VARIATION AND SELECTION IN THE CERVICAL CENTRAL ARTICULATIONS OF LIVING TURTLES

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INTRODUCTION

STATEMENT OF THE PROBLEM

THE EVOLUTION of the retractile neck in turtles is of interest as a phenomenon of adaptation, nearly the whole history of which is known; it thus offers an unusual opportunity for the study of an adaptive structure in terms of a continuous and continuing process. The study from this point of view of cervical structure in turtles, fossil and recent, will be the subject of a series of papers.

A primary advantage in the use of the Testudinata as material for the study of adaptation is the fact that they are a small order. Perhaps 300 species are recognized among living forms, and, while more fossil species have been described, it is reasonably certain that many of these are synonyms. The order can therefore be studied as a whole with fair convenience.

At the same time, in spite of being rather uniform in certain features (the presence of a shell of some sort, for example), the turtles are quite diversely adapted, having a wide variety of habits (carnivorous, omnivorous, herbivorous) and living in widely differing habitats (marine, fresh-water, and terrestrial). Inevitably the turtles have reacted to these diverse conditions by changes in structure. The neck in particular is a region that has reacted by structural modification to varying needs. In fact the evolution of mechanisms for the retraction of the neck is probably the most significant advance within the order since Triassic times. Yet the mechanisms of neck retraction are notably different in the several major phyletic lines; the problems connected with the mechanical difficulties of a retractile neck have been solved in several ways within the order.

One apparent difficulty is, however, present. In many living species of turtles the neck vertebrae in a number of respects are quite variable, even to the extent of polymorphism. Under such circumstances it is possible to doubt that vertebral structure is correlated with function, that it is adaptive. A first task therefore—the task of the present paper—is the demonstration that such variation is consistent with the designation of the neck of turtles as an adaptive structure.

Testudinate cervical vertebrae are known to vary intraspecifically in the following ways: (1) in number; (2) in length-width ratio[1]; (3) in the shape and relative height of the neural spines; (4) in the shape, number, and relative height of the ventral keels; (5) in the number and degree of development of intervertebral ossicles; (6) in the character and degree of development of the transverse processes; (7) in the presence or absence of separately ossified ribs; (8) in the curvature and placement of the zygapophyses; (9) in the size and shape of the zygapophysial articular surfaces; (10) in the breadth-height ratio of the central joints; (11) in the presence or absence of doubling (ginglymoidy) of the central joints; (12) in the placement of the convexities and concavities which unite in the formation of the central joints.

Of these variations the last two are very much better for intensive investigation than any of the others. They are, for example, the only ones easily recognized and at the same time so frequent that the species that contain them must be called polymorphic. In contrast, variation in number of cervical vertebrae is rare, and variation in zygapophysial angle and surface is as a rule neither very obvious nor at all easy to describe or to measure, while variations such as those in length-width ratios are made difficult to study by the complicating factor of growth changes of the same sort. In addition, variations of the central joints are the only variants that have received previous mention in the literature. They are therefore the material of choice for investigation of the significance of polymorphism in the neck of turtles. If the central articulations can be shown to be adaptive, in spite of being so highly variable, the way is cleared for the continuation of the study of the testudinate neck as an adaptive structure continuing to evolve.

[1] Variations in dimensions and degree of development when mentioned here are not merely growth and age changes but substantial differences in the proportion of parts in animals of comparable size and age.

HISTORICAL SUMMARY

The classic description of testudinate cervical osteology was given in 1881 by Leon Vaillant. In a meticulous memoir he delineated, with unrivaled accuracy in both text and figures, representatives of all testudinate families except the still to be discovered *Carettochelys* and the uncommon *Dermatemys*. He made clear for the first time the complexity and diversity within the order.

Appropriately Vaillant was the first to call attention to intraspecific variation in the cervical central articulations of turtles. This he did in a lengthy footnote appended to his important paper just before publication. He had examined more than 84 specimens belonging to 46 species; in this number he found intraspecific variation in the position of the anterior biconvex centrum in single specimens of *Pseudemys scripta ornata*, *Testudo graeca*, *Testudo ibera*, and *Testudo radiata*.

Vaillant's observations were extended by George Baur in his series of "Osteologische Notizen über Reptilien" (1886–1889), a very important record of both normal and variant conditions in turtles. Baur's pronouncements on the subject of cervical centra were, however, in the nature of general summaries, and, except in the case of *Dermatemys*, of which he was the first to describe the cervical central pattern correctly, it is not possible to discover how many specimens of any species he examined. He reported cervical central variations in *Testudo leithii* and *Testudo denticulata* and mentioned also one found by Dollo in *Chelonia mydas*.

The next important contribution was that of Siebenrock (1906). Working with material gathered by Voeltskow's expeditions to East Africa and Madagascar, he was able to examine 630 specimens of the single species *Bellemys*[1] *arachnoides*, previously considered rare. In 85 of his specimens of *Bellemys* he could study the vertebral column. Eighty cervical columns showed one central pattern; five, another. He was also able to examine 22 specimens of *Testudo radiata*; 20 of these had one pattern; two, another. He studied much additional material of *Testudo* and related genera. This, unfortunately, he did not report fully except in the cases of *Testudo denticulata*, *T. graeca*, and *T. ibera*.

As a source of data Siebenrock's work is very valuable; he did not, however, discuss the significance of his findings. He was, it would appear from his text, solely interested in determining what conditions were most frequent in each species and therefore "normal."

A last contribution to this very limited literature of testudinate cervical central variation is that of Hans Virchow (1926). Examining a very small series of skeletons (nine specimens of eight species belonging to five families), he found spectacular differences in the central articulations in two specimens of *Testudo pardalis*. The value of his work was much diminished not only by the extreme paucity of his material, but also by his apparent total ignorance of the work of Vaillant, Baur, and Siebenrock. He ventured, however, interesting generalizations on the range of structure possible to turtles.

These four contributions only, of Vaillant, Baur, Siebenrock, and Virchow, are the scanty record of cervical central variation in turtles. The present paper is able to amplify this record substantially and place it on a new footing.

MATERIAL

The osteological collections of Lafayette College, Columbia University, Cornell University, Yale University, the American Museum of Natural History, the Academy of Natural Sciences of Philadelphia, the Carnegie Museum at Pittsburgh, the Chicago Natural History Museum, the Kansas Natural History Museum, the Museum of Comparative Zoölogy at Harvard University, the University of Michigan Museum of Zoology, the United States National Museum, and the Laboratoire d'Anatomie Comparée of the Museum National d'Histoire Naturelle at

[1] *Pyxis* Bell, 1825, the generic name used by Siebenrock and other authors, is preoccupied by *Pyxis* Chemnitz, 1784. *Bellemys*, new name, is therefore proposed.

TABLE 1

LIST OF SPECIMENS RECORDED

Family[a]	Total Recorded: Literature and Personal Examination	Total Personally Examined	Intraspecific Variants[b] Recorded	Variants Personally Seen
Dermatemydidae	6	2	0	0
Chelydridae				
Chelydrinae	117	114	2	2
Staurotypinae	2	2	0	0
Kinosterninae	109	104	18	16
Testudinidae				
Platysterninae	5	2	0	0
Emydinae	687	664	71	70
Testudininae	352	263	55	34
Cheloniidae	41	35	2	1
Dermochelyidae	9	6	0	0
Carettochelyidae	2	0	0	0
Trionychidae	65	58	0	0
Pelomedusidae	39	24	0	0
Chelidae	27	15	0	0
Total	1461	1289	148	123

[a] For the classification here employed, see Appendix 2.
[b] Variant is here understood as any condition differing from the condition thus far most frequently observed in a species.

Paris have provided the author with the opportunity to examine more than 1000 turtle skeletons, while over 100 more have been personally prepared. The observations made on these specimens have been combined and collated with all the information given by Vaillant, Baur, Siebenrock, and Virchow as well as with the incidental mentions of the cervical centra in the works of Boulenger (1889), Wieland (1902), Bienz (1896), Hay (1908), Völker (1913), Walther (1922), and others.

Table 1 lists by family or subfamily the number of specimens reported herein.

TERMINOLOGY

CENTRA

Anyone not completely familiar with testudinate osteology has but slight conception of the complexities that doubling (ginglymoidy) of certain of the joints, though occurring only in cryptodires, has introduced into the testudinate cervical vertebral column. To take the simplest case, the statement that all the cervical centra of certain specimens of *Bellemys arachnoides* are "procoelous" confounds four types of centra under one name: some of the centra described as "procoelous" have single articulations cranially and caudally, one has a single articulation cranially and a double articulation caudally, one has double articulations cranially and caudally, and one has a double articulation cranially and a single articulation caudally.

A system of naming centra that could adequately describe all the mentioned types and all the others possible in turtles was devised by Wieland in 1899. He suggested the device of indicating double articulations by the prefix "bi-." The simple type of centrum called "procoelous" by Owen is called "coelocyrtean"[1] by Wieland; the more complex types,

[1] "Cyrtean" here is from the Greek κυρτός, meaning convex; it was independently suggested by Virchow
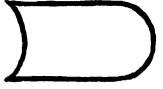
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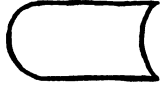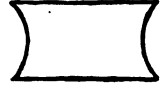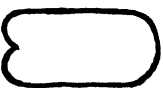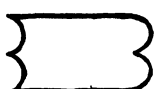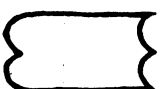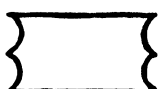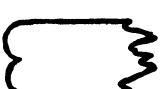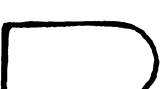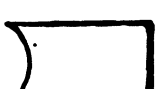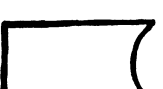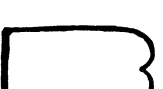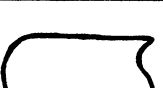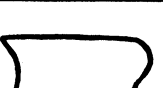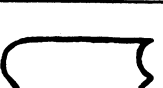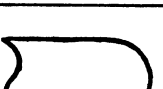
	BICONVEX	PROCOELOUS	OPISTHOCOELOUS	AMPHICOELOUS
SIMPLE				
DOUBLED POSTERIORLY				
DOUBLED ANTERIORLY				
DOUBLED AT BOTH ENDS				
POSTERIOR SURFACE NON-ARTICULAR				
PLATYAN ON ONE SURFACE				
"				
ASYMMETRICAL DOUBLE JOINT				
"				

FIG. 1. Some of the types of centra known to occur in turtles. Only spheroidal and plane joints are shown. As a convention for placement, plane and partly convex surfaces are treated as though convex.

cited for *Bellemys*, usually described under the same name with the preceding, then become, respectively, "coelobicyrtean," "bicoelobicyrtean," and "bicoelocyrtean."

The unfamiliarity of this system, the formidable appearance of the compounded names, and their lack of special usefulness except for the posterior cervicals of cryptodiran turtles, two of the centra of some Salientia, and the sacral centra of a few lizards rather certainly put this simplest verbal description of doubled joints outside any probability of popular use.

Fortunately there are available visual methods of description which are as accurate and much more satisfactory. One such method, that of schematic frontal section, was independently employed by Vaillant and by Virchow. Figure 1 portrays by this method more than 20 types of centra[1] that normally or as individual variants are known in turtles.

This method of description, of course, presents a difficulty: each description is in this case a drawing and as such cannot be readily incorporated into the body of a text. Another method of visual description is possible which avoids or minimizes this difficulty: a series of central convexities and concavities (conveniently called a "cervical central pattern") may be represented by such formulas as have been used, for example, by Walther (1922) in which parentheses stand for the convexities and concavities. In such a formula the condition found in the genera *Pelusios* and *Pelomedusa*, which have a biconvex second centrum and the remainder procoelous, is shown as (2))3))4))5))6))7))8). (See the comparison in fig. 3 of these formulas and schematic frontal sections.) Such a formula is easily modified to show doubling or other conditions. Thus the 14 specimens of *Emys orbicularis* so far described exhibit the condition (2((3((4))5))6))7))8). Plane joints may be shown as | and saddle and cylindrical joints by s and c.

This device is so obviously superior to any purely verbal description that it will be a method often employed in the tabulations of the present paper (Appendix 1 and table 6).

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(1926) but not in the combinations listed above. "Amphicyrtienne" was also used by Vaillant (1881).

[1] Only spheroidal and flat articular surfaces are shown. Cylindrical and saddle joints may also occur.
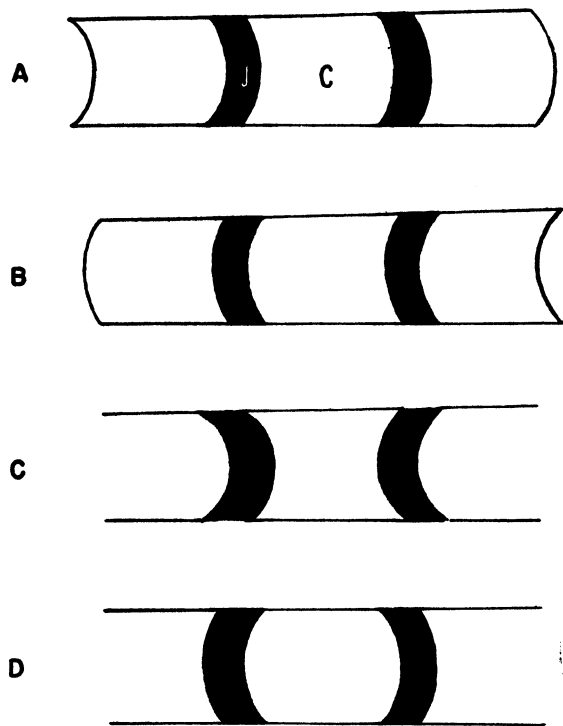
FIG. 2. Diagram to illustrate a method of description of joints between centra according to the shape of the joint apparatus. A. Procoelous centra and procoelous joints. B. Opisthocoelous centra and opisthocoelous joints. C. An amphicoelous centrum and surrounding joints. D. A biconvex centrum and surrounding joints. *Abbreviations:* C, centrum; j, joint apparatus.

In Appendix 1, in order to reveal more clearly the character of the centra, commas are placed between the joint surfaces of successive centra. In table 6 (in which the joints rather than the centra are objects of attention) Walther's formulas are employed without such modification and in their simplest form.

JOINTS

It will be important in some of the following discussion to consider joints as well as centra as distinct entities. Certain definitions and formulations are therefore desirable:

When the joints of the neck are enumerated, it is convenient to give them the number of the posterior of the two centra participating in them. Thus the first joint of the neck is that between the occipital condyle and the first vertebra (this may be also called

FIG. 3. Diagram to explain the notation for joint variation here adopted. Numbers of joints are in Roman numerals. Numbers of centra in arabic numerals. Variation in any cervical column is indicated by the Roman numeral of the variant joint.

the occipito-cervical joint).[1] The second cervical joint is that between the odontoid bone (always distinct in turtles and always with a distinct though feeble posterior articular surface) and the second centrum. The third joint lies between the second and third centra, the fourth is in front of the fourth centrum, and so on. The ninth cervical joint is also the cervico-dorsal. In each case the numerical position of the joint can be designated by a roman numeral.

The simplest terminology describing the character of individual joints is that based on the shape of the joint apparatus[2] itself (see fig. 2). In this terminology joints between procoelous centra are procoelous; between opisthocoelous centra, opisthocoelous. Note,

however, that procoelous and opisthocoelous are for spheroidal joints the only possible alternatives. The joint anterior to a biconvex centrum is opisthocoelous, that posterior to it procoelous, while in the case of those amphicoelous centra that occur in modern turtles the anterior joint is procoelous, the posterior opisthocoelous.

For the discussion of joint variation or of the evolution of cervical central patterns, where either the most frequent or the truly primitive pattern is known, a simple notation is useful (fig. 3). If the most frequent condition be designated N, or the primitive condition P, deviation from either type may be shown by roman numerals indicating the ordinal position of the joints that have varied. Thus in *Testudo pardalis* the most frequent condition is that with the fourth and eighth centra biconvex. This, then, is condition N. The most common variation has the third centrum biconvex, a situation brought about by modification of joint IV. This variation, therefore, is sufficiently described by the numeral IV. More complex variants of the primitive pattern are shown by the same rule as III, IV and IV, VIII. (See fig. 3.) This notation is used extensively in tables 2, 3, and 4 and in Appendix 1.

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[1] The occipito-cervical joint will not be discussed further here; it is highly specialized and mistaken ideas are held regarding it. One correction pertinent to this paper may be made. Several authors have described the first vertebra of turtles as amphicoelous. The posterior articulation of the vertebra so described, that between the odontoid bone and the second centrum, is indeed a true central joint, but the anterior joint called attention to by these authors is not a central joint at all but an articulation between the atlas arches and the occipital condyle without parallel elsewhere in the vertebral column.

[2] By joint apparatus is here understood the soft tissue surrounding the joint cavity between two articulating bones.

To AVOID OVERBURDENING the reader the basic data which are summarized in the following text have been placed in Appendix 1. A summary of the classification here employed is given in Appendix 2.

In the present section concentration of attention is on intraspecific variation and its characters. This is reported in a factual manner without more discussion than is essential to the understanding of the observed conditions themselves. (Theoretical considerations are taken up in the concluding section.) Decription of the characters of intraspecific variation is by groups. These groups are defined by possession of basically or primitively similar cervical central patterns. They are sometimes coterminous with families as understood here, but just as often they are suprafamilial, even by the standards of the present work.

Both sorts of variation of the central articulations are reported, variation in doubling, and variation in the placement of convexities and concavities (called for the sake of brevity "convexo-concave" variation).

GROUP 1. TESTUDINIDAE

The three subfamilies of the Testudinidae have in common a single most frequent cervical central pattern, that with the fourth and eighth centra biconvex. Other valid generalizations, however, are difficult. The Platysterninae, only five specimens of which have been examined for the characters of the cervical vertebrae, are too inadequately known to be further discussed. The Testudininae and Emydinae, on the other hand, although they are the best known of all turtle groups, are also the most polymorphic, with regard to convexo-concave variation. The Testudininae especially present a high frequency of polymorphic forms. *Testudo pardalis* exhibits five cervical central patterns in only 36 specimens, *T. denticulata* four in 24, *Gopherus berlandieri* three in 19, *T. leithii* three in six. In the Emydinae only species of *Pseudemys*, *Clemmys*, and *Terrapene* are known to approach this frequency of polymorphic forms.

It must be recognized, of course, that the size of the sample is for most species quite insufficient for accurate calculations of the frequency of polymorphic forms to be made. For many species it is impossible to say on present evidence what cervical central pattern is truly the most frequent condition. Such is the case, for example, in *Hardella thurjii*, the species of *Geoemyda*, *Testudo angulata*, and *T. leithii*. Indeed only in the case of those five species with samples of over 50 (*Chrysemys picta*, *Pseudemys scripta*, *Terrapene carolina*, *T. ornata*, and *Bellemys arachnoides*) is there any statistical probability of close approach to the real intrapopulational frequency of the various recorded patterns. In the remaining species extreme sampling error is too probable to be ignored, especially in the case of species represented by fewer than 25 specimens.

A few general observations may nevertheless be made with fair assurance:

1. Polymorphic forms differing by but one step (variation of a single joint) from the presumed primitive pattern with the fourth and eighth centra biconvex occur in both Emydinae and Testudininae, but polymorphic types involving two or more modifications from the primitive are, as far as known, restricted to the Testudininae.

2. The single-step variation involving joint IV and resulting in the biconvexity of the third centrum is much the commonest alternate to the otherwise most prevalent and probably primitive condition with a biconvex fourth centrum. This commonest alternate is the norm of certain of the Testudininae, *Testudo radiata*, the genus *Kinixys*, and perhaps also the genus *Homopus*. (A more extreme departure from the primitive, a biconvex second centrum, a variant in *T. radiata*, is the norm in the genus *Bellemys*.)

3. Other known single-step variant types involve modification of joints II, V, VII, or VIII. In no instance have variants involving III alone or VI alone or in any combination been detected.

4. The known multiple-step variants have, with the single rare exception of IV, VII, VIII,

TABLE 2

PATTERN VARIATION WITHIN SPECIES (EMYDINAE)

Species[b]	Patterns[a]							Total No. of Specimens
	N	II	IV	V	VII	VIII	9th Cervical	
Batagur baska	3	—	—	—	—	—	—	3
Hardella thurjii	1	—	—	—	—	—	—	1
Orlitia borneensis	1	—	—	—	—	—	—	1
Siebenrockiella crassicollis	1	—	—	—	—	—	—	1
Chinemys reevesii	3	—	—	—	—	—	—	3
Hieremys annandalii	1	—	—	—	—	—	—	1
Chrysemys picta	181	—	9	2	3	—	—	195
Pseudemys floridana	33	—	6	1	—	—	—	40
Pseudemys rubriventris	10	—	—	—	—	—	—	10
Pseudemys scripta	72	1	5	—	3	1	1	83
Graptemys barbouri	4	—	—	—	—	—	—	4
Graptemys geographica	17	—	—	—	—	—	—	17
Graptemys pseudogeographica	24	—	1	—	1	—	—	26
Malaclemys terrapin	19	—	—	—	1	—	—	20
Deirochelys reticularia	6	—	—	—	—	—	—	6
Clemmys caspica	1	—	—	—	—	—	—	1
Clemmys guttata	11	—	—	—	—	2	—	13
Clemmys insculpta	20	2	—	2	—	3	—	27
Clemmys leprosa	3	—	—	—	—	—	—	3
Clemmys marmorata	10	—	1	—	—	1	—	12
Clemmys muhlenbergii	5	—	—	—	—	—	—	5
Emys blandingii	27	—	—	—	—	—	1	28
Emys orbicularis	14	—	—	—	—	—	—	14
Terrapene carolina	81	—	13	3	4	2	—	103
Terrapene klauberi	1	—	—	—	—	—	—	1
Terrapene ornata	56	—	3	—	—	1	—	60
Terrapene mexicana	1	—	—	—	—	—	—	1
Geoemyda annulata	1	—	1[c]	—	—	—	—	2
Geoemyda grandis	1	—	—	—	—	—	—	1
Geoemyda pulcherrima	1	—	—	—	—	—	—	1
Geoemyda punctularia	1	—	—	—	—	—	—	1
Geoemyda spinosa	1	—	—	—	—	—	—	1
Geoemyda trijuga	5	—	—	—	—	—	—	5
Cuora amboinensis	3	—	—	—	—	—	—	3
Cuora flavomarginata	1	—	—	—	—	—	—	1

[a] For notation, see page 517.
[b] Groupings of genera are here intended to call attention to relationship, although the affinities of some forms are not certainly with the forms with which they are here grouped (e.g., *Hieremys, Emys blandingii*).
[c] Centra 5 to 8 are missing.

the effect of increasing the number of procoelous centra in the cervical column. Certain of the single-step variants (variations of joints V and VII) have the effect of decreasing the number of procoelous centra.

These statements concern only the arrangement of convexities and concavities; polymorphism exists also in the doubling of the joints.

The Emydinae almost always have joints VII and VIII double. Joint VII becomes simple only in a *Terrapene carolina* in which the convexo-concave relations in this joint have also varied. Joint VIII is simple only in a

TABLE 3

PATTERN VARIATION WITHIN SPECIES (TESTUDININAE)

Species	Patterns[a]											Total No. of Specimens
	N	II	IV	V	VIII	II IV	III IV	II III IV	IV VIII	IV VII VIII	II III IV VIII	
Acinixys planicauda	—	—	1	—	—	—	—	—	—	—	—	1
Homopus areolatus	—	—	2	—	—	—	—	—	—	—	—	2
Kinixys belliana	—	—	14	—	—	—	—	—	1	—	—	15
Kinixys erosa	—	—	10	—	—	—	—	—	—	—	—	10
Kinixys homeana	—	—	3	—	—	—	—	—	—	—	—	3
Bellemys arachnoides	—	—	—	—	—	—	81	—	—	—	7	88
Testudo angulata	—	—	—	—	1	—	1	—	—	—	—	2
Testudo calcarata	4	—	—	—	—	—	—	—	—	—	—	4
Testudo oculifera	1	—	2	—	—	—	—	—	—	—	—	3
Testudo pardalis	22	—	8	—	1	—	1	—	4	—	—	36
Testudo radiata	1	—	31	—	—	—	4	—	1	—	—	37
Testudo tornieri	5	—	1	—	—	—	—	—	—	—	—	6
Testudo leithii	4	1	—	—	—	—	—	1	—	—	—	6
Testudo graeca+ibera	28	—	7	—	—	—	—	—	—	—	—	35
Testudo marginata	5	—	—	—	—	—	—	—	—	—	—	5
Testudo horsfieldii	—	—	1	—	—	—	—	—	—	—	—	1
Testudo elegans	—	—	—	—	—	1	—	—	—	—	—	1
Testudo emys	1	—	—	—	—	—	—	—	—	—	—	1
Testudo denticulata	7	—	16	1	—	—	1	—	—	—	—	25
Testudo elephantopus	27	1	4	—	—	—	—	—	—	—	—	32
Testudo gigantea	—	—	4	—	—	—	—	—	—	1	—	5
Gopherus agassizii	9	—	—	—	—	—	—	—	—	—	—	9
Gopherus berlandieri	10	—	6	—	3	—	—	—	—	—	—	19
Gopherus polyphemus	12	—	—	—	—	—	—	—	—	—	—	12

[a] For notation, see page 517.

Pseudemys scripta in which convexo-concave relations in that joint have similarly varied.

Joint VI in emydines is quite variable; in European and Asiatic species, as noticed by Bienz (1896), there is apparently some tendency for this joint to be simple more frequently than in American forms.

In the Testudininae joint VI is regularly simple, and variation in doubleness commonly involves two joints, joint VII and the cervico-dorsal.

Polymorphism in regard to doubling of joint VIII is seen most prominently in the genus *Kinixys*. In the various species of *Testudo* joint VII is typically double and infrequently variant, but in *Kinixys* simple, double, and intermediate conditions of this joint occur in a continuous series so that no "normal" condition can be described.

The cervico-dorsal joint tends to be broad in all the land turtles and is often double-oval

or vaguely double. A perfect double joint in this position has been described by Wieland (1902) in *Gopherus polyphemus*. (A similar condition has been seen by the author in a *Chrysemys picta*.)

Rarely joint VIII, normally double in all land turtles, may become simple, and with the abolition of doubling in this joint there may no longer be any double joints in the cervical series.

In a single instance joint IV varies in the direction of doubleness. In *Testudo pardalis* (A.M.N.H. No. 24354) joint IV is asymmetrically double: the posterior end of the third centrum is concave on one side, convex on the other, while the anterior end of the fourth centrum is reciprocally convex on one side, concave on the other.

Plane joints are rarely present; joint II of a *Pseudemys floridana suwanniensis* and joint IV of a *Terrapene carolina carolina* are the

FIG. 4. Cervicals 2 to 8 of *Testudo gigantea*. A.M.N.H. No. 64021. Upper row: anterior view. Middle row: ventral view. Lower row: posterior view. ×⅔.
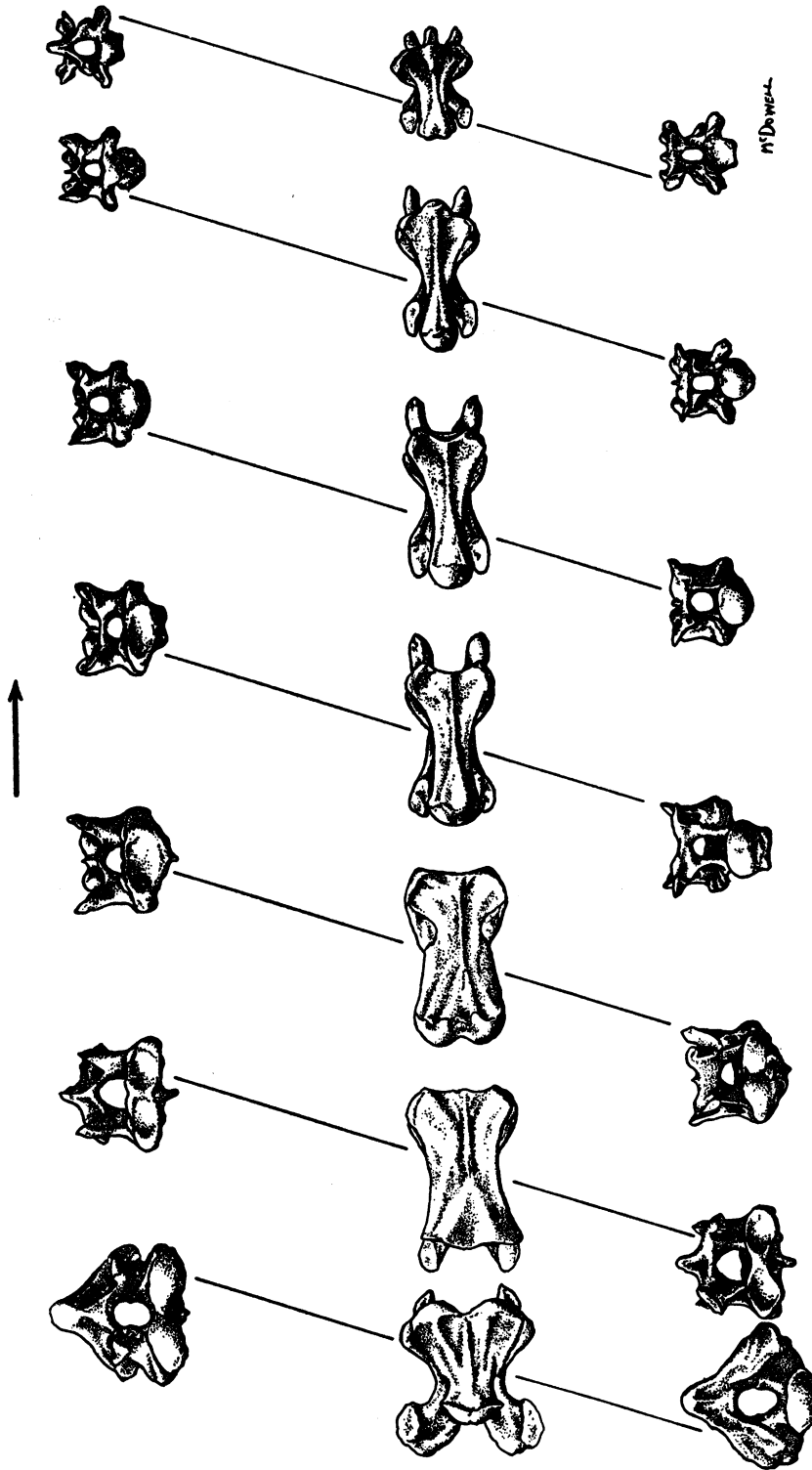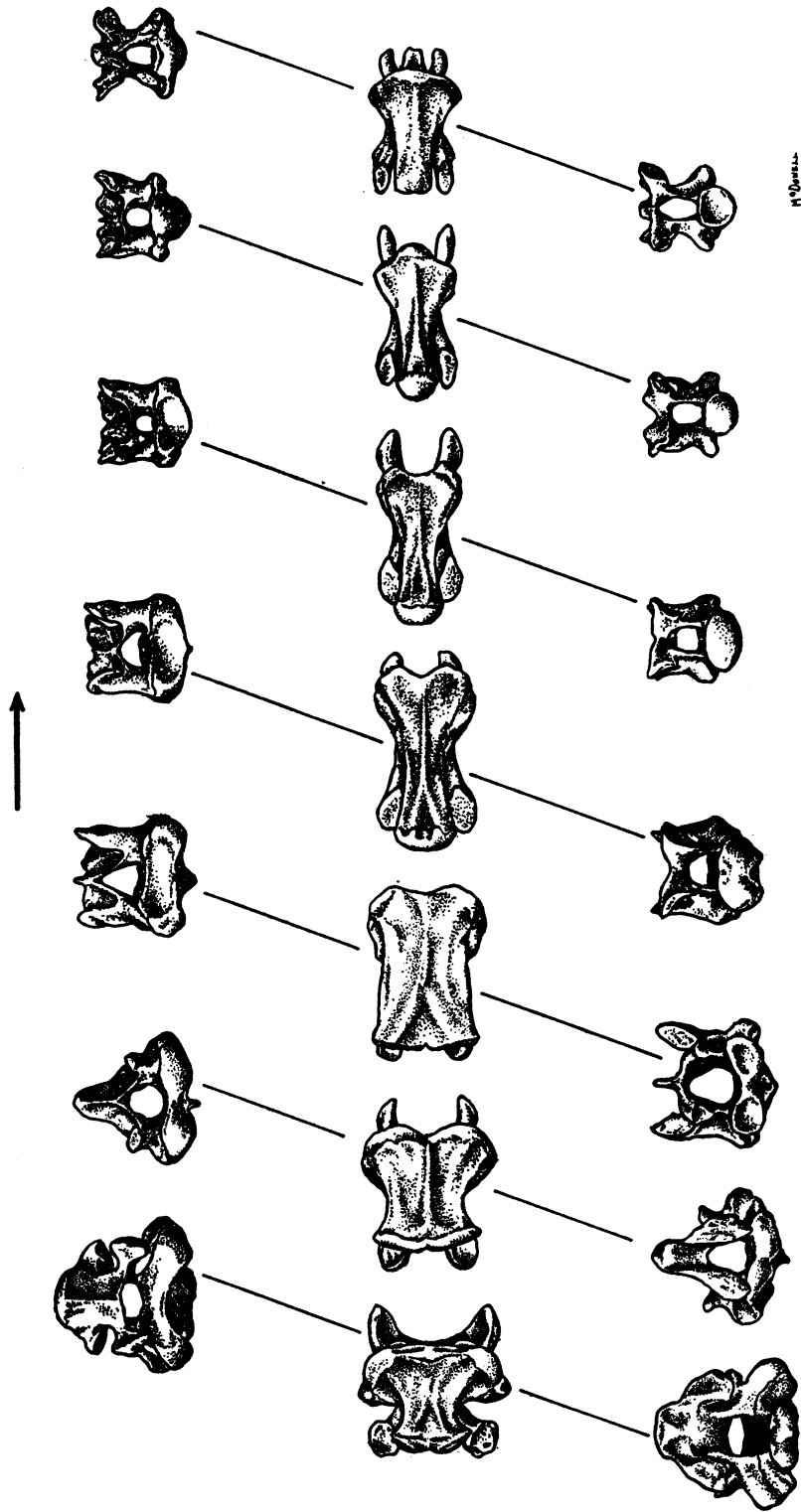
FIG. 5. Cervicals 2 to 8 of *Testudo gigantea*. A.M.N.H. No. 64020. Upper row: anterior view. Middle row: ventral view. Lower row: posterior view. ×⅔
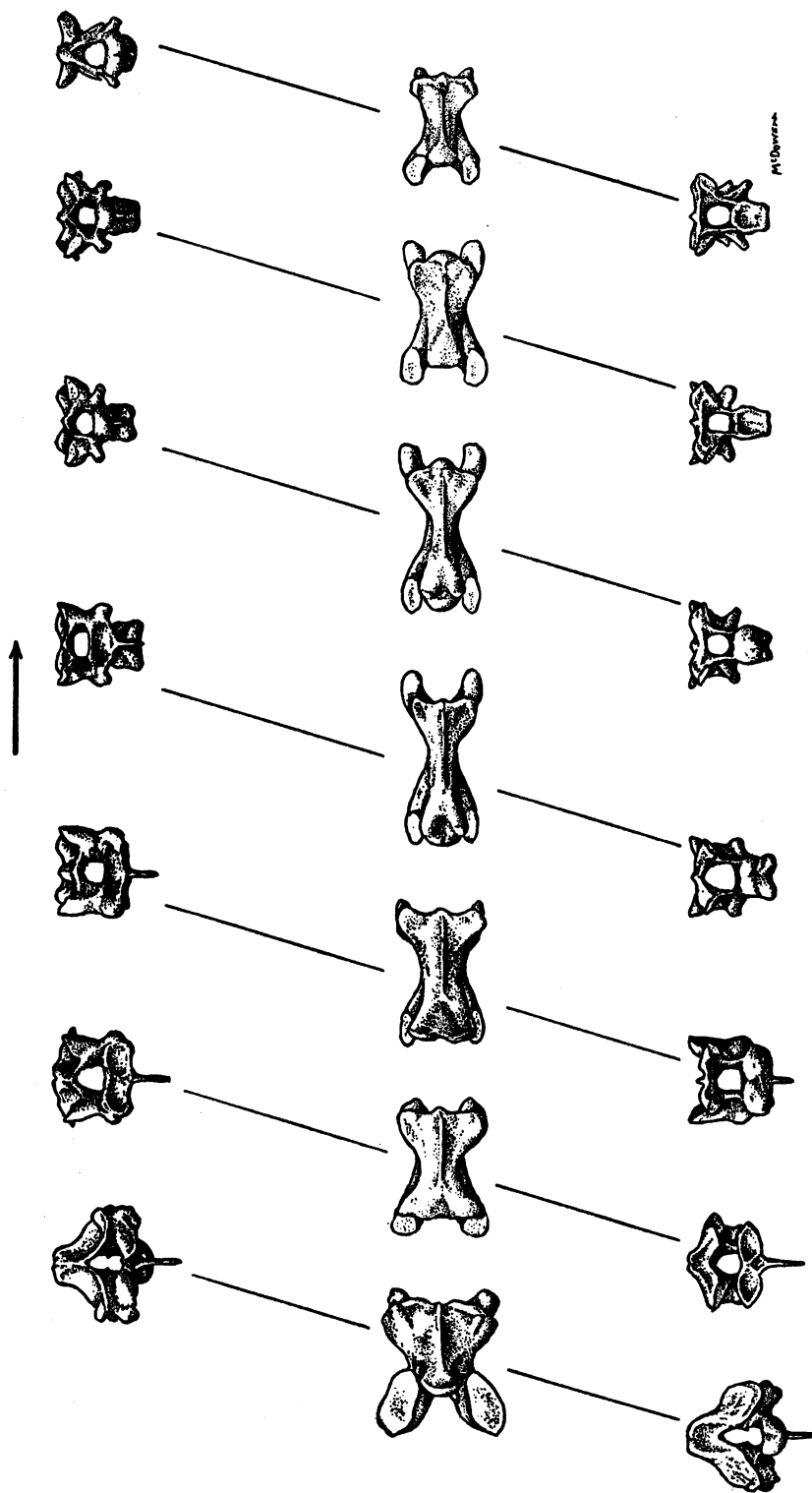
Fig. 6. Cervicals 2 to 8 of *Hieremys annandalii*. Columbia University. Upper row: anterior view. Middle row: ventral view. Lower row: posterior view. ×⅔.
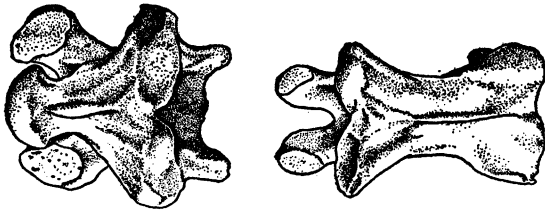
FIG. 7. Cervicals 7 and 8 of *Testudo pardalis*. A.M.N.H. No. 32824. An asymmetrical double joint is shown. Cervical 8 is at the left.

only examples in this group of such plane joints. Saddle joints are even rarer; only joint II of a *Pseudemys scripta troosti* can be so interpreted.

Certain special conditions are unique or nearly unique in turtles of this group:

1. Asymmetrical double joints. One of these has been mentioned above, and other examples are known (see Appendix 1). In these convexo-concave change has been confined to one side of a double joint only. Though this condition is never normal, in most instances the joints on the two sides are, in spite of the asymmetry, as well formed and perfectly adapted as normal, symmetrical joints. Exception to this rule must be made for the variant joint IV of *Testudo pardalis* cited above. Here the combination of variation in doubling with partial (one-sided) con-

vexo-concave variation has resulted in poorly adapted, misshapen joints on both sides.

A further elaboration of this type of variation is seen in a *Gopherus berlandieri* (Kansas Natural History Museum No. 2674) in which convexo-concave variation is confined to a portion of one-half of a doubled joint, a variation, so to speak, of a quarter joint.

2. "Amphicoelous"[1] joints. Examples are known in both the Emydinae (*Clemmys insculpta* and *Terrapene carolina major*) and Testudininae (*Testudo pardalis*) of apparent "amphicoelous" joints in which a cavity in one centrum is opposed to a cavity on another centrum. In the specimen of *Clemmys* and that of *Terrapene* indications exist of a cartilage filling the intervening space; probably in all three cases a ball of cartilage occupied the place of a joint head.

Vaillant (1881, p. 90) in one instance found the anterior condyle of an *Emys orbicularis* "constituée par une portion osseuse parfaitement sphérique," called by him an epiphysis and compared by him with similar epiphyses in the Salientia first discovered by Dugès (1834). The difference between Vaillant's case and the instances cited just above is that Vaillant's element ossifies separately and the cartilage spheres in the latter cases fail to ossify.

GROUP 2. DERMATEMYDIDAE, CHELYDRIDAE

The two families Dermatemydidae and Chelydridae have two characters of their cervical central columns in common. There is always an anterior biconvex centrum, and the eighth centrum is always procoelous. Neither intraspecific variation nor species or generic differences violate this rule, as stated, in any known instance. To this degree, therefore, these families are more homogeneous, less polymorphic (and possibly more primitive) than the Emydinae and Testudininae.

The position of the anterior biconvex vertebra is not, however, constant. The biconvex centrum may be the second as in *Dermatemys* and frequently in *Kinosternon*, rarely in *Sternotherus*, or the third as in *Sternotherus* and usually in *Kinosternon*, rarely in *Chelydra*, or the fourth as in *Chelydra* and *Macrochelys* and rarely in *Kinosternon*.

For *Chelydra serpentina* a rather good series of specimens permits us to say that a single most frequent or "normal" condition exists with a low frequency for one alternate. The case is similar in *Sternotherus odoratus*, but here the normal condition is the same as the scarce variant in *Chelydra*, and the alternate is a condition unknown in *Chelydra*. *Kinosternon flavescens* resembles *Sternotherus* but differs in the much higher incidence of the less frequent class of central pattern.

A rare variation in *Chelydra* is an apparently "amphicoelous" joint IV. This is obvi-

[1] Use of the term "amphicoelous" here does not follow the usage proposed in the section on terminology (p. 517). Strictly the joints should be described as biconvex, but it is so unusual to think of joints and centra separately that I have here followed familiar but illogical usage, placing the term, however, in quotation marks.

TABLE 4

PATTERN VARIATION WITHIN SPECIES (DERMATEMYDIDAE, CHELYDRIDAE)

Species	Patterns[a]			Total No. of Specimens
	P	IV	III, IV	
Dermatemys mawii	—	—	6	6
Chelydra serpentina	97	2	—	99
Macrochelys temminckii	18	—	—	18
Staurotypus salvinii	—	1[b]	—	1
Claudius angustatus	—	1	—	1
Kinosternon baurii	—	8	1	9
Kinosternon cruentatum	—	1	1	2
Kinosternon flavescens	—	49	10	59
Kinosternon integrum	—	1	—	1
Kinosternon leucostomum	—	3	1	4
Kinosternon sonoriense	—	3	—	3
Kinosternon subrubrum	1	7	2	10
Sternotherus carinatus	—	3	—	3
Sternotherus odoratus	—	69	1	70
Sternotherus minor	—	2	—	2

[a] For notation, see page 517.
[b] Centra 5 to 8 are missing.

ously comparable to the "amphicoelous" joints of the Testudinidae; a cartilaginous joint head is to be inferred.

In both Dermatemydidae and Chelydridae joints VII and VIII are usually double, but the alternative condition of simplicity is not uncommon, and in a cryptodire so typical as *Chelydra serpentina* the double joints taxonomically so diagnostic of the Cryptodira may occasionally be completely absent.

GROUP 3. CHELONIIDAE, DERMOCHELYIDAE

Dermochelys and the four genera of modern Cheloniidae sometimes exhibit a cervical central pattern precisely like that typically exhibited by *Chelydra* and *Macrochelys*. More frequently they differ in having less mobility at joint VII in which, in such cases, two plane surfaces are united in what is very nearly a synchondrosis.

As in the Chelydridae, *sensu lato*, the position of the anterior biconvex centrum has been observed to vary. Usually it is the fourth, but once in seven recorded specimens of *Eretmochelys imbricata* it has been the third, and once in 15 *Chelonia mydas* it has been the fifth. Little reliance can be placed in these stated frequencies of variation; the observation of Baur (1889, p. 186) that ". . . unter mindestens 50 Exemplaren von Seeschildkröten . . . habe ich immer nur den vierten bikonvex gefunden" suggests that the

real frequencies may be considerably lower.

Certainly common, however, are lesser variations of joints VII and VIII. In joint VIII, for example, in neither *Dermochelys* nor the Cheloniidae can any one condition be described as "normal." Sometimes the joint is double, sometimes broadly simple, sometimes cylindrical.[1]

The cylindrical modification of this joint is unique. The only other cylindrical joints occur in the Pleurodira, and in that suborder are vertical, not transverse as in these turtles. In the Cheloniidae this type of joint was first noticed by Virchow (1926), who found in *Chelonia mydas* a posterior transverse cylinder on the seventh centrum fitting into an

[1] In one instance, in a *Lepidochelys kempi* from Long Island (fig. 8), the seventh centrum is doubly convex behind, the eighth centrum singly concave in front; both joint surfaces are in this case feebly differentiated.
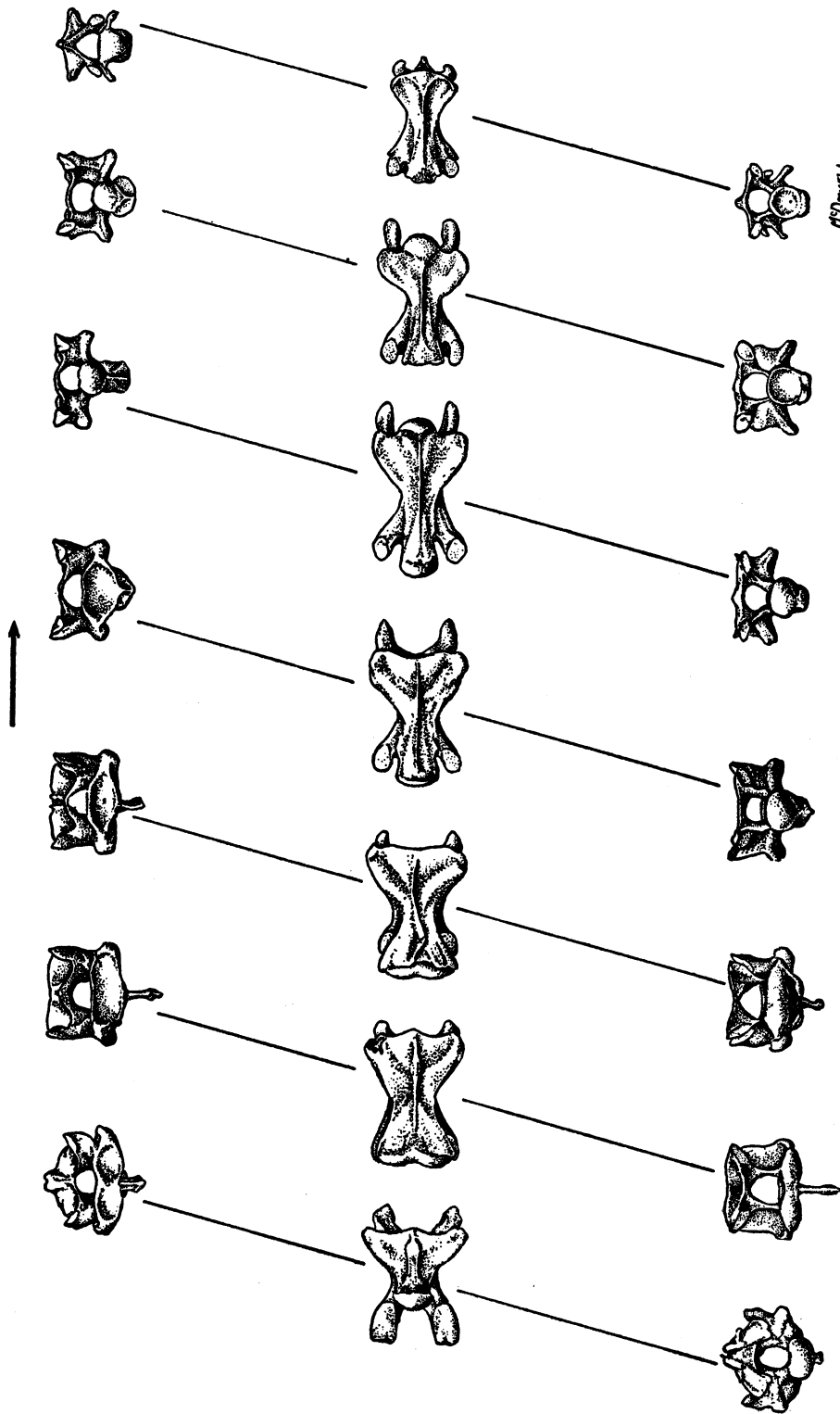
FIG. 8. Cervicals 2 to 8 of *Chelydra serpentina*. Collection of the author. Upper row: anterior view. Middle row: ventral view. Lower row: ventral view. ×⅘.
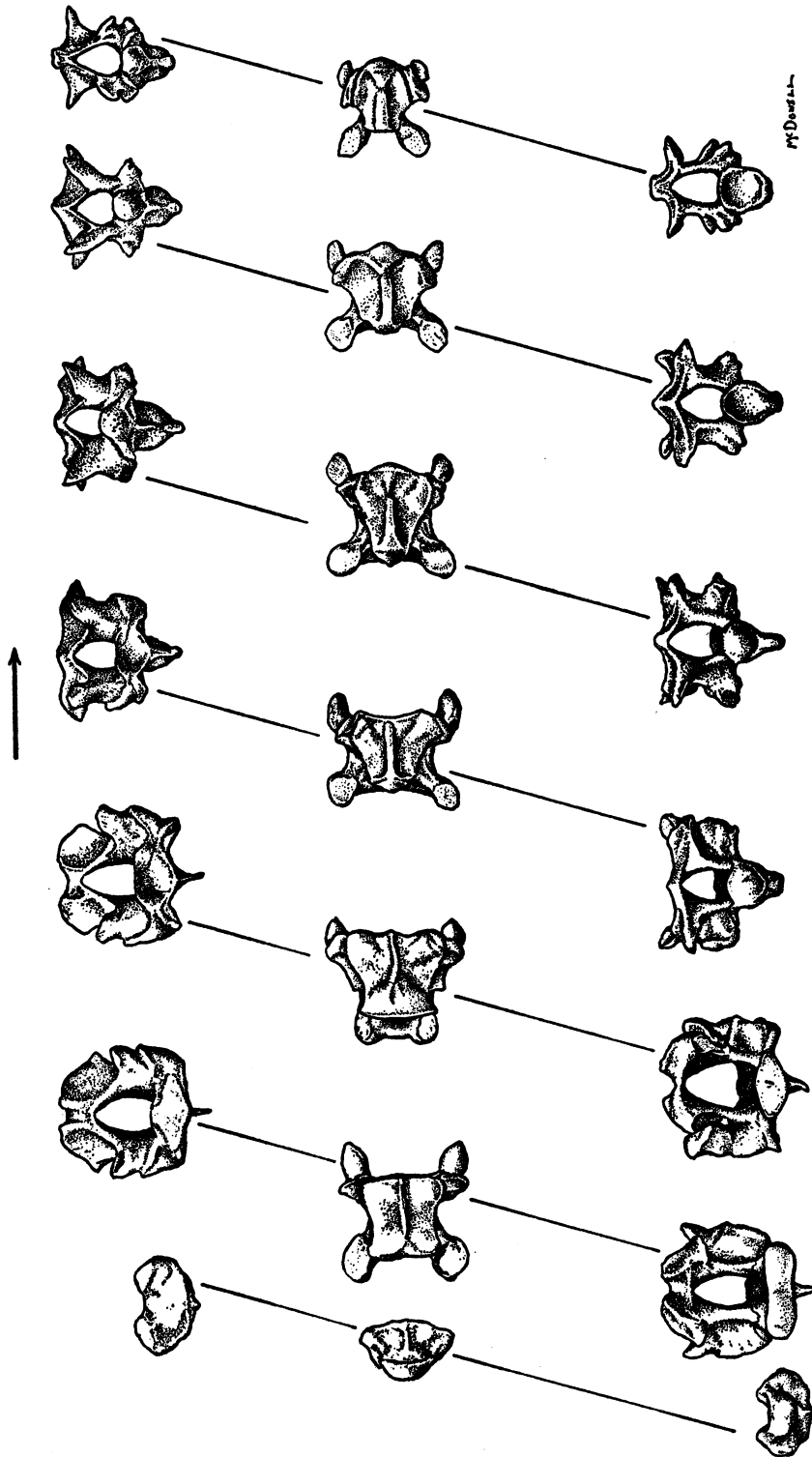
FIG. 9. Cervicals 2 to 8 of *Lepidochelys kempii*. Collection of the author. Upper row: anterior view. Middle row: ventral view. Lower row: posterior view. The neural arch of the eighth vertebra has been lost in the specimen. ×1.

anterior cylindrical concavity on the eighth centrum.

The present author has not seen any such perfect cylindrical joint as Virchow describes, but ambiguous conditions intermediate between truly cylindrical articulations and broadened simple spheroidal joints are frequent.

Joint VII is, as has been mentioned, more frequently amphiplatyan than procoelous; when it is procoelous, doubling is weak or absent.

GROUP 4. CARETTOCHELYIDAE, TRIONYCHIDAE

The two families Trionychidae and Carettochelyidae agree in having mostly opisthocoelous cervical centra. The vertebrae are, however, very slender in the Trionychidae, rather broad in the Carettochelyidae; the cervico-dorsal connection is also radically different in the two families.

Because of the extreme rarity of the single species, *Carettochelys insculpta* from the Fly River in New Guinea, the cervical centra of this family were for a long time unknown. When at last the eighth centrum of an incomplete specimen was described and figured by Waite (1905) the ginglymoidy of both anterior and posterior faces of this doubly biconvex centrum was at once accepted as critical evidence that this turtle could not belong to the Pleurodira with which Boulenger had ranked it in spite of the stubborn opposition of Baur. The doubling of the cervico-dorsal joint is nearly unique, being elsewhere known only as an infrequent variant in the Testudinidae.

The osteology of a complete specimen was made known by Walther in 1922, but the range of variation of this form, of which so few specimens have been examined, is still not known.

The distinctive character of the cervico-dorsal joint in the Trionychidae is correlated with the fact that in these forms the maximum flexure of the testudinate neck is attained. As Vaillant noticed, and the present author can confirm, in extreme flexion the haemal (morphologically ventral) surfaces of the centra of the eighth cervical and the first dorsal are in contact.

Such a condition, of course, precludes a true joint between the posterior face of the eighth centrum and the anterior face of the centrum of the first dorsal, and, in fact, these centra are united only by a tubular ligament, the bony connection of the two vertebrae being assured by the zygapophyses. (This condition was first described and the eighth vertebra of a trionychid figured by Sir Richard Owen in 1851.)[1]

Variation in this condition or in the opisthocoely of the remaining cervical centra is not known, but the doubling of joint VII is subject to peculiar modification: In a *Lissemys punctata* examined by Vaillant a single posterior concavity on the sixth centrum was matched with a double anterior head on the seventh centrum, but encrusting cartilage made the latter in the fresh condition a simple head and united the two bones in amphiarthrosis.

A simple posterior concavity on the sixth centrum articulating with a double anterior head on the seventh centrum has been seen also by Virchow in *Cycloderma frenatum* and by the present author in *Trionyx triunguis*.

Joint VIII is always perfectly double.

GROUP 5. PELOMEDUSIDAE

So far as known, the second centrum of the Pelomedusidae is always biconvex. The succeeding centra are all simply procoelous in species of the Ethiopian region, but in Neotropical species some of them possess saddle joints.

Undoubtedly the saddle joints of the South American species have been derived from simple joints of the African species. In fact, the cervical series of *Podocnemis expansa*, for example, is not a complete series of saddle joints but bears traces of its origin from the unspecialized African type of pelomedusid series in simple as well as cylindrical and

[1] This condition, unique to the Trionychidae, deceived Virchow (1926) into believing that the posterior end of the eighth centrum of his *Cycloderma frenatum* was broken.

FIG. 10. Cervicals 2 to 8 of *Trionyx triunguis.* A.M.N.H. No. 36599. Upper row: anterior view. Middle row: ventral view. Lower row: posterior view. ×⁴⁄₃.
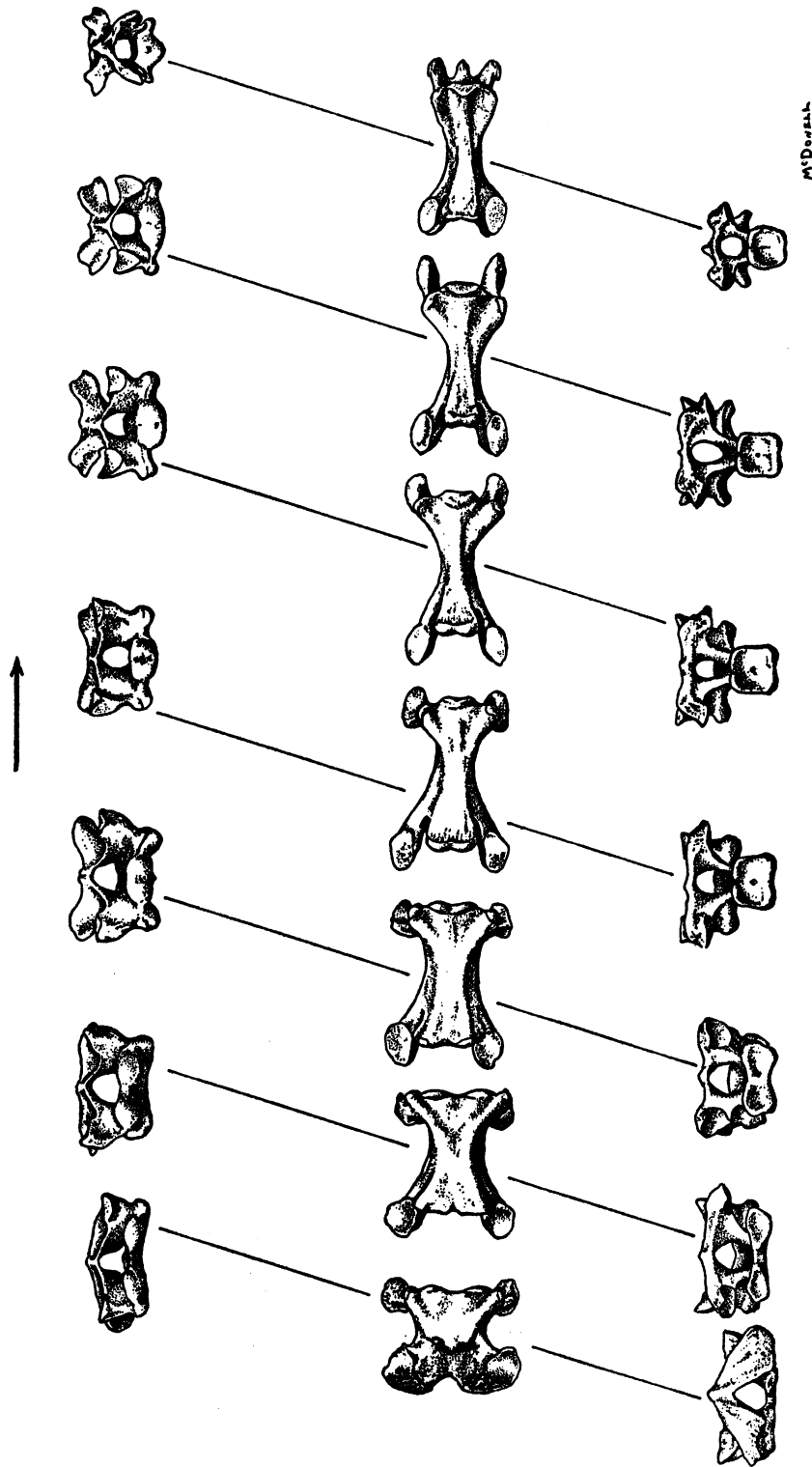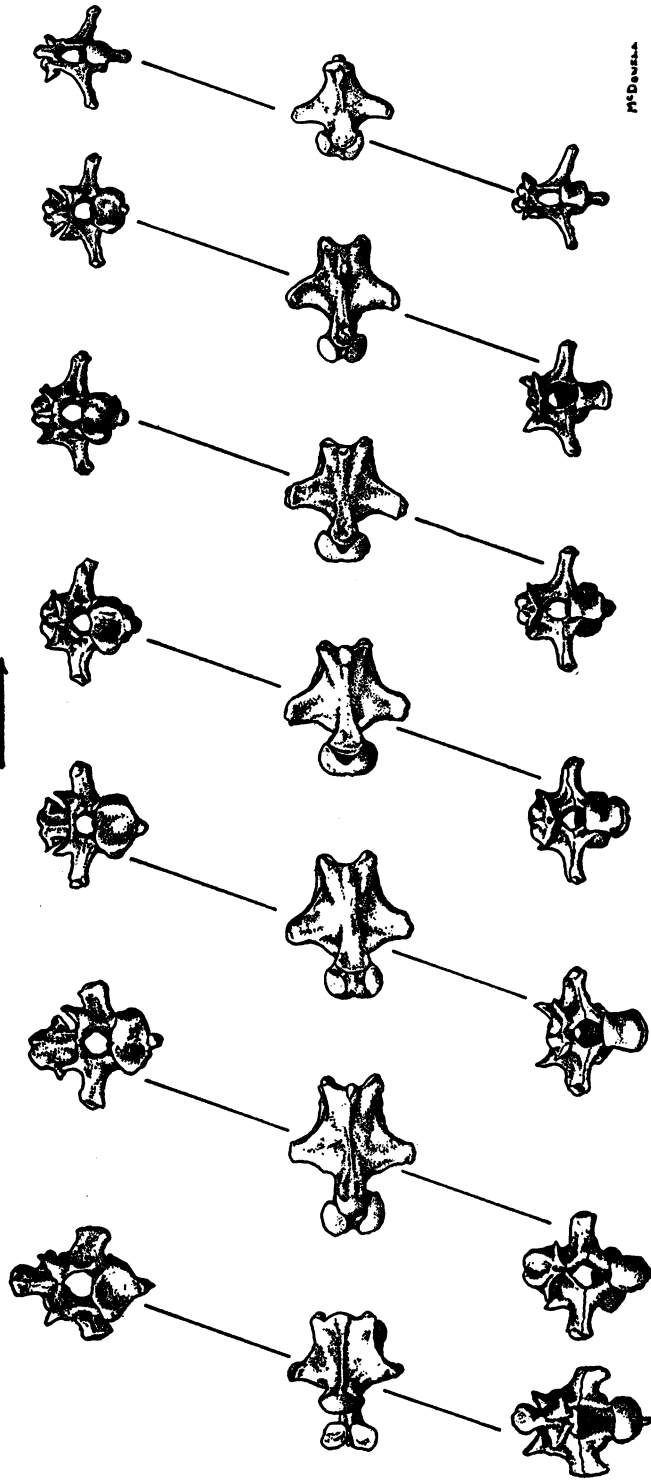
Fig. 11. Cervicals 2 to 8 of *Podocnemis expansa*. A.M.N.H. No. 6823. Upper row: anterior view. Middle row: ventral view. Lower row: posterior view. X⅔.
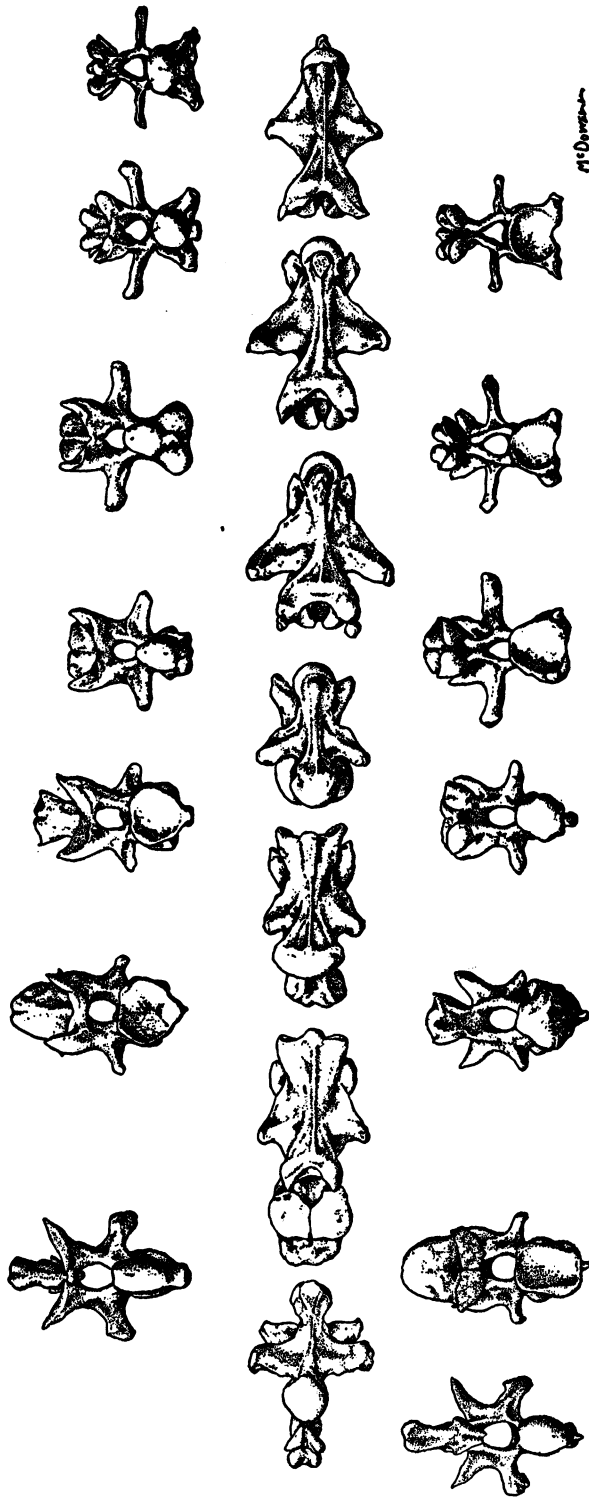
FIG. 12. Cervicals 2 to 8 of *Chelus fimbriata*. A.M.N.H. No. 6596. Upper row: anterior view. Middle row: ventral view. Lower row: posterior view. ×⅘.

other transitional joints at the two ends of the neck, perfect saddle joints occurring only on the middle centra.

Different authors (Baur, 1888c; Wieland, 1902) have described such columns in very different terms. In part these divergent de-scriptions are a consequence of the difficulty of describing a complex situation in simple terms; in part they probably reflect real, though slight, differences in the shape of the joints in individual specimens.

Double joints are unknown.

GROUP 6. CHELIDAE

The Chelidae in all certainly known instances[1] have the fifth and eight centra biconvex, but the specimen list is by no means extensive enough to rule out even fairly high frequencies of variation.

The cervical central joints of *Chelus fimbriata*, usually classed as simple and spheroidal, are at best modified, even distorted, versions of such joints. Joint VIII, in particular, is very much modified: it is elongate dorsoventrally and better interpreted as cylindrical than spheroidal. In *Chelodina longicollis*, on the other hand, as Vaillant observed in one specimen available to him and as the author has seen on one specimen at Yale University, joint VII is truly spheroidal, tending to be broadened transversely. The significance of this character in the two species is unknown.

Double joints are not, so far as the present author has seen, ever present in these pleu-rodires. One such joint was, however, recorded by Sir Richard Owen (1853, p. 186) in *Chelus fimbriata*. According to Owen joint VII of this specimen was double: "The sixth vertebra is concave before and presents two convexities behind; the seventh vertebra has a corresponding double concavity in front and a deep vertical groove in back." Although this observation ascribes to a pleurodire a character supposedly characteristic of, and unique in, the other living suborder, yet, since this description is circumstantial and in other respects (position of biconvex centra, vertical elongation of joint VIII) in complete agreement with the observations of other authors, and in view of the fact that only 14 other cervical columns of this species (only 30 of the entire family) have been described, it is not possible to dismiss out of hand Owen's statement as mistaken.[2] Conspicuously, much more material needs to be studied.

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[1] Nopcsa (1923, p. 34) lists the third and eighth centra as biconvex in *Chelus fimbriata*, but his table does not profess to be more than a compilation, and as such there is at least one other error in the list (*Chisternon*), as Wiman (1933) has already noticed.

[2] The statement is so anomalous, however, that it has been omitted from the tabulations of this paper (table 1, Appendix 1).

DISCUSSION

THE FOREGOING DATA in the case of many species fully satisfy Ford's (1940) definition of polymorphism: "the occurrence together in the same habitat of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation." Three hypotheses may be presented in explanation of this observed phenomenon: (1) random unselected variation, (2) somatic plasticity, and (3) balanced polymorphism.

The first explanation would have us believe that the observed variations, though present in an actively functioning structure and of such a character that they would influence its function, are neutral in selective value and their frequencies the result of an equilibrium between mutation and reverse mutation with perhaps the added effect of genetic drift.

The second explanation would have us believe that the observed cervical central patterns are environmental effects, the result of the plasticity of bone during use. In this case the general plasticity of bone would be selected, not individual cervical central patterns.

The third explanation requires that specific cervical central patterns be specially adapted to special conditions and that polymorphism represents a conflict of advantages resulting in a balance of equilibrium of pattern frequencies.[1]

The present discussion will begin an analysis of the observed facts in terms of these alternatives. Critical evidence is lacking to settle all points. It is, however, possible to eliminate certain hypotheses on the bases of the facts placed in evidence and to define the remaining problems of the observed polymorphism in more precise terms. Selection can be shown to be a major factor in the determination of all cervical patterns, variant and normal. In the immediately following sections, therefore, discussion will be in terms of the presumed effects of selection considered at three levels: (1) adult structure, (2) genetic mechanisms, (3) ontogenetic mechanisms. A final section will very briefly summarize the results of these sections and state the remaining problems. All discussion in these sections will be necessarily inferential; direct evidence of selective effects, such as might, for example, be gained from comparison of the frequencies of cervical patterns in young populations and in adults, must await additional material and study. The data here assembled are derived from adult specimens only, on which selection has presumably already acted and from which the effects of selection can be inferred only negatively from the absence of expected classes.

OBSERVED FACT: INTRASPECIFIC VARIABILITY

Type	Random (unselected) genetic variation, or neutral polymorphism	Environmental effects, or somatic plasticity	Channeled genetic variation, or balanced polymorphism
Adaptive value	Non-adaptive	Adaptive but non-specific in adaptation	Adaptive and specific in adaptation
Cause	Mutation and genetic drift	Selection	Selection

SELECTION AND ADULT STRUCTURE

In beginning the interpretation of adult cervical central patterns it is necessary to have in mind that the differentiation of each joint apparatus is essentially independent of the formation of the main bodies of the centra between which it lies and that in consequence the shapes of the centra in macerated skele-tons, whether procoelous, opisthocoelous, amphicoelous, or biconvex, are the secondary and rather accidental result of the differentia-

[1] It is not possible as a practical matter to distinguish between balanced polymorphism as here defined and long-term transitional polymorphism (see Ford, 1940). The important feature in both these possible conditions is specific adaptation of specific patterns.

tion of the joint apparatuses. Figure 13 will make this visually clearer. A and B indicate the changes that occur in convexo-concave variation: the modification of the joint and the resulting change in central shape. C and D show that the change from double to simple joints, or the reverse, is rather similar and is equally independent of the centra themselves.

Thus, while functionally the shapes of the centra considered as unit elements are highly
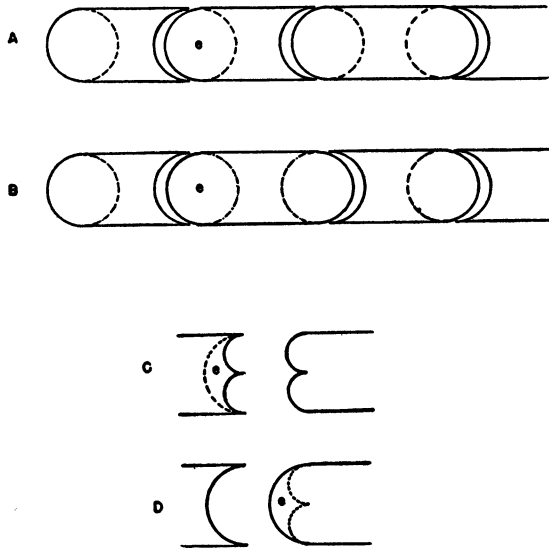

FIG. 13. Diagram to show the nature of the changes involved in joint variation. A, B. Convexo-concave variation. C, D. Variation in doubling. *Abbreviation:* e, an epiphysis that may be attached to one vertebra or the other.

significant, ontogenetically efficiency of function is dependent upon the shaping of the individual joint apparatuses between them. If, therefore, natural selection has been effective in building up or conserving the functionally most efficient series of central shapes, it has acted by means of and on joint variability. The special characters of joint variability that have been recorded in the previous section are explained in terms of the effects of selection.

Let us now examine the observed characters of joint variability to see how far they fit this concept.

In the placement of convexities and concavities usually changes are abrupt; lessened convexities and concavities and plane joints,

although not absent, are far less frequent than modifications which transform a perfectly formed procoelous joint into a perfectly formed opisthocoelous joint, or the reverse. Changes of this sort could be classified without hesitation and with perfect correctness by someone wholly unfamiliar with the material. In the case of doubled joints, on the contrary, intermediate conditions are commoner than completed changes. Classification of these changes is often a dubious and difficult matter of judgment.

In terms of selection, and in no other terms, the explanation of this difference appears to be rather simple: special shapes of centra have more or fewer advantages, but the general mobility of the neck is more important still. All changes that limit the general mobility of the neck are therefore at a considerable disadvantage and tend to be suppressed. The structural intermediate between convexities and concavities are weakened convexities and concavities or plane joints, conditions that would limit the mobility of the neck. These types of joints tend therefore to be infrequent or rare.

Doubleness, on the contrary, has as its reason for being a specific kind of restriction of joint mobility, restriction of lateral motion. The same purpose can, however, be served, at least to some degree, by other modifications of the vertebrae, for example, by changes in the angulation of the zygapophyses, or very simply by mere broadening of the appropriate cervical joints.

This restriction of lateral motion, while it is certainly of some importance, is probably not of such fundamental functional significance as the presence of well-formed convexities and concavities. In this connection it may be noted that changes in doubling are usually in the direction of simplicity, less frequently towards increase in the number of double joints.

Changes in doubleness are thus less important in the first place and more easily compensated in the second than changes in the character of convexities and concavities. Selection acts less severely, and a wide range of variability is permitted to be expressed.

This permitted range of variability is markedly regional; variation in doubling, indeed the doubled condition itself, is almost

restricted to posterior joints (table 5). (That it does very rarely occur elsewhere we have seen from the extraordinary asymmetrical doubling of joint IV in *Testudo pardalis*.) Even in posterior joints variation in doubleness is usually restricted to the marginal joints of that series in which doubling occurs, though this again has exceptions.

The effects of selection seem rather evident here. The implication would seem to be that the capacity to vary is present in all joints alike, but that functionally doubling is most useful in joint VIII and of marginal utility for other posterior joints and probably distinctly unfavorable for anterior joints. Very likely the real range of variation in doubling, of which the observed variation that has been cited here is an imperfect sample, reflects rather accurately for each joint in each species the selective value, positive, negative, or neutral, of the doubled character.

Variability in the placement of convexities and concavities is similarly different in different joints. It is a clear-cut, though complex case, worth analyzing in some detail.

In table 5 is marked every joint that has

TABLE 5

INCIDENCE OF VARIATION AND DIFFERENCE

	Intra-specific	Supra-specific
Variation and difference in doubling		
II	—	—
III	—	—
IV	x	—
V	—	—
VI	x	x
VII	x	x
VIII	x	x
Cervico-dorsal	x	x
Convexo-concave variation and difference		
II	x	x
III	x	x
IV	x	x
V	x	x
VI	—	x
VII	x	x
VIII	x	x
Cervico-dorsal	—	x

varied intraspecifically in the position of its convexities and concavities and every joint that is different in different taxonomic groups. It will be seen that all but two of the joints vary intraspecifically, and none is without difference between groups (at least at the superfamily level). Since there is every reason to believe that those differences which are taxonomic characters are not different in kind or origin from intraspecific variation but are, in fact, the more or less completely fixed results of the latter, this must mean that every joint in the neck is potentially variable in the placement of its convexities and concavities.[1]

As a trial hypothesis let us assume completely random variation in the placement of the convexities and concavities of the central joints. Considering for the moment spheroidal conditions of the joints only, each joint may be either of two forms: procoelous or opisthocoelous. Leaving out of account, as always, the occipitocervical articulation, there remain eight joints, II to IX, which theoretically may vary. There should be then 2^8, or 256, possible combinations of individual joint conditions, that is to say, 256 possible cervical central patterns with spheroidal joints only.

Compare now this hypothetical potential of variation with the observed facts. In reality, when every known cervical central column is taken into account, only 16 of the supposed 256 possible patterns are known, whether as normal characters of species or as intraspecific variants. Consideration of plane and saddle joints (which should increase the

[1] The argument which the above paragraph is intended to counter is the often-proposed alternative explanation of the absence of certain conceptually possible conditions in living populations: that these conditions are for unknown reasons genetically impossible. It might be supposed, for example, that the observation that certain joints in turtles are never opisthocoelous is analogous to the observation that roses are never blue and is true for a similar reason (because mutation to the unknown condition is, or seems to be, impossible). This is, of course, not an explanation; it merely removes the problem from one level to another, without, indeed, ruling out the hypothesis of selective effect. Aside from that point, however, the conception would not seem to be pertinent here. The required changes did occur in the past in the origin of certain taxonomic groups and their non-appearance in other lines today requires explanation.

potential of variation to 4^8, or 65,536) increases the known number of patterns to only 21.

Table 6 lists the 16 major cervical central patterns. This table is worth considerable attention; certain regularities and recurrences are very evident in it.

TABLE 6

SUMMARY OF ALL TYPES OF CERVICAL CENTRAL PATTERNS KNOWN TO OCCUR IN TURTLES NORMALLY OR AS INTRASPECIFIC VARIATION (OMITTING THE FACTOR OF DOUBLING)

1. (2(3(4)5)6)7)8)
   Known in *Chelydra, Macrochelys, Kinosternon, Clemmys, Gopherus, Testudo, Caretta, Dermochelys*

1a. (2(3(4)5)6|7)8)
   Known in *Chelonia, Eretmochelys, Caretta, Lepidochelys, Dermochelys*

2. (2(3)4)5)6)7)8
   Known in *Kinosternon, Sternotherus, Chelydra, Kinixys, Testudo Staurotypus, Claudius*

2a. (2(3)4)5)6|7)8)
   Known only in one specimen of *Eretmochelys imbricata*

3. (2)3)4)5)6)7)8)
   Known in *Dermatemys, Kinosternon, Erymnochelys, Pelomedusa, Pelusios*

3a. (2)3s4s5s6s7)8)
   Known only in *Podocnemis*

4. (2(3(4)5)6)7(8)
   Known in *Batagur, Chrysemys, Clemmys, Cuora, Deirochelys, Emys, Chinemys, Geoemyda, Malaclemys, Orlitia, Pseudemys, Siebenrockiella, Hieremys, Terrapene, Gopherus, Testudo, Platysternon, Ocadia*

5. (2(3)4)5)6)7(8)
   Known in *Chrysemys, Clemmys, Hardella, Pseudemys, Terrapene, Gopherus, Acinixys, Homopus, Kinixys, Testudo*

6. (2)3)4)5)6)7(8)
   Known in *Bellemys* and *Testudo*

7. (2(3(4(5)6)7(8)
   Known in *Clemmys, Chrysemys, Terrapene, Chelys, Chelodina, Emydura, Phrynops, Batrachemys, Hydraspis, Hydromedusa, Mesoclemmys, Platemys, Testudo*

7a. |2(3(4(5)6)7(8)
   Known only in one specimen of *Pseudemys floridana*

8.)2(3(4)5)6)7(8)
   Known only in one specimen each of *Testudo leithii, Testudo elephantopus,* and *Clemmys insculpta*

8a. s2(3(4)5)6)7(8)

TABLE 6—*Continued*

Known only from a single specimen of *Pseudemys scripta*

9.)2(3)4)5)6)7(8)
   Known only from one specimen of *Testudo elegans*

10.)2)3)4)5)6)7(8)
    Known only from one specimen of *Testudo leithii*

11.)2)3)4)5)6)7)8)
    Known from seven specimens of *Bellemys arachnoides*

12. (2(3(4)5)6(7(8)
    Known from *Chrysemys, Graptemys, Pseudemys, Terrapene*

13. (2(3)4)5)6(7)8)
    Known from one specimen of *Testudo gigantea*

14. (2(3(4(5(6(7(8)
    Known only in *Carettochelys*

15. (2(3(4(5(6(7(8–
    Known in *Chitra, Cycloderma, Dogania, Lissemys, Pelochelys, Trionyx*

16. (2(3(4(5)6|7)8)
    Known only in *Chelonia mydas*

First, the same patterns occur time and again, sometimes in genera and families not at all closely related, and both as normal patterns and as intraspecific variants.

Second, every joint in the testudinate neck except the cervico-dorsal may adopt either of the two alternatives, procoelous or opisthocoelous. The cervico-dorsal is either absent (a ligamentous connection only) as in the Trionychidae or always procoelous as in the majority of turtles, cryptodire and pleurodire alike.

Third, joint VI is procoelous without variation in most turtles, cryptodire and pleurodire. It is opisthocoelous only in the Carettochelyidae and Trionychidae.

Fourth, centra 3, 4, 5, and 8 are never amphicoelous. Centra 2, 6, and 7 may be amphicoelous.

Fifth, centrum 6 is never biconvex, centrum 7 may rarely be biconvex, but centrum 2 may be procoelous, opisthocoelous, amphicoelous, or biconvex, or may have a plane or a saddle joint in front.

Sixth, alternations of biconvex and amphicoelous centra never occur in the middle of the cervical column, though they may occur at either end.

Such very general statements are, of course, not completely justified by present material.

The number of species and of specimens examined is certainly not sufficient to present these inductions as truths not to be questioned. They should stand rather as indications supported by the weight of the present evidence.

Evidence of the action of selection can be seen in all these regularities. The frequent occurrence of the same pattern as a taxonomically constant feature of one species or family and as an intraspecific variant in some species not at all closely related is, for example, rather certainly meaningful. The pattern of the Chelidae of the Suborder Pleurodira is repeated as an intraspecific variant in *Chrysemys*, *Pseudemys*, *Clemmys*, *Terrapene*, and *Testudo*. The pattern of the primitive pelomedusids of the Suborder Pelurodira is mimicked by certain individuals of the genus *Kinosternon* of the Suborder Cryptodira. Such parallel phenomena surely imply that the patterns repeated in this fashion are superior functionally and so selectively favored over their theoretical alternates of the "potential of variation."

Again the fact that the cervico-dorsal joint is never opisthocoelous must be correlated with the fact that this joint as the point of connection between the immobile dorsal column and the mobile neck is the most important center of motion of the neck in every testudinate. Similarly the fact that joint VI is in most turtles the second most important center of motion of the neck must be the explanation of its constancy within species, indeed within superfamilies (see fig. 14).[1]

These joints are presumed to be held constant because of their rigid functional requirements. The converse of this should also be true: joints less restricted in their functional requirements should be less constant. Joint VII, which is often plane in the

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[1] The cervico-dorsal joint in turtles would seem to be an example of the general rule often noticed that the condyle is on the more distal, mobile element, the cotyle on the proximal, immobile part. In most turtles joint VI is similar, the three vertebrae, the sixth, seventh, and eighth, remaining usually relatively rigid in their relation to one another, acting as a unit.
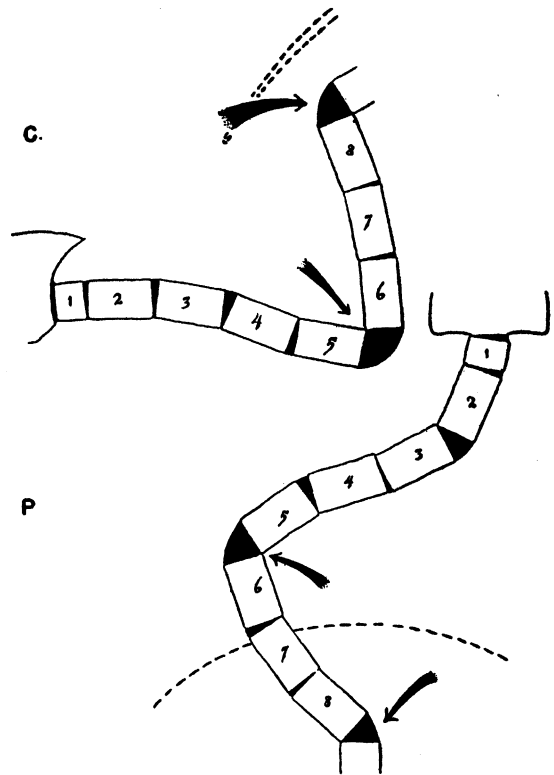
FIG. 14. Centers of motion in the testudinate neck. Arrows indicate points of greatest flexure or centers of motion. Dotted lines indicate edges of shells. *Abbreviations:* C, cryptodire; P, pleurodire.

Cheloniidae and Dermochelyidae and variable in emydines, may be an example of this condition, and so may be joint II, which is always feeble and sometimes plane.

Even variable joints, however, seem to be prohibited from varying in certain combinations which might produce unfavorable central shapes. This, for example, would seem to be the most reasonable explanation of the absence of amphicoelous vertebrae in certain positions.

In summary, all that we learn from adult structure tends to eliminate the idea of randomness in the incidence of patterns. Patterns are at least negatively controlled; some types of patterns, presumably deleterious in their effects, are never observed.

SELECTION AND GENETIC MECHANISMS

There are a few bits of evidence that can be pieced together from the data that bear on genetic mechanisms.

A first such bit of evidence is the fact that peculiar variants and peculiar frequencies of variation tend to be highly characteristic of taxonomic units. A condition with all the cervical centra procoelous is, for example, unique to the peculiar Malagasy species, *Bellemys arachnoides*, occurring in seven out of 88 specimens of that species. The one other pattern known in *Bellemys*, that with the second centrum biconvex, though very frequent in this species, is rare in most related forms. In another Malagasy tortoise, *Testudo radiata*, there is similarly a very special and characteristic frequency of patterns. In this instance the condition with the second centrum biconvex alternates with one with the third centrum biconvex, the latter being much the more frequent condition. A third condition in which the fourth centrum is biconvex, unknown in *Bellemys*, is present, though rarely, in *T. radiata*. In the South American *T. denticulata* this third condition occurs in about one-third of the studied specimens, while the typical condition of *T. radiata* is that of most of the remaining two-thirds; the condition so frequent in *Bellemys*, that with the second centrum biconvex, is in its turn rare in *T. denticulata*. In the Galápagos tortoises 86 per cent of the studied specimens show the fourth centrum biconvex as in one-third of *T. denticulata;* 14 per cent show the third centrum biconvex as in 84 per cent of *T. radiata*, while the condition with the second centrum biconvex, present in 92 per cent of *Bellemys*, is unknown in the Galápagos forms. The sample sizes for these cases, while not consistently large, are suf-ficient to dismiss the hypothesis of sampling error. Nor are these cases at all atypical. Compare the marked differences in frequencies of patterns between *Chelydra serpentina*, *Sternotherus odoratus*, and *Kinosternon flavescens*, or between *Terrapene carolina* and *Terrapene ornata*.[1]

Only a few (two to six) of the 256 theoretically possible patterns are found in any species, although several samples exceed 75, and one approaches 200. Further, of these few classes existing in any species, the two most frequent account for over 90 per cent of the sample in every case except one, and in this single exception (*Testudo pardalis*) the two most frequent classes account for over 80 per cent of the sample, while the third most frequent class carries the total well over the 90 per cent mark.

These facts would seem to narrow the possibilities for genetic explanation of the variations that have been described here. The hypothesis of complete phenotypic lability (somatic plasticity) would seem to be rejected. On the other hand it is not safe, in absence of breeding experiments or analysis of broods, to espouse without qualification an explanation of these differences in terms of gene frequency. Alternative genetic explanations are possible (see footnote, p. 545), but no evidence exists upon which to choose among them.

For the present it suffices to recognize that a determinate type of inheritance is indicated and that in all species the character of the central articulations is apparently of sufficient selective importance that the number of phenotypes resulting from the underlying genotypes, whatever they may be, is of a limited and defined character.

SELECTION AND ONTOGENETIC MECHANISMS

Since selection, if it has been effective at all, has certainly been effective at still another level, the level of the ontogenetic mechanisms which determine directly the character of the central joints, it will be valuable to examine the little that is known about these mechanisms, their action, and their evolution.

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[1] There is even a hint of very local racial differences in pattern frequency. All three of the only known instances of variation of joint VII in *Chrysemys picta* were obtained in the same collection from the same lake in New Jersey. Two of the three are asymmetrical double joints. All three are subadult specimens. The asymmetric joints might, in this case at least, be reasonably interpreted as examples of incomplete "penetrance."

In rough outline the descriptive embryology of the joint apparatuses is well understood. In early stages the vertebral centra are joined by dense masses of precartilage or early cartilage cells, the intervertebral discs. Within these discs, in later stages, the joint cavities appear by lysis *in situ*, the resulting joint surfaces having from the first essentially the shapes they will have in the adult. Ultimately ossification extends from the main bodies of the centra into the joint heads and joint sockets which have been outlined by the formation of the joint cavities. Completion of this ossification may, however, be long delayed, so that in young turtles the largest portion of both the cup and ball of each joint may still be cartilaginous.[1]

The mechanism of determination of the shape of the joint cavity, and thus the placement of cup and ball, is not known nearly so well. From various evidences, it may, however, be inferred that the differentiation of the central joints in testudinates involves two separate and successive processes.

There must be, first, a basic developmental mechanism (supported by a genetic control which is rarely ineffective) that has the function of determining joint areas that have the potentiality of becoming either procoelous or opisthocoelous but that do not yet have fixed fates. There must be, second, a mechanism, superimposed upon the first, acting triggerwise to complete the differentiation of the joint areas, coverting them from regions prepared to differentiate in one of two ways into regions set definitely upon that course that will result in the adult condition.

Such a succession of two levels of central determination would provide simultaneously the necessary ontogenetic basis for complexity in central patterns and a possibility of varying these patterns. For the turtles, however, this succession is hypothetical, logically inferred but not concretely demonstrated.

As the description of the embryology of testudinate joints immediately above plainly shows, the first of the two processes must in turtles normally be the determination of an area without well-marked boundaries, not

manifesting any visible signs of independence. Apparently only very rarely, as in the case of Vaillant's "epiphysis" (e in fig. 13), cited on page 524 above, does this area become so distinctly differentiated that it has its own center of ossification, while somewhat less rarely, as in the "amphicoelous" joints of the Emydinae, Testudininae, and Chelydrinae, the same areas may assert their independence by remaining cartilaginous in the adult.

Perhaps in older forms, as paleontological evidence tends to show, "epiphyses" in Vaillant's sense may have been more frequently, if still imperfectly, realized. In several of the later Amphichelydia in which most of the joints between centra were completely formed and well differentiated, the fourth centrum (which in many modern turtles is biconvex) was biconcave, forming "amphicoelous" joints with the third centrum in front and the fifth centrum behind. This condition is known in *Baena riparia* (May, 1908), *Chisternon hebraicum* (A.M.N.H. No. 5904), both of the North American Bridger Eocene, and in *Meiolania platyceps* (Anderson, 1925) of the Australian Pleistocene.

It is quite improbable that joints IV and V in these late and advanced Amphichelydia were notochordal. It is more reasonable to interpret the condition of these extinct forms in terms of the "amphicoelous" joints known in modern cryptodires and to assume, therefore, that the spaces left between the third and fourth and fourth and fifth centra were filled in life by epiphyses, probably cartilaginous and probably the normal adult condition in these forms.

The fact remains, however, that in no turtle has a free "epiphysis" actually been seen, such that it might attach to one centrum or to another. Vaillant's "epiphysis" in *Emys orbicularis* was already fused, and even in the Amphichelydia mentioned above the concavities of the fourth centrum were feebler than those of the opposed third and fifth, probably indicating that the cartilaginous epiphyses were fused and that ossification had to some degree extended into them from the body of the fourth centrum. Thus it would appear that in turtles the second part of the postulated ontogenetic process, the determination of the fusion of epiphyses, must have its effect so early that epiphyses

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[1] These phenomena are described from slides of developing vertebrae in *Emys orbicularis* examined by the courtesy of Dr. B. W. Kunkel and from skeletons of very young *Chrysemys picta* personally prepared.

VERTEBRA
6 ⟶

ARTICULAR
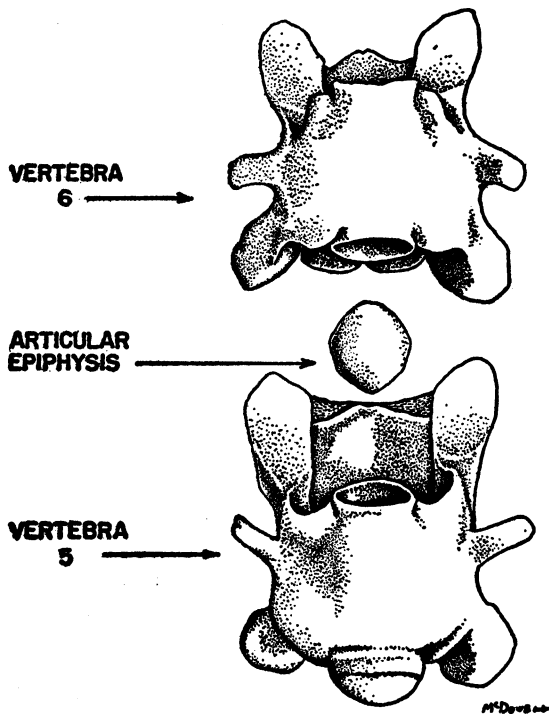EPIPHYSIS ⟶

VERTEBRA
5 ⟶

FIG. 15. Vertebrae 5 and 6 of *Megophrys boettgeri*. A.M.N.H. No. 28801.

are virtual rather than real.

Fortunately there are in other orders instances in which the conjectured two-level ontogenetic mechanism is more satisfactorily demonstrable. In the Salientia, for example, in certain forms, at least—as was first shown by Dugès in 1834—the embryonic intervertebral discs regularly ossify as distinct elements, little spheres of bone, which, if they attach to the centra in front of them, make these centra procoelous, or, if they attach to the centra behind them, make these centra opisthocoelous.

This condition, as Boulenger (1908), Noble (1931), and others have pointed out, is easily demonstrated in the genus *Megophrys* (Pelobatidae). Figure 15 shows the intervertebral sphere that belongs between the fifth and sixth centra of *Megophrys boettgeri* (A.M.N.H. No. 28801). When these vertebrae were first disarticulated the ball was apparently part of the posterior (sixth) vertebra. It proved, however, to be readily movable in its socket and was teased out for the illustration here presented. The vertebral column of this specimen has a most peculiar central pattern, the

second through sixth centra being opisthocoelous, the seventh biconvex, the eighth, ninth, and tenth procoelous. The intervertebral spheres were in every case attached to one or another vertebra, but not coössified. A second specimen of the same species examined (A.M.N.H. No. 28778) has the spheres so attached as to make all the vertebrae procoelous.

Such conditions as these are clearly visual verifications of the sort of two-level mechanism that we have supposed to exist in the turtles. In these Salientia it is accompanied (as is already apparent) by many instructive parallels to the situations that have been reported in the turtles. The ontogenetic means to achieve complexity exists, and in advanced forms (the Diplasiocoela of Nichols, 1916) normal complexity has been achieved: the ninth vertebra is normally biconvex and the eighth normally bicoelous in *Rana* and its relatives. Intraspecific variation like that of the turtles is also possible, and, as we have already seen in *Megophrys*, does occur. Even the extraordinary asymmetrical double articulations of the Testudinidae (above, p. 524) have an exact parallel (C. L. Morgan, 1886).

In the Caudata also a two-level mechanism of joint determination is a matter of direct observation (Moore, 1900), and, as J. Anderson (1878, p. 849) found in *Tylototriton verrucosus*, both complexity and intraspecific variation are present in this order also. Anderson describes a biconvex vertebra in the tail of *Tylototriton*, the vertebrae in front of it being opisthocoelous, those behind it procoelous; in one of the two specimens he examined, the biconvex centrum was the sixteenth caudal, in the other the twenty-fifth. (Anderson's observations have not apparently been repeated by any one else.)

In the Sauria, on the other hand, there is not known to the present author any example either of complexity or of intraspecific variation. In this suborder wherever formed joints exist (and in a large subdivision, the Gekkota, they are mostly absent) they are always procoelous. The vertebrae in this group have, it appears, always been either procoelous or, as primitively in all reptiles, amphicoelous; there has, so far as known, never been in any lizard anything but a uniform series of joints

formed on a uniform plan. There has been, therefore, no necessity for, and there is no indication of, an ontogenetic mechanism providing for complexity in central pattern by means of a two-level determination of joint surfaces. Apparently both the capacity to achieve complexity and the correlated capacity to vary central joints intraspecifically are absent in this group. If this be true, it is a genuine limitation upon the variability of lizards—a genuine limitation of their evolutionary potential.

An ontogenetic mechanism providing for the possibility of complex central patterns has, it would seem, never been a selective necessity in the lizards. In the turtles it has apparently been of importance since the Cretaceous. When for the first time formed joints between centra appear in turtles (in the Baenoidea of the Cretaceous; see Appendix 2) the joint heads and joint sockets are not yet perfectly differentiated, the bony convexities are small and feeble, the concavities disproportionately large, but already the placement of convexities and concavities is complex.

Complexity is thus primitive in turtles. The reason would seem to be the special mechanical problems which the presence of a shell entails for turtles. Two facts are important here: (1) the neck of turtles is fixed to an immovable block of dorsal vertebrae embedded in the shell; (2) the neck must compensate by its own mobility for the locomotor inadequacies of the remainder of the body. Special mobility in a structure fixed to an immovable fulcrum results in important consequences in the thrust relationships of the centra. Under such circumstances the intercalation of a biconvex centrum at some place in the neck, even in very primitive forms, is readily interpreted as an adaptive necessity, and the evolution of the ontogenetic mechanism required to produce such a centrum is similarly a phenomenon of adaptation and selection.

A complex pattern had in primitive turtles, it appears, a considerable selective advantage over a simple one. Nevertheless it was no easy matter to arrive by random change at the delicate balance of competing ontogenetic processes that would constitute a developmental mechanism which could

evoke the functionally most efficient complex pattern in the adult. The evolution of complexity in central pattern must have involved several stages.

In the Tetrapoda formed joints between centra appear to have an advantage over an amphicoelous condition. Formed joints have been several times evolved in unrelated groups—independently in the Salientia, Caudata, Crocodilia, Sauria, Saurischia, Ornithischia, Aves, and Mammalia, as well as in the Testudinata. It was probably advantageous to the early turtles of the period of beginning modernization to evolve formed joints even if the optimal condition was not immediately achieved. Selection would operate against the maintenance of this non-optimal condition, and lability to the extent that it permitted closer approaches to the optimum would be selectively favorable. At such a period the ontogenetic mechanism to which we refer the possibility of central variation in modern forms must have been built up.

We are suggesting here an early period of experimental variability, such as has been well documented for certain forms (†*Henricosbornia*, Simpson, 1937). For the turtles and especially for their cervical vertebrae (so infrequently preserved) such a period is largely an inference, but there is in at least one case a hint of such a condition. †*Neurankylus bauri* of the Cretaceous of North America, in the single specimen in which the neck is known, shows the pattern (2((3((4))5))6((7((8) (Wiman, 1933), a pattern otherwise known as a rare abnormality in modern testudinids. If this condition is an abnormality in †*Neurankylus* it bespeaks either extreme sampling error or a higher frequency of intraspecific variation in these older turtles. If it was normal for the species it indicates that patterns no longer of sufficient selective value to be fixed in any living species were during the Cretaceous being tried out, later to be lost. In either case the specimen points with some probability to a period of experimental variability, whether at the infraspecific or the specific level.

Thus from the point of view suggested here the two-part ontogenetic mechanism which makes possible the variability of modern species is a survival from an older period of variability which preceded the achievement

	II	III	IV	V	VI	VII	VIII	IX
Emydinae Testudininae								
Emydinae Testudininae								
Bellemys Testudo								
Testudo Chelidae								
Testudo								
Testudo								
Testudo								
Chrysemys Terrapene								
Testudo								
Chelydrinae Cheloniidae Testudo								
Staurotypinae Kinosterninae, Testudo								
Dermatemys Kinosternon								
Bellemys								
Carrettochelys								
Trionychidae								
Chelonia								

FIG. 16. An interpretation of the 16 cervical central patterns in terms of morphogenetic fields. Solid: field of opisthocoely; stippled: field of procoely. Roman numerals indicate joints affected.

of the complex patterns of modern forms.

Complex central patterns are made possible by the two-step process that has been suggested, but they are probably organized as patterns by morphogenetic fields. Readers may have already arrived at an interpretation of central change in turtles in terms of the field concept from the inspection of figure 3, showing an apparent change in the position of the biconvex vertebra. Figure 16 interprets in terms of advancing and retreating fields of procoely and opisthocoely all the 16 major cervical central patterns. The fields are conceived of as acting trigger-wise in the second step of the two-step process of joint differentiation. It will be noted that in several instances the fields involved are small. Such small fields must be matters of such delicate ontogenetic balance that a priori (on thermodynamic grounds) they would be expected to be subject to much disturbance unless maintained and defended by selection pressure. This argument, of course, applies to all the sets of complex fields indicated in the figure. Complex fields, simply because of their organized complexity, are more liable to deterioration and disorganization than any simple field. They are unlikely to be maintained except by constant selection pressure. From this point of view, therefore, the perpetuation of complexity is per se evidence of selection.

SELECTION AND POLYMORPHISM

The discussion thus far enables us to circumscribe and define the limits of polymorphism in cervical central patterns and to assess the problems involved with greater clarity. It should be evident, for example, that theories, whether of environmental effects or of neutral polymorphism, that assume that every joint in the neck may be labile are conspicuously out of harmony with the facts. The places and modes of action of environmental effects or of neutral genotypic polymorphism are limited, if they are not absent. Generalized environmental effects and generalized neutral polymorphism are ruled

TABLE 7

Pattern Frequencies of Various Testudinidae in Per Cent

Species	Patterns*											Total No. of Specimens
	N	II	IV	V	VII	VIII	III IV	II III IV	IV VIII	II III IV VIII	9th Cervical	
Emydinae												
Chrysemys picta	93	—	4	1	2	—	—	—	—	—	—	195
Clemmys insculpta	74	7	—	7	—	12	—	—	—	—	—	27
Emys blandingii	96	—	—	—	—	—	—	—	—	—	4	28
Graptemys pseudogeographica	94	—	3	—	—	3	—	—	—	—	—	26
Pseudemys floridana	83	—	15	2	—	—	—	—	—	—	—	40
Pseudemys scripta	88	1	6	—	3	1	—	—	—	—	1	82
Terrapene carolina	78	—	13	3	4	2	—	—	—	—	—	103
Terrapene ornata	93	—	5	—	—	2	—	—	—	—	—	60
Testudininae												
Testudo elephantopus	84	3	13	—	—	—	—	—	—	—	—	31
Testudo graeca group	77	—	19	—	—	—	2	2	—	—	—	47
Testudo pardalis	64	—	19	—	—	3	3	—	11	—	—	36
Testudo denticulata	28	—	64	4	—	—	4	—	—	—	—	25
Testudo radiata	3	—	84	—	—	—	10	—	3	—	—	37
Bellemys arachnoides	—	—	—	—	—	—	92	—	—	8	—	88

* For notation, see page 517.

TABLE 8

PATTERN FREQUENCIES OF CHELYDRIDAE IN PER CENT

Species	Patterns[a]			Total No. of Specimens
	P	IV	III, IV	
Chelydrinae				
Chelydra serpentina	98	2	—	95
Kinosterninae				
Sternotherus odoratus	—	99	1	70
Kinosternon flavescens	—	83	17	59

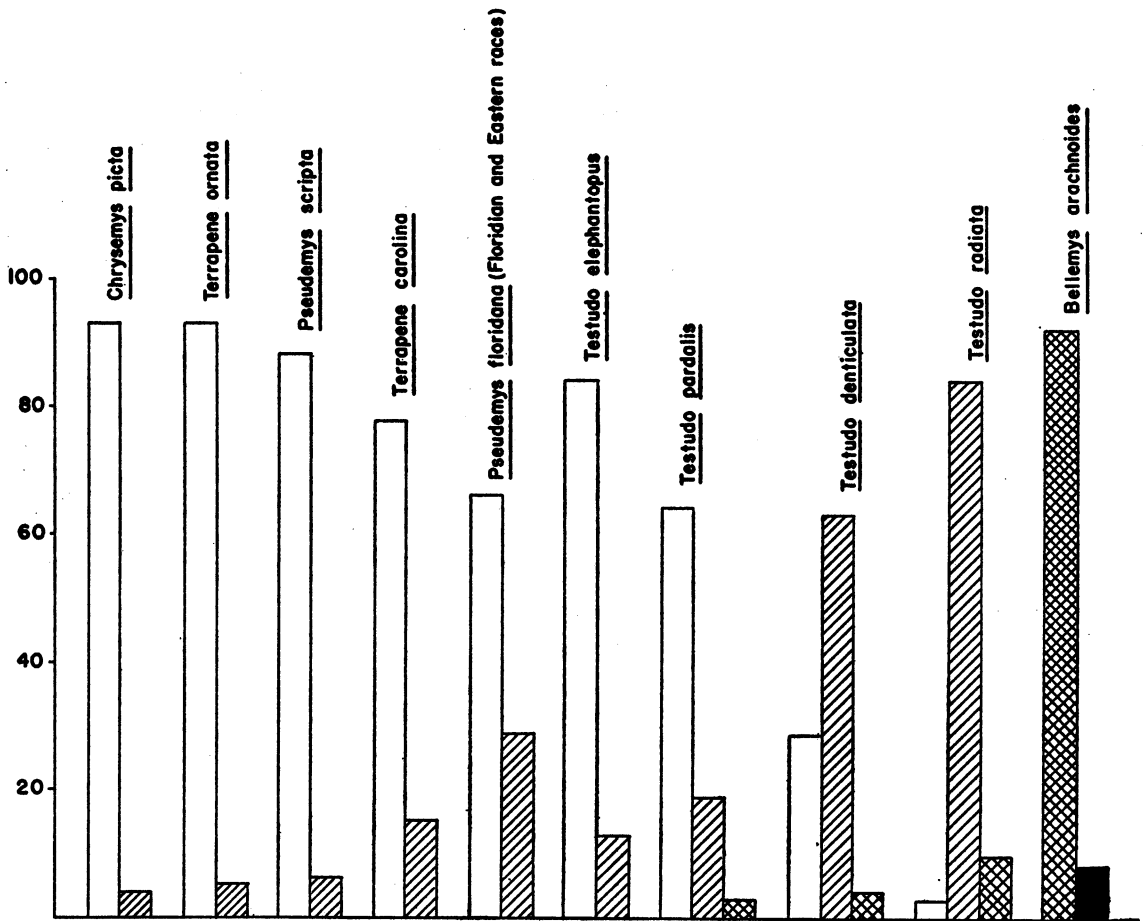[a] For notation, see page 517.

FIG. 17. Frequencies in per cent of certain patterns in some testudinids. Rare patterns are not shown. White: pattern N; hatched: IV; cross-hatched: III, IV; black: II, III, IV, VIII.

out as factors in testudinate cervical structure.[1] Selection has held certain joints constant while permitting or promoting polymorphism in others.

The determination of the neutrality or the selective advantage of the remaining undoubted instances of polymorphism is difficult. Many avenues of analysis have been explored, but none in the present state of evidence give a quite unequivocal answer to the question propounded. A review of the facts will nevertheless be useful.

It must first be realized that polymorphism is known only in three families, Testudinidae, Chelydridae, and Cheloniidae. Polymorphism may occur in the remaining testudinate families; the number of representatives of these that have been studied is not large enough to eliminate that possibility, but obviously the phenomenon in these cannot be discussed. Indeed only for the two families in which it is best known, the Testudinidae and Chelydridae, is any analysis possible, so all the following discussion is of necessity restricted to the two families.

For the reader's convenience tables 7 and 8 repeat in terms of per cent of the sample the better numerical data of tables 2, 3, and 4. The histograms of figure 17 present the same

[1] One sort of environmental effect, however, is not ruled out. It is possible that the environment—perhaps temperature during development—determines increase in the extent of a morphogenetic field and that the latter, acting trigger-wise in the determination of joints, changes a joint that otherwise would have been opisthocoelous to procoelous. In certain cases such an environmental effect might be of a marginal sort so that the field is brought up to threshold strength on one side of a vertebra but not on the other. There should result in such cases asymmetrical double joints of exactly the sort that have been observed. Genetically this phenomenon would be one of "penetrance," and the underlying genotype would in these cases be the same for instances in which a certain joint was symmetrically opisthocoelous, symmetrically procoelous, or asymmetrical.

No known facts contradict this possibility, and it is a reasonable explanation of an important class of observed variations (the asymmetrical double joints). Such a mechanism might be a method of attaining polymorphism that, given a rigorously genetically controlled percentage of penetrance (a condition known to occur; Wright, 1934, 1935), could be even more stable than the alternatives of allelic or inversion polymorphism. In the absence of breeding data the reality of this possible condition cannot be definitely decided, and no further discussion of this point is possible.

information visually for certain members of the Testudinidae.

A very suggestive approach to the examination of these data is a study of the pattern of variation characteristic of the several subfamilies.

To indicate the pattern of variation in a group all the variations known within the group are recorded and placed in a diagram in the relation of their phenotypic divergence from one another (see figs. 18 and 19 for the subfamilies Emydinae and Testudininae).

As was stressed previously (p. 518), in the Emydinae all changes from N, the most frequent, probably primitive pattern, involve only single joints. One variant from the condition of N is very much commoner than any other: this is the pattern designated IV in which joint IV has varied, with the resulting increase by one of the number of procoelous vertebrae in the neck.

Again, as was stressed previously, the Testudininae present a very different picture. Changes from N, still the most frequent condition of most of the species, include not only the same changes of single joints that were present in the Emydinae but also a whole series of apparent combinations of some of these single changes. Further, as figure 19 shows, these combinations can be arranged
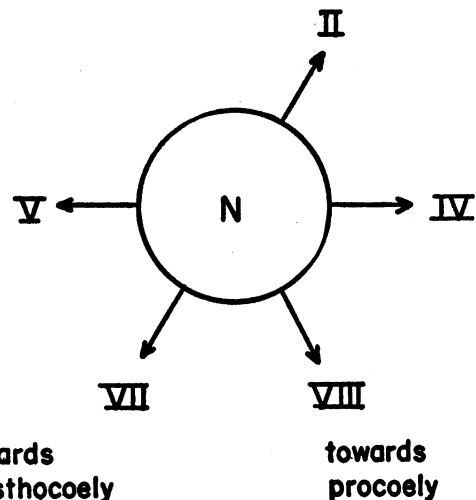

FIG. 18. Pattern of variation in the Emydinae. N and Roman numerals indicate patterns so designated on pages 550 to 552 of Appendix 1. Arrows indicate direction of structural change.
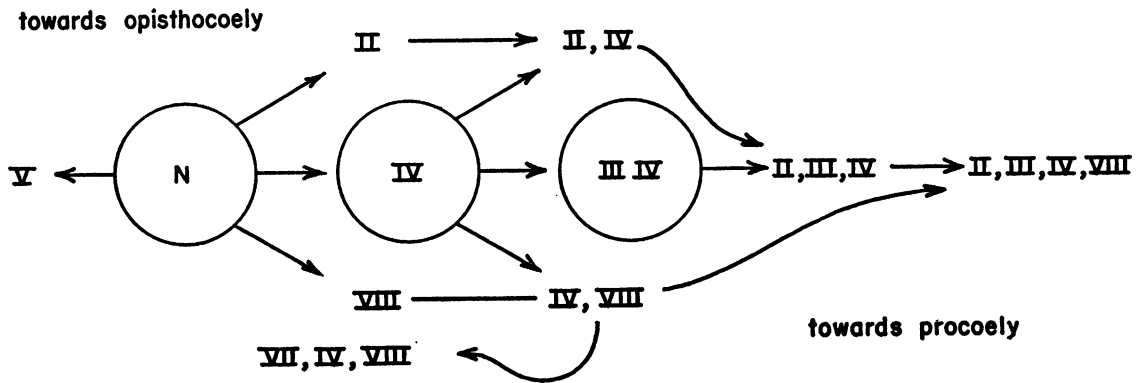
towards opisthocoely

FIG. 19. Pattern of variation in the Testudininae. N and Roman numerals indicate patterns so designated on pages 550 to 552 of Appendix 1. Arrows indicate direction of structural change. See text for further explanation.

in the order of their increasing complexity until they seem to reach a climax in the II, III, IV, VIII variant which occurs in perhaps 10 per cent of the endemic Madagascan tortoise, *Bellemys arachnoides*. Every one of these combinations of joint changes has the effect of increasing procoely in the column, and indeed in every individual species, as in the subfamily as a whole, all the commonest variants, i.e., all those that principally contribute to the polymorphism rampant in this subfamily, have the same effect.

Descriptively as regards phenotypes there can be no doubt that the most advanced variants of the subfamily Testudininae are aggregations or accumulations of single joint changes such as are seen in the Emydinae as well as in the Testudininae. That these more complex changes are also accumulations of genetic changes is certainly a dubious assumption in the absence of all breeding data and all genetic analysis. It will seem a naive identification of gene and character. But, phrased in terms of multiple factors, morphogenetic fields, and thresholds, it is not an improbable hypothesis. Multiple factors could be assumed to have small plus or minus effects on the extent of morphogenetic fields, but given a threshold phenomenon they would be manifest only if the totality of their effects passed a given threshold. The passage of this threshold would mimic the effect of a single gene controlling the affected joints. Changes from the norm involving more than one joint would require a greater accumulation of multiple factors and the passing of

thresholds for more than one joint; the result would mimic because of the threshold mechanism accumulations of genes each controlling a single joint.

This concept, however, lacks proof and is unnecessary for our immediate analysis. A fact of considerable importance emerges from consideration of the phenotypic variants independently of their genotypic basis: Variation in both Emydinae and Testudininae and in every well-studied species within these groups is parallel in trend, differing only in the degree to which that trend is realized. In the Emydinae the trend towards increasing procoely in the cervical column is feeble and only in a few species (*Terrapene carolina*, *Clemmys insculpta*, and perhaps the eastern and Floridian races of *Pseudemys floridana*) is an important element. In the Testudininae on the contrary this trend is always important, and in some forms, e.g., *Testudo radiata* and *Bellemys arachnoides*, has been carried very far.

A trend in variation exactly similar in direction occurs also in the Chelydridae. Figure 20 exhibits the pattern of variation of this family as displayed in two of its subgroups.

Thus we have in the two families Testudinidae and Chelydridae parallelism on an impressive scale in the kinds of change that have gone on in certain osteological patterns. There is parallelism at the generic level and at the family level. What is the explanation of such a condition?

Note that the parallelism goes beyond

osteology, that in general the kind of evolution in the two families is similar. The Emydinae are ancestral to the Testudininae, and the Chelydrinae through the Staurotypinae to the Kinosterninae, and in each case the trend of evolution has been, in general, from an aquatic to a terrestrial habitat and probably also from a more carnivorous to a more herbivorous food habit. In reality of course the course of evolution has been more complex than this, but this general picture is not without value as a suggestion of some of the functional shifts which may account for the tendency to structural shift.

Parallelism suggests similar selective pressures acting on similar genotypes. Let us look again at the data from the point of view of Simpson's (1944) concept of "centripetal" and "asymmetric" selection.

In both families it would appear from the pattern of variation that selection must be described as asymmetric. In the Chelydridae it could be regarded as very nearly centripetal, and so also for some of the Emydinae. For some of the latter subfamily, however, it is to an important degree asymmetric. In the Kinosterninae a major displacement of the norm has taken place (pattern IV is commoner by far than P), but selection tends to be asymmetric even with regard to this new norm. In the Testudininae the norm has shifted only in certain species, but again in all selection is asymmetric.

Here also the author believes that no quarrel is possible with the description of the conditions postulated above for phenotypes. Very considerable doubt will, however, attach, in the absence of breeding data, to the interpretation of these conditions in terms of gene frequency and change in gene frequency. Yet, while it cannot be demonstrated, no evidence contradicts it, and it is in the author's opinion the most probable interpretation.

Specifically, utilizing the multiple factor hypothesis proposed above, it may be supposed that asymmetric selection would tend towards the accumulation of, let us say, plus factors affecting morphogenetic fields for procoely. Given again threshold phenomena there could result, depending upon the intensity and degree of asymmetry of the selection in the various forms and upon the availability in each of suitable plus mutations, precisely
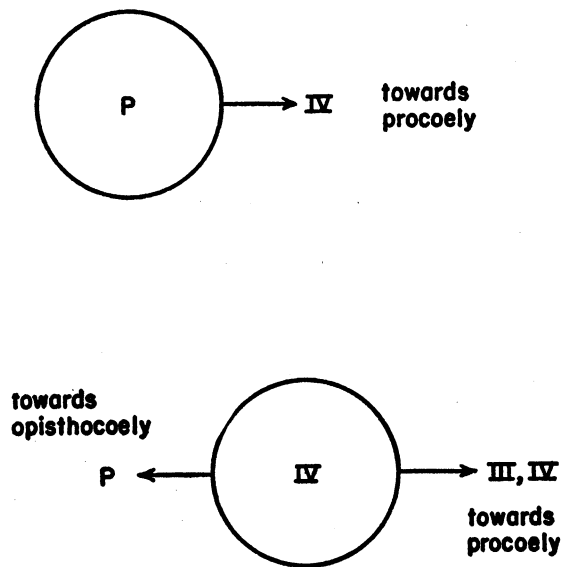

FIG. 20. Patterns of variation in the Chelydridae. P and Roman numerals indicate patterns so designated on page 552 of Appendix 1. Arrows indicate direction of structural change.

the array of diverse polymorphic frequencies in the several species which has been described for the Testudininae.

This again is wholly speculative, but it is thought to be useful as showing the possibility of a reasoned interpretation of the anatomical data in terms of selection and evolution.

It will perhaps clarify many of the issues that have been raised to reëxamine the data in terms of the "adaptive peak" concept (Wright, 1932; Dobzhansky, 1941; Simpson, 1944). According to this concept in most Emydinae one phenotype, pattern N, is in terms of cervical structure the highest adaptive peak. Neighboring peaks exist, for example, pattern IV, and patterns V and VIII, which are lower than the major peak but which are easily reached from that peak, i.e., envolve little remolding of the genotype. These peaks are available to the Emydinae because they are so close to the major peak and because they are not very far down its slope; individuals are therefore found which occupy these peaks. Other peaks exist, for example, that which is characteristic of the Trionychidae, but these are not available to the Emydinae, even though they might, could they be attained, be as high or higher

than N. They are not available, first, because they are distant and involve greater remolding of the genotype, and, second, because they involve as intermediate steps conditions which are far down in the adaptive valleys, e.g., pattern V, VI, in the transition to the trionychid peak. Still other conditions exist which are in no sense peaks at all or even saddles between peaks. These are the conditions that are radically defective in a mechanical sense (as fused centra), are therefore never viable, and can be appropriately described as lying in "chasms of lethality."

In those Emydinae of which this adaptive picture is true no evolutionary trend is to be expected. For the Testudininae, however, and certain Emydinae a very different situation may be suggested. In these animals it must be assumed either that the height of the subpeaks associated with N has risen markedly, or alternatively that the height of N has been lowered. On either interpretation there results not a single adaptive peak but a ridge or chain of peaks.

This ridge represents, at one end of its length, pattern N, then successively varying frequencies of N and IV, then IV as a nearly fixed phenotype, then varying frequencies of IV and III, IV, and finally III, IV, as a nearly fixed type. Neighboring conditions are in each part of the ridge more easily reached than more distant conditions. Local differences in slope are probable. Adjacent to this ridge are other peaks of less but still closely similar height, VIII and IV, VIII and II, III, IV, VIII: the ridge is almost a plateau. Surrounding this favored area, however, are steeper slopes, and here also there are chasms of lethality.

The evolutionary significance of this condition is profoundly different from that of the typical Emydinae. A species may here wander very easily from point to point upon the ridge under the varying influences of slope and drift; it is not, as in the typical Emydinae, isolated upon a single peak.

The situation so described will be regarded probably as "relaxation of selection." It is necessary to realize, however, that it is such in a peculiar and limited sense. It may be valuable to present in contrast a condition that may more genuinely and more broadly represent a lifting of selection pressure. The central articulations of the pelobatid frog *Megophrys* may be such a case. The author has examined the central articulations in only two specimens of *Megophrys boettgeri;* these differed, however, in five joints. Boulenger (1908) has cited other examples of intraspecific variation in this genus quite as extreme. The matter needs further investigation, but it may really be that the central articulations in this genus are quite inconstant and that the position of convexities and concavities between centra is of little or no functional importance. We may at least for purposes of argument assume this to be so and utilize *Megophrys* as a model of lability in central articulations. The difference between the character of variability in the frog and in the turtles is easily seen to be extreme. Intraspecific transformation of more than two joints is, even in the testudines, quite rare, while intraspecific differences involving many more central joints have attracted the attention of all who have dealt with the osteology of *Megophrys*. The polymorphism of the testudines can be thought of in terms of slow advance along an adaptive gradient; the erratic variation of the frog genus cannot. In the testudines we can speak with some possibility of approach to truth of an adaptive ridge having length and slope; in the frog genus, in regard to this character, the whole concept of adaptive peaks seems to have little relevance.

Enough has now been said to indicate that in the polymorphism seen in testudinate cervical central articulations the polymorphic species of each monophyletic taxonomic unit can be arranged in series which are interpretable with some show of probability as the result of evolution under selection.

This is as far as it is possible to go within the scope and by the methods of the present paper. The remaining problems—the possible selective value of the several polymorphic classes and their possible differential importance in diverse situations—will require, in addition to the anatomical and systematic analysis which alone has been attempted here, a careful and thoroughgoing investigation of the correlation of function and habit with structure. Preliminary studies of this sort have been begun; it is intended to report these studies in a later paper.

SUMMARY

1. THE ARTICULATIONS of the centra are an easily studied character of the neck of turtles that shows considerable diversity among species and higher groups and at the same time considerable intraspecific variation.

2. The taxonomic diversity and the intraspecific variation do not differ in elements.

3. Structurally and probably also genotypically a certain frequency distribution of variants is characteristic for each species, and for higher groups certain included sets of frequency distributions are characteristic.

4. In certain groups the frequency distributions characteristic of the contained species can be arranged in series which simulate or represent evolutionary series.

5. The profound effects of selective forces in the origin and perpetuation of these frequency distributions and sets of distributions are on many grounds inferred.

6. It is therefore considered probable that the observed structural series represent real stages in evolution under selection, and that the high intraspecific variability observed in some forms may be only evolution caught in process.

TABULATION of central patterns below is made under the group headings recognized in the section Systematic Record above. Under the group heading in each case is listed one pattern in the placement of convexities and concavities, designated by N or P, which is believed to be the most frequent or most primitive in the group. All other convexo-concave patterns occurring in that group are thereafter listed in such sequence as appears reasonable. Each of these secondary patterns is given a roman numeral indicating the joint or joints in it that have varied from the conditions of pattern N or P. Patterns in doubling are shown as subscript varieties of convexo-concave patterns. All patterns are expressed in Walther's formulas (see p. 515).

The number of specimens of any species conforming to a pattern is listed directly under that pattern. If two numbers are given for a species, the first number derives from the present author's personal observation on museum material or on material personally prepared, while the second number represents a literature record.[1] In most cases, in the interests of brevity, neither museum or other source nor literature citation is given, but for rare variants exception is made to this rule, and literature citations are given by author and records from major museums and the author's personal collection under these standard abbreviations:

A.M.N.H., the American Museum of Natural History
C.M., Carnegie Museum
C.N.H.M., Chicago Natural History Museum
C.U.M., Cornell University Museum
E.W., author's personal collection
K.N.H.M., Kansas Natural History Museum
L.A.C., Laboratoire d'Anatomie Comparée, Paris
M.C.Z., Museum of Comparative Zoölogy, Harvard University
U.M.M.Z., University of Michigan Museum of Zoology
U.S.N.M., United States National Museum
Yale, Peabody Museum, Yale University

[1] Whenever, in the report of any cervical pattern in the literature, the author has not stated how many specimens he has examined, it has been assumed for the purposes of record here that only one specimen was examined.

Supporting all numerical data reported here is a detailed list, specimen by specimen, in the possession of the author.

The generic and specific names used here are those in current use. Forms currently recognized as subspecies are listed only by the specific names. Thus *Chrysemys picta* includes *marginata* and *belli*, *Pseudemys scripta* includes *troosti* and *ornata*, *P. floridana* includes *concinna*, *suwanniensis*, and *texana*, and *Terrapene carolina* includes *triunguis*, *major*, and *bauri*. In all cases note has been made of subspecific identifications, but since statistically significant differences in central characters have not been found,[2] the identifications are not here recorded.

GROUP 1. TESTUDINIDAE

N1 (2(,(3(,(4),)5},}6},}7{,{8)
N2 (2(,(3(,(4),)5),)6},}7{,{8)

Platysterninae
2+3 *Platysternon megacephalum*

Emydinae
2+1 *Batagur baska;* 176 *Chrysemys picta;* 4 *Chinemys reevesii;* 0+1 *Clemmys caspica;* 11 *C. guttata;* 20 *C. insculpta;* 1 *C. japonica;* 2+1 *C. leprosa;* 10 *C. marmorata;* 5 *C. muhlenbergii;* 2+1 *Cuora amboinensis;* 1 *C. flavormarginata;* 6 *Deirochelys reticularia;* 27 *Emys blandingii;* 5+9 *E. orbicularis;* 1 *Geoemyda annulata;* 1 *G. grandis;* 1 *G. pulcherrima;* 1 *G. punctularia;* 1 *G. spinosa;* 5 *G. trijuga;* 4 *Graptemys barbouri;* 17 *G. geographica;* 24 *G. pseudogeographica;* 1 *Hieremys annandalii;* 16+2 *Malaclemys terrapin;* 1 *Ocadia sinensis;* 1 *Orlitia borneensis;* 33 *Pseudemys floridana;* 9 *P. rubriventris;* 69+3 *P. scripta;* 1 *Siebenrockiella crassicollis;* 78+2 *Terrapene carolina;* 1 *T. klauberi;* 56 *T. ornata;* 1 *T. mexicana*

Testudininae
9 *Gopherus agassizii;* 10 *G. berlandieri;* 10+2 *G. polyphemus;* 3+1 *Testudo calcarata;* 5+2 *T. denticulata;* 5+22 *T. graeca* (+*ibera*)[3]; 0+4 *T. leithii;* 2+3 *T. marginata;* 0+1 *T. oculifera;* 20+1 *T. pardalis;* 1 *T. radiata;* 5 *T. tornieri;* 16+10 *T. elephantopus*[4]

[2] It is possible that the subspecies of *P. floridana* may be an exception to this; see page 546 and figure 17.

[3] Because of an error by Boulenger (Flower, 1926), literature and museum records of *graeca* and *ibera* are likely to be confused; they are therefore here combined.

[4] The name "*elephantopus*" is here used in the sense of Rothschild (1931), Mertens (1934), and Flower (1937) to include all Galápagos "species."

N3 (2(,(3(,(4)5},}6},}7{,{8}

Emydinae

1 *Chrysemys picta,* (E.W.); 0+1 *Pseudemys rubriventris,* (Martin and Moale, 1881)

N4 (2(,(3(,(4),)5)6},}7{,{8}

Testudininae

0+1 *Gopherus polyphemus,* (Wieland, 1902)

N5 (2(,(3(,(4),)5),)6),)7(,(8)

Testudininae

0+1 *Testudo pardalis,* (Virchow, 1926)

II₁)2(,(3(,(4),)5},}6},}7{,{8)

Emydinae

2 *Clemmys insculpta,* (U.M.M.Z., Yale)

II₂)2(,(3(,(4),)5),)6},}7{,{8)

Testudininae

1 *Testudo elephantopus,* (U.S.N.M.); 0+1 *T. leithii,* (Yale = Baur, 1889)

II₃ s2(,(3(,(4),)5},}6},}7{,{8)

Emydinae

1 *Pseudemys scripta,* (E.W.)

IV₁ (2(,(3),)4),)5},}6},}7{,{8)

IV₂ (2(,(3),)4),)5),)6},}7{,{8)

IV₃ (2(,(3),)4),)5),)6),)7{,{8)

Emydinae

9 *Chrysemys picta;* 1 *Clemmys marmorata;* 1 *Geoemyda annulata;* 1 *Graptemys pseudogeographica;* 1 *Hardella thurjii;* 6 *Pseudemys floridana;* 4+1 *P. scripta;* 13 *Terrapene carolina;* 3 *T. ornata*

Testudininae

0+1 *Acinixys planicauda;* 0+2 *Homopus areolata;* 12+2 *Kinixys belliana;* 9+1 *K. erosa;* 1+1 *K. homeana;* 6 *Gopherus berlandieri;* 11+4 *Testudo denticulata;* 3+5 *T. graeca* (including *ibera*); 1 *T. horsfieldii;* 0+2 *T. oculifera;* 7 *T. pardalis;* 3+28 *T. radiata;* 1+1 *T. tornieri;* 3+1 *T. elephantopus;* 2+2 *T. gigantea*

IV₄ (2(,(3|,|4),)5},}6},}7{,{8)

Emydinae

1 *Terrapene carolina,* (C.U.M.)

IV₅ (2(,(3{,{4),)5),)6},}7{,{8)

Testudininae

1 *Testudo pardalis,* (A.M.N.H.)

V₁ (2(,(3(,(4(,(5},}6},}7{,{8)

Emydinae

2 *Chrysemys picta,* (K.N.H.M.); 2 *Clemmys insculpta,* (C.M., U.M.M.Z.); 3 *Terrapene carolina,* (K.N.H.M., C.U.M.)

V₂ (2(,(3(,(4(,(5),)6},}7{,{8)

Testudininae

1 *Testudo denticulata,* (U.S.N.M.)[1]

V₃ |2(,(3(,(4(,(5},}6},}7{,{8)

Emydinae

1 *Pseudemys floridana,* (A.M.N.H.)

VII₁ (2(,(3(,(4),)5},}6{,{7{,{8)

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¹ This specimen is believed to be the one recorded by Baur (1889) as showing this condition.

Emydinae

1 *Chrysemys picta,* (E.W.); 1 *Graptemys pseudogeographica,* (K.N.H.M.); 2 *Pseudemys scripta,* (K.N.H.M.); 1 *Terrapene carolina,* (Yale)

VII₂ (2(,(3(,(4),)5},}6(,(7{,{8)

Emydinae

1 *Terrapene carolina,* (U.M.M.Z.)

VII₃ (2(,(3(,(4),)5},}6},}7{,{8)

Emydinae

2 *Chrysemys picta,* (E.W.); 1 *Pseudemys scripta,* (K.N.H.M.); 2 *Terrapene carolina,* (K.N.H.M., Yale)

VIII₁ (2(,(3(,(4),)5},}6},}7},}8)

Emydinae

1 *Clemmys insculpta,* (U.M.M.Z.); 1 *C. marmorata,* (M.C.Z.); 2 *Terrapene carolina,* (K.N.H.M., Yale); 1 *T. ornata,* (K.N.H.M.)

VIII₂ (2(,(3(,(4),)5),)6},}7},}8)

Testudininae

1 *Testudo angulata,* (L.A.C.); 1 *Gopherus berlandieri,* (K.N.H.M.)

VIII₃ (2(,(3(,(4),)5},}6},}7{,{8)

Emydinae

1 *Clemmys guttata* (C.N.H.M.)

VIII₄ (2(,(3(,(4)),)5},}7},}7{,{8)

Emydinae

2 *Clemmys insculpta,* (C.M.)

VIII₅ (2(,(3(,(4),)5),)6},}7{,'8)

Testudininae

1 *Testudo pardalis,* (A.M.N.H.)

VIII₆ (2(,(3(,(4),)5),)6},}7},,}8)

Testudininae

1 *Gopherus berlandieri,* (K.N.H.M.)

VIII₇ (2(,(3(,(4)5},}6},}7{,}8)

Emydinae

1 *Clemmys guttata,* (U.M.M.Z.)

VIII₈ (2(,(3(,(4),)5},}6},}7),)8)

Emydinae

1 *Pseudemys scripta,* (U.M.M.Z.)

VIII₉ (2(,(3(,(4),)5),)6),)7),)8)

Testudininae

1 *Gopherus berlandieri,* (U.S.N.M.)

II, IV)2(,(3),)4),)5),)6},}7{,{8)

Testudininae

1 *Testudo elegans,* (A.M.N.H.)

III, IV (2),)3),)4),)5),)6},}7{,{8)

Testudininae

1+80 *Bellemys arachnoides;* 0+1 *Testudo angulata,* (Siebenrock); 1 *T. denticulata,* (U.S.N.M.); 1 *T. pardalis,* (U.S.N.M.); 4 *T. radiata,* (L.A.C. 1, Vaillant 1, Siebenrock 2)

II, III, IV)2),)3),)4),)5),)6},}7{,{8)

Testudininae

1 *Testudo leithii,* (Yale = Baur, 1889)

IV, VIII₁ (2(,(3),)4),)5),)6},}7},}8)

Testudininae

1 *Kinixys belliana,* (A.M.N.H.); 1 *Testudo pardalis,* (U.S.N.M.)

IV, VIII₂ (2(,(3),)4),)5),)6},}7),)8)

Testudininae
   1 *Testudo pardalis*, (A.M.N.H.)
IV, VIII$_3$ (2(,(3),)4,),)5),)6},}7},{8)
Testudininae
   2 *Testudo pardalis*, (A.M.N.H., Virchow); 1
   T. radiata, (Vaillant)
IV, VII, VIII (2(,(3),)4,),)5),)6{,{7},}8)
Testudininae
   1 *Testudo gigantea*, (A.M.N.H.)
II, III, IV, VIII)2),)3),)4,),)5),)6},}7},}8)
Testudininae
   7 *Bellemys arachnoides*, (Vaillant 1, Boulenger
   1, Siebenrock 5)
A ninth cervical vertebra present (2(,(3(,(4),)5},}
   6},}7},}8},}9)
Emydinae
   1 *Emys blandingii*, (U.M.M.Z.); 1*Pseudemys
   scripta*, (Lafayette College)

GROUP 2. DERMATEMYDIDAE, CHELYDRIDAE

P1 (2(,(3(,(4),)5),)6),)7),)8)
P2 (2(,(3(,(4),)5),)6},}7},}8)
Chelydrinae
   88+5 *Chelydra serpentina*; 16+2 *Macro-chelys temminckii*
Kinosterninae:
   0+1 *Kinosternon subrubrum*, (Vaillant 1881)
IV$_1$ (2(,(3),)4,),)5),)6},}7},,}8)
Chelydrinae
   1 *Chelydra serpentina*, (U.M.M.Z.)
Staurotypinae
   1 *Staurotypus salvinii*,[1] (U.M.M.Z.); 1 *Clau-dius angustatus*, (A.M.N.H.)
Kinosterninae
   8 *Kinosternon baurii*; 1 *K. cruentatum*; 49 *K. flavescens*; 1 *K. integrum*; 2+1 *K. leucosto-mum*; 4 *K. sonoriense*; 7 *K. subrubrum*; 3 *Sternotherus carinatus*; 66+3 *S. odoratus*; 2 *S. minor*
IV$_2$ (2(,(3(,)4),)5),)6},}7},}8)
Chelydrinae
   1 *Chelydra serpentina*, (K.N.H.M.)
III, IV (2),)3),)4,),)5),)6},}7},}8)
Dermatemydidae
   2+4 *Dermatemys mawii*
Kinosterninae
   1 *Kinosternon cruentatum*, (K.N.H.M.); 1 *K. baurii*, (C.U.M.); 9+1 *K. flavescens*; 1 *K. leucostomum*, (L.A.C.); 2 *K. subrubrum* (C.U.M.); 1 *Sternotherus odoratus*, (C.U.M.)

GROUP 3. CHELONIIDAE, DERMOCHELYIDAE

N1 (2(,(3(,(4),)5),)6|,|7},}8)

N2 (2(,(3(,(4),)5),)6|,|7),)8)
N3 (2(,(3(,(4),)5),)6),)7),)8)
Cheloniidae
   13+2 *Caretta caretta*; 12+2 *Chelonia mydas*; 5+1 *Eretmochelys imbricata*; 3 *Lepidochelys kempii*
Dermochelyidae
   6+3 *Dermochelys coriacea*
N4 (2(,(3(,(4),)5),)6|,|7},)8)
Cheloniidae
   1 *Lepidochelys kempii*, (E.W.)
IV (2(,(3),)4,),)5),)6|,|7},}8)
Cheloniidae
   1 *Eretmochelys imbricata*, (M.C.Z.)
V (2(,(3(,(4(,(5),)6|,|7},}8)
Cheloniidae
   1 *Chelonia mydas*, (Dollo)

GROUP 4. CARETTOCHELYIDAE, TRIONYCHIDAE

N1 (2(,(3(,(4(,(5(,(6{,{7{,{8}
Carettochelyidae
   2 *Carettochelys insculpta*, (Waite, Walther)
N$_2$ (2(,(3(,(4(,(5(,(6{,{7{,{8–
N3 (2(,(3(,(4(,(5(,(6(,(7{,{8–
N4 (2(,(3(,(4(,(5(,(6(,(7{,{8–
Trionychidae
   1 *Chitra indica*; 0+1 *Cycloderma aubryi*; 0+1 *C. frenatum*; 1 *Dogania subplana*; 2+1 *Lis-semys punctata*; 1 *Pelochelys bibroni*; 2+2 *Trionyx*[2] *cartilaginea*; 8 *T. emoryi*; 7 *T. ferox*; 1 *T. hurum*; 18 *T. mutica*; 1+1 *T. triunguis*; 27 *T. spinifer*

GROUP 5. PELOMEDUSIDAE

N1 (2),)3),)4,),)5),)6),)7),)8)
Pelomedusidae
   7+2 *Pelomedusa subrufa*; 4+7 *Pelusios sub-niger*; 2+1 *P. gabonensis*; 2+2 *Podocnemis (Erymnochelys) madagascarensis*
N2 (2),)3s,s4s,s5s,s6s,s7),)8)
Pelomedusidae
   2+2 *Podocnemis dumeriliana*; 8 *P. expansa*; 1 *P. sextuberculata*

GROUP 6. CHELIDAE

N (2(,(3(,(4(,(5),)6),)7(,(8)
Chelidae
   0+1 *Batrachemys nasuta*; 12+2 *Chelus fim-briata*; 1+2 *Chelodina longicollis*; 0+2 *Emydura latisternum*; 1 *E. macquarrii*; 0+1 *Hydraspis hilarii*; 0+2 *Hydromedusa maxi-miliani*; 1 *Mesoclemmys gibba*; 1+1 *Phry-nops geoffrayana*; 0+1 *Platemys platycephala*

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[1] Baur, Boulenger, and Siebenrock all state that the Staurotypinae have the third cervical centrum bi-convex; in no case, however, do they cite species or number of specimens. Their general statements are therefore ignored here.

[2] The use of the generic name *Trionyx* is involved in controversy. Purely as a convenience, without admitting to an opinion on the merits of these questions of nomen-clature, the author has adhered to the names used by Malcolm Smith (1931).

APPENDIX 2. A SUMMARY OF CLASSIFICATION

THE CLASSIFICATION here adopted is not a conventional one. It is in certain respects new and expresses the author's views of the taxonomic implications of the data here assembled. As regards living forms differences from the more familiar systems of Boulenger (1889), Siebenrock (1909), and Lindholm (1929) are, however, minor and are in almost all cases differences as to the systematic rank of categories universally recognized. In the Cryptodira some union of currently recognized families is suggested to make the family category in this suborder comparable with the same unit in the other living suborder.

With regard to fossils also there are a few suggestions made here which have not been previously made by one authority or another. The most important novelty is the erection of the †Baenoidea, new superfamily, for those amphichelydians in which centra with formed joints are known. In this action the author betrays his preoccupation with, and the extreme importance he attaches to, cervical structure. Since in whole groups of (especially European) forms cervical structure is imperfectly or not at all described, the content of this superfamily as here recognized is provisional only. The plesiochelyids are, for example, more modernized in shell characters than the baenids, but they are excluded from the baenoids and retained in the more primitive pleurosternoids because Andrews (1921) has described as amphicoelous the few cervicals which have been preserved of the plesiochelyid †*Tholemys*. The European thalassemydids are similarly assigned to the pleurosternoids, primarily because they seem closely affiliated to the plesiochelyids.

Table 9, which attempts to record the time and place of the first and of the latest appearance of the various groups, excluding from consideration forms doubtfully referred or poorly known, introduces some other considerations which have influenced the author's placement of forms. From the tabulation it seems possible that the baenoids originated from the pleurosternoids and the Cryptodira from the baenoids on the North American continent or in neighboring east Asia. The plesiochelyids and thalassemydids, both of which are European, would on this hypoth-

esis be remote from this line. †*Kallokibotion* of the later Cretaceous of Europe with its amphicoelous vertebrae seems to be an isolated survivor of a primitive group (Nopcsa, 1923a).

The importance of the baenoids in the author's estimation has been a factor in the erection of two new families in this superfamily. Neither †*Neurankylus* nor †*Eubaena* can with any propriety be assigned to the same family with †*Baena*. In both shell and cervical characters the two first genera differ very much from the latter. They apparently differ from each other also in characters which in other testudinate groups are of family grade; they are therefore provisionally made the representatives of monotypic families here.

In the listing of groups below the primary purpose has been to display the usefulness of characters of the cervical vertebrae in helping to delimit natural taxonomic units in the Testudinata. The definitions are not intended to be exhaustive, nor is the classification a final one. It is quite possible that some of the subdivisions, especially of the fossil forms, may prove to be artificial.

Previous work has had, of course, a profound effect on this classification. Boulenger, Baur, Hay, Nopcsa, and Woodward (*in* Zittel, 1932) in particular have been frequently consulted in the course of its construction. Discussions with Dr. Rainer Zangerl have had determining influences in the disposition of several groups. The final classification is, however, the responsibility solely of the author.

Table 9 indicates the geologic range of the groups recognized. Table 10 lists in an informal key some of the characters used by the author in separating his groups.

Below are summarized the principal taxonomic changes recommended:

1. *Bellemys*, new name, replaces *Pyxis* Bell, 1825, preoccupied.

2. The superfamilies †Triassochelyoidea, †Pleurosternoidea, †Baenoidea, Testudinoidea, Chelonioidea, Dermochelyoidea, Carettochelyoidea, and Trionychoidea are recognized with somewhat novel content or are newly erected.

TABLE 9

Order Testudinata
 Suborder †Amphichelydia; Triassic to Pleistocene
  Superfamily †Triassochelyoidea; Triassic
   Family †Triassochelyidae; Triassic
    Subfamily †Triassochelyinae; Triassic, Europe
    Subfamily †Proterochersinae; Triassic, Europe
  Superfamily †Pleurosternoidea
   Family †Pleurosternoidae; Jurassic to Cretaceous
    Subfamily †Pleurosterninae; Jurassic to Cretaceous, Europe, North America
    Subfamily †Desmemydinae; Cretaceous, Europe
    Subfamily †Kallokibotinae; Cretaceous, Europe
   Family †Plesiochelyidae; Jurassic to Cretaceous, Europe
   Family †Thalassemydidae; Jurassic to Cretaceous, Europe
  Superfamily †Baenoidea; Cretaceous to Pleistocene
   Family †Baenidae; Cretaceous to Pleistocene
    Subfamily †Baeninae; Cretaceous to Eocene, North America
    Subfamily †Meiolaniinae; ?Cretaceous to Eocene, South America, Pleistocene, Australia
   Family †Neurankylidae; Cretaceous, North America
   Family †Eubaenidae; Cretaceous, North America
 Suborder Cryptodira; Cretaceous to Recent
  Superfamily Testudinoidea; Cretaceous to Recent
   Family Dermatemydidae; Cretaceous, North America, east Asia, to Recent, North America
   Family Chelydridae; Eocene to Recent
    Subfamily Chelydrinae; Eocene to Miocene, Europe, Miocene to Recent, North America
    Subfamily Staurotypinae; Oligocene to Recent, North America
    Subfamily Kinosterninae; Pliocene, North America, to Recent, North America, South America
   Family Testudinidae; Cretaceous to Recent
    Subfamily Platysterninae; Cretaceous to Recent, east Asia
    Subfamily Emydinae; Paleocene, North America, to Recent, North America, Asia, Africa, Europe, South America
    Subfamily Testudininae; Eocene, North America, Asia, Africa, to Recent, North America, Asia, Africa, Europe, South America
  Superfamily Chelonioidea
   Family †Toxochelyidae; Cretaceous to Eocene
    Subfamily †Toxochelyinae; Cretaceous, North America
    Subfamily †Lytolominae; Cretaceous, North America, to Eocene of Europe
   Family †Protostegidae; Cretaceous, North America
   Family Cheloniidae; Cretaceous to Miocene, North America, Europe, Recent, Oceanic
  Superfamily Dermochelyoidea; Eocene to Recent
   Family Dermochelyidae; Eocene to Miocene, Europe, Recent, Oceanic
  Superfamily Carettochelyoidea; Paleocene to Recent
   Family Carettochelyidae; Paleocene to Recent
    Subfamily †Anosteirinae; Paleocene to Oligocene, Europe, Eocene, North America, Asia
    Subfamily Carettochelyinae; Miocene to Recent, east Asia
  Superfamily Trionychoidea; Cretaceous to Recent
   Family Trionychidae; Cretaceous to Recent
    Subfamily †Plastomeninae; Cretaceous to Eocene, North America
    Subfamily Trionychinae; Cretaceous to Recent, North America, Eocene to Pliocene, Europe, Oligocene to Recent, Asia, Recent, Africa
    Subfamily Lissemydinae; Miocene to Recent, Africa, Pliocene to Recent, Asia
 Suborder Pleurodira; Cretaceous to Recent
  Family Pelomedusidae; Cretaceous to Recent
   Subfamily †Bothremydidae; Cretaceous to Miocene, North America
   Subfamily Pelomedusinae; Cretaceous, North America, Cretaceous to Miocene, Europe, Eocene to Pliocene, Asia, Paleocene to Recent, Africa, Cretaceous to Recent, South America
  Family Chelidae; geological occurrence before the late Cenozoic uncertain

TABLE 10

Order Testudinata

Reptilia with skull roof complete or emarginate, never truly fenestrated, shoulder girdle internal to the ribs, cervical vertebrae eight, dorsal vertebrae 10

Suborder †Amphichelydia

Skull roof complete, rarely emarginated from behind; pterygoids excluding quadrates from basisphenoid; two pairs of, one pair of, or no mesoplastra; pelvis always in strong contact with plastron; neck not retractile; posterior cervical vertebrae with high spines; cervical postzygapophyses never united; cervical centra amphicoelous or of varied types, formed joints, if present, never double

Superfamily †Triassochelyoidea

Skull roof complete, a parietal-squamosal arch; two pairs of mesoplastra; free cervical ribs; last cervical neural arch fused to nuchal; cervical centra amphicoelous

Family †Triassochelyidae

Shell very convex; marginals very numerous, supramarginals present

Subfamily †Triassochelyinae

Pelvis not fused with plastron

Subfamily Proterochersinae

Pelvis fused with plastron

Superfamily †Pleurosternoidea

Skull roof complete, a parietal-squamosal arch present; one pair or no mesoplastra; no free cervical ribs; last cervical free of nuchal; cervical vertebrae amphicoelous

Family †Pleurosternidae

Shell with or without fontanelles; one pair of mesoplastra; pelvis not fused to plastron

Subfamily †Pleurosterninae

Shell without fontanelles; acromion long

Subfamily †Desmemydinae

Shell with fontanelles; acromion long

Subfamily †Kallokibotinae

Shell without fontanelles; acromion short

Family †Plesiochelyidae

Shell without fontanelles; no mesoplastra; pelvis sometimes fused to plastron?

Family †Thalassemydidae

Shell with fontanelles; no mesoplastra; pelvis not fused to plastron

Superfamily †Baenoidea, new superfamily

Skull roof complete or emarginated from behind; one pair of or no mesoplastra; no free cervical ribs; last cervical free of nuchal; cervical centra with formed joints

Family †Baenidae

Skull roof complete, a parietal-squamosal arch present; one pair of mesoplastra; fourth cervical amphicoelous; eighth cervical procoelous

Subfamily †Baeninae

Skull roof without horns

Subfamily †Meiolaniinae

Skull roof with horns

Family †Neurankylidae, new family

Skull roof unknown; one pair of mesoplastra; fourth and eighth cervical centra biconvex

Family †Eubaenidae, new family

Skull roof emarginate from behind, no parietal-squamosal arch; no mesoplastra; fourth cervical centrum?; eighth cervical centra biconvex

Suborder Cryptodira

Skull roof, if complete, probably secondarily so, usually much emarginated from behind; pterygoids excluding quadrates from basisphenoid; never any mesoplastra; pelvis always free from plastron; neck retractile vertically to a greater or less degree; posterior cervical spines low; postzygapophyses wide apart; cervical central articulations well developed, always broad and typically double on posterior cervicals

Superfamily Testudinoidea

Epidermal scutes always present; armor thecal; limbs not modified as paddles; skull roof

TABLE 10—*continued*

complete or emarginate behind; basisphenoid not in contact with palatines; maxillary in contact with quadratojugal or not; one or two biconvex centra in the neck; two or three joints of the neck usually double

Family Dermatemydidae

Nuchal without costiform processes; plastron not cruciform; alveolar surface of maxilla broad and ridged; marginal shields 25; only one biconvex centrum in the neck; eighth centrum doubly concave in front

Family Chelydridae

Nuchal with costiform processes; plastron often cruciform; alveolar surface of maxilla typically broad without ridges; marginal shields 23 or 25; only one biconvex vertebra in the neck, eighth centrum concave in front, the concavity usually double

Subfamily Chelydrinae

Entoplastron present; marginal shields 25

Subfamily Staurotypinae

Entoplastron present; marginal shields 23

Subfamily Kinosterninae

Entoplastron absent; marginal shields 23

Family Testudinidae

Nuchal plate without costiform processes; plastron never cruciform; alveolar surface of maxilla broad or narrow, ridged or not; marginal shields 23, 24, or 25; typically two biconvex centra in the neck; eighth centrum typically doubly convex in front

Subfamily Platysterninae

A complete series of inframarginals present; digits with three phalanges; skull roof complete, postorbital large but no parietal-squamosal arch; marginal shields 25

Subfamily Emydinae

Never with complete series of inframarginals; at least some digits with three phalanges; skull roof very incomplete, postorbital small, no parietal-squamosal arch; marginal shields 25

Subfamily Testudininae

Never with complete series of inframarginals; digits never with more than two phalanges; skull roof very incomplete, postorbital small, no parietal-squamosal arch; marginal shields 23, 24, or 25

Superfamily Chelonioidea

Epidermal scutes present; armor thecal; limbs modified as paddles; skull roof more or less complete; maxillary not in contact with quadratojugal; basisphenoid not in contact with palatines; one biconvex vertebra in the neck; one or no joints double

Family †Toxochelyidae

Humerus not specialized; xiphiplastra unreduced; the fourth cervical centrum biconvex; the joint between the sixth and seventh centra not plane; the eighth centrum doubly concave in front; a secondary palate developed or not

Subfamily †Toxochelyinae

A secondary palate not developed; epithecal cones on neurals

Subfamily †Lytolominae

A secondary palate developed; no epithecal cones on neurals

Family †Protostegidae

Humerus specialized; xiphiplastra reduced; fourth centrum biconvex?; joint VII not plane; the eighth centrum concave in front, the articulation not double; a secondary palate not developed

Family Cheloniidae

Humerus specialized; xiphiplastra unreduced; fourth centrum typically biconvex; joint VII typically plane; eighth centrum concave in front, the articulation double or not; secondary palate developed

Superfamily Dermochelyoidea

Epidermal scutes absent; thecal armor very reduced, a mosaic epithecal armor developed; limbs modified as paddles; skull roof complete; maxillary not in contact with quadratojugal; basisphenoid not in contact with palatines; only one biconvex vertebra in the neck; one or no cervical joints double

TABLE 10—*continued*

Family Dermochelyidae
> Typically the fourth cervical centrum biconvex; the joint between the sixth and seventh centra more often not plane; eighth centrum simply or doubly concave in front

Superfamily Carettochelyoidea
> Epidermal scutes reduced or absent; thecal armor unreduced; limbs modified as paddles; skull roof emarginate behind; maxillary in contact with the quadratojugal; basisphenoid in contact with the palatines; one biconvex centrum in the neck; two cervical joints double

Family Carettochelyidae
> All cervicals except the eighth opisthocoelous; eighth cervical doubly convex in front and behind; vertebrae broad

Subfamily Anosteirinae
> Epidermal scutes reduced, sometimes absent; atlas not fused to odontoid bone

Subfamily Carettochelyinae
> Epidermal scutes absent; atlas fused to odontoid bone

Superfamily Trionychoidea
> Epidermal scutes absent; armor largely epithecal; limbs modified as paddles; skull deeply emarginate behind; maxillary not in contact with quadratojugal; basisphenoid in contact with palatines; no biconvex centrum in the neck; one or two cervical joints double

Family Trionychidae
> All cervical vertebrae opisthocoelous except the eighth; eighth centrum doubly convex in front, united to the centrum of the first dorsal only by ligament; vertebrae slender

Subfamily †Plastomeninae
> Posterior plastral elements closely united in the midline; cutaneous femoral flaps absent?

Subfamily Trionychinae
> Posterior plastral elements separated in the midline; cutaneous femoral flaps absent

Subfamily Lissemydinae
> Posterior plastral elements separated in the midline; cutaneous femoral flaps present

Suborder Pleurodira
> Skull roof complete or not usually emarginate from below; pterygoids not excluding quadrate from basisphenoid; one pair of or no mesoplastra; pelvis always fused to plastron; neck retractile laterally; posterior cervical spines rather high; cervical postzygapophyses close or fused; cervical central articulations well developed, never double

Family Pelomedusidae
> Nuchal scute absent; quadratojugal present; vomer present or absent; second cervical centrum biconvex, others procoelous or with saddle articulations

Subfamily †Bothremydinae
> Vomer present; deep pit in triturating surfaces of maxillae and mandible

Subfamily Pelomedusinae
> Vomer absent; no pits in maxillae or mandible

Family Chelidae
> Nuchal scute present or absent; quadratojugal absent; vomer present; fifth and eighth centra biconvex, never any saddle joints

3. The previously recognized families †Proterochersidae, †Meiolaniidae, Platysternidae, and Kinosternidae are reduced to subfamily rank.

4. The fossil genera †*Neurankylus* and †*Eubaena* are regarded as being so distinct that each requires family rank. †**Neurankylidae** and †**Eubaenidae**, new families, are therefore proposed.

ACKNOWLEDGMENTS

BIBLIOGRAPHY

ANDERSON, C.
1925. Notes on the extinct chelonian Meiolania with a record of a new occurrence. Rec. Australian Mus., vol. 14, pp. 223–242.

ANDERSON, J.
1878. Anatomical and zoological researches: comprising an account of the zoological results of the two expeditions to the western Yunnan in 1868 and 1875. London.

ANDREWS, C. W.
1921. On a new chelonian from the Kimmeridge Clay. Ann. Mag. Nat. Hist., ser. 9, vol. 7, pp. 145–153.

BAUR, G.
1886a. Osteologische Notizen über Reptilien. Zool. Anz., vol. 9, pp. 685–690.
1886b. Osteologische Notizen über Reptilien. Fortsetzung I. *Ibid.*, vol. 9, pp. 733–743.
1887. Osteologische Notizen über Reptilien. Fortsetzung II. *Ibid.*, vol. 10, pp. 96–102.
1888a. Osteologische Notizen über Reptilien. Fortsetzung III. *Ibid.*, vol. 11, pp. 417–424.
1888b. Osteologische Notizen über Reptilien. Fortsetzung IV. *Ibid.*, vol. 11, pp. 592–597.
1888c. Osteologische Notizen über Reptilien. Fortsetzung V. *Ibid.*, vol. 11, pp. 736–740.
1889a. Osteologische Notizen über Reptilien. Fortsetzung VI. *Ibid.*, vol. 12, pp. 40–47.
1889b. Revision meiner Mittheilungen im Zoologischen Anzeiger mit Nachträgen. *Ibid.*, vol. 12, pp. 238–243.
1889c. Die Systematische Stellung von *Dermochelys* Blainville. Biol. Centralbl., vol. 9, pp. 149–153, 180–191, 618–619.
1891a. Notes on some little known American fossil tortoises. Proc. Acad. Nat. Sci. Philadelphia, 1891, pp. 411–430.
1891b. On the relationships of *Carettochelys* Ramsay. Amer. Nat., vol. 25, pp. 631–639.
1893a. Notes on the classification and taxonomy of Testudinata. Proc. Amer. Phil. Soc., vol. 31, pp. 210–225.
1893b. Notes on the classification of the Cryptodira. Amer. Nat., vol. 27, pp. 672–675.

BERRY, C. T.
1937. More complete remains of a chelonian, *Syllomus crispatus* Cope, from the Miocene of Virginia. Amer. Mus. Novitates, no. 953, pp. 1–12.

BIENZ, A.
1896. *Dermatemys mavii* Gray, eine osteologische Studie mit Beiträgen zur Kenntnis der Schildkröten. Rev. Suisse Zool., vol. 3, pp. 61–135.

BISHOP, S. C., AND F. J. W. SCHMIDT
1931. The painted turtles of the genus *Chrysemys*. Field Mus. Nat. Hist., zool. ser., vol. 18, pp. 121–139.

BOJANUS, L. H.
1819–1821. Anatome testudinis Europae. Wilno, vols. 1, 2.

BOULENGER, G. A.
1887. Notes on the osteology of *Platysternum*. Ann. Mag. Nat. Hist., ser. 5, vol. 19, pp. 461–463.
1888. On the characters of the chelonian families Pelomedusidae and Chelydidae. *Ibid.*, ser. 6, vol. 1, pp. 346–347.
1889. Catalogue of the chelonians, rhyncocephalians and crocodiles in the British Museum (Natural History). London.
1908. A revision of the oriental pelobatid batrachians (genus *Megalophrys*). Proc. Zool. Soc. London, pp. 407–430.

CARR, A. F.
1935. The identity and status of two turtles of the genus *Pseudemys*. Copeia, 1935, pp. 147–148.
1937. The status of *Pseudemys scripta* and *Pseudemys troosti*. Herpetologica, vol. 1, pp. 75–77.
1938. Notes on the *Pseudemys scripta* complex. *Ibid.*, vol. 1, pp. 131–135.
1942a. Notes on sea turtles. Proc. New England Zool. Club, vol. 21, pp. 1–16.
1942b. The status of *Pseudemys floridana texana* with notes on parallelism in *Pseudemys*. *Ibid.*, vol. 21, pp. 69–76.

CASE, E. C.
1939. A nearly complete turtle skeleton from the Upper Cretaceous of Montana. Contrib. Mus. Paleont. Michigan, vol. 6, pp. 1–19.

CHABANAUD, P.
1934. Contribution a l'osteologie des cheloniens pleurodires de la familie des pelomedusides. Faune des colones françaises, vol. 5, pp. 237–308.

DOBZHANSKY, T.
1941. Genetics and the origin of species. New York.

DOLLO, L.
1887. *Psephophorus*. Ann. Soc. Sci. Bruxelles, vol. 11, pp. 139–176.

DugÈs, A.
1834. Recherches sur la osteologie et la myologie des batraciens a leurs differents ages. Mem. Inst. France, Sci. Math. Phys., vol. 6, pp. 111–216.

Flower, S.
1926. Species of land tortoises of the genus Testudo found in countries bordering the Mediterranean Sea. Copeia, p. 133.
1937. Further notes on the duration of life in animals. III. Reptiles. Proc. Zool. Soc. London, ser. A, pp. 1–39.

Ford, E. B.
1940. Polymorphism and taxonomy. In Huxley, J. S., The new systematics. Oxford.

Gervais, P.
1872. Osteologie du Sphargis luth. Nouv. Arch. Mus. Hist. Nat. Paris, vol. 8, pp. 199–228.

Harassowitz, H.
1922. Die Schildkrotengattung Anosteira von Messel bei Darmstadt und ihre stammesgeschichtliche Bedeutung. Abhandl. Hessischen Geol. Landesanst., vol. 6, pp. 137–238.

Hay, O. P.
1905. On the group of fossil turtles known as the Amphichelydia with remarks on the origin and relationships of the suborders, superfamilies and families of testudines. Bull. Amer. Mus. Nat. Hist., vol. 21, pp. 137–175.
1908. Fossil turtles of North America. Washington.
1922. On the phylogeny of the shell of the Testudinata and the relationships of Dermochelys. Jour. Morph., vol. 36, pp. 421–441.

Jaekel, O.
1918. Die Wirbeltierfunde aus dem Keuper von Halberstadt. Ser. II. Testudinata. Paleont. Zeitschr., vol. 2, pp. 89–214.

Kasper, A.
1903. Ueber den Atlas und Epistropheus bei den Pleurodiren Schildkröten. Arb. Zool. Inst. Wien, vol. 14, pp. 137–172.

Lindholm, W. A.
1929. Revidiertes Verzeichnis der Gattungen der rezenten Schildkröten nebst Notizen zur Nomenklatur der Arten. Zool. Anz., vol. 81, pp. 275–295.

Loveridge, A.
1941. Revision of the African terrapins of the family Pelomedusidae. Bull. Mus. Comp. Zool., vol. 88, pp. 467–524.

Martin, H. N., and W. A. Moale
1881. Handbook of vertebrate dissection. Part I. How to dissect a chelonian. New York.

Mertens, R.
1934. Die Inselreptilien, Ihre Ausbreitung, Variation und Ausbildung. Zoologica, Leipzig, no. 84, pp. 1–209.

Moore, J. P.
1900. Postlarval changes in the vertebral articulations of Spelerpes and other salamanders. Proc. Acad. Nat. Sci. Philadelphia, vol. 52, pp. 613–622.

Morgan, C. L.
1886. Abnormalities in the vertebral column of the common frog. Nature, vol. 35, p. 53.

Nichols, G. C.
1916. The structure of the vertebral column in the Anura Phaneroglossa and its importance as a basis of classification. Proc. Linnaean Soc. London, 128th session, pp. 80–91.

Noble, G. K.
1931. The biology of the Amphibia. New York.

Nopcsa, F.
1923a. On the geological importance of the primitive reptilian fauna of the uppermost Cretaceous of Hungary; with a description of a new tortoise (Kallokibotion). Quart. Jour. Geol. Soc., vol. 79, pp. 100–116.
1923b. Kallokibotium, a primitive amphichelydean tortoise from the uppermost Cretaceous of Hungary. Palaeont. Hungarica, vol. 1, pp. 1–34.
1923c. Die Familien der Reptilien. Fortschr. Geol. Paleont., no. 2, pp. 1–210.
1928. Genera der Reptilien. Paleobiologica, vol. 1, pp. 163–188.

Owen, R.
1851. On the Megatherium (Megatherium americanum Blumenbach) Part I. Preliminary report on the exogenous processes of vertebrae. Phil. Trans. Roy. Soc., London, vol. 141, pp. 719–764.
1853. Descriptive catalogue of the osteological series contained in the museum of the Royal College of Surgeons of England. London, vol. 1.

Pope, C. H.
1935. The reptiles of China. Natural History of Central Asia, New York, vol. 10.
1939. Turtles of the United States and Canada. New York.

Ramaswami, L. S.
1933. The vertebral column of South Indian frogs. Current Sci., vol. 1, pp. 306–309.

Rothschild, L.
1931. Exhibition of specimens of the saddlebacked races of Galapagos tortoises. Proc. Zool. Soc. London, vol. 2, p. 1208.

SIEBENROCK, F.
    1906.   Schildkröten aus Ostafrika und Mada-
            gascar. *In* Voeltskow, A., Reise in
            Ostafrika . . . . Wissenschaftliche Er-
            gebnisse. Stuttgart, vol. 2, Systemati-
            scher Arbeit., pp. 1–40.
    1907.   Die Schildkrötenfamilie Cinosternidae
            m. monographisch bearbeitet. Sitz. Ber.
            Akad. Wiss. Wien, vol. 116, pt. 1, pp.
            528–596.
    1909.   Synopsis der rezenten Schildkröten mit
            Berücksichtigung der in historischer
            Zeit ausgestorbenen Arten. Zool. Jahrb.,
            suppl., vol. 10, pp. 427–618.
SIMPSON, G. G.
    1937.   Superspecific variation from the point
            of view of paleontology. Amer. Nat.,
            vol. 71, pp. 236–237.
    1938.   *Crossochelys*, Eocene horned turtle from
            Patagonia. Bull. Amer. Mus. Nat. Hist.,
            vol. 74, pp. 221–254.
    1944.   Tempo and mode in evolution. New York.
SMITH, M. A.
    1931.   Loricata, Testudines. The fauna of
            British India. Reptilia and Amphibia.
            London, vol. 1.
THOMSON, J. S.
    1932.   The anatomy of the tortoise. Roy.
            Dublin Soc. Proc., new ser., vol. 20,
            pp. 359–461.
VAILLANT, L.
    1881.   Memoire sur la disposition des vertebres
            cervicales chez les cheloniens. Ann. Sci.
            Nat., ser. 6, vol. 10, pp. 1–106.
    1894.   Essai sur la classification generale des
            cheloniens. *Ibid.*, ser. 7, vol. 16, pp.
            331–345.
VERSLUYS, J.
    1914.   On the phylogeny of the carapace and
            on the affinities of the leathery turtle,
            Dermochelys coriacea. Rep. Brit. Assoc.
            Adv. Sci., vol. 83, pp. 1–17.
    1922.   Eine lebende Anosteiride *Carettochelys
            insculpta* Ramsay. Paleont. Zeitschr.,
            vol. 5, pp. 97–99.
VIRCHOW, H.
    1926.   Die Halswirbelsäule der Schildkröten.
            Verhandl. Anat. Gesellsch., vol. 35,
            pp. 215–221.
VOLKER, H.
    1913.   Ueber das Stamm-, Gliedmassen- und
            Hautskelet von *Dermochelys coriacea*.
            Zool. Jahrb., Anat. Abt., vol. 33, pp.
            431–542.
WAITE, E.
    1905.   Osteology of the New Guinea turtle.
            Rec. Australian Mus., vol. 6, pp. 110–118.
WALTHER, W. G.
    1922.   Die Neu Guinea Schildkröte *Caret-
            tochelys insculpta* Ramsay. Nova Guinea,
            vol. 13, pp. 607–702.
WEGNER, T.
    1911.   *Desmemys bertalmanni*, ein Beitrag zur
            Kenntniss der Thalassemydidae. Pale-
            ontographica, 1911.
WHITE, T. E.
    [MS.]   The osteology of the recent turtles of
            central North America. Master's Thesis,
            Univ. Kansas, Univ. Kansas Library,
            unpubl.
WIELAND, G. R.
    1899.   The terminology of vertebral centra.
            Amer. Jour. Sci., ser. 4, vol. 8, pp.
            163–164.
    1902.   Notes on the Cretaceous turtles *Toxo-
            chelys* and *Archelon* with a classification
            of the marine Testudinata. *Ibid.*, ser.
            4, vol. 14, pp. 95–108.
    1904.   Structure of the upper Cretaceous
            turtles of New Jersey: Adocus, Osteo-
            pygis and Propleura. Amer. Jour. Sci.,
            ser. 4, vol. 17, pp. 112–132.
WIMAN, C.
    1933.   Schildkröten aus der oberen Kreide in
            New Mexico. Nova Acta Reg. Soc.
            Upsala, ser. 4, vol. 9, pp. 1–34.
WRIGHT, S.
    1932.   The roles of mutation, inbreeding, cross-
            breeding and selection in evolution.
            Proc. Sixth Internatl. Congr. Genetics,
            vol. 1, pp. 356–366.
    1934a. On the genetics of subnormal develop-
            ment of the head (otocephaly) in the
            guinea pig. Genetics, vol. 19, pp. 471–
            505.
    1934b. An analysis of variability in number of
            digits in an inbred strain of guinea pigs.
            Ibid., vol. 19, pp. 506–536.
    1934c. The results of crosses between inbred
            strains of guinea pigs differing in num-
            ber of digits. *Ibid.*, vol. 19, pp. 537–551.
    1934d. Genetics of abnormal growth in the
            guinea pig. Cold Spring Harbor Sym-
            posia, vol. 2, pp. 137–147.
    1935.   A mutation of the guinea pig tending to
            restore the pentadactyl foot when
            heterozygous, producing a monstrosity
            when homozygous. Genetics, vol. 20,
            pp. 84–107.
ZANGERL, R.
    1939.   The homology of the shell elements in
            turtles. Jour. Morph., vol. 65, pp.
            383–406.
ZITTEL, K. A.
    1932.   Textbook of paleontology. Vol. 2.
            Vertebrata. (Translated and edited by
            Charles R. Eastman, revised by Arthur
            Smith Woodward.) London.