PARTITION OF THE GENUS *CLEMMYS* AND RELATED PROBLEMS IN THE TAXONOMY OF THE AQUATIC TESTUDINIDAE

BY

SAMUEL B. McDOWELL

Rutgers University, Newark, New Jersey, U.S.A.

[Accepted 11th June 1963]

(With 11 figures in the text)

On the basis of presence or absence of a muscular apophysis of the basisphenoid in the floor of the recessus scalae tympani, contact of the angular bone with Meckel's cartilage, nature of the joint between the fifth and sixth cervical centra, and pygal pattern, the testudinid subfamily Emydinae as currently recognized may be divided into two subfamilies, the Batagurinae and the Emydinae. The Batagurinae are almost entirely Old-World, but have one New-World genus, *Rhinoclemys* (the New-World turtles generally referred to *Geoemyda*). The Emydinae are almost entirely New-World, with a single Old-World genus, *Emys*. The genus *Clemmys* is emydine and entirely North American ; the Old-World species usually referred to *Clemmys* are batagurines and are here referred to two genera : *Mauremys* Gray for *caspica*, *japonica* and *mutica* [=*nigricans* of most authors most of the time], and *Sacalia* Gray for *bealei*. A reclassification of the genera of Batagurinae and Emydinae is presented ; the classification is based mainly on skull characters. *Annamemys* and *Pseudocadia* are considered synonyms of *Mauremys mutica*.

CONTENTS

INTRODUCTION

As presently defined, the genus *Clemmys* contains both New-World and Old-World species of small testudinid turtles inhabiting shallow water.

New-World species are *Clemmys guttata* (the type of the genus), *C. insculpta*, *C. muhlenbergi*, and *C. marmorata*. The Old-World species are *C. caspica* (including *leprosa*), *C. bealei* (including *quadriocellata*), *C. japonica*, and *C. mutica*.* The osteology of these turtles indicates they are not congeneric ; indeed, I would place the New- and Old-World species of present "*Clemmys*" in different subfamilies. The reasons will be given below, but it may be stated here that *Clemmys* should be restricted to the New-World species *C. guttata*, *C. muhlenbergi*, *C. insculpta*, and *C. marmorata;* the Old-World species *caspica*, *mutica*, and *japonica* are referred to *Mauremys* Gray ; and *bealei* is referred to *Sacalia* Gray. These genera are compared in Table 1.

The differences between *Sacalia* and *Mauremys* (12, 13, 14, and 15 of Table 1) seem sufficient to justify generic separation of *bealei* from *caspica*, *japonica* and *mutica*, but are not inconsistent with the belief that *Mauremys* and *Sacalia* are closely related. More interesting are some of the differences between *Clemmys* on the one hand and *Sacalia* and *Mauremys* on the other ; these differences suggest that *Clemmys* is part of a primarily New-World radiation and only convergent to *Sacalia* and *Mauremys*, which are part of an Old-World radiation.

BATAGURINAE AND EMYDINAE

Characters 1, 2, 3, and 4 of Table 1 not only serve to distinguish *Clemmys* from *Mauremys* and *Sacalia*, but separate the conventional Emydinae into two series, one almost entirely New-World and the other almost entirely Old-World in distribution. It is here proposed that these two series be recognized taxonomically as two subfamilies, the Batagurinae and the Emydinae.

The Batagurinae includes all of the Old-World turtles now referred to the Emydinae with the exception of the genus *Emys;* it also includes the Neotropical turtles generally referred to the genus *Geoemyda* (for reasons to be given later, these turtles must be referred to the genus *Rhinoclemys*). In the exclusion of the angular from Meckel's cartilage, the Batagurinae appear to be more specialised than the emydines, but the retention of a strong basioccipital tuberosity that forms the floor of the recessus scalae tympani and the simple joint between the fifth and sixth cervical centra mark this subfamily as more primitive that the Emydinae. Furthermore, the Batagurinae includes *Hardella*, a genus of living turtles that resembles Mesozoic turtles in lacking any bony wall around the paracapsular sac, aside from the flooring provided by the basioccipital and pterygoid.

The Emydinae includes *Emys* of Europe, Western Asia and North Africa and all the New-World forms previously referred to the Emydinae except *Rhinoclemys*. It should be noted that the land tortoises (subfamily Testudininae) show the distinctive characters of the Batagurinae, except that some of the genera show a peculiar pygal pattern with the supracaudal scute falling short of the pygal–suprapygal suture ; it is nearly certain that the

*Although the name *Emys nigricans* Gray 1834 has clear priority over *Emys muticus* Cantor 1842, I regard *nigricans* as a "tainted" name because it has been used for *Chinemys kwangtungensis* and is thus made ambiguous.

Testudininae are derived from a batagurine, rather than emydine, ancestor. *Platysternon* (subfamily Platysterninae) shows the distinctive features of the Emydinae ; it is the only member of the rich South-east Asiatic turtle fauna showing emydine, rather than batagurine affinities (I hope to show in a later paper that the affinities of *Platysternon* are with the North American genera *Chelydra* and *Macroclemys*).

Character 10 is almost a distinction between Batagurinae and Emydinae, but a few Emydinae are like the batagurines in having a strong backward extension of the pterygoid. These emydines are the genus *Malaclemys* (including *Graptemys*) and the subgenus *Trachemys* of *Chrysemys* (that is, the *Chrysemys scripta* group). Even here the condition is not precisely as in the batagurines, since in the absence of the basioccipital tuberosity the pterygoid

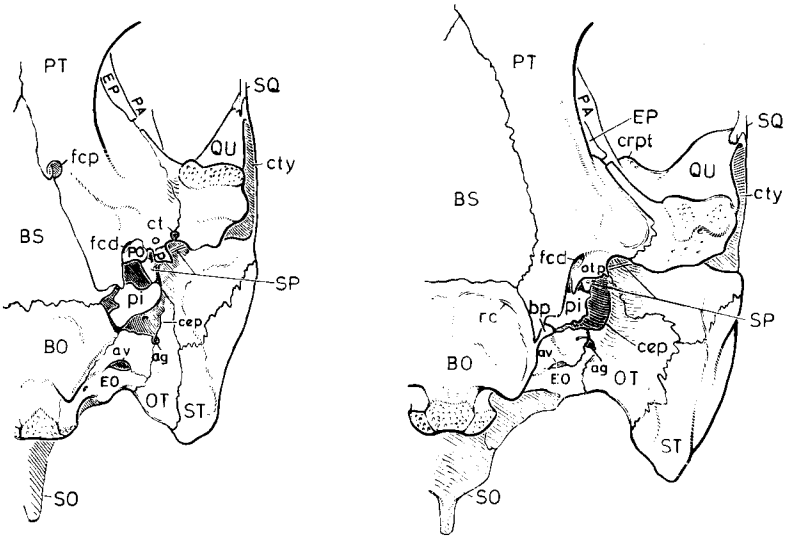

Fig. 1—Basiocranium of *Clemmys guttata* (left) and *Mauremys caspica* (right). Note the large foramen caroticopharyngeale (fcp) in *Clemmys* and its absence in *Mauremys* ; the greater backward extent of the pterygoid in *Mauremys* ; the presence of a " batagurine process " (bp) of the basioccipital in *Mauremys*, forming the floor of the recessus scalae tympani. (For key to lettering see p. 279.)

is barely in contact with the basioccipital or separated from that bone by an extension of the basisphenoid. Probably the posterior extension of the pterygoid in *Malaclemys* and *Chrysemys* (*Trachemys*) is secondary and shortening of the posterior end of the pterygoid was a primary accompaniment of loss of the basioccipital tuberosity in the Emydinae. If this be so, then it is possible that the double joint between the fifth and sixth cervical centra and the absence of the basioccipital tuberosity with accompanying forward migration of the rear of the pterygoid are functionally related and reflect some modification of the neck-retraction mechanism ; for the rear of the pterygoid is the point of insertion of the most anterior slip of the retrahens capitis collique muscle. Forward migration of the insertion of the retrahens would increase the efficiency of action by the muscle, but only if the greater pull resulting

from increased leverage is not translated into transverse, rather than vertical, bending of the neck ; the double joints in the rear of the cryptodire cervical column appear to be a provision against transverse bending of the neck during contraction of the long retractors running from the rear of the carapace to the anterior cervicals and head.

Characters 6, 5, 7, 8, and 9 are specialised features of the Old-World species referred to *Clemmys* that not only distinguish these species from Emydinae,

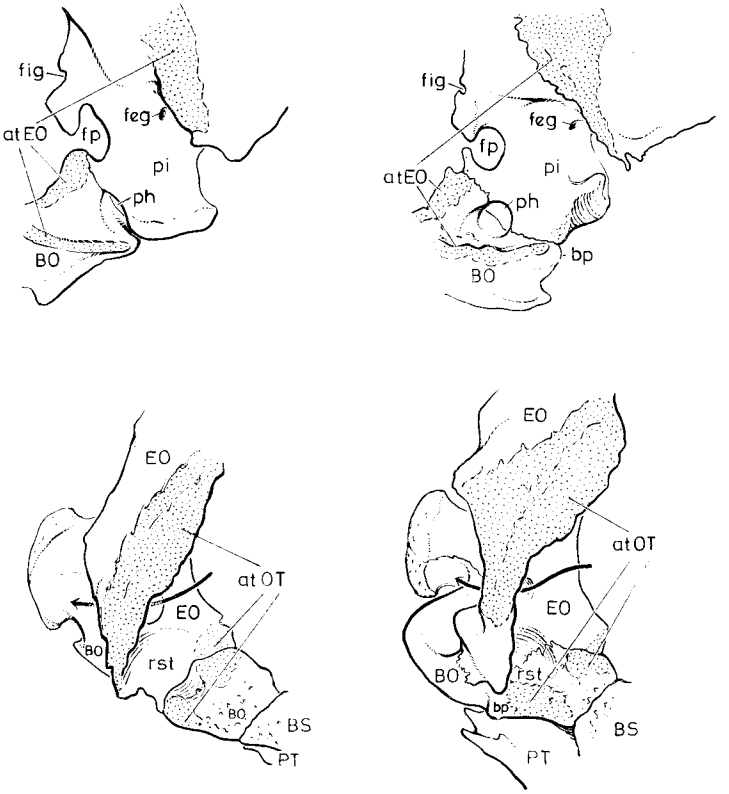

Fig. 2—The recessus scalae tympani of *Clemmys guttata* (left-hand figures) and *Mauremys caspica* (right-hand figures). The upper row shows the anterior wall of the recessus, as viewed from directly behind after removal of the exoccipital ; the lower row shows the posterior, medial, and ventral row in three-quarter view after removal of the opisthotic. The arrow in the lower figures shows the course of the vagus. (For key to lettering see p. 279.)

but set them apart from some Batagurinae. That is, they are the result of evolution within the Batagurinae that has further increased divergence from the Emydinae, including New-World *Clemmys*.

The batagurine genera *Hardella*, *Morenia*, and *Geoclemys* have the anterior opening of the Vidian canal between the epipterygoid and the inferior process of the parietal, well posterior to the anterior edge of the latter ; in this feature, as well as others, these three genera appear to be the most primitive among the Batagurinae. In the other batagurines there is a progressive usurpation of the role of the epipterygoid by the parietal. This is seen in its simplest state

in *Batagur*, *Kachuga*, and *Callagur*, where the anterior edge of the inferior process of the parietal is not thickened and the only specialisation beyond the condition in *Hardella* is the contact of a sliver of the parietal with the palatine lateral to the Vidian nerve and artery. In the other genera the anterior edge of the inferior process of the parietal is more or less thickened and the epipterygoid shortened, but in " *Pyxidea* " *mouhoti* anteroposterior shortening of the lateral wall of the cranial cavity eliminates this thickened part of the parietal and brings the anterior orifice of the Vidian canal back to between the epipterygoid and the palatine.

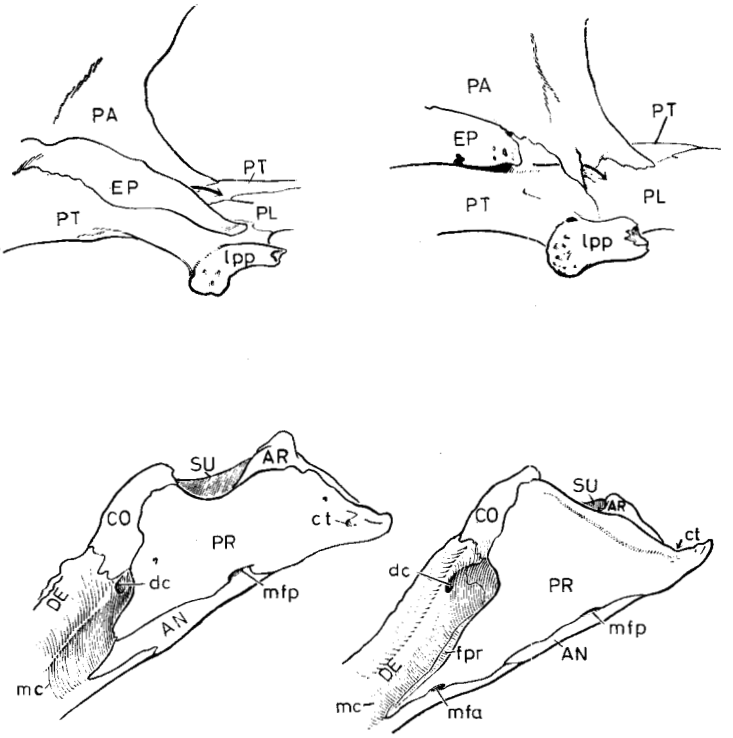

Fig. 3—*Clemmys guttata* (left-hand figures) and *Mauremys caspica* (right-hand figures). The upper row shows the anterior edge of inferior process of the parietal and the epipterygoid; the arrow shows the course of the Vidian canal. The lower row shows the medial aspect of the posterior end of the mandible, showing the flange on the prearticular (fpr) in *Mauremys* that excludes the angular from Meckel's cartilage. (For key to lettering see p. 279.)

Shortening of the angular is a characteristic of all the Batagurinae except *Hardella*, *Morenia*, *Batagur*, *Callagur*, *Kachuga*, and *Hieremys*.

The reduction of jugal–squamosal [" quadratojugal "] contact and development of slight kinesis in the horizontal temporal arch characterize a group of turtles presently referred to the genera *Cyclemys*, *Pyxidea*, *Cuora*, *Geoemyda*, *Notochelys*, *Annamemys* [see discussion beyond], and (Old-World) *Clemmys* (that is *Mauremys* and *Sacalia*). This group, which may be termed the *Geoemyda* Complex, appears to be a quite natural group of genera, primarily,

but not entirely, Old-World in distribution. In addition to the characteristic temporal arch, they share several other common features, such as : small nasopalatine foramen, narrow and unridged triturating surfaces, parietal in contact with quadrate posterolateral to the trigeminal foramen ; failure of the palatine to form a strong upward lamina to meet the inferior process of the parital (in some, the palatine does not meet the parietal at all), entoplastron usually transected by humeropectoral sulcus, and presence of but two phalanges in the fifth digit of the manus. It may be noted that these

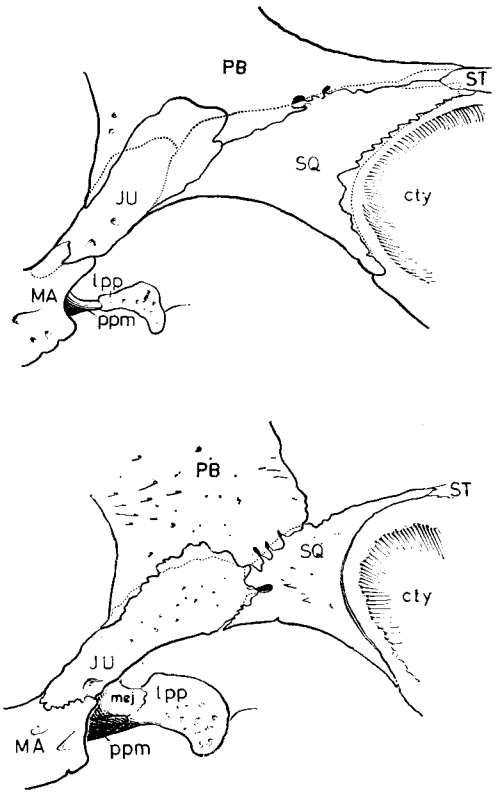

Fig. 4—Construction of the temporal arch in *Clemmys guttata* (upper) and *Mauremys caspica* (lower). The solid lines indicate the sutural pattern on the outer surface of the arch, the dotted lines the pattern on the inner surface of the arch. In some *Mauremys* the contact between jugal and squamosal below the conspicuous foramen is absent. Note the slightly open suture between squamosal and quadrate in *Mauremys*, permitting slight kinesis.

characters are essentially those that have been used to ally the New-World and the Old-World species of *Clemmys*. It is here suggested that the resemblance between true (New-World) *Clemmys* and Old-World "*Clemmys*" (*Sacalia* and *Mauremys*) in these features is convergent, and that these characters of Old-World "*Clemmys*" are better interpreted as resemblances to the *Geoemyda* Complex.

The enlarged and rounded postlagenar hiatus and the strip of granular skin extending from ear to eye are features shared not only with most of the

Table 1—Comparison of *Clemmys*, *Mauremys* and *Sacalia*

	Clemmys	*Mauremys*	*Sacalia*
1. Angular bone.	Forms the floor of the canal for Meckel's cartilage.	Excluded from contact with Meckel's cartilage by a longitudinal flange of the prearticular (but in contact with the articular).	As in *Mauremys*.
2. Basioccipital.	Without strong lateral tuberosity, not extending lateral to lagena, contributing to the medial wall of the recessus scalae tympani, but not to the floor of that recess; instead, the exoccipital curves downward and forward to form the floor, as well as the posterior wall of that recess.	With a strong lateral tuberosity that extends lateral to the lagena and forms the floor of the recessus scalae tympani.	As in *Mauremys*.
3. Joint between centra of fifth and sixth cervical vertebrae.	A double joint, with a pair of condyles.	A simple joint, with a single condyle.	As in *Mauremys*.
4. Supracaudal scutes.	Fall short of suture between pygal and suprapygal.	Extend forward on to suprapygal.	As in *Mauremys*.
5. Anterior border of inferior process of parietal, and anterior end of epipterygoid.	Anterior border of inferior process not thickened, with single attachment to the pterygoid medial to the Vidian canal; anterior end of epipterygoid equals or exceeds inferior process in anterior extent, forming lateral part of wall of the anterior end of the Vidian canal.	Anterior border of inferior process thickened and ventrally with two attachments to the pterygoid, a medial attachment and a more lateral one, with the anterior end of the Vidian canal between them; epipterygoid shortened anteriorly, its anterior end behind the thickened anterior edge of inferior process of parietal.	As in *Mauremys*.

[*Continued.*]

Table 1—*continued*

	Clemmys	*Mauremys*	*Sacallia*
6. Angular bone.	Unreduced in length ; equals or exceeds prearticular in anterior extent.	Reduced in length and conspicuously exceeded in anterior extent by prearticular.	As in *Mauremys*.
7. Postlagenar hiatus (a gap in the suture between basioccipital and processus interfenestralis of opisthotic, filled with connective tissue in life, ventral to the perilymphatic foramen, and immediately posterior to the lagena of the membranous labyrinth).	A small vertical slit.	A large round hole, more than half as big as perilymphatic foramen.	As in *Mauremys*.
8. Skin overlying lower end of jugal.	Evenly cornified, firmly adherent to the bone.	Broken up into finely granular skin that extends from eye to ear and is only loosely attached to the underlying bone.	As in *Mauremys*.
9. Squamosal (=quadratojugal of most authors).	Large and firmly anchored to surrounding bones by sutures with extensive squamous overlap ; its anterior end nearer to orbit than to tympanic cavity ; most of its anterior border firmly joined to jugal and most of its dorsal border firmly joined to postorbital.	Weakly joined to surrounding bones by sutures with little squamous overlap, relatively small, and apparently slightly kinetic ; its anterior end nearer to tympanic cavity than to orbit ; jugal contact, if present, taking up less than half the anterior border of squamosal.	As in *Mauremys*, but jugal contact constantly (?) absent.

10. Pterygoid.	With posterior end extending but little posterior to jaw articulation, failing to meet the basioccipital, exposing the foot of the processus interfenestralis of the opisthotic, and failing to exclude the basisphenoid from the border of the ear region.	With posterior end extending well posterior to jaw articulation, meeting basioccipital, partially concealing processus interfenestralis, and excluding basisphenoid from border of ear region.	As in *Mauremys*.
11. Foramen caroticopharyngeale.	Present as a large gap in the suture between pterygoid and basisphenoid; or entirely within pterygoid; transmitting a large pharyngeal branch of the carotid artery.	Absent.	Absent.
12. Ventral end of jugal.	Tapering to a point, not meeting pterygoid, so that maxillary enters border of temporal fossa.	Expanded inward to meet lateral process of pterygoid, excluding maxilla from border of temporal fossa.	As in *Mauremys*, but inward expansion more extensive, in contact with inferior process of parietal, which is broadly flared out.
13. Fissura ethmoidalis (between descending processes of prefrontals).	Abruptly narrowed beneath the small round dorsal passage for olfactory and profundus nerves, so as to be keyhole-shaped.	As in *Clemmys*.	Broadly triangular.
14. Scutellation of forearm.	With numerous transversely enlarged scales separated by granular scales.	As in *Clemmys*.	A few very large scutes without intervening granules.
15. Plastral buttresses.	Rather weak, the axillary extending only a short distance on to first pleural, the inguinal buttress extending a short distance on to fifth pleural.	Stronger than in *Clemmys*, the axillary buttress extending well on to first pleural, the inguinal buttress extending well on to fifth pleural (in some *caspica*, also making contact with sixth pleural).	Very weak, scarcely extending beyond marginal bones.

Geoemyda Complex, but also with *Orlitia* and *Siebenrockiella*. I believe the latter two genera are close to the ancestry of the *Geoemyda* Complex, not only because of the above resemblances, but because of the following features : failure of the vomer to extend back into the floor of the cranial cavity ; deep emargination of the triturating surfaces from behind along the midline, so that the vomer fails to support the rhamphotheca and the prepalatine foramina are exposed ventrally in the upper jaw, and the symphysis of the dentaries extends posterior to the symphysial part of the lower triturating surface. Williams (in Loveridge & Williams, 1957, pp. 185, 188) suggests *Ocadia* as the ancestor of the *Geoemyda* Complex, but of the characters used by Williams (plastral buttressing, width and crests of triturating surfaces, relation of humero-pectoral sulcus to entoplastron), *Siebenrockiella* agrees better than *Ocadia* with the *Geoemyda* Complex, since it lacks crests on the triturating surfaces. Moreover, *Ocadia* has the vomer expanded anteriorly to support the rhamphotheca, so that the prepalatine foramina are concealed from below ; has the vomer extended back to contribute to the floor of the cranial cavity ; has the lower triturating surface extended back on the midline beyond the level of the dentary symphysis ; has the postlagenar hiatus small and laceriform ; and lacks any strip of granular skin from ear to eye. The skull of *Ocadia* is very similar to that of the *tecta* group of *Kachuga*, and I believe this is the real affinity of *Ocadia*.

Characters 11 and 12 are specialisations of true (New-World) *Clemmys* shared with some, but not all Emydinae. The foramen for the pharyngeal artery is present, but minute, in *Chrysemys* (*sensu lato*) and only slightly larger and more conspicuous in *Deirochelys*. In *Emys* and *Emydoidea* the foramen is conspicuous but not quite so large as in *Clemmys*. *Terrapene* is as in *Clemmys* in the size of the foramen, and *Clemmys* and *Terrapene* are alone among Emydinae (*sensu stricto*) in the narrowness of the ventral end of the jugal.

As I conceive the relationship among aquatic Testudinidae, the approach of the Batagurinae to the Emydinae is not through the narrow-jawed forms, such as *Mauremys* and *Clemmys*, but through the broad-jawed batagurines *Hardella* and *Morenia* and the broad-jawed emydines of the subgenus *Pseudemys* of the genus *Chrysemys*. The pattern of ridges on the triturating surfaces of *Hardella* is very similar to that on the triturating surface of *Chrysemys* (*Pseudemys*) *alabamensis*.

Both *Chrysemys alabamensis* and *Hardella* have very broad triturating surfaces, with a pair of longitudinal middle ridges on both the upper and lower triturating surfaces. In both turtles the middle ridge of the upper surface ends anteriorly in a strong cusp close to the common meeting point of vomer, premaxillary, and maxillary, and in both turtles a crest runs forward from this cusp close to the maxillo-premaxillary suture to connect with the " tooth " on the tomium flanking the median premaxillary notch ; in both turtles the cusp is joined by a short commissural ridge to a median keel on the vomerine contribution to the triturating surface. In both the American and the Indian turtle, the middle crest of the lower triturating surface ends anteriorly in a cusp that bites posterolateral to the cusp of the upper surface ;

and in both turtles, the cusp on the lower surface is connected by a commissural ridge to a median keel that runs forward to the strong terminal hook of the dentary.

The general appearance of the skull of *Hardella* is also like that of *Chrysemys alabamensis,* with conspicuously flattened ventral surface of the

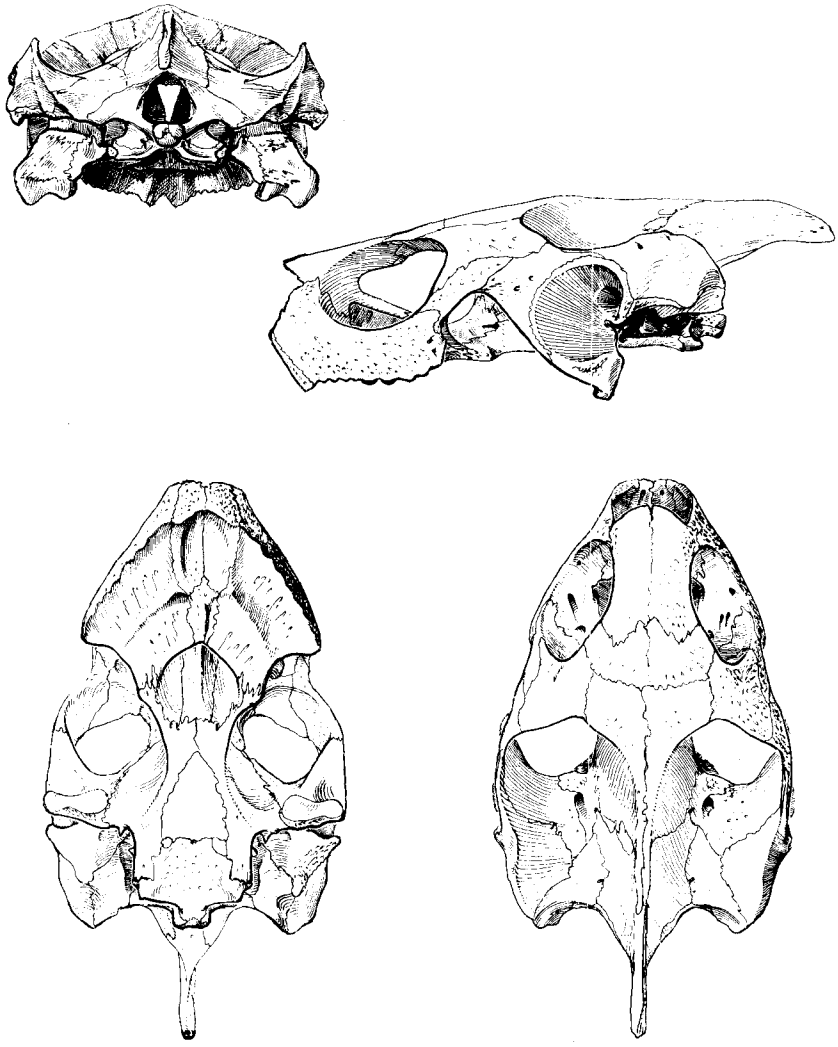

Fig. 5—*Hardella thurgii.* Occipital, lateral, ventral, and dorsal views of skull.

dentary, deep excavation on the lateral surface of the dentary for the adductor mandibulae, large and fenestra-like nasopalatine foramen and small posterior palatine foramen, and large orbits that face somewhat upward as well as outward. Most interesting, however, are the differences, for the construction of the canal for Meckel's cartilage and of the recessus scalae tympani differ

in the same way the corresponding parts of *Sacalia* and *Mauremys* differ from those of *Clemmys*.

Fig. 6—*Chrysemys* (*Pseudemys*) *alabamensis*. Occipital, lateral, ventral, and dorsal views of skull.

The angular forms parts of the floor of the canal for Meckel's cartilage in *Chrysemys alabamensis*, but in *Hardella* a lamina of bone grows laterally from the prearticular to meet the dentary and surangular, thus nearly excluding the angular from the floor of the Meckelian canal.

In *Hardella* the basioccipital is broad and forms the floor of the recessus scalae tympani, the chamber behind the auditory capsule containing the sac of perilymph (scala tympani) that projects out of the perilymphatic foramen and the posteromedial end of the paracapsular sac (the paracapsular sac, found in all turtles, is a fluid-filled vesicle surrounding the base of the stapes ; see Baird, 1960 for discussion of this structure). The basioccipital flooring of the recessus scalae tympani extends far lateral to the postlagenar hiatus (new term ; proposed for a gap in the suture between the basioccipital and the processus interfenestralis of the opisthotic, ventral to the perilymphatic foramen and immediately posterior to the lagena ; the hiatus is present in all turtles except Kinosternids (including *Dermatemys*), where the processus interfenestralis meets the basioccipital by squamous overlap, but in some testudinines and in *Kachuga tecta* the hiatus is minute ; the hiatus is filled by connective tissue in life). The basioccipital has a lateral extension

distinctly set-off from the muscular tuberosity ; this extension, which I term the " batagurine process ", is largely concealed from below by the posterior end of the pterygoid and represents the lateral end of the portion of the basioccipital flooring the recessus scalae tympani. This portion of the basioccipital has some resemblance to the vestigial rib-heads found on the cervical vertebrae of cryptodires and the " batagurine process " and basi-occipital flooring of recessus scalae tympani may represent an ossified cranial rib.

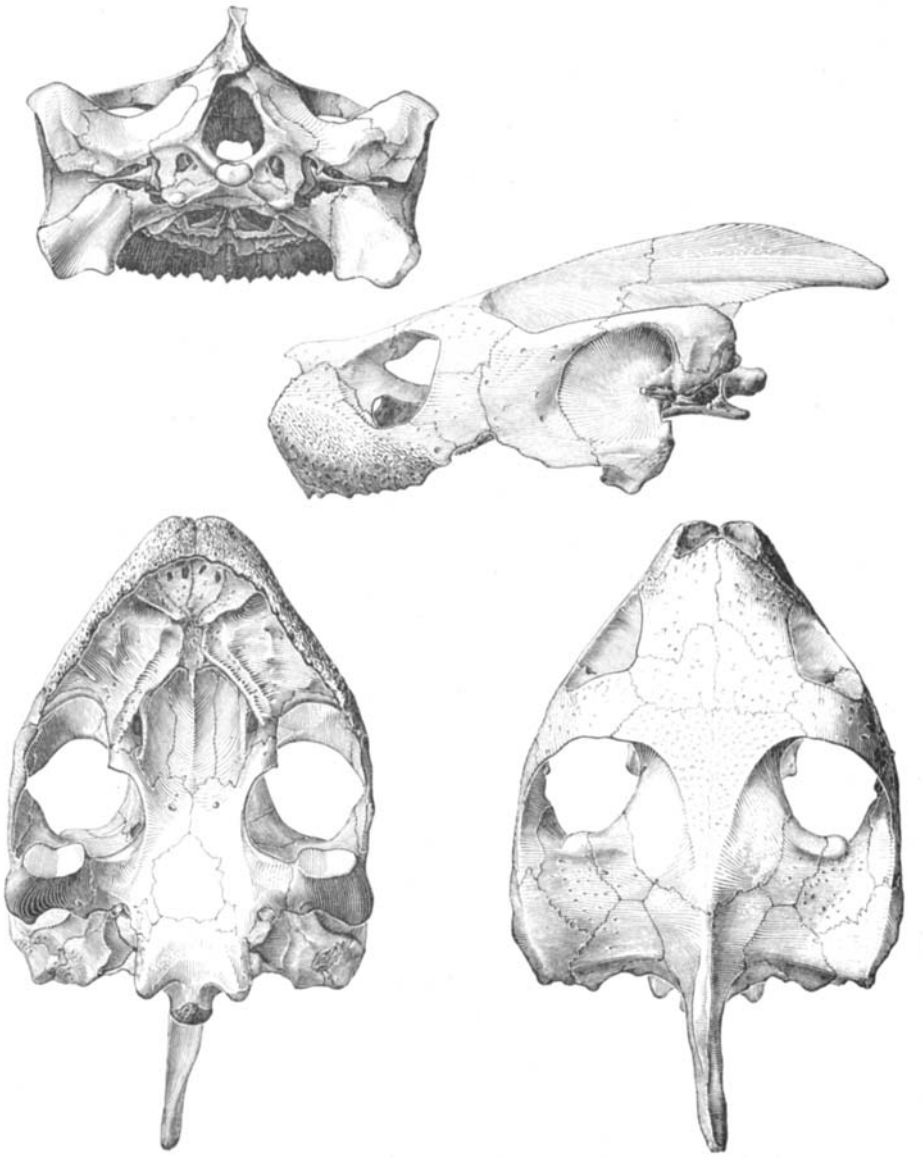

Fig. 7—*Dermatemys mawi.* Occipital, lateral, ventral, and dorsal views of skull.

In *Chrysemys alabamensis* the ossified basioccipital is relatively narrow and does not extend lateral to the postlagenar hiatus ; in fact, it does not even quite complete the ventral border of the hiatus. The exoccipital curls forward to meet the foot of the processus interfenestralis of the opisthotic, thus forming the floor of the recessus scalae tympani. The pterygoid does not extend back to the basioccipital, so that the posterolateral corner of the basisphenoid is exposed ventrally entering the floor of the otic capsule and the entire ventral end of the process interfenestralis is similarly exposed ventrally. This is substantially the same construction of the recessus scalae tympani found in other Emydinae (*sensu stricto*).

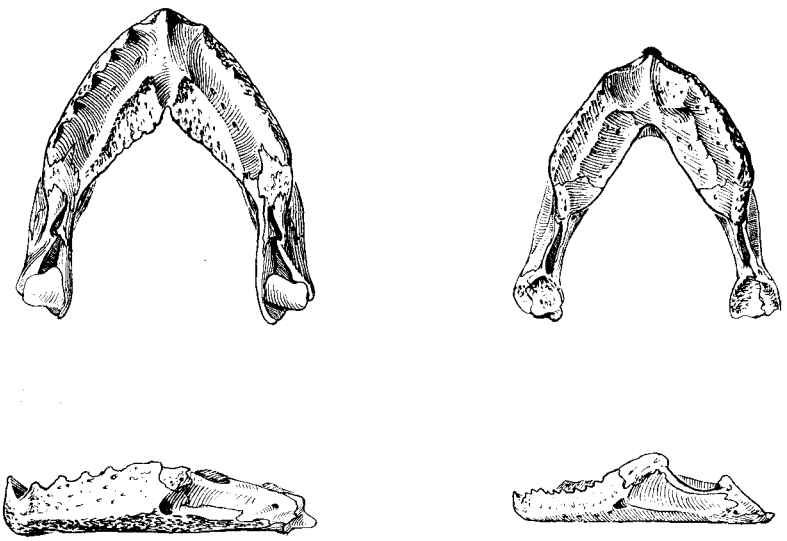

Fig. 8—Dorsal and lateral views of the mandible of *Hardella thurgii* (left-hand figures) and *Chrysemys* (*Pseudemys*) *alabamensis* (right-hand figures).

Elsewhere (McDowell, 1961) I have argued that *Dermatemys* is the most primitive member of the kinosternid group, and it is noteworthy that the general appearance of the skull of *Dermatemys* is much like that of *Hardella* and *Chrysemys alabamensis*. This is probably the primitive facies of the skull for Testudinoidea. The points of difference that are stressed here are relatively minor, and if the adaptive radiation of the kinosternids, the batagurines, and the emydines had proceeded no further than the stage represented by *Dermatemys, Hardella,* and the subgenus *Pseudemys,* then no more than generic distinction would be demanded. However, each of these lines has had an adaptive radiation of some consequence. The much modified arterial circulation of the head, reflected in the modified pattern of cranial foramina, distinguish the kinosternid radiation ; the emydine radiation is characterized by the unusual construction of the recessus scalae tympani, the joint between fifth and sixth cervicals, and pygal pattern ; the batagurine radiation is marked by no constant departure from the primitive condition except the

exclusion of the angular from contact with Meckel's cartilage, and in *Hardella* this exclusion is incomplete.

Starting from the primitive facies, with broad triturating surfaces that possess cusps and pits as well as coarsely dentate crests, both emydines and batagurines have developed narrow-jawed genera. At least, this seems the easiest explanation. Adaptive radiation and convergent evolution in feeding mechanisms is well known (e.g. various " edentates " among mammals, Darwin's finches in the Galapagos Archipelago, and the vangids in Madagascar) and nothing unprecedented is called for in saying the basicranial differences between Batagurinae and Emydinae reflect the primary phyletic splitting and that the resemblances in triturating surfaces between *Clemmys* and *Mauremys* are convergent. On the other hand, it seems inexplicable to me that several phyletic lines of turtles entering North America should all become convergent to one another in details of basicranial construction.

NOTES ON *MAUREMYS*, *PSEUDOCADIA*, AND *ANNAMEMYS*

Within the genus *Mauremys*, each species has its own peculiarities ; thus, in *M. japonica* the inferior process of the parietal does not quite meet the palatine ; in *M. caspica* the pterygoid fails to send up a snag of bone lateral to the paracapsular sac. But the chief peculiarity of *Mauremys mutica* is its geographic and individual variability in characters that have been used to diagnose genera among the *Geoemyda* Complex. It has been shown by Nakamura (1934) that this species is geographically variable in the relationship of the entoplastron to the humeropectoral sulcus, northern specimens usually having the entoplastron transected by the sulcus (as in most of the *Geoemyda* Complex) and southern specimens having the sulcus posterior to the entoplastron. This is an important discovery, not only to herpetology but to archaeology, for it leads to a reinterpretation of a turtle shell found in the ruins of Anyang Hsien in northern Honan. This shell, originally described by Ping (1930) as *Testudo anyangensis*, was recognized as a pond turtle by Lindholm (1932), who placed it in a new genus *Pseudocadia* and regarded it as most closely related to *Ocadia sinensis*. *Ocadia sinensis* is not known from north of Fukien Province on the Chinese Mainland (the species also occurs on Formosa), about 800 miles south of Anyang Hsien.

Lindholm was under the impression that it is a constant feature of *Mauremys mutica* for the humeropectoral sulcus to pass behind the entoplastron (he placed this species in a monotypic genus *Cathaiemys* on these grounds). Had he been aware of the conditions in north Chinese *M. mutica* he would probably have noted that there is nothing in Ping's excellent detailed description and figures of *anyangensis* that would distinguish that form from a north Chinese *Mauremys mutica* ; on the other hand, several features, such as the great forward extent of the inguinal aperture and the slightly projecting, rather than truncate, gular region of the plastron, give the Anyang turtle a very different appearance from that of *Ocadia*. On geographic grounds reference of *Pseudocadia anyangensis* to the synonymy of *Mauremys mutica* is plausible, since *mutica* is known from southern Japan and from at least as far north as Kiangsu and Anhwei Provinces on the mainland.

It has not been reported previously that *Mauremys mutica* is individually variable in the hexagonal neural bones being short-sided anteriorly or posteriorly. In a series from Hainan Island (American Museum of Natural History collection) three are normal (30154, 30166, 30171) and two have the second neural octagonal and succeeding neurals short-sided behind (30160, 30168) ; in 30172 the third neural is octagonal and followed by neurals that are short-sided behind ; in 30165 the fourth neural is octagonal and followed by hexagonal neurals that are short-sided behind. This is a feature which has been relied on extensively in distinguishing a *Geoemyda–Cuora–Cyclemys* group within the *Geoemyda* Complex, and the discovery of such individual variation in *M. mutica* suggests that the taxonomic value of the neural bones has been overrated in this group. In a later section of this paper a reclassification of the genera of the *Geoemyda* Complex will be given.

The plastral buttresses of *Mauremys mutica* are quite strong and define between them a pair of deep pulmonary recesses ; however, the condition is not quite as in *Hardella*, *Batagur*, and *Orlitia*, for the inguinal buttress is attached to the middle of the fifth pleural rather than to the suture between the fifth and sixth pleurals, and the axillary buttress does not make direct contact with the first rib but is connected to the rib by a prominent ridge on the inner face of the first pleural. This is more conspicuous in large than in small specimens. The turtle described by Bourret (1939, 1941) as *Annamemys merkleni* appears to agree with *Mauremys mutica* in scutellation, skull structure (*fide* Bourret's plate), colour pattern, and all but one feature of shell-structure : the axillary buttress is said to be in contact with the first rib. But Bourret's diagram of the carapace, with a + marking the position of the end of the buttress, shows the tip of the axillary buttress as near the posterior border of the first pleural, quite unlike the condition in *Batagur*, *Orlitia*, or *Hardella*, where the tip of the buttress has a more anterior position ; Bourret's figure would be well in accord with *Mauremys mutica* if it is assumed he failed to note the inconspicuous suture between the tip of the axillary buttress and the ridge on the first pleural.

Savage (1953) has shown that *Cyclemys annamensis* Siebenrock is actually the juvenile of Bourret's *Annamemys merkleni* (and is a senior name). The appearance of *Cyclemys annamensis* as figured is so like that of juvenile *Mauremys mutica*, particularly in head colour-pattern, that it is more likely than not that *Annamemys* is a synonym of *Mauremys mutica*.

REDEFINITIONS OF GENERA OF TURTLES OF THE BATAGURINAE AND EMYDINAE

The following classification is based mainly on the skull structure, but also makes use of cloacal bursae, condition of the second ceratobranchial, shell structure, and scutellation.

Subfamily Batagurinae

Diagnosis : Testudinidae with axillary or inguinal scent glands, or both ; at least two digits of each appendage with three phalanges ; prearticular with

a lateral flange that nearly (*Hardella*) or quite (remaining genera) separates angular from Meckel's cartilage ; basioccipital with ossified lateral tuberosity that forms floor of recessus scalae tympani and is in contact with paracapsular sac ; posterior end of pterygoid in contact with basioccipital tuberosity ; a simple articulation between fifth and sixth cervical centra ; supracaudal scutes extending up onto suprapygal.

Hardella Complex

Diagnosis : triturating surfaces very broad, the upper surface a pair of middle ridges that end anteriorly in a pair of cusps (but the sculpture of the triturating surface only faintly indicated in *Geoclemys*) ; lower triturating surface extending back behind the dentary symphysis along the midline ; vomer large, its rear forming part of floor of cranial cavity, its anterior end with a shelf contributing to the triturating surface, this shelf concealing the foramina praepalatina from below ; nasopalatine foramen a large fenestra ; *anterior opening of Vidian canal between epipterygoid (laterally) and palatine (medially), posterior to anterior border of inferior process of parietal, the anterior border of the inferior process of the parietal entirely medial to Vidian canal ; coronoid bone flattened dorsally, scarcely rising above prearticular ;* squamosal firmly attached to surrounding bones.

Genus *Hardella* Gray

Hardella Gray, Suppl. Cat. Shield Rept. 1870 : 58. Type : *Emys thurgii* Gray.

Diagnosis : carotid canal between pterygoid and proötic ; *chamber for paracapsular sac completely open posteriorly ;* frontal entering orbital border ; frontals not underarching olfactory nerves ; sculpture of triturating surfaces sharply defined, the lower triturating surface with a middle ridge ; squamosal (" quadratojugal " Auct.) firmly sutured to postorbital ; plastral buttresses very strong, the axillary reaching the first rib, the inguinal attached half-way up the suture between the fifth and sixth pleurals.

Probably two species : *H. thurgii* (Gray) of the Ganges and Brahmaputra systems, with a weak vertebral keel ; and *H. indi* Gray of the Indus system, with an angulation on each lateral scute, forming a pair of low and discontinuous pleural keels in addition to the vertebral keel (three specimens examined).

In the lack of any bony wall behind the paracapsular sac, *Hardella* differs from all other Testudinidae and resembles Mesozoic turtles and cheloniids.

Genus *Morenia* Gray

Morenia Gray, Suppl. Cat. Shield Rept. 1870 : 62. Type : *Emys berdmorei* Blyth=*Emys ocellata* Duméril & Bibron.

Diagnosis : carotid canal entirely within pterygoid ; a lobe of the exoccipital, bolstered by a lobe of the opisthotic, descending behind the paracapsular sac to define an apertura vagi ; frontal broadly excluded from orbital border by prefrontal and postorbital ; frontals meeting beneath the olfactory nerves just posterior to fissura ethmoidalis ; sculpture of triturating surfaces sharply defined ; lower triturating surface without middle ridge ; squamosal firmly

sutured to postorbital ; plastral buttresses weak, the axillary barely reaching the first pleural, the inguinal barely reaching the fifth or sixth pleural.

Two species : *M. ocellata* (southern Burma and Tenasserim) and *M. petersi* (Bengal) ; I have not seen the latter species.

Genus *Geoclemys* Gray

Geoclemys Gray, Cat. Shield Rept. **1**, 1855 : 17. Type : *Emys hamiltonii* Gray.

Diagnosis : carotid canal entirely within pterygoid ; a lobe of the exoccipital, bolstered by a lobe of the opisthotic, descending behind the paracapsular sac to define an apertura vagi ; frontal broadly excluded from orbital border by prefrontal and postorbital ; frontals nearly meeting beneath the olfactory nerves just posterior to fissura ethmoidalis ; sculpture of triturating surfaces only faintly indicated on bone, somewhat more distinct on the rhamphotheca, the triturating surface nearly flat ; no middle ridge on lower triturating surface ; squamosal completely separated by jugal from postorbital ; plastral buttresses moderate, the axillary attached to the first pleural, the inguinal to the suture between the fifth and sixth pleurals.

One species, *G. hamiltoni* of the Indus and Ganges Systems. Although *Geoclemys* is generally said to have " alveolar surfaces of jaws very broad, without median ridge " (Smith, 1931, p. 111), the traces of a cusp-and-ridge pattern much like that of *Morenia* can be made out clearly on the rhamphotheca and is discernible on the bony surfaces. The complete enclosure of the carotid canal within the pterygoid and the underarching of the olfactory nerves by the frontals are features common to *Morenia* and *Geoclemys* that I have not seen in any other Batagurinae. But in some respects *Geoclemys* more resembles *Hardella* : in *Geoclemys* there is a discontinuous pleural keel, suggested in the carapace of *Hardella indi* but not visible in *Morenia* ; and the head colour-pattern of *Geoclemys*, with all stripes broken up into a series of pale blotches, is approached by *Hardella*, where the anterior ends of the supraorbital stripe are isolated as a supranasal blotch and the anterior ends of the suborbital stripe are isolated as a subnasal blotch (in *Morenia* all the head stripes are complete).

There is no doubt that *Geoclemys* is distinct from *Chinemys* and *Malayemys*, for the coronoid process and epipterygoid region of those turtles is as in the next group, the Batagur Complex, and the feeble indications of a middle crest on the upper triturating surface of *Malayemys* show no indications of an anterior cusp ; in *Chinemys* there are no indications of a crest on the triturating surface.

Batagur Complex

Diagnosis : triturating surfaces moderately broad to very broad, with or without longitudinal denticulated ridges, but without specially enlarged cusps ; vomer large, its posterior end extending back to the level of the cranial cavity, its anterior end with a shelf that makes up part of the triturating surface and conceals the foramina praepalatina from below ; lower triturating surface equalling or exceeding dentary symphysis in backward extent along the midline ; coronoid bone with distinct coronoid process that rises above prearticular and surangular (but may not rise above dentary) ; anterior

opening of Vidian canal in palatine, in inferior process of parietal, or in parieto-palatine suture, the anterior part of the inferior process of the parietal attached to the palatine both lateral and medial to the Vidian canal ; squamosal firmly attached to neighbouring bones or absent ; postlagenar hiatus a narrow horizontal slit ; posterior palatine foramen a small hole.

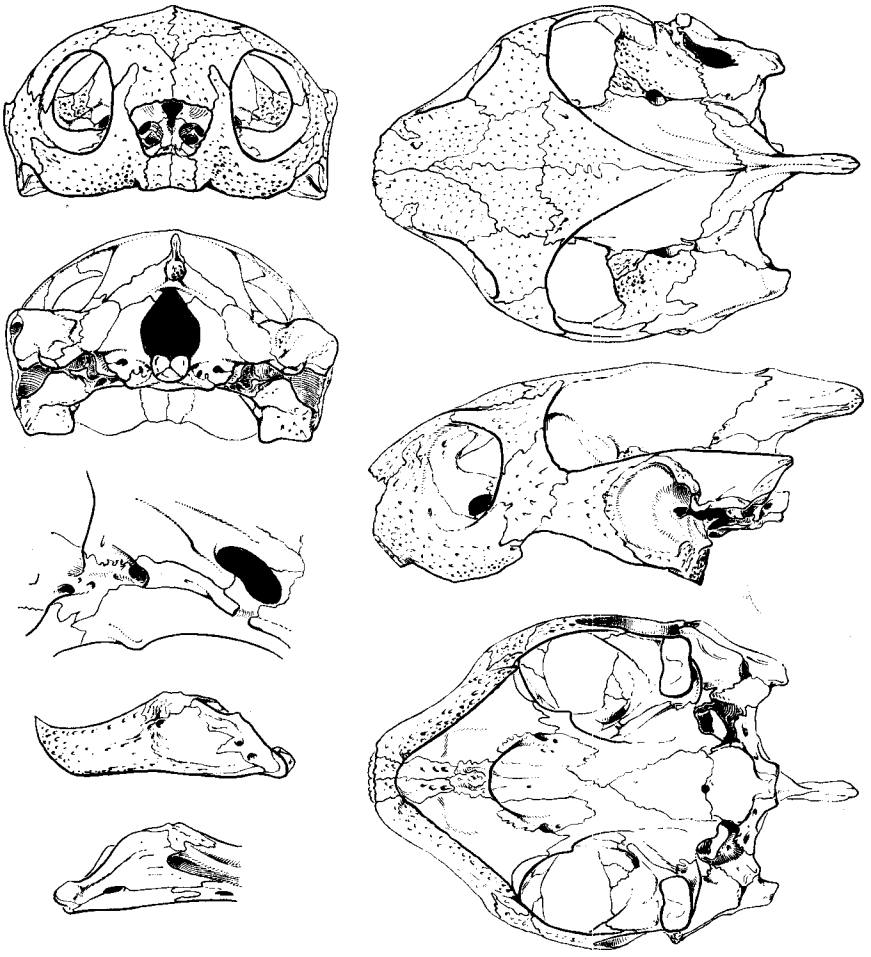

Fig. 9—*Geoclemys hamiltoni*, adolescent specimen : frontal, occipital, dorsal, lateral, and ventral views of skull ; left epipterygoid and adjacent bones ; lateral view of mandible and medial view of posterior mandibular ramus.

Genus *Kachuga* Gray

Kachuga Gray, Proc. zool. Soc. Lond. 1869 : 186, 200. Type : *Kachuga trilineata* Gray = *Emys trivittata* Duméril & Bibron.

Diagnosis : upper triturating surface with one sharply defined and denticulated middle ridge ; nasopalatine foramen a large fenestra ; maxilla excluded from inferior process of parietal by palatine ; inferior temporal emargination

deep, the maxilla excluded from the squamosal ; squamosal present, except as an abnormality (observed on the left side of one *K. tecta* skull prepared by the author from a spirit-specimen) ; posterior temporal emargination deep, the squamosal excluding postorbital from supratemporal ; frontal broadly excluded from posterior temporal emargination by parieto-postorbital contact ; fossa on quadrate process of pterygoid for the medial pterygoid muscle facing ventro-laterally or directly ventrad, the pterygoid bone falling short of the articular surface of the quadrate ; prearticular and angular subequal in forward extent ; coronoid process of coronoid bone moderate, barely rising above dentary ; plastral buttresses very strong, the axillary reaching the first rib, the inguinal extending half-way up the suture between fifth and sixth pleural ; entoplastron anterior to sulcus between humeral and pectoral scutes ; posterior neural bones not elongated, the fourth central (vertebral) scute overlying parts of four or five neural bones, as is usual in Batagurinae ; fifth finger with three phalanges.

This genus contains six or seven species : *K. trivittata* (Duméril & Bibron) of the Irrawaddy and Salween Systems of Burma ; *K. kachuga* (Gray) of the eastern Ganges System (and Kistna and Godavari Systems ?) ; *K. dhongoka* (Gray) of the eastern Ganges System ; *K. smithi* (Gray) of the Indus and western Ganges System ; *K. sylhetensis* (Jerdon) of the Annamese hills ; and *K. tecta*. *Kachuga tecta* is generally regarded as forming two geographic races : *K. t. tecta* (Gray) of the Indus, Ganges, and Brahmaputra Systems ; and *K. t. tentoria* (Gray) of the peninsular Mahanadi, Godavari, and Kistna Systems. However, a specimen in the Harvard Museum of Comparative Zoology from Bengal is plainly *tentoria*, with pale and indistinct head stripes, short second central scute, and nearly unmarked limbs ; this specimen, originally identified as *K. smithi*, suggests that *tentoria* and *tecta* occur together in Bengal and are distinct species. I have seen no material of *K. kachuga* and *K. sylhetensis*, and for *K. dhongoka* I have seen only two shells and one juvenile, now living in my home. This juvenile *K. dhongoka* has only three claws on each hand, and for that reason the number of claws is not used in the generic diagnosis to distinguish *Kachuga* from *Batagur*.

Within the genus *Kachuga*, the differences between the two extremes represented by *K. trivittata* and *K. tecta* are so great as to suggest generic separation. In *K. trivittata* the fissura ethmoidalis gradually narrows ventrally, the tomium of the upper jaw is notched medially, the fifth toe has four phalanges, the fourth central scute is of normal form and the carapace has only an obscure dorsal ridge, the anterior neural bones are elongated, and the adult size is very large (carapace reaching 580 mm, *fide* Smith, 1931, p. 133). In *K. tecta* the fissura ethmoidalis is abruptly narrowed beneath the passage of the olfactory and profundus nerves, the tomium of the upper jaw forms a truncated median beak set-off by a pair of lateral notches, the fifth toe has three phalanges, the fourth central scute is elongated and tapers anteriorly to a point behind a sharp dorsal crest on the anterior carapace, all the neurals are short, and the adult size is small (carapace reaching 230 mm, *fide* Smith, 1931, p. 128). However, *K. dhongoka* and *K. smithi* partially bridge this gap. *K. dhongoka* is similar to *K. trivittata* but has nodosities on the first three central scutes, suggesting an incipient anterior carapacial crest, and is smaller

(carapace to 400 mm, *fide* Smith, 1931, p. 130) ; *K. smithi* is similar to *K. tecta* but has elongated anterior neural bones, has no notches setting-off the beak from the lateral maxillary tomium, and has a discontinuous carapacial crest.

Genus *Callagur* Gray

Callagur Gray, Suppl. Cat. Shield Rept. **1**, 1870 : 53. Type : *Batagur picta*=Gray *Emys borneoensis* Schlegel & Müller.

Similar to *Kachuga*, but neural bones under fourth central scute elongated, so that fourth central overlies three neural bones.

It is with the gravest misgivings that I keep *Callagur* separate from *Kachuga*. The single species, *C. borneoensis* (Schlegel & Müller), is closely related to *Kachuga trivittata* and is geographically representative of that species, being found in the Malay Peninsula, Sumatra, and Borneo. *Callagur borneoensis* differs from *Kachuga trivittata* principally in the elongated neural bones, narrower triturating surfaces, and in reaching an even greater size (carapace to 760 mm, *fide* de Rooij, 1915, p. 291). The triturating surfaces are distinctly narrower than those of *K. trivittata*, although they are not appreciably narrower than those of *K. tecta*, and appear to have become narrowed by reduction of the lingual border, so that the middle ridge has come to lie close to the lingual border of the triturating surface. In respect to the triturating surfaces, as well as in respect to size and geographical distribution, *K. trivittata* seems to be intermediate between *K. kachuga* and *Callagur borneoensis*. Only someone with plentiful material of *Kachuga* and *Callagur* can make a definite statement, but I suspect that *Callagur borneoensis*, *Kachuga trivittata*, and *K. kachuga* will turn out to be a single superspecies.

Genus *Batagur* Gray

Batagur Gray, Cat. Shield Rept. **1**, 1855 : 35. Type : *Emys batagur* Gray=*Emys baska* Gray.

Diagnosis : posterior neurals elongated, the fourth central scute overlying three neurals (as in *Callagur*) ; skull similar to that of *Kachuga* and *Callagur*, but with an additional denticulated middle ridge above and below ; constantly with only four claws on manus.

A single species, *B. baska* (Gray), of the marine estuaries and deep rivers on the coast of the Indian Ocean from Bengal to the Malay Peninsula and also Cochin-China and Sumatra.

Genus *Hieremys* M. Smith

Hieremys M. Smith, J. Nat. Hist. Soc. Siam, **2**, 1916 : 50. Type : *Cyclemys annandalii* Boulenger.

Diagnosis : upper triturating surface with middle ridge indistinct and reduced to a mound-like swelling along the lingual border ; nasopalatine foramen a large fenestra ; maxilla excluded from inferior process of parietal by palatine ; squamosal bone absent, so that the inferior temporal emargination is confluent dorsally with the posterior temporal emargination ; latter deep ; postorbital widely separated from supratemporal ; frontal broadly excluded from posterior temporal emargination by parieto-postorbital contact ; fossa

on pterygoid for medial pterygoid muscle facing ventrolaterally, the pterygoid falling short of the articular surface of the quadrate ; prearticular and angular subequal in forward extent ; coronoid process of coronoid bone moderate, not rising above dentary ; plastral buttresses short, the axillary attached to the ventrolateral end of the first pleural, the axillary to the ventrolateral end of the fifth pleural ; entoplastron crossed by humeropectoral sulcus ; posterior neural bones not elongated, the fourth central scute resting on four neural bones ; fifth finger with two phalanges ; fourth to sixth neurals hexagonal and short-sided behind.

This genus contains only *H. annandali* (Boulenger) of Cambodia, central Siam, and northern Malaya. This is a very distinct genus with no close relatives, but I believe it closer to *Kachuga* than to any other living genus. This is not the opinion of Williams (*in* Williams & Loveridge, 1957), who allies *Hieremys* to " *Geoemyda* " (essentially *Heosemys* of the present classification). The absence of the squamosal and presence of hexagonal neurals with the posterolateral surface shorter than the anterolateral are certainly resemblances to *Heosemys*, as are the reduced plastral buttresses, transection of the entoplastron by the humeropectoral sulcus, and the presence of but two phalanges in the fifth finger.

On the other hand, the large nasopalatine fenestra and small posterior palatine foramen, the presence of a triturating shelf on the vomer that conceals the incisive foramina from below, the long angular bone, the backward extension of the lower triturating surface behind the dentary symphysis on the midline, all are more suggestive of *Kachuga* than of any member of the *Geoemyda* Complex. The mound-like swelling along the lingual border of the upper triturating surface of *Hieremys* is not seen in any member of the *Geoemyda* Complex and seems to represent the middle ridge of the triturating surface of *Kachuga* and *Callagur*, but lacking denticulations and so close to the lingual border of the surface as to merge with the border.

Genus *Ocadia* Gray

Ocadia Gray, Suppl. Cat. Shield Rept. **1**, 1870 : 35. Type : *Emys sinensis* Gray.

Diagnosis : upper triturating surface with one sharply defined and denticulated middle ridge ; nasopalatine foramen a large fenestra ; maxilla excluded from inferior process of parietal by palatine ; inferior temporal emargination deep, the maxilla excluded from the squamosal ; squamosal present ; posterior temporal emargination shallow, the postorbital in contact with the supratemporal ; frontal broadly separated from the posterior temporal emargination by parieto-postorbital contact ; fossa for medial pterygoid muscle facing ventrolaterally ; pterygoid falling short of articular surface of quadrate ; angular shortened, much exceeded in anterior extent by prearticular ; coronoid process of coronoid bone moderate, rising only slightly above dentary ; plastral buttresses moderately strong, the axillary inserted high on first pleural (but not attached to first rib), the inguinal inserted about half-way up the suture between the fifth and sixth pleurals ; humeropectoral sulcus transecting entoplastron ; neural bones not elongated, the fourth central scute overlying four neurals ; fifth finger with two phalanges.

One species, *O. sinensis* (Gray), of Formosa, southern China, and northern Indo-China. This turtle resembles the smaller species of *Kachuga* in having the fissura ethmoidalis abruptly narrowed ventrally, in having only three phalanges in the fifth toe, and in the lack of elongation of the neurals. *Ocadia* differs from *Kachuga*, principally in the less extensive posterior temporal emargination, shortened angular, loss of a phalanx from the fifth finger, position of the humero-pectoral sulcus, and somewhat reduced buttresses. Another feature that sets *Ocadia* apart from all the Batagurinae described above is the lengthened tail, quite elongate in the young and moderately long in the adult.

Genus *Malayemys* Lindholm

Malayemys Lindholm, Zool. Anz. **97**, 1932 : 30. Type : *Emys subtrijuga* Schlegel & Müller. (A substitute name for *Damonia* as used by M. Smith, Fauna Brit. India., Rept. Amph. **1**, 1931 : 103.)

Diagnosis : upper triturating surface very broad, with middle ridge reduced to a slight flexure in plane of the nearly flat surface ; nasopalatine foramen small ; maxilla in contact with inferior process of parietal ; inferior temporal emargination very shallow, the maxilla in extensive contact with squamosal ; posterior temporal emargination very deep, nearly meeting the frontal bone and broadly separating the postorbital from the supratemporal ; the ridge of the pterygoid forming the lateral margin of the fossa for the medial pterygoid muscle much enlarged, reaching to the articular facet of the quadrate, so that the fossa for the medial pterygoid muscle faces ventromedially ; angular shortened, much exceeded by prearticular in anterior extent ; coronoid process of coronoid very high, rising far above other bones of mandible, recurved terminally ; plastral buttresses moderately strong, the axillary attached to the lateroventral surface of the first pleural, the inguinal extending about a third of the way up the suture between the fifth and sixth pleurals ; entoplastron anterior to humero-pectoral sulcus ; neural bones not elongated, the fourth central scute overlying parts of four neurals ; fifth finger with two phalanges.

This genus contains *M. subtrijuga* of southern Siam and Indo-China, northern Malaya and Java. Although *Malayemys* is generally said to lack a middle ridge on the upper triturating surface, there is a distinct, though blunt, convexity running along the surface, better defined in the rhamphotheca than in the bone. This convexity seems to be a vestigial middle ridge and is nearer to the tomium than to the lingual border. The middle neural bones are short-sided behind, as in *Hieremys*, but there is little resemblance between *Hieremys* and *Malayemys* in other respects, apart from features shared with other members of the *Batagur* Complex. As noted by Parsons (1960), *Malayemys* is quite peculiar in lacking any trace of a papilla or fold lateral to the choana.

Genus *Chinemys* M. Smith

Chinemys M. Smith, Fauna Brit. India, Rept. Amph. **1**, 1931 : 116. Type : *Damonia reevesii* (Gray).

Diagnosis : upper triturating surface broad to very broad, without trace of a middle ridge ; nasopalatine foramen small ; maxilla separated from

inferior process of parietal by palatine ; inferior temporal emargination shallow, the maxilla in contact with the squamosal (but this contact concealed laterally by the jugal) ; posterior temporal emargination deep ; frontal broadly excluded from posterior temporal emargination by parieto-postorbital contact ; squamosal nearly or quite excluding postorbital from supratemporal ; ridge on pterygoid forming lateral border of fossa for medial pterygoid muscle much enlarged, reaching to the articular surface of the quadrate, so that the fossa faces ventromedially ; angular shortened, much exceeded by prearticular in anterior extent ; coronoid process of coronoid bone very high, riding far above other bones of mandible, but blunt and not recurved terminally ; plastral buttresses moderately strong, the axillary attached to the middle of the first pleural, the inguinal running about a third of the way up the suture between fifth and sixth pleurals ; entoplastron intersected by humero-pectoral sulcus ; neural bones not elongated, parts of four underlying the fourth central scute ; fifth finger with two phalanges.

This genus contains two species : *C. reevesi* (Gray) of southern and central China and Japan ; and *C. kwangtungensis* (Pope) of Kwangtung and northern Indo-China. I have not seen the latter species, but the illustration of its skull given by Fang (1934) under the name *Chinemys nigricans* considerably resembles the skull figured by Bourret (1941) as *Geoclemys palaeannamitica* from a cave deposit in Annam.

The high coronoid process, inwardly inflected fossa for the medial pterygoid muscle, and small nasopalatine foramen are all resemblances to *Malayemys*, and this is perhaps the phyletic affinity of *Chinemys*. On the other hand, *Chinemys* agrees with *Ocadia* and differs from *Malayemys* in having a long tail (particularly in the young), an entoplastron transected by the humero-pectoral sulcus, and (as a variation) contact between the postorbital and supratemporal. It is possible that *Chinemys* is most closely related to *Ocadia* and has merely paralleled *Malayemys* in the development of flattened triturating surfaces.

Although *Callagur* is questionably distinct from *Kachuga* and the very close relationship between *Kachuga* and *Batagur* is obvious and generally accepted, the cross-resemblances between *Hieremys*, *Malayemys*, *Chinemys*, and *Ocadia* make it impossible to subdivide this grouping with any assurance.

Orlitia Complex

Diagnosis : triturating surfaces moderate or broad posteriorly, but narrowed along the midline, without cusps, with middle ridge on upper surface distinct or vestigial ; vomer reduced, its posterior end excluded from floor of cranial cavity by pterygoids, its anterior end not participating in the triturating surface ; foramina praepalatina fully exposed ventrally ; dentary symphysis extending well behind lower triturating surface along midline ; coronoid bone with strong coronoid process that rises above the neighbouring bones ; anterior opening of Vidian canal in palatine, the anterior part of the inferior process of the parietal attached to the palate both medially and laterally to the Vidian canal ; squamosal firmly attached to neighbouring bones and extending well forward ; posterior palatine foramen at least slightly

enlarged ; postlagenar hiatus a large round hole, nearly as large as perilymphatic foramen ; fifth finger with three phalanges.

Genus *Orlitia* Gray

Orlitia Gray, Ann. Mag. nat. Hist. (4) **11**, 1873 : 156. Type : *Orlitia borneensis* Gray.

Diagnosis : nasopalatine foramen a large fenestra exceeding the posterior palatine foramen in size ; upper triturating surface broad posteriorly, with sharply defined middle ridge ; neural bones elongated ; entoplastron anterior to humero-pectoral sulcus ; plastral buttresses very strong, the axillary attached to the first rib, the inguinal inserted over half-way up the suture between fifth and sixth pleurals.

This genus contains *O. borneensis* Gray of the Malay Peninsula, Borneo, and Sumatra. In many ways *Orlitia* resembles *Kachuga*, but the ways in which it differs from *Kachuga* appear to be approaches to the *Geoemyda* Complex. Thus, there is a strip of granular skin from eye to tympanum, whereas in *Kachuga* this area has small shields ; in *Orlitia* the posterior palatine foramen is distinctly enlarged, although still smaller than the nasopalatine foramen ; the narrowing of the triturating surfaces along the midline, thus exposing the foramina praepalatina to ventral view and the dentary symphysis to dorsal view, is a marked resemblance to the *Geoemyda* Complex and a departure from the *Hardella* and *Batagur* Complexes ; and the enlargement of the postlagenar hiatus into a large round fenestra is a strong resemblance to the more primitive members of the *Geoemyda* Complex and quite unlike other Testudinidae.

Orlitia shares with *Callagur* the distinction of being the largest aquatic testudinid, as indicated by carapace length, and because the head of *Orlitia* is relatively larger than that of *Callagur*, *Orlitia* is probably the largest of the Batagurinae. Yet in many ways *Orlitia* is more like the smaller members of *Kachuga* than like the large *K. trivittata* ; thus, the fifth toe has only three phalanges, the vertebral keel is very distinct, and the tail is evenly granular ventrally and without three rows of small scutes, and the crista praetemporalis (setting-off the fossa for the adductor mandibulae posterior from that for the adductor mandibulae externus) is broad and heavy. On the other hand, the fissura ethmoidalis is gradually narrowed ventrally as in *K. trivittata*, *Callagur*, and *Batagur*.

Genus *Siebenrockiella* Lindholm

Siebenrockiella Lindholm, Zool. Anz. **81**, 1929 : 280. Type : *Emys crassicollis* Gray. (Substitute name for *Bellia* Gray, preoccupied.)

Diagnosis : nasopalatine foramen small, exceeded in size by the large and fenestra-like posterior palatine foramen ; triturating surfaces moderately narrow, without distinct middle ridge, although a convexity on the posterior part of the upper triturating surface may be a vestige of the ridge ; neural bones short and nearly square in the middle of the series ; humero-pectoral sulcus transecting entoplastron ; plastral buttresses moderate, the axillary attached to the middle of the first pleural, the inguinal attached about one-third of the way up the suture between fifth ans sixth pleurals.

One species, *S. crassicollis* (Gray), of the Indo-Chinese and Malay Peninsula, Sumatra, Borneo, and Java.

Geoemyda Complex

Diagnosis : triturating surfaces narrow, without bony ridging (vestigial longitudinal ridging of the rhamphotheca in *Melanochelys*) ; dentary symphysis

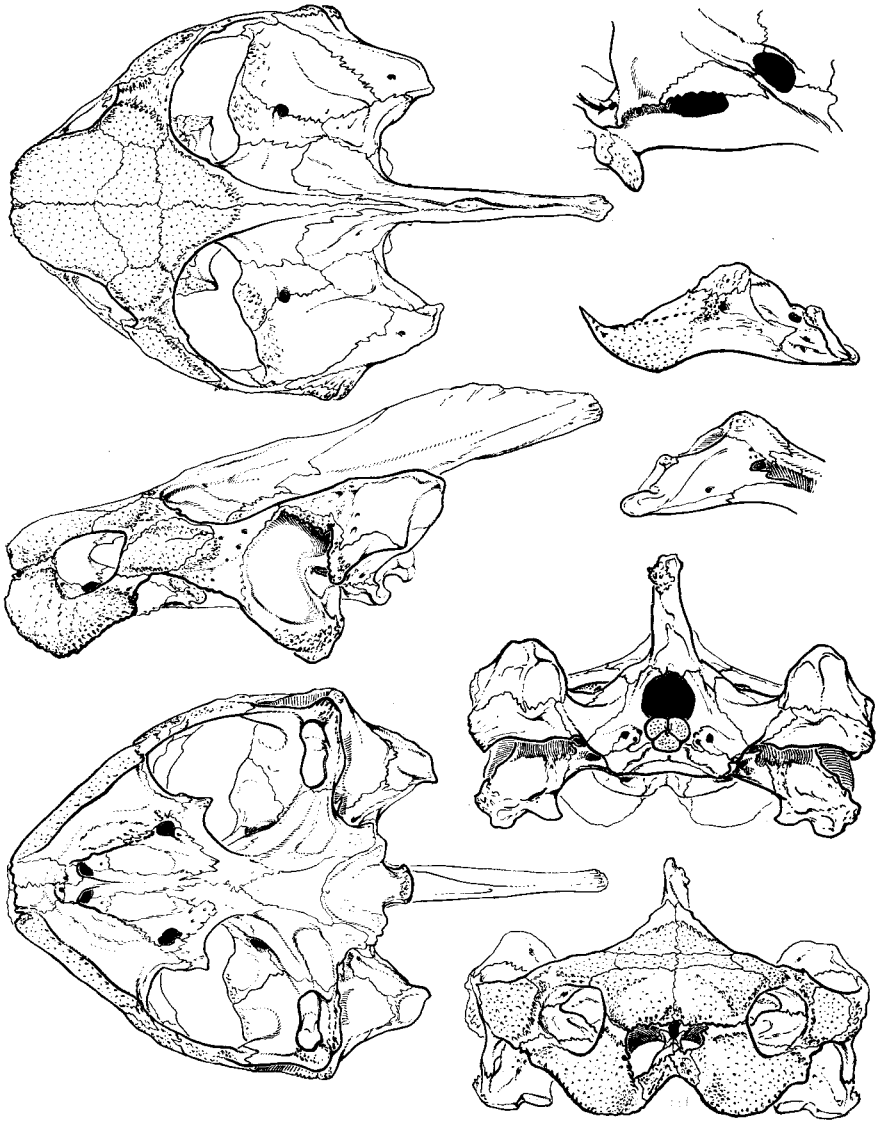

Fig. 10—*Orlitia borneensis*, adult skull with pathological erosion of premaxilla : dorsal, lateral, ventral, occipital, and frontal views of skull ; left epipterygoid region (the large fenestra in the lateral wall of the Vidian canal beneath the epipterygoid is not present in a younger skull ; the arrow points to the anterior opening of the Vidian canal) ; lateral view of mandible and medial view of mandibular ramus.

extending posterior to triturating surface along midline ; vomer small, not supporting rhamphotheca or extending back to contribute to floor of cranial cavity ; foramina praepalatina well exposed to central view ; nasopalatine foramen small ; anterior orifice of Vidian canal opposite extreme anterior edge

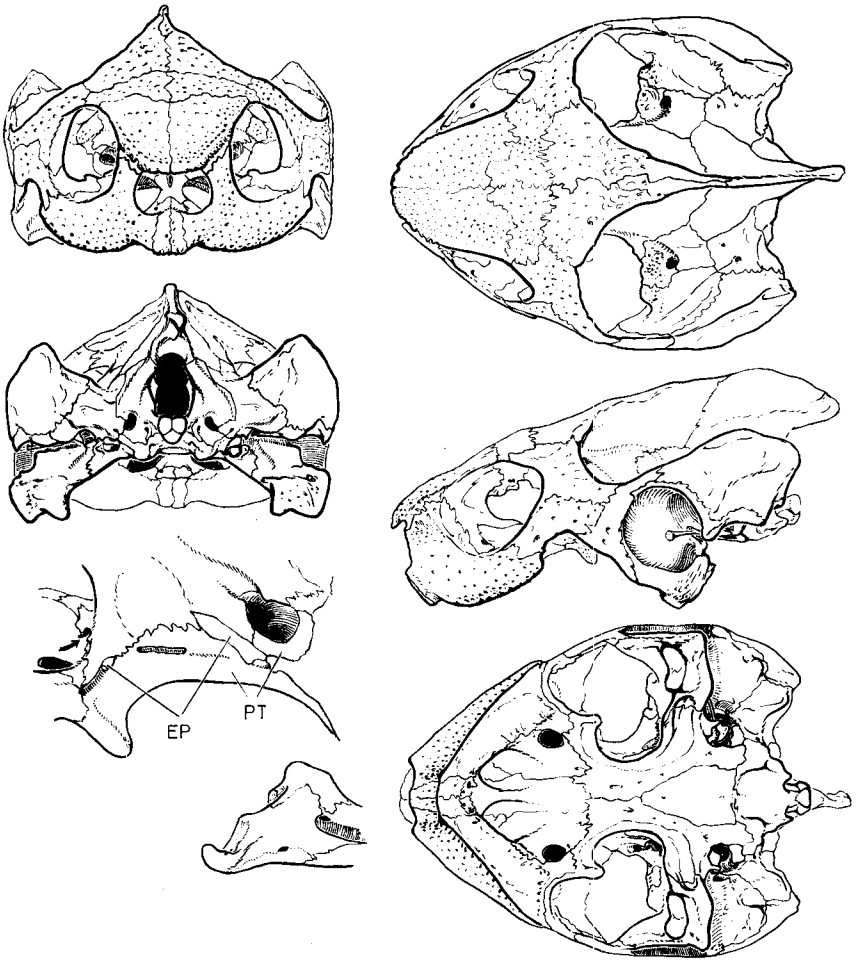

Fig. 11—*Siebenrockiella crassicollis*, adult skull : frontal, occipital, dorsal, lateral, and ventral views of skull ; left epipterygoid region (the arrow points to the anterior end of the Vidian canal) ; and medial view of mandibular ramus. (For key to lettering see p. 279).

of inferior process of parietal ; parietal meeting quadrate posterolateral to the trigeminal foramen ; squamosal (=quadratojugal Auct.) with much reduced jugal contact or quite separated from the jugal, or absent, slightly kinetic when present ; fifth digit of manus with two phalanges ; fifth digit of pes with three phalanges.

Genus *Notochelys* Gray

Notochelys Gray, Proc. zool. Soc. Lond. 1863 : 177. Type : *Notochelys platynota* (Gray).

Squamosal absent or present* and separated from jugal by postorbital ; foramen arteriopalatinum placed on the floor of the canalis cavernosus well lateral to border of basisphenoid and anterior to foramen caroticum primitivum; fissura ethmoidalis broad and drop-shaped ; postlagenar hiatus large and rounded ; anterior edge of inferior process of parietal strongly flared outward to meet the expanded ventral end of the jugal ; crista praetemporalis forming a strong shelf overhanging trigeminal foramen ; plastral buttresses absent in adult, the plastron bound to the carapace by ligament ; adult with hinge between hyoplastron and hypoplastron ; second ceratobranchial ossified ; *one or two additional central scutes intercalated between homologues of fourth and fifth centrals ;* extensor surface of forearm with numerous narrow and crescentic transverse scutes separated by conspicuous granular skin ; cloacal bursae present.

One species, *N. platynota* of Malaya, Sumatra, and Borneo.

The genus is characterized by the fixation of a not uncommon variation of other turtles, additional central scutes. Unlike chance variations of other turtles, the additional central scute or scutes of *Notochelys* have a symmetrical connection with the adjacent lateral scutes and a definite position in the central row. It is not so easy to guess which genus of turtles may have given rise to *Notochelys*, for although the plastral hinge and the position of the foramen arteriopalatinum (for the palatine artery and an anastomotic artery that joins the artery of the Vidian canal) suggest *Cyclemys*, the scutellation of the arm is as in *Siebenrockiella* and unlike that of the other genera of the *Geoemyda* Complex.

Genus *Cyclemys* Bell

Cyclemys Bell, Proc. zool. Soc. Lond. 1834 : 17. Type : *Cyclemys orbiculata* Bell=*Cyclemys dentata* (Gray).

Squamosal present, usually not touching jugal ; horizontal temporal arch complete and continuous ; foramen arteriopalatinum as in *Notochelys* ; fissura ethmoidalis narrowly triangular or keyhole-shaped ; postlagenar hiatus moderately large and rounded ; anterior edge of inferior process of parietal not flexed outward, not in contact with jugal or palatine ; ventral end of jugal broad ; crista praetemporalis moderately strong ; plastral buttresses resorbed in adult, the plastron attached to the carapace by ligament ; adult with hinge between hyoplastron and hypoplastron ; hexagonal neurals short-sided behind ; second ceratobranchial ossified ; scutes of carapace

* Malcom Smith says the " quadratojugal " may be present or absent, and the statement is repeated here, although the two young Sumatran individuals I have examined both had the bone. I am very sceptical of the statements in the literature about variable occurrence of the squamosal in this group of turtles because the bone is so loosely attached that it is easily lost in preparation and leaves little or no mark on the quadrate to hint at its very former presence. Proof of individual variability in presence of this bone based on alizarin clearings or dissection of whole heads needs to be presented.

normal ; extensor surface of forearm with transversely oval scutes separated by narrow bands of granular skin ; cloacal bursae present.

One species, properly called *Cyclemys dentata* (Gray), but with an extensive and valuable literature under the name *C. dhor* (Gray) ; Burmese-Malayan region, Sumatra, Java, Borneo, and Philippines.

The juvenile turtle described by Bourret as *Geoemyda tcheponensis* appears to be a variation of this turtle with the entoplastron abnormally far forward, perhaps because it has not yet grown back between the hyoplastra. The figures of *Geoemyda tcheponensis* given by Bourret (1941) compare almost perfectly with AMNH 58423 (Upper Chindwin River, Burma), a specimen that is plainly a juvenile *Cyclemys*. Juvenile *Cyclemys* possess plastral buttresses and lack a plastral hinge, making it very easy to misassign them generically.

Genus *Rhinoclemys* Gray

Rhinoclemys Gray, Ann. Mag. nat. Hist. (3) **12,** 1863 : 182. Type : *Rhinoclemys annulata* Gray.

Squamosal (=quadratojugal Auct.) probably always present, but loosely attached and easily lost from prepared skulls, barely if at all in contact with jugal, but meeting postorbital ; foramen arteriopalatinum as in *Notochelys* and *Cyclemys* ; fissura ethmoidalis broadly triangular or oval ; postlagenar hiatus small to moderate in size, rounded in form ; anterior edge of inferior process of parietal not flexed outward, well separated from jugal but in contact with palatine ; ventral end of jugal broad ; crista praetemporalis moderately to very strong ; plastron without hinge, attached to carapace by well-ossified buttresses ; hexagonal neurals short-sided behind ; carapace with or without neural keel, without pleural keels ; second ceratobranchial cartilaginous ; scutes of shell normal ; forearm scutellation as in *Cyclemys* ; cloacal bursae present ; tail very short.

The precise number of biological species is still to be determined, but the following are conventionally recognized : *R. annulata* (Southern Central America and northwestern South America) ; *R. areolata* (southeastern Mexico and northern Central America) ; *R. funerea* (Costa Rica) ; *R. pulcherrima* (Mexico and Central America) ; *R. punctularia* (northern South America) ; *R. rubida* (southwestern Mexico).

This genus is entirely Tropical American and contains all the Batagurinae known from the New-World. In all recent literature these species are referred to the genus *Geoemyda*, but the type of that genus (*spengleri*) is a very different turtle, lacking cloacal bursae, with a long tail, with a characteristic narrowing of the ventral part of the cranial cavity, and a very weak crista praetemporalis. The Indian *Melanochelys* is closely related to *Rhinoclemys*, but is more specialised. The genus *Rhinoclemys* has been in the New-World since at least the Eocene, for Hay (1908 : 337–339) described as *Echmatemys pusilla* a shell that certainly belongs to this genus from the Bridger B of Grizzly Buttes, Wyoming.

The genera *Cyclemys*, *Rhinoclemys*, and *Melanochelys* seem to be closely related ; not only do they agree in having the foramen arteriopalatinum well lateral to the basisphenoid and the hexagonal neurals quite constantly

short-sided behind, but *Cyclemys dentata*, *Rhinoclemys funerea*, and *R. punctularia* are the only members of the *Geoemyda* Complex with a choanal papilla (see Parsons, 1906).

Genus *Melanochelys* Gray

Melanochelys Gray, Proc. zool. Soc. Lond. 1869 : 187. Type : *Emys trijuga* Schweigger.

As in *Rhinoclemys*, but fissura ethmoidalis may be narrowed to approach a keyhole-like form ; ventral end of jugal narrow, well separated from pterygoid by maxilla ; and carapace tricarinate, with a pair of pleural keels.

Two species : *M. trijuga* (India, Ceylon, and Burma) ; *M. tricarinata* (Central India to Assam). I have not seen the latter.

Genus *Sacalia* Gray

Sacalia Gray, Suppl. Cat. Shield Rept. **1**, 1870 : 35. Type : *Emys bealii* Gray.

Squamosal present, in contact with postorbital but not jugal ; foramen arteriopalatinum bordered by basisphenoid, anterior to foramen caroticum primitivum ; fissura ethmoidalis broadly triangular ; postlagenar hiatus large and rounded ; anterior edge of inferior process of parietal flared outward, in contact with palatine and the broad ventral end of the jugal ; crista praetemporalis moderately heavy, partially overhanging trigeminal foramen ; plastral buttresses retained throughout life, but weak, barely extending beyond marginal bones ; no plastral hinge ; hexagonal neurals short-sided in front ; carapace with neural keel but no pleural keels ; second ceratobranchial ossified ; scutes of shell normal ; forearm covered by a few very large scutes without intervening areas ; cloacal bursae present ; noticeably elongate tail in young, the tail moderate in adult.

One species, *S. bealei* of Annam and southern China.

Genus *Mauremys* Gray

Mauremus Gray, Proc. zool. Soc. Lond. 1869 : 500. Type : *fuliginosa* Gray = *Mauremys caspica leprosa* (Schweigger).

Pseudocadia Lindholm, Zool. Anz. **97**, 1932 : 31. Type : *Testudo anyangensis* Ping = *Mauremys mutica* (Cantor).

Cathaiemys Lindholm, *ibid.* : 29. Type : *Emys muticus* Cantor.

Annamemys Bourret, Bull. Instr. publ. Hanoi **4**, 1939 : 15. Type : *Annamemys merkleni* Bourret = *Mauremys mutica* (Cantor).

Emmenia Gray, Suppl. Cat. Shield Rept. **1**, 1870 : 38. Type : *Emys grayi* Gunther = *Mauremys caspica* (Schweigger).

Eryma Gray, *ibid.* : 44. Type : *Emys laticeps* Gray = *Mauremys caspica leprosa* (Schweigger).

Squamosal present, in contact with postorbital, may or may not be in contact with jugal ; foramen arteriopalatinum as in *Sacalia* ; fissura ethmoidalis narrowly keyhole-shaped ; postlagenar hiatus rounded, moderate to large ; anterior edge of inferior process of parietal not flared out, separated from the expanded ventral end of the jugal by the pterygoid, in contact with the palatine (*caspica*, *mutica*) or narrowly separated from the palatine (*japonica*) ; crista praetemporalis moderately heavy, partially overhanging trigeminal foramen ; plastral buttresses retained throughout life, moderate to strong, firmly joined to pleurals ; no plastral hinge ; hexagonal neurals

short-sided anteriorly or posteriorly ; carapace with neural keel and at least faint pleural keels ; second ceratobranchial ossified ; forearm with transversely oval scutes separated by granules ; cloacal bursae present ; tail long in young, moderate in adult.

Three species : *M. caspica* (Caspian region west to the Balkans ; Iberian Peninsula and northwestern Africa) ; *M. mutica* (southern Japan, Formosa, central and southern parts of eastern China, and Annam) ; and *M. japonica* (southern Japan).

Genus *Cuora* Gray

Cuora Gray, Cat. Shield Rept. **1**, 1855 : 41. Type : *Testudo amboinensis* Daudin.

Squamosal present, in contact with postorbital, not in contact with jugal ; fissura ethmoidalis and foramen arteriopalatinum as in *Mauremys* ; postlagenar hiatus moderate, rounded ; anterior edge of inferior process of parietal not flared out, separated from the expanded ventral end of the jugal by the pterygoid, in contact with palatine ; *pterygoid failing to grow up over the medial face of the quadrate to exclude that bone from the wall of the canalis cavernosus ;* crista praetemporalis as in *Mauremys* ; plastral buttresses resorbed, the plastron joined to the carapace by ligament in the adult ; plastron with hinge between hyoplastron and hypoplastron ; hexagonal neurals short-sided behind ; carapace with weak neural and pleural keels ; posterior margin of carapace smooth ; second ceratobranchial ossified ; forearm as in *Mauremys* ; cloacal bursae present ; tail moderate.

Three species : *C. yunnanensis* (Northeastern Yunnan) ; *C. trifasciata* (southern China to Sungai Kroh, Perak, Malaya [AMNH 49933]) ; and *C. amboinensis* (Indo-China to Celebes). I have not seen *C. yunnanensis*.

Cuora is generally regarded as closely related to *Cyclemys*, but the skull of *Cuora* is much more similar to that of *Mauremys*, particularly *M. mutica*, and the external appearance of juvenile *M. mutica* is much like that of juvenile *Cuora trifasciata*. The figure of the head of *Cuora yunnanensis* given by M. Smith is even more suggestive of juvenile *M. mutica*. Since hexagonal neurals with the short side posterior are now known to occur within *Mauremys mutica*, this turtle can no longer be dismissed from comparison with *Cuora*. *Cuora* appears to differ from *Mauremys mutica* in two features : first, the development of a plastral hinge, a feature developed independently in many groups of turtles ; and second, the entry of the quadrate into the lateral wall of the canalis cavernosus, a feature in which *Cuora* is unique among Testudinoidea.

Genus *Geoemyda* Gray

Geoemyda Gray, Proc. zool. Soc. Lond. 1834 : 100. Type : *Testudo spengleri* Gmelin.
Nicoria Gray, Cat. Shield Rept. **1**, 1855 : 17. Type : *spengleri*.
Pyxidea Gray, Proc. zool. Soc. Lond. 1863 : 175. Type : *Cyclemys Mouhotii* Grya.
Cistoclemmys Gray, *ibid.* Type : *Cistoclemmys flavomarginata* Gray.
Cuora Auct., part.

Squamosal present or absent ; fissura ethmoidalis as in *Mauremys* and *Cuora* or broadly triangular (*G. mouhoti*) ; *inferior processes of parietals strongly*

convergent ventrally, encroaching on groove for trabecular cartilage, so that cranial cavity is markedly narrowed ventrally ; anterior edge of inferior process of parietal thin, separated from the narrow ventral end of the jugal by the pterygoid and maxilla ; crista praetemporalis weak, not overhanging the trigeminal foramen ; plastral buttresses weak and barely extending beyond marginal bones (*spengleri*) or unattached to carapace and ending freely ; a weak hyoplastral hinge or not (*spengleri*) ; hexagonal neurals short-sided behind ; carapace with neural and pleural keels ; posterior margin of carapace weakly to strongly serrated ; second ceratobranchial ossified (*flavomarginata*) or cartilaginous ; forearm with a shingle-like panoply of large overlapping scutes, as in some Testudininae ; strip of granular skin to the eye much narrowed to a single tier of granules over the jugal ; *cloacal bursae reduced to small nipples* (*flavomarginata*, one examined) *or absent* (*splengeri*, two examined ; *mouhoti*, one examined) ; tail long in young, long to moderately short in adult ; sole of pes with enlarged scutes.

Three species here referred definitely to the genus : *G. flavomarginata* [*Cuora flavomarginata* of other authors], native to Formosa and the Ryukyus ; *G. mouhoti* [*Cyclemys* or *Pyxidea mouhoti* of other authors] of Assam, Indo-China, and Hainan ; and *G. spengleri* of the Ryukyus, Borneo, Sumatra, Natuna, Malaya, Indo-China and southern China. Bourret's (1941) figures and description of *Cuora galbinifrons* Bourret of Annam strongly suggest that this species is close to *flavomarginata* and belongs in *Geoemyda*, but since I have not examined this species, it is not considered in this discussion.

The three species here included differ much from one another in anatomical features, and perhaps each should be referred to its own genus. Thus, whereas *flavomarginata* has the foramen arteriopalatinum placed as in *Cuora*, *Mauremys*, and *Sacalia*, *mouhoti* has the foramen more posterior (level with the foramen caroticum primitivum) and *spengleri* lacks the foramen ; *mouhoti* also differs from the others in its broad fissura ethmoidalis and in the forward extension of the epipterygoid to the level of the anterior border of the cranial cavity. *Geoemyda spengleri* differs from the others in retaining plastral buttresses connected to the carapace and lacking a plastral hinge in the adult stage and in the failure of the inferior process of the parietal to meet the palatine ; *G. spengleri* may be primitive in lacking a plastral hinge, but in its skull features it is more specialised than the well-hinged *G. flavomarginata* and it may be suggested that *spengleri* is paedomorphic and that the absence of hinging is merely the retention into adult life of a juvenile character ; this theory would account for the very feeble condition of the buttresses, which may have lost their definitive pleural attachments in phylogeny. *Geoemyda flavomarginata* retains ossification in the second ceratobranchial, whereas *spengleri* and *mouhoti* resemble *Rhinoclemys*, *Melanochelys*, and the Testudininae in having the second ceratobranchial cartilaginous throughout life. In *flavomarginata* vestiges of the cloacal bursae are retained that are lost in the other species of *Geoemyda* ; but *flavomarginata* is more specialised than the other species in the loss of the squamosal, so that the horizontal temporal arch is incomplete.

The genus *Geoemyda* is here defined as held together by the common possession of a number of features. The reduction or absence of the cloacal

bursae is the most striking, and recently Smith & James (1958) resurrected the name *Pyxidea* for "*Clemmys*" *mouhoti* largely because of the absence of bursae. In separating *mouhoti* from the genus *Cyclemys* they were fully justified, but they were unaware that *Geoemyda spengleri*, a turtle with a remarkable external resemblance to *mouhoti*, also lacks the bursae and that the bursae are vestigial in "*Cuora*" *flavomarginata*, a turtle with some external similarity to *spengleri*. Also striking is the ventral narrowing of the cranial cavity in *Geoemyda* ; this is accompanied by a conspicuous elevation of the dorsal profile of the skull over the large orbits ; these two cranial features are probably only one, for the lower portion of the cranial cavity of turtles houses the rectus muscles of the eyes, and elevation of the eyes is probably responsible for moving the eye-muscles from the ventral part of the cranial cavity.* The shingle-like scutes of the forearm, the enlarged scutes on the sole of the pes, and the extreme narrowing of the granule-strip to the eye are external features that set the genus *Geoemyda* as here defined apart from the rest of the *Geoemyda* Complex, but are approached by the next genus, *Heosemys*.

The unexpanded ventral end of the jugal in *Geoemyda* is suggestive of *Melanochelys*, and it is possible that *Geoemyda* is derived from *Melanochelys* ; but I think it more likely that *Geoemyda* is derived from *Cuora* ; the placing of *flavomarginata* in *Geoemyda* rather than *Cuora* is more a reflection of a personal perference for vertical over horizontal classifications than a disagreement with previous workers on the affinities of this turtle. In *flavomarginata* the quadrate is excluded from the canalis cavernosus by the pterygoid, making it unlikely that this species is derived from the existing species of *Cuora* as here defined, but *Cuora*, *Geoemyda* and *Mauremys mutica* share the common feature of tuberculate scales around the cloaca (in *G. spengleri* and *G. mouhoti* these tubercles are drawn out into papillae) ; this is not suggested in *Melanochelys*.

The reduction of cloacal bursae, narrowing of the ventral end of the jugal, reduction of the anterior part of the cavum epiptericum, shingle-like scutellation of the arm, and the permanently cartilaginous second ceratobranchial of *spengleri* and *mouhoti* are features in which *Geoemyda* resembles most or all Testudininae. The existence of some testudinines (e.g. *Geochelone*, *Gopherus*) with broad and ridged triturating surfaces makes it unlikely that the testudinines are derived from *Geoemyda*, and the resemblance seems the result of convergence. *Geoemyda* appears to be a batagurine genus that has taken over in East Asia a niche taken by testudinines in Africa, and is an Asiatic genus of small terrestrial tortoises ; in North America, the emydine genus *Terrapene* has taken a similar rôle.

* Cranial cavity is here used in a loose sense to refer to the space in the dried skull housing the brain and some other structures. If cranial cavity is used in the strict sense to mean the chamber for the brain defined by the dura mater, then it cannot be said that the rectus muscles of turtles occupy the cranial cavity ; instead, the rectus muscles, as well as the profundus, trochlear, oculomotor, and abducent nerves, occupy a chamber, the cavum epiptericum, bounded medially by the dura and laterally by the inferior process of the parietal. Using this terminology, it may be said that the anterior part of the cavum epiptericum, spacious in the majority of turtles, is nearly obliterated and collapsed in *Geoemyda*.

Genus *Heosemys* Stejneger

Heosemys Stejneger, Proc. biol. Soc. Wash. **15,** 1902 : 238. Type : *Emys spinosa* Gray.

Entire horizontal temporal arch, including the squamosal bone, absent ; fissura ethmoidalis broadly oval ; postlagenar hiatus small but round ; anterior edge of inferior process of parietal not flared out, separated from the expanded lower end of the jugal by the pterygoid ; crista praetemporalis as in *Geoemyda* ; palatine in contact with inferior process of parietal ; plastral buttresses persistent, firmly joined to pleurals ; no plastral hinge ; hexagonal neurals short-sided behind ; carapace with at least traces of neural and pleural keels ; posterior margin of carapace serrated ; second ceratobranchial ossified ; cloacal bursae present ; tail short at all ages ; foramen arterio-palatinum as in *Geoemyda mouhoti*, placed at the level of the foramen caroticum primitivum and bordered medially by the basisphenoid.

Five species : *H. depressa* (Arakan) ; *H. grandis* (Burma, Indo-China, Siam, and Malaya) ; *H. leytensis* (Leyte Island) ; *H. silvatica* (Cochin forests at tip of Indian Peninsula) ; and *H. spinosa* (Malay Peninsula to Sumatra, Natuna, and Borneo). This genus corresponds precisely to the genus *Geoemyda* of Boulenger (1889), with the addition of *sylvatica* and *leytensis*, described after Boulenger's publication.

This is an isolated genus, without clear affinity to any other particular genus of the *Geoemyda* Complex, although clearly a member of the complex. The pleural keels of the carapace are vestigial, sometimes not distinguishable in the adult, and the lower end of the jugal is dilated and reaches the pterygoid ; but otherwise it is to *Geoemyda* that *Heosemys* shows nearest resemblance in osteology. Thus, the total loss of the horizontal temporal arch in *Heosemys* is approached by *Geoemyda flavomarginata*, which lacks the squamosal, and the strong serration of the carapacial border is a similarity between *Geoemyda* and *Heosemys*, as is the weakness of the shelf (crista praetemporalis) formed by the quadrate and proötic and defining the fossa for the adductor posterior muscle dorsally.

Subfamily Emydinae

Diagnosis : Testudinidae with axillary or inguinal scent glands, or both ; except in some *Terrapene*, at least two digits of each appendage with three phalanges ; prearticular without lateral flange, the angular broadly in contact with Meckel's cartilage ; basioccipital relatively narrow, not extending lateral to lagena, without tuberosity forming floor of recessus scalae tympani, not in contact with paracapsular sac ; pterygoid not in contact with basioccipital (but may reach exoccipital ; in which case, the basioccipital and pterygoid separated by an open fissure) ; a double articulation between fifth and sixth cervical centra ; supracaudal scutes not extending on to suprapygal.

The following features distinguish the Emydinae from the Platysterninae : pterygoids with an extensive area between pterygoid muscles that is in contact with the pharyngeal mucosa ; posterior temporal emargination extending anterior to tympanic cavity ; anterior end of pterygoid cartilage (and the groove in the pterygoid for its reception) curved outward but not backward ; stapedial notch of quadrate open posteriorly or, if closed, with persistent

suture-like fissure ; sella turcica broad ; premaxillary pit shallow, not containing an inter-premaxillary foramen ; anterior caudals procoelous, but condyles poorly defined, nearly flat.

In addition to the above diagnosis, it may be noted that the Emydinae are structurally much less varied than the Batagurinae and are constant for the following features : plastral buttresses, even when strongly developed, not in contact with first rib or sixth pleural ; hexagonal neurals not short-sided behind ; fissura ethmoidalis abruptly narrowed below passage of olfactory and profundus nerves ; exoccipital at least partially walling in paracapsular sac posteriorly ; angular equalling or exceeding prearticular in anterior extent ; fifth finger with two phalanges.

Chrysemys Complex

Diagnosis : triturating surfaces broad to very broad, the upper receiving contributions from palatine and pterygoid ; lower triturating surface defined lingually by a sharp angulation setting-off the horizontal triturating surface from the vertical medial surface of the dentary ; nasopalatine foramen enlarged into a fenestra, larger than posterior palatine foramen ; interorbital region broader than nasal chamber ; inferior process of parietal touching palatine except in some *Chrysemys picta* ; cervical vertebrae not elongated, vertebrae II to VIII subequal in length ; entoplastron anterior to humero-pectoral sulcus ; thoracic rib-heads normal.

Genus *Chrysemys* Gray

Chrysemys Gray, Cat. Tort. Crocod. Brit. Mus. 1844 : 27. Type : *Testudo picta* Schneider.

Triturating surface of maxilla with sharply defined middle ridge ; anterior edge of inferior process of parietal thin ; posterior end of pterygoid usually not in contact with exoccipital.

The biological species of this genus have still to be determined. The genus falls into three groups, which are here termed the subgenera *Pseudemys*, *Trachemys*, and *Chrysemys*. Current practice maintains *Chrysemys* as distinct, but groups *Pseudemys* and *Trachemys* together under the name *Pseudemys*. This does not appear defensible to me, for in many ways *Pseudemys* (*sensu stricto*) is more distinct than is *Chrysemys*, and it must be three genera or one ; I prefer the latter course, using subgenera to indicate groupings.

The subgenus *Pseudemys* Gray, 1856, contains species that resemble *Hardella* in having the mandible flattened ventrally, a well-defined cusp at the anterior end of the middle ridge of the upper triturating surface, and four phalanges in the fifth toe. The skull is specialised in being unusually short and deep, with strong sutural union between maxilla and squamosal. Within this genus there are two series of forms : a *rubriventris* series, with the vomer contributing to the triturating surface and with the middle ridge of the lower triturating surface set well lateral to the lingual margin of the surface ; and a *floridana* series, without a triturating shelf on the vomer, so that the foramina praepalatina are exposed ventrally, and with the middle crest of the lower triturating surface indistinctly set-off from the margin of the surface. At present, members of the *rubriventris* group are assigned to three species :

C. (*P.*) *rubriventris* (Le Conte), sporadically distributed along the Atlantic coast of the United States ; *C.* (*P.*) *nelsoni* (Carr), Florida Peninsula ; and *C.* (*P.*) *alabamensis* (Baur), Gulf Coast of the United States. The *floridana* series is assigned to two species : *C.* (*P.*) *floridana* (Le Conte) of the south-eastern and south central United States, and *C.* (*P.*) *concinna* (Le Conte) of the south-eastern and south central United States and extreme north-eastern Mexico.

The subgenus *Trachemys* Agassiz, 1857, contains forms with rounded ventral surface of the dentary, no anterior cusp on the middle ridge of the upper triturating surface, and three phalanges on the fifth toe ; the maxilla is separated from the squamosal. Frequently the pterygoid extends back near the exoccipital and the crista praetemporalis is heavier than in other *Chrysemys* ; these are resemblances to *Malaclemys*, to which genus *Trachemys* may be ancestral. The carapace has a sculpture of longitudinal ridges. Following Williams (1956), the species of *Trachemys* may be listed as : *C.* (*T.*) *scripta* (Schoepff), eastern United States to Colombia and Venezuela ; *C.* (*T.*) *dorbigni* (Duméril & Bibron), extreme southern Brazil and adjacent Argentina ; *C.* (*T.*) *decussata* (Gray), Cuba, Hispaniola, Puerto Rico, and Cayman ; *C.* (*T.*) *terrapen* (Lacépède) (Jamaica) ; and *C.* (*T.*) *decorata* (Barbour & Carr), Hispaniola.

Subgenus *Chrysemys* is much like *Trachemys*, but the posterior palatine foramen is larger and the nasopalatine fenestra smaller, the first central scute is unconstricted anteriorly, the triturating surfaces are narrower, and the shell is unsculptured. The pterygoid does not extend back to the level of the exoccipital. There is a single species, *C.* (*C.*) *picta* (Schneider), of southern Canada, the whole of the northern United States and most of the central United States.

Genus *Malaclemys* Gray

Malaclemys Gray, Cat. Tort. Crocod. Brit. Mus. 1844 : 28. Type : *Emys concentrica* (Gray) = *Malaclemys terrapin* (Schoepff).

Graptemys Agassiz, Contr. Nat. Hist. U.S. **1**, 1857 : 436. Type : *Testudo geographica* Le Sueur.

Diagnosis : triturating surfaces nearly flat, with only a vague mound-like indication of a middle ridge ; anterior border of inferior process of parietal thickened ; pterygoid forming a suture with exoccipital.

This genus contains ten species : *M. pseudogeographica* (Gray), Mississippi, western Ohio, eastern Missouri, and Sabine Systems ; *M. versa* (Stejneger), Colorado System of Texas ; *M. kohni* (Baur), southern and middle Mississippi and adjacent more western area ; *M. oculifera* (Baur), Pearl River System ; *M. flavomaculata* (Cagle), Alabama–Black Warrior–Tombigbee System ; *M. pulchra* (Baur), streams of north coast of Gulf of Mexico, from Pearl to Escambria Systems ; *M. barbouri* (Carr & Marchand), Gulf Coast streams from Escambria to Apalachicola Systems ; *M. geographica* (Le Sueur), Great Lakes–St. Lawrence, Susquehanna, Ohio, and north and middle Mississippi Systems ; and *M. terrapin* (Schoepff), Atlantic and Gulf Coasts of the United States.

I do not recognize *Graptemys* even as a subgenus, because the differences between *M. terrapin* and, for example, "*Graptemys*" *kohni* are certainly no greater than those between "*Graptemys*" *kohni* and "*Graptemys*" *geographica*. Partition of *Malaclemys* (*sensu lato*) into two groups does not adequately express the structural diversity within the group, and I do not have sufficient material to divide the genus into its many natural groupings.

Deirochelys Complex

Diagnosis : triturating surfaces very narrow and unridged, the upper surface not involving palatine or pterygoid ; lower triturating surface not sharply defined medially, the rhamphotheca-bearing part of the dentary sloping into the vertical medial surface of the dentary ; nasopalatine foramen small, the posterior palatine foramen expanded into a large fenestra ; interorbital width less than the width of the nasal chamber ; inferior process of parietal touching palatine ; cervical vertebrae II to VII are conspicuously longer than cervical VIII ; humero-pectoral sulcus passing either just in front of or just behind the posterior end of the entoplastron ; thoracic rib-head extremely long, slender and bowed out ventrally.

Genus *Deirochelys* Agassiz

Deirochelys Agassiz, Contr. Nat. Hist. U.S. **1**, 1857 : 441. Type : *Testudo reticulata* Daudin = *Testudo reticularia* Latreille.

Diagnosis : plastron without hinge ; carapace with vermiculate sculpture as in *Chrysemys* (*Trachemys*) ; plastral buttresses present ; entoplastron usually slightly anterior to humero-pectoral sulcus.

One species, *D. reticularia* (Latreille) of the south-eastern United States. *Deirochelys* may have the pterygoid produced backward to the level of the exoccipital or even beyond ; this, the vermiculate sculpture of the carapace, and the coloration suggest that *Deirochelys* is derived from the subgenus *Trachemys* of *Chrysemys*, but has become very much modified, particularly in the narrowing of the triturating surfaces and elongation of the neck. Elongation of the neck is probably responsible for the modification of the rib-heads, expanding the space for epaxial musculature that inserts on the neck.

Genus *Emydoidea* Gray

Emydoidea Gray, Suppl. Cat. Shield Rept. **1**, 1870 : 19. Type : *Cistuda blandingii* Holbrook.

Diagnosis : plastron with hinge between hyoplastron and hypoplastron ; carapace smooth ; plastral buttresses absent, the plastron connected to the carapace by ligament ; entoplastron usually meeting humero-pectoral sulcus.

One species, *E. blandingi* (Holbrook), sporadically distributed over the north-eastern and north central United States. I am in thorough agreement with Williams (*in* Loveridge & Williams, 1957) that this turtle is probably derived from *Deirochelys* and has no very close affinity with the Old-World genus, *Emys*, apart from relationship to *Emys* also shared by *Deirochelys*. I have been unable to find significant cranial differences between *Deirochelys* and *Emydoidea*.

Emys Complex

Diagnosis : triturating surfaces very narrow, without ridges ; upper triturating surface without contributions from palatine or pterygoid ; inferior triturating surface without distinct lingual border on dentary, sloping gradually into the vertical medial face of the dentary ; nasopalatine foramen small, the posterior palatine foramen expanded into a large fenestra except in *Terrapene* ; interorbital region broader than nasal chamber ; inferior process of parietal well separated from palatine by pterygoid ; cervical vertebrae not elongated, vertebrae II to VIII subequal in length ; humero-pectoral sulcus crossing the broad part of the entoplastron ; thoracic rib-heads normal.

Genus *Emys* Duméril

Emys Duméril, Zool. analyst. 1806 : 76. Type : *Testudo lutaria* Linné = *Testudo orbicularis* Linné.

Diagnosis : lower end of jugal expanded inward along the posterior border of the maxilla to meet the pterygoid ; frontal excluded from orbital border by strong contact between prefrontal and postorbital ; posterior palatine foramen a large fenestra ; foramina caroticopharyngeales small to moderate, remote from pterygoid–basisphenoid suture ; no plastral buttresses in adult, the plastron connected to the carapace by ligament ; a plastral hinge between hyoplastron and hypoplastron ; cloacal bursae large.

One species, *E. orbicularis* (Linné), of central and southern Europe, northwestern Africa, and western Asia east to the Aral Sea. Although *Emys* appears to be closely related to *Clemmys*, as defined here, it cannot be derived from *Clemmys*, for the latter genus is more specialised than *Emys* in the form of the jugal bone and the enlarged caroticopharyngeal foramina. In having a firm union between prefrontal and postorbital *Emys* differs from all New-World Emydinae, where the frontal normally enters the orbital margin and there is, at most, a point-to-point contact between prefrontal and postorbital.

Genus *Clemmys* Ritgen

Clemmys Ritgen, Nova Acta Acad. Leopold-Carol. **14**, 1828 : 272. Type (by a later designation) : *Testudo punctata* Schoepff = *Testudo guttata* Schneider.

Diagnosis : lower end of jugal narrowing to a point, not meeting pterygoid and not excluding maxilla from border of inferior temporal fossa ; frontal entering orbital margin ; posterior palatine foramen expanded into a large fenestra ; caroticopharyngeal foramen large and conspicuous, either on the pterygoid–basisphenoid suture or connected to it by a short suture ; plastron without hinge, joined to carapace by inguinal and axillary buttresses ; well-developed cloacal bursae.

Four species : *C. guttata* (Schneider), Great Lakes, Atlantic Coastal, and New England regions of the United States ; *C. insculpta* (Le Conte), New England, Middle Atlantic, and Great Lakes regions of the United States ; *C. muhlenbergi* (Schoepff), Middle Atlantic and Appalachian regions of the United States ; and *C. marmorata* (Baird & Girard), Pacific Coast of North America from Vancouver to northern Baja California.

Genus *Terrapene* Merrem

Terrapene Merrem, Tent. Syst. Amph. 1820 : 27. Type : *Testudo clausa* Gmelin = *Testudo carolina* Linné.

Diagnosis : jugal tapering to a point ventrally, not in contact with pterygoid, not excluding maxilla from border of inferior temporal fossa ; frontal entering orbital margin ; posterior palatine foramen little, if at all, expanded ; caroticopharyngeal foramen large, on pterygoid–basisphenoid suture, or connected to it by a short suture ; plastron with a hinge between hyoplastron and hypoplastron ; plastron connected to carapace by suture, the buttresses absent ; cloacal bursae very small or absent.

The precise number of species is uncertain in the absence of definitive information on the Mexican forms. The following species are certainly distinct : *T. carolina* (Linné), United States and adjacent Canada east of the Rockies ; *T. ornata* (Agassiz), western prairie region of the United States and adjacent Mexico ; *T. mexicana* (Gray), Mexico ; and *T. coahuila* Schmidt & Owens, Quatro Cienegas in Coahuila. The status of the forms *yucatana* (Boulenger), *nelsoni* Stejneger, and *klauberi* Bogert remains to be determined.

Terrapene is almost certainly an offshoot of *Clemmys*, which it particularly resembles in the large caroticopharyngeal foramina, and in spite of its hinged plastron seems much less closely related to *Emys* than to *Clemmys*.

SKULLS EXAMINED
(NOT INCLUDING SPOT DISSECTIONS OF PRESERVED SPECIMENS)

BATAGURINAE

Hardella thurgii (1), *H. indi* (1) ; *Geoclemys hamiltoni* (1) ; *Morenia ocellata* (5) ; *Callagur borneoensis* (2) ; *Batagur baska* (1) ; *Kachuga trivittata* (2), *K. tecta* (3), *K. tentoria* (1), *K. smithi* (1) ; *Ocadia sinensis* (2) ; *Malayemys subtrijuga* (3) ; *Chinemys reevesi* (4) ; *Hieremys annandali* (3) ; *Orlitia borneensis* (2) ; *Siebenrockiella crassicollis* (6) ; *Notochelys platynota* (1) ; *Cyclemys dentata* (3) ; *Melanochelys trijuga* (3) ; *Rhinoclemys punctularia* (3), *R. pulcherrima* (2), *R. annulata* (2), *R. funerea* (1) ; *Sacalia bealei* (2) ; *Mauremys caspica* (5), *M. japonica* (1), *M. mutica* (3) ; *Cuora trifasciata* (1), *C. amboinensis* (2) ; *Geoemyda flavomarginata* (1), *G. spengleri* (2), *G. mouhoti* (1) ; *Heosemys spinosa* (1), *H. grandis* (6).

EMYDINAE

Chrysemys alabamensis (2), *C. floridana* (5), *C. concinna* (9), *C. rubriventris* (6), *C. nelsoni* (1), *C. decussata* (5), *C. scripta* (8), *C. picta* (10) ; *Malaclemys terrapin* (6), *M. barbouri* (1), *M. kohni* (1), *M. pseudogeographica* (2), *M. geographica* (5) ; *Deirochelys reticularia* (3) ; *Emydoidea blandingi* (3); *Emys orbicularis* (3) ; *Clemmys guttata* (10), *C. insculpta* (5), *C. muhlenbergi* (3), *C. marmorata* (3) ; *Terrapene mexicana* (1), *T. carolina* (19), *T. ornata* (4).

ACKNOWLEDGMENTS

I am most grateful to the following people for the use of material from their institutions : Dr Doris Cochran, United States National Museum ; Mr Charles Bogert, American Museum of Natural History ; and Dr Ernest Williams,

Harvard Museum of Comparative Zoology. I am also grateful to Dr Wayne Frair for turtles from his private collections.

REFERENCES

BAIRD, I. L. (1960). A survey of the periotic labyrinth in some representative recent reptiles. *Kans. Univ. Sci. Bull.* **41** (9) : 891–981.

BOULENGER, G. A. (1889). *Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History)*. London : Brit. Mus. (Nat. Hist.).

BOURRET, R. (1939). Notes herpétologiques sur l'Indochine français. XVIII. Reptiles et batraciens reçus au Laboratoire des Sciences Naturelles de l'Université au cours de l'année 1939. Descriptions de quatre espèces et d'une variété nouvelles. *Bull. Gen. Instr. publ. Hanoi* **4** : 5–39.

BOURRET, R. (1941). Les tortues de l'Indochine. *Inst. Océanogr. Indochine* **38** : 1–235.

FANG, P. W. (1934). Notes on some chelonians of China. *Sinensia* **4** : 145–208.

HAY, O. P. (1908). The fossil turtles of North America. *Spec. Publ. Carneg. Instn. Washington* **75** : iv+568.

LINDHOLM, W. A. (1932). Über eine angebliche Testudo-Art aus Südchina. *Zool. Anz.* **97** : 27–30.

LOVERIDGE, A. & WILLIAMS, E. E. (1957). Revision of the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. comp. Zool. Harv.* **115** (6) : 163–557.

MCDOWELL, S. B. (1961). On the major arterial canals in the ear-region of testudinoid turtles and the classification of the Testudinoidea. *Bull. Mus. comp. Zool. Harv.* **125** : 23–39.

NAKAMURA, K. (1934). On *Clemmys mutica* (Cantor) with special reference to its variation and distribution. *Annot. zool. jap.* **14** : 425–432.

PARSONS, T. S. (1960). The structure of the choanae of the Emydinae (Testudines, Testudinae). *Bull. Mus. comp. Zool. Harv.* **123** : 113–127.

PING, C. (1930). Notes on the shell of a land tortoise from the ancient ruins of Annyang. *Bull. Fan Inst. Biol., Peking* **1** : 217–226.

ROOIJ, N. DE (1915). *The reptiles of the Indo-Australian Archipelago.* **1.** Leiden : E. J. Brill.

SAVAGE, J. M. (1953). Remarks on the Indo-Chinese turtle *Annamemys merkleni* ; with special reference to the status of *Cyclemys annamensis*. *Ann. Mag. nat. Hist.* (12) **6** : 468–472.

SMITH, M. A. (1931). The fauna of British India including Ceylon and Burma. Reptilia and Amphibia. Vol. I. Loricata, Testudines. London.

SMITH, H. M. & JAMES, L. F. (1958). The taxonomic significance of cloacal bursae in turtles. *Trans. Kans. Acad. Sci.* **61** (1) : 86–96.

WILLIAMS, E. (1956). *Pseudemys scripta callirostris* from Venezuela with a general survey of the *scripta* series. *Bull. Mus. comp. Zool. Harv.* **115** : 145–160.

KEY TO LETTERING OF THE FIGURES

ag	apertura glossopharyngei.
AN	angular bone.
AR	articular bone.
atEO	attachment for exoccipital bone.
atOT	attachment for opisthotic bone.
av	apertura vagi.
BO	basioccipital bone.
bp	" batagurine process " of basioccipital, flooring the recessus cavum tympani.
BS	basisphenoid (or fused basisphenoid and parasphenoid) bone.
cep	crista exoparacapsularis, separating the (more medial) recess for the paracapsular sac from the (more lateral) passage for the vena capitis lateralis and stapedial artery.
CO	coronoid bone.
crpt	crista praetemporalis.
ct	notch or foramen for chorda tympani nerve.
cty	cavum tympani of quadrate bone.
dc	dentary canal.
DE	dentary bone.
EO	exoccipital bone.
EP	epipterygoid bone.
fcd	foramen caroticum definitivum.
fcp	foramen caroticopharyngeale.
feg	foramen externum glossopharyngealis.
fig	foramen (or incisura) internum glossopharyngealis.
fp	foramen perilymphaticum.
fpr	flange of prearticular separating angular bone from Meckel's cartilage.
JU	jugal bone.
lpp	lateral process of pterygoid.
MA	maxillary bone.
mc	Meckelian canal.
mej	mediad expansion of jugal.
mfa	anterior mylohyoid foramen.
mfp	posterior mylohyoid foramen.
OT	opisthotic bone.
otp	process of pterygoid bearing the medial end of the operculum tubae.
PA	parietal bone.
PB	postorbital bone.
ph	postlagenar bone.
pi	processus interfenestralis of opisthotic.
PL	palatine bone.
PO	proötic bone.
ppm	pterygoid process of maxillary bone.
PR	prearticular bone.
PT	pterygoid bone.
rc	scar for insertion of rectus capitis muscle.
rst	recessus scalae tympani.
SO	supraoccipital bone.
SP	stapes.
SQ	squamosal bone.
ST	supratemporal bone.
SU	surangular bone.