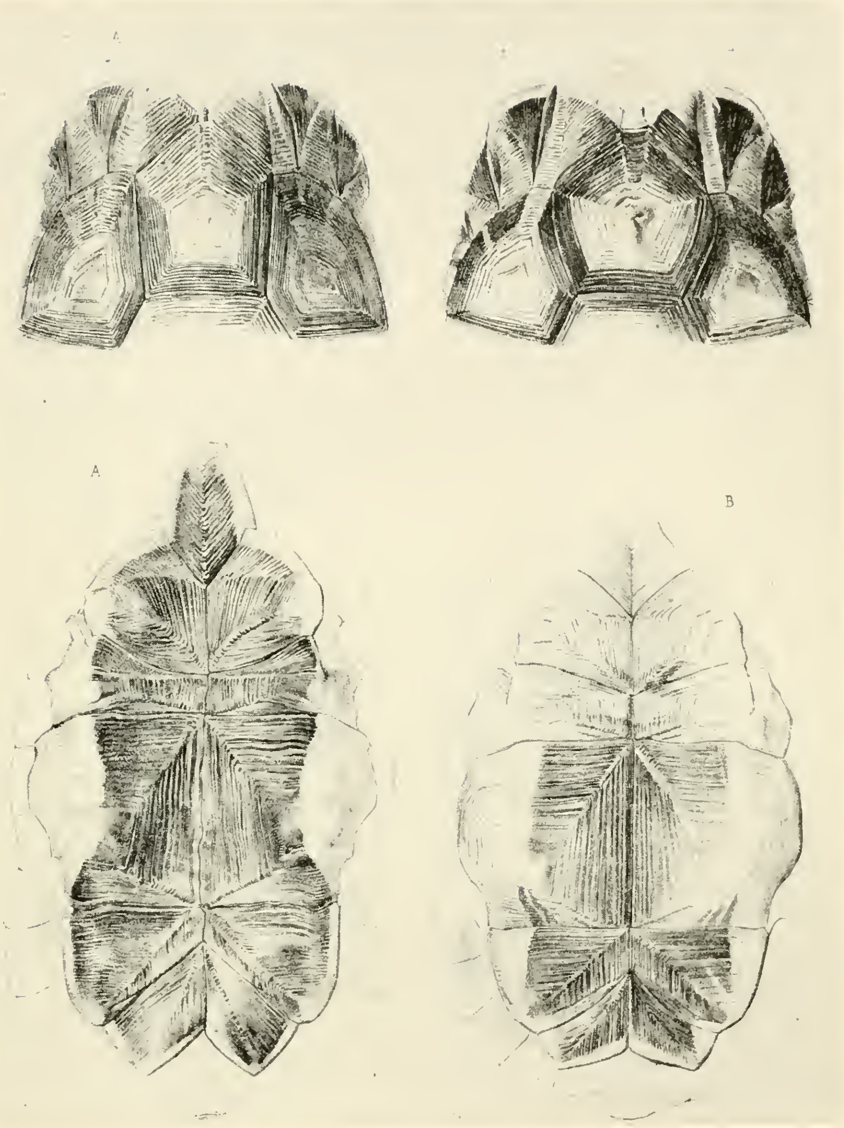

PLATE 12

PLATE 13

Homopus species: dorsal views of carapaces.

A. *H. signatus* (M.C.Z. 42218) ex Steinkop.

B. *H. boulengeri* (M.C.Z. 42231) ex "Cape Province."

C. *H. areolatus* (M.C.Z. 17525) ex Tootabi.

D. *H. femoralis* (M.C.Z. 17523) ex Hanovr.

(Frank White, photographer.)

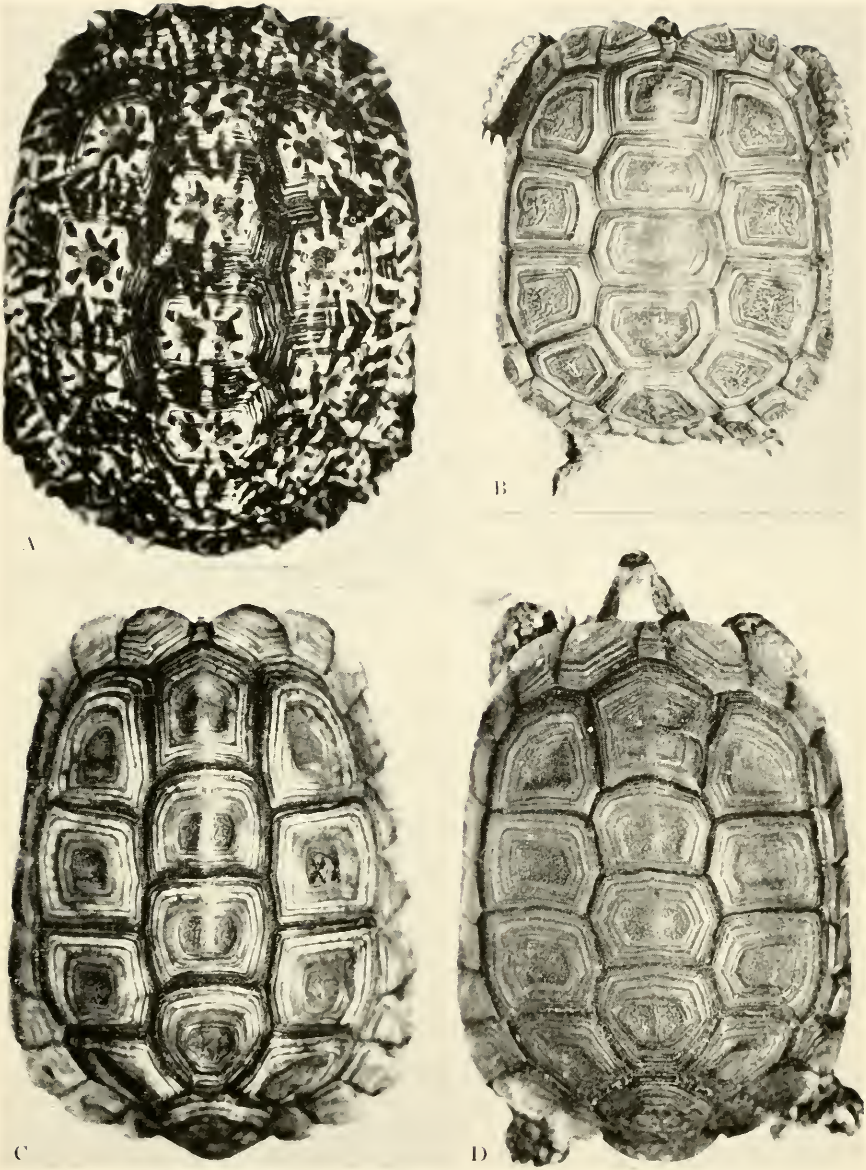

PLATE 13

PLATE 14

Kinixys species: dorsal views of carapaces.

A. *K. b. belliana* (M.C.Z. 42852) ex Lukafa, Belgian Congo.
B. *K. homeana* (M.C.Z. 38371) ex Ifan. Ondo, Nigeria.
C. *K. erosa* imm. (M.C.Z. 22486) ex Lenga, Liberia.
D. *K. b. belliana* (M.C.Z. 40015) ex Voi, Kenya Colony.

(Frank White, Photographer.)

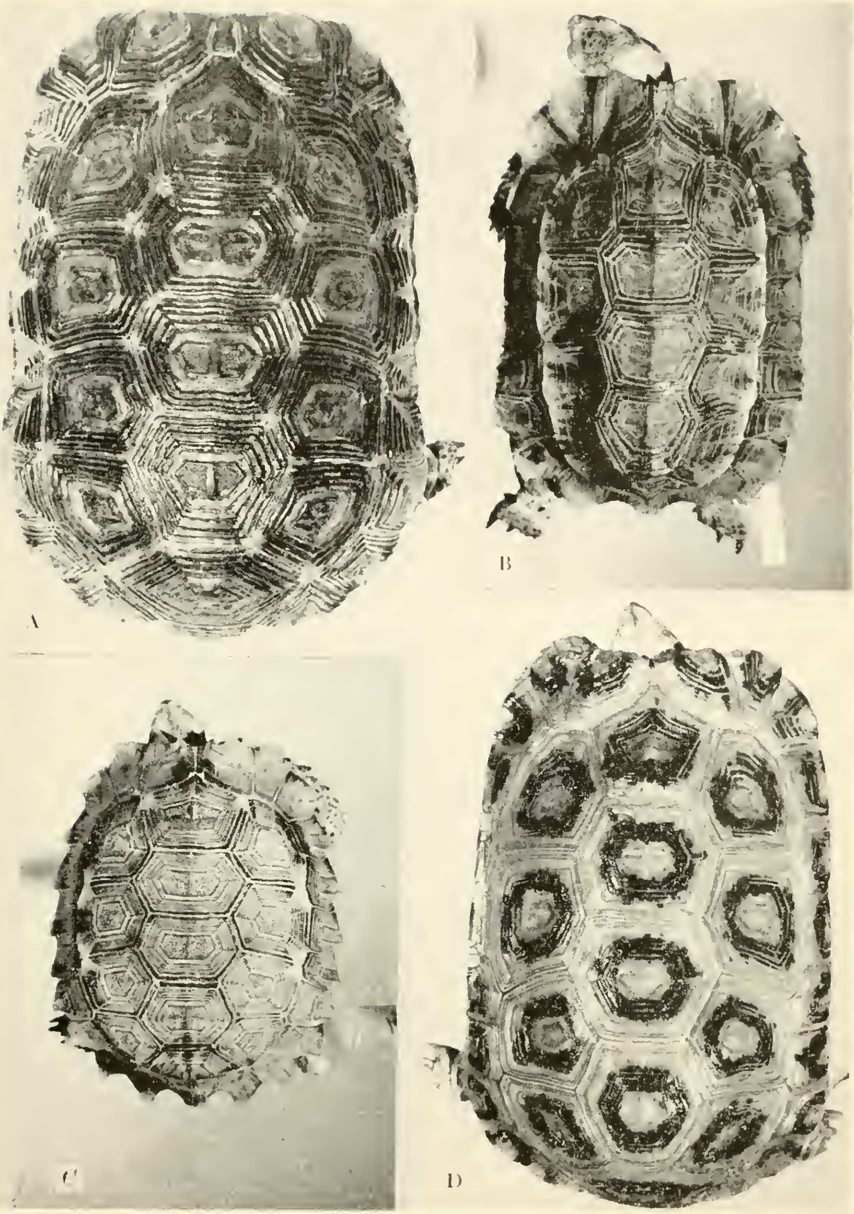

PLATE 14

PLATE 15

Trionyx triunguis
Juvenile ex Wadi Halfa, Nile, Egypt.

(From J. Anderson.)

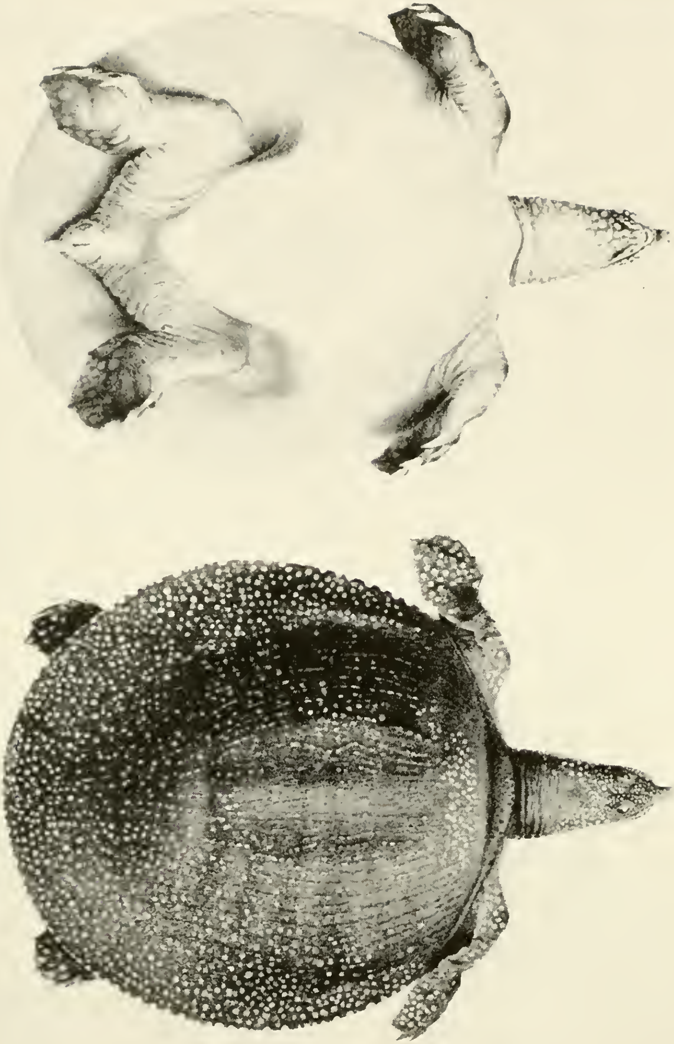

PLATE 15

PLATE 16

Cyclanorbis species: juveniles for comparison.

A. *C. elegans* (B.M. 1908.4.7.3) ex Anglo-Egyptian Sudan.
B. *C. elegans* same specimen, plastral view.
C. *C. senegalensis* (B.M. 1907.7.16.26) ex Gambia.
D. *C. senegalensis* same specimen, plastral view.

(Courtesy of British Museum. Peter Green, photographer.)

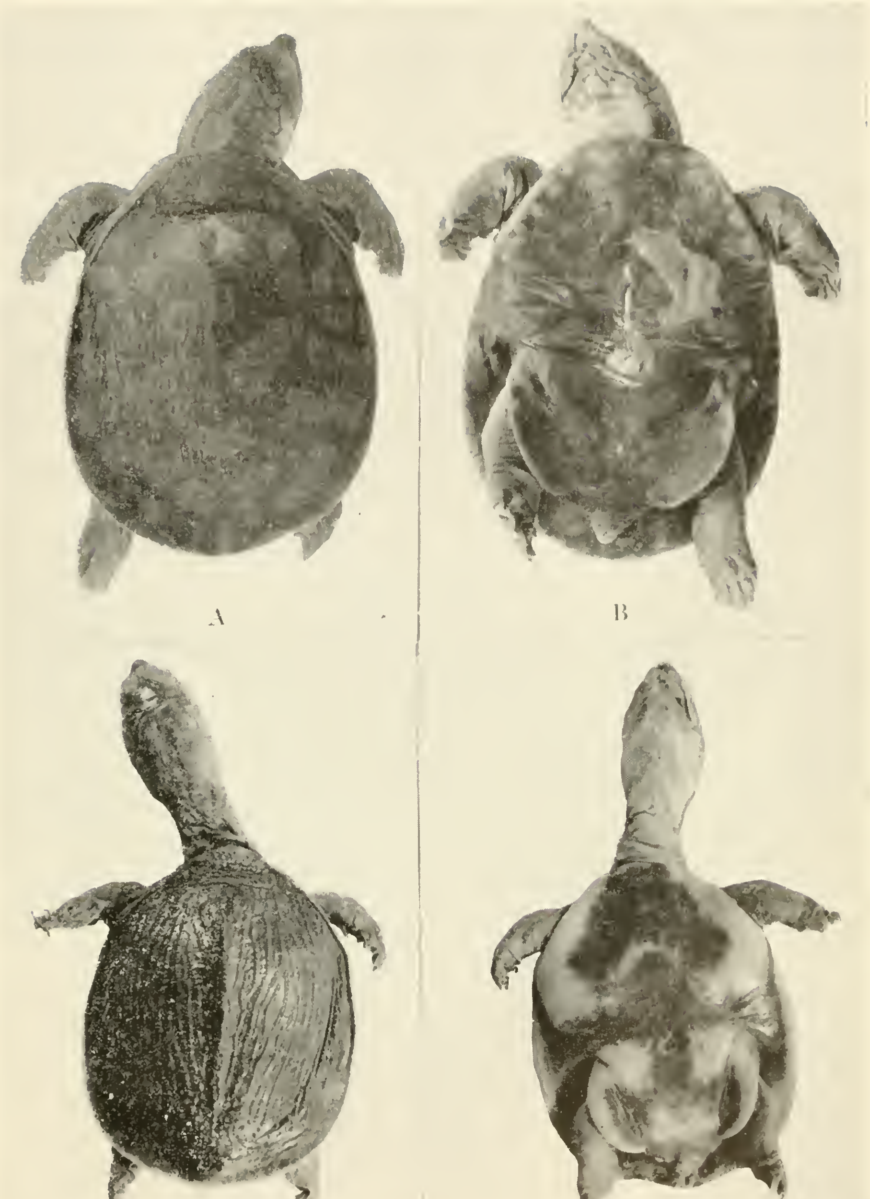

PLATE 16

PLATE 17

Cycloderma species: juveniles for comparison.

A. *C. frenatum* (M.C.Z. 50360) ex Chowe, Nyasaland.

B. Same specimen, plastral view.

(Frank White, photographer.)

C. *C. aubryi* (B.M. 1908.5.25.3) ex Zombo, Congo River, Belgian Congo.

D. Same specimen, plastral view.

(Courtesy of British Museum. Peter Green, photographer.)

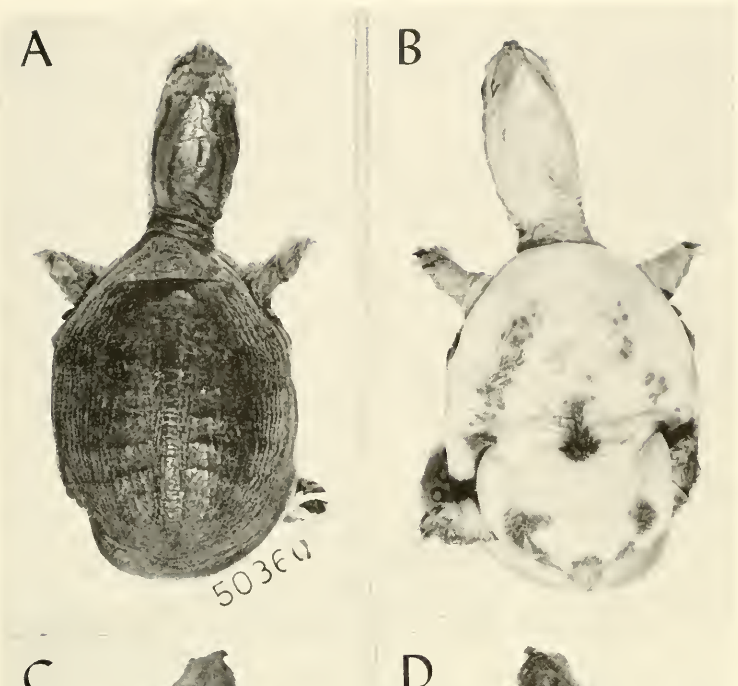

PLATE 17

PLATE 18

Cycloderma species: adults for comparison.

A. *C. aubryi* (Type: Paris Museum) ex Gabon, French Congo.
(Reduced. From A. Duméril.)

B. *C. frenatum* (Cotype: Z.M.U.) ex Zambezi River, Mozambique.
(From W. K. H. Peters.)

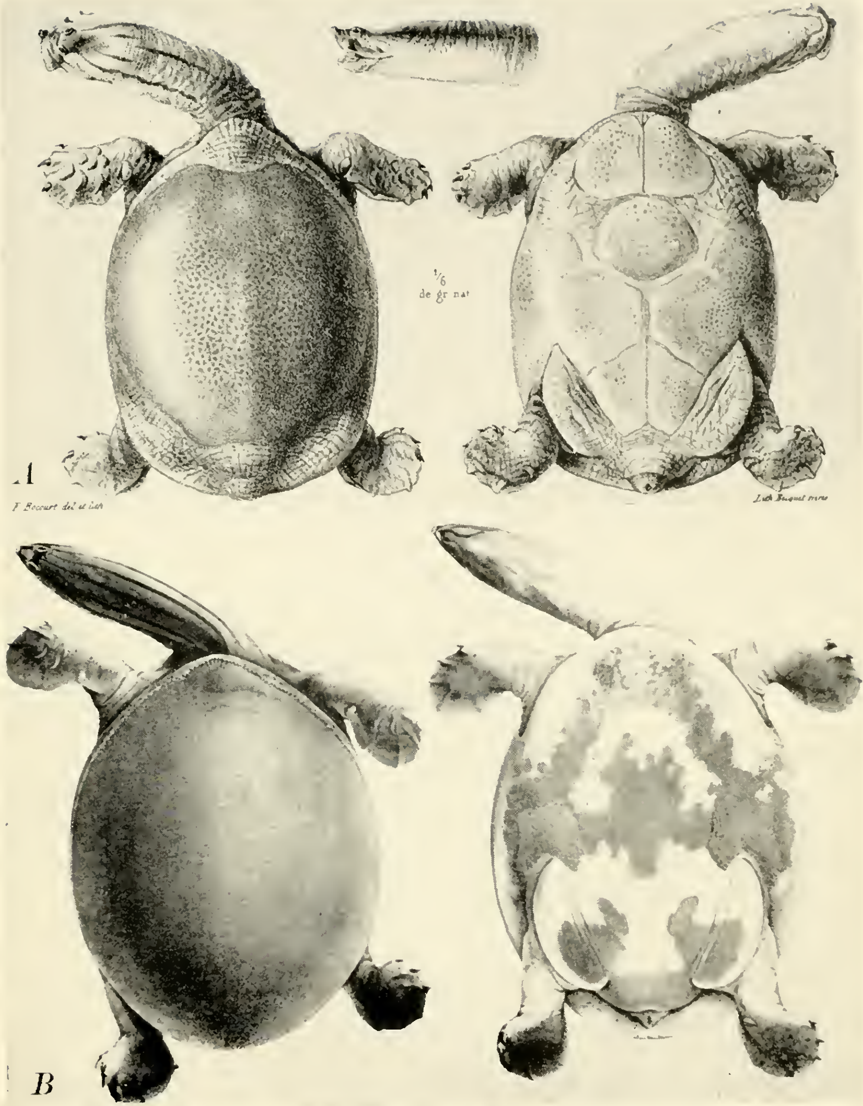

PLATE 18