

PAREIASAURS VERSUS PLACODONTS AS NEAR ANCESTORS
TO THE TURTLES

WILLIAM KING GREGORY

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INTRODUCTION: THE APPROACH TO THE PROBLEM

THAT THE TURTLES, especially the sea turtles, were more or less closely related to the plesiosaurs has been the view of certain authors, including Baur (1887b, pp. 97-99), but, according to Williston (1907, p. 487), "It is chiefly because of the external resemblances of form and similarity in mode of locomotion in the water that it has been generally and indefinitely assumed from Buckland's time to the present that the plesiosaurs were related to the turtles." In

called *Otocoelus* and *Conodectes*, in which the region of the auricular meatus (otic notch) "resembled those of the Loricata and Testudinata." On top of the neural spines were placed "transverse osseous arches," which even overlapped the scapular arch (as does the carapace of turtles), while the temporal region of the skull was "complex and with no longitudinal bars." Cope (1898) therefore proposed a new order, the Chelydosauria, to include this family (Otocoelidae) and sug-

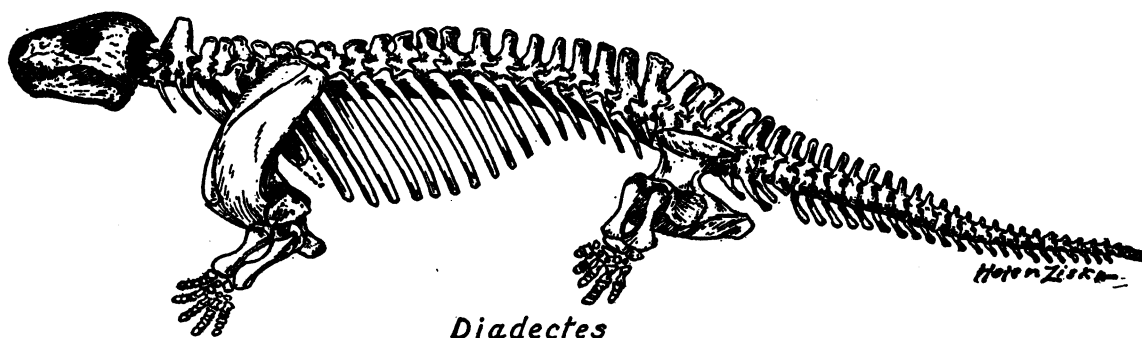


FIG. 1. Skeleton of *Diadectes phaseolinus* Cope. \times About 1/12. Data from American Museum material and from Case (1905, 1911). Length about 1.7 m.

opposition to this view, Williston (*loc. cit.*) pointed out many supposedly inadapative differences between the plesiosaurs and the turtles and concluded that "Whatever of resemblance there may be in the form and habits of these two orders of animals has been due solely to parallel evolution, to similar aquatic adaptations. In their internal structure they are really remote from each other and neither could have been derived from the other type, not even in a remotely antecedent stage."

A new phase in the development of this already old problem began with Cope's discoveries in the Texas Permian (or Permian-Carboniferous) of the very primitive reptiles (fig. 1) which he named *Diadectes*, *Empedocles*, and *Empedias* and for which he erected (1880) the suborder Cotylosauria, of the "order Theromorpha." Case (1905, p. 127) states that in 1896 Cope described two other genera from the Permian of Texas, which he

gested that "the order is probably ancestral to the Testudinata and the Pseudosuchia." Eventually it was shown that the Otocoelidae (Dissorophidae) were rhachitomous labyrinthodonts, and Cope subsequently abandoned the name Chelydosauria, retaining the name Cotylosauria for *Diadectes* and its relatives.

Case (1905), restricting the "Chelydosauria" to the Diadectidae and Otocoelidae, pointed out seven important points in which the diadectid skull indicates affinities to the Testudinata and concluded: "In just the characters in which the Chelydosauria (Otocoelidae, Diadectidae) approach the turtles they are distinct from the Cotylosauria (Pareiasauridae and Pariotichidae) and so it seems very probable that we have in the Diadectidae forms very closely related to the ancestral stem of the turtles, which tell us much regarding the development of the Testudinata directly from the Cotylosauria"

[sic ?Chelydosauria]. The conclusion of Cope and Case that the chelonians have indeed been derived from the Cotylosauria (*sensu lato*) has been sustained by Williston (1904; 1907; 1917; 1925, pp. 209, 210), Watson (1914b), Hay (1905), von Huene (1936b), and others.

The older view that the turtles are somehow related to the Sauropterygia has been defended by Jaekel (1902, pp. 135-144) and independently by Broom (1924). Both these authors cite the turtle-like skull characters of the Upper Triassic placodont *Placochelys* (see p. 314), and Jaekel also attempted to homologize certain parts of the carapace and plastron of *Placochelys* with those of chelonians. Jaekel (*ibid.*, p. 143) explained the contemporaneity of the heavily toothed placodonts and the virtually toothless beaked chelonians in Upper Triassic times by the assumption that the ancestors of the chelonians had undergone a severe transformation together with a change in food habits. The traces of some such transformation were indeed evident in the much later discovered skulls of *Henodus chelyops* from the Lower Jurassic of Europe, described by von Huene (1936a, 1938). In this genus only the last upper and lower crushing teeth of the placodonts remained. The oral borders were evidently covered with a horny beak which, on the evidence cited by von Huene, may have borne parallel ridges (fig. 31) for sifting food from the water, as in certain ducks. The carapace and plastron of *Henodus* in general form were remarkably like those of certain turtles. Nevertheless von Huene showed that *Henodus* is only a highly specialized placodont and the last of its order. The earlier placodonts, including *Paraplacodus* (Peyer, 1935), are far less turtle-like and, on the other side, I shall presently cite decisive evidence that in the girdles and limbs as well as in the construction of the temporal region the older placodonts were related to the nothosaurs and plesiosaurs. Von Huene, therefore, even in his latest phylogenetic diagrams (1936b, 1940) continues to place the Testudinata as a derivative of the Cotylosauria, its line starting between the pareiasaurs and the seymouriamorphs.

Until recently I was content to accept the

general conclusion that the turtles have been derived from the cotylosaurian order, without making any serious effort to find out which cotylosaurs, if any, were the nearest to the undiscovered pre-Triassic line that led to *Eumotosaurus* (fig. 4) and the chelonians. Nor did a cursory first review of the evidence reveal anything further. The Procolophonia, which have been ably reviewed by Colbert (1946), were a distinct suborder of cotylosaurs, running their course to their extinction in the Upper Triassic, retaining the great otic notch of *Diadectes* but remaining quite different from the contemporary amphichelydian turtles. The captorhinomorphs, another suborder of cotylosaurs, had lost the otic notch and the curved quadrate which were characteristic of *Diadectes* (fig. 6A) and which would be expected in an ancestral chelonian, nor did either the rest of the skull or the postcranial skeleton indicate a very close connection with the turtles. For that matter, *Diadectes* itself, although quite turtle-like in its large otic notch and curved quadrate, was well provided with highly specialized jaws and dentition; its very large vertebrae (fig. 16) bore complex hyposphenehypantral articulations, while a bony carapace and plastron were either lacking or not sufficiently coherent to be preserved.

When I turned my attention to the pareiasaurs (figs. 2, 3), I was surprised to find that apart from their gigantic size they seemed on the whole to afford an excellent starting point for the chelonian line, both in their general construction and in many features of the skull, vertebrae, ribs, girdles, limb bones, hands, and feet.

Seeley (1887-1895) made many comparisons between pareiasaurs and anomodonts, pareiasaurs and protorosaurs, pareiasaurs and mammals, and the like, but, strange to say, neither his text nor his figures compare pareiasaurs and chelonians. Houghton and Boonstra's thorough systematic and comparative studies on South African pareiasaurs (1929, 1930, 1932, 1933) have supplied indispensable material for the present study, but they do not touch upon the major problem of the possible relationships of pareiasaur to chelonian.

The present paper is in part a continuation of the series on comparative osteology and

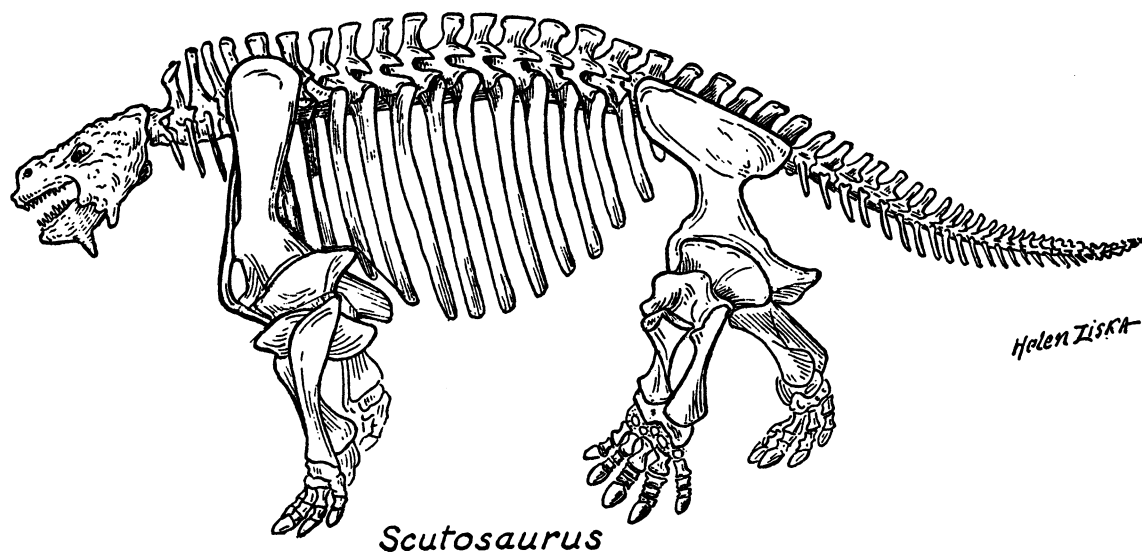


FIG. 2. Skeleton of *Scutosaurus karpinskyi* (Amalitsky). Based on American Museum skeleton mounted by Mr. Charles Lang under the direction of Dr. Barnum Brown. Length about 3.05 m.

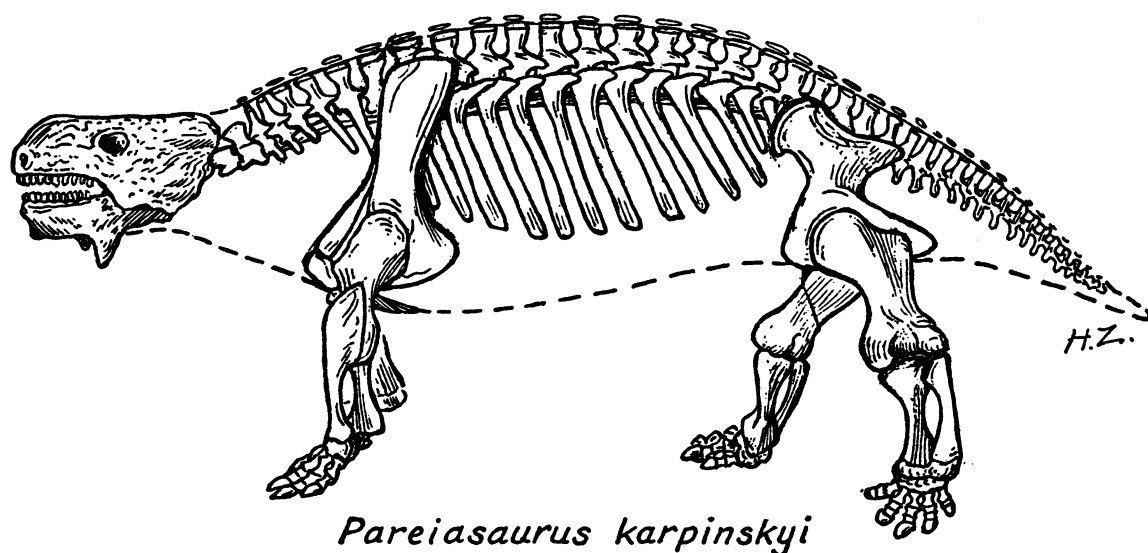


FIG. 3. Skeleton of "*Pareiasaurus karpinskyi*." Based largely on unpublished lithographic plates of Amalitsky's, with changes indicated by comparative study. The line along the middle of the back indicates the position of the neural or middorsal bony scutes. The transverse rows of scutes are not indicated.

myology by the author and his collaborators, especially L. A. Adams (1919), Charles L. Camp (Gregory and Camp, 1918), R. W. Miner (1925), G. K. Noble (Gregory and Noble, 1924), A. S. Romer (1922), H. O. Elftman (1929), H. C. Waterman (1929), B. Schaeffer (1941), H. C. Raven (Gregory and Raven, 1941), and F. G. Evans (1939),

transformation of organic designs: a review of the origin and deployment of the earlier vertebrates" (1936).

The skeletons of various chelonians in the American Museum have been studied with special reference to the skull, vertebral column, girdles, and limbs, especially in their adjustments to the presence of a fixed cara-

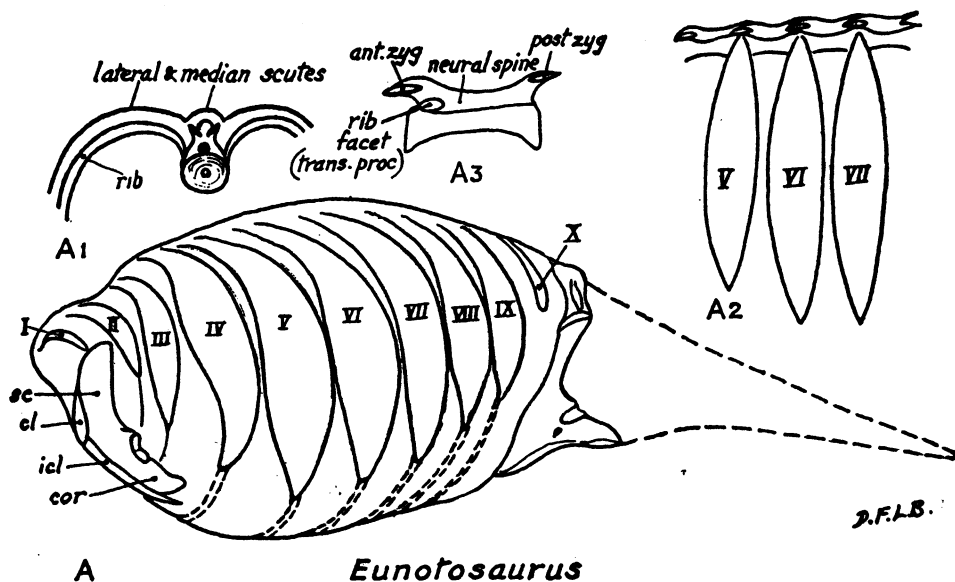


FIG. 4. Sketches of thoracic skeleton of Upper Permian chelonian, *Eunotosaurus* Seeley. Based on description and figures by Watson (1914b). Of the 10 dorsal ribs, no. I was small and apparently had not yet overlapped the top of the scapula; nos. III–VIII were greatly widened, no. IX was less so, no. X was very small. The narrow pelvis was behind the carapace. The latter consisted of thin median and lateral ossified plates. The centra were slender and somewhat hour-glass-shaped, with reduced neural spines, low neural arches, closely interlocking zygapophyses. The prominent rib facets were near the front end of the centra in vertebrae II–VII but near or at the middle in VIII and IX, all essentially as in later chelonians.

which dealt with the evolution of various parts of the vertebrate skeleton on the diverging lines of ascent from the crossopterygian fishes to the amphibians, reptiles, and mammals.

The accepted general principles of evolution and the methods of analysis and synthesis applied in the present investigation are discussed in earlier papers, especially "The orders of mammals" (1910, pp. 105–107), "Fish skulls: a study of the evolution of natural mechanisms" (1933, pp. 443–449), "Reduplication in evolution" (1935b), "The

pace and plastron and in comparison with the corresponding parts of cotylosaurs, placodonts, sauropterygians, and other extinct reptiles. Some excellent pareiasaurian material in the American Museum, including a skeleton of the Russian *Scutosaurus*, mounted under the direction of Dr. Barnum Brown, and casts of the limb bones of the South African *Propappus*, received from Dr. Robert Broom, have also been studied and are here figured. Numerous courtesies from Dr. Edwin H. Colbert and Mr. Charles M. Bogert are gladly acknowledged.

COMPARISON OF DIADECTID, PAREIASAUR, AND TURTLE SKELETONS

GENERAL BODY FORM AND HABITS

THE CONSENSUS OF RECENT AUTHORS is that the most primitive turtles living today are not the flattened, wide, marine leathery turtles (*Dermochelys*, *Sphargis*), or even the hawksbill and loggerhead sea turtles (Cheloniidae) but the terrestrial tortoises (fig. 5A), with high, well-rounded carapace, short, elephant-like feet, and strong blunt claws. These features were already foreshadowed in at least some of the pareiasaurs, which, according to Boonstra (1933b), were also provided with a partial carapace of bony scutes along the midline of the back and sides. The outer surface of the skull of both diadectids and pareiasaurs was often heavily furrowed or wrinkled by the under side of a massive integument. In certain diadectids (*Chilonyx*) and many pareiasaurs there were conical protuberances around the rear borders of the skull, which also indicate a great development of an integumental skeleton. Clear traces of such a condition are seen also on the surface of the skull in *Triassochelys* (fig. 6C), as figured by Jaekel.

A ventral armature of gastralium or abdominal ribs seems to be unknown among the diadectids and pareiasaurs, as well as among the chelonians, and it may be conjectured that, in spite of analogies with the plesiosaur gastralium (Owen, 1849), the plastron of chelonians, which was well developed in the Upper Triassic *Triassochelys*, arose from a rapid spreading of bone-producing power of the integument on the ventral surface of the body across the integumental "bridges" between the humeral and femoral notches. The pareiasaurs, as far as known, were gigantic animals, at least in their adult stage, and the lack of a firmly knit carapace and plated plastron apparently did not endanger their existence. But the turtles in their beginnings were small animals which could easily be turned over by aggressive pelycosaurs and theriodonts, and for them a stout plastron of broad plates must have been a much needed addition to their armor.

The bony rib plates in chelonians were not developed as such in diadectids or pareiasaurs and probably originated within the order, in part as lateral extensions of the bony perichondral husks of the ribs, within the widening periosteal membranes (Goette, 1899, p. 415), in part through an invasion of surface scutes into the intercostal spaces (see fig. 3).

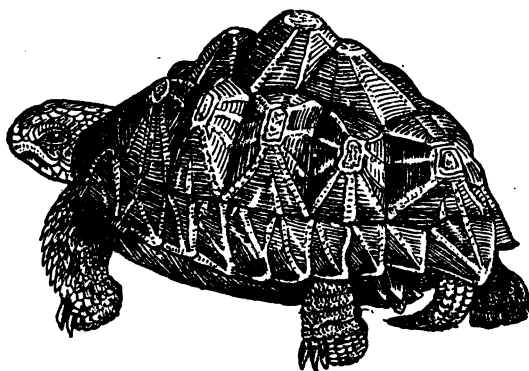
The marginal teeth of pareiasaurs were small, laterally compressed, cuspidate, and close set, unlike the transversely oval cheek teeth and nipping incisors of *Diadectes* (fig. 7) and less restricted to the cutting of tough, resistant substances; while their powerful jaws and strong bony palates (fig. 8A) should have enabled them to smash and devour a variety of animal and vegetable foods. The change to the horny beak and powerful cutting and crushing jaws of turtles may be paralleled more or less among other reptiles of carnivorous to omnivorous habits (e.g., endothiodonts among anomodonts, *Psittacosaurus* among dinosaurs).

In walking, the body of pareiasaurs (figs. 2, 3) could be raised farther from the ground than it was in the sharply bent-limbed *Diadectes* (fig. 1), and both the forearm and the shank could be more widely extended than in that primitive cotylosaur. The turtles, in spite of their extreme development of carapace and plastron, exhibit even greater mobility of the limbs than did the pareiasaurs and have advanced well beyond the diadectid grade.

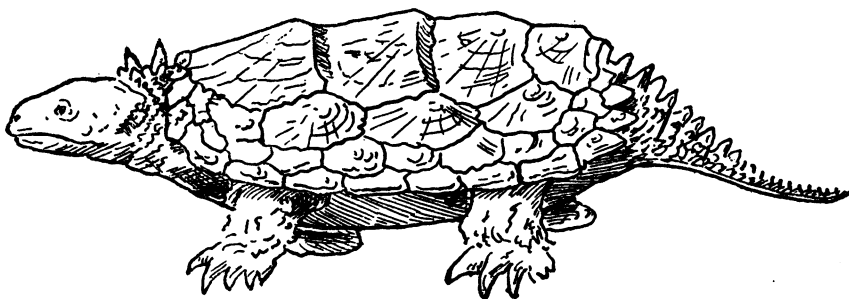
SKULL

The general form of the skull in *Diadectes* suggests that of *Triassochelys* and the sea turtle *Chelone* in all views (figs. 6, 7, 8, 9), but retains many more primitive features, such as the ascending rami of the premaxillae and the full complement of primitive reptilian elements. Of the latter, modernized turtles have lost the supratemporals, tabulars, nasals, postorbitals, and ectopterygoids.

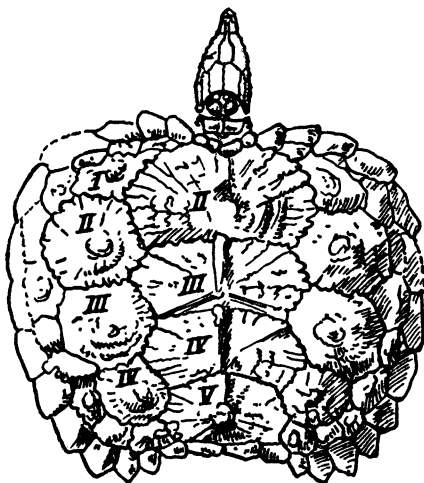
The dentition of diadectids is of course



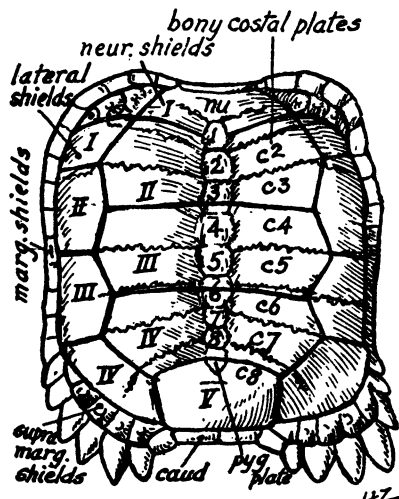
A *Testudo elegans*



B *Triassochelys*



B₁



C *Proganochelys*

FIG. 5. Modern tortoise and Mesozoic amphichelydians. A, After Lydekker; B, B 1, after Jaekel; C, after E. Fraas. Horny shields are here designated by roman, bony plates by arabic, numbers.

highly specialized but, as noted above, the reduction of crushing teeth in the later placodonts (*Henodus*), together with other evidence, suggests that the possession of specialized crushing teeth in *Diadectes* does not necessarily exclude it from ancestry to secondarily beaked forms without teeth.

closely with the basic plan of this region in pareiasaurs (fig. 8A).

The secondary bony palate was only beginning in *Triassochelys* (fig. 8B), and in fact the entire under side of the skull in this form suggests that, apart from its development of horny upper and lower beaks, it was

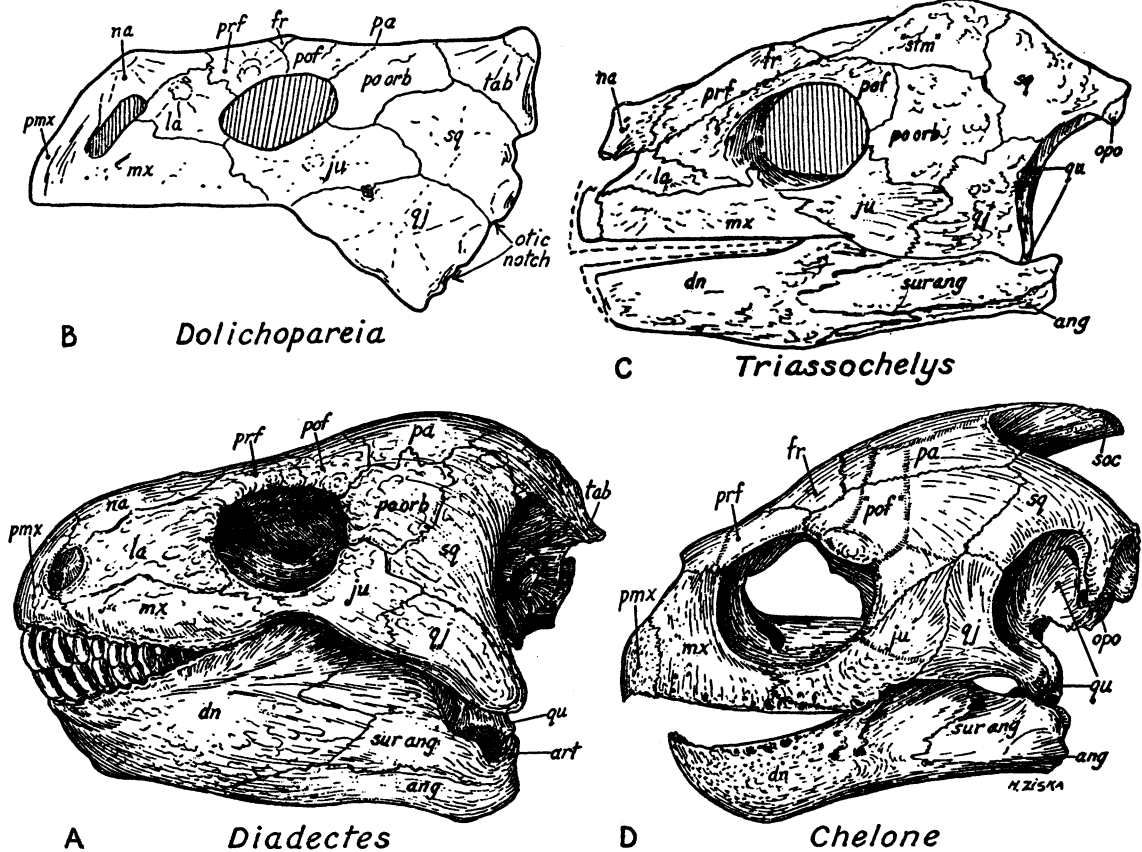
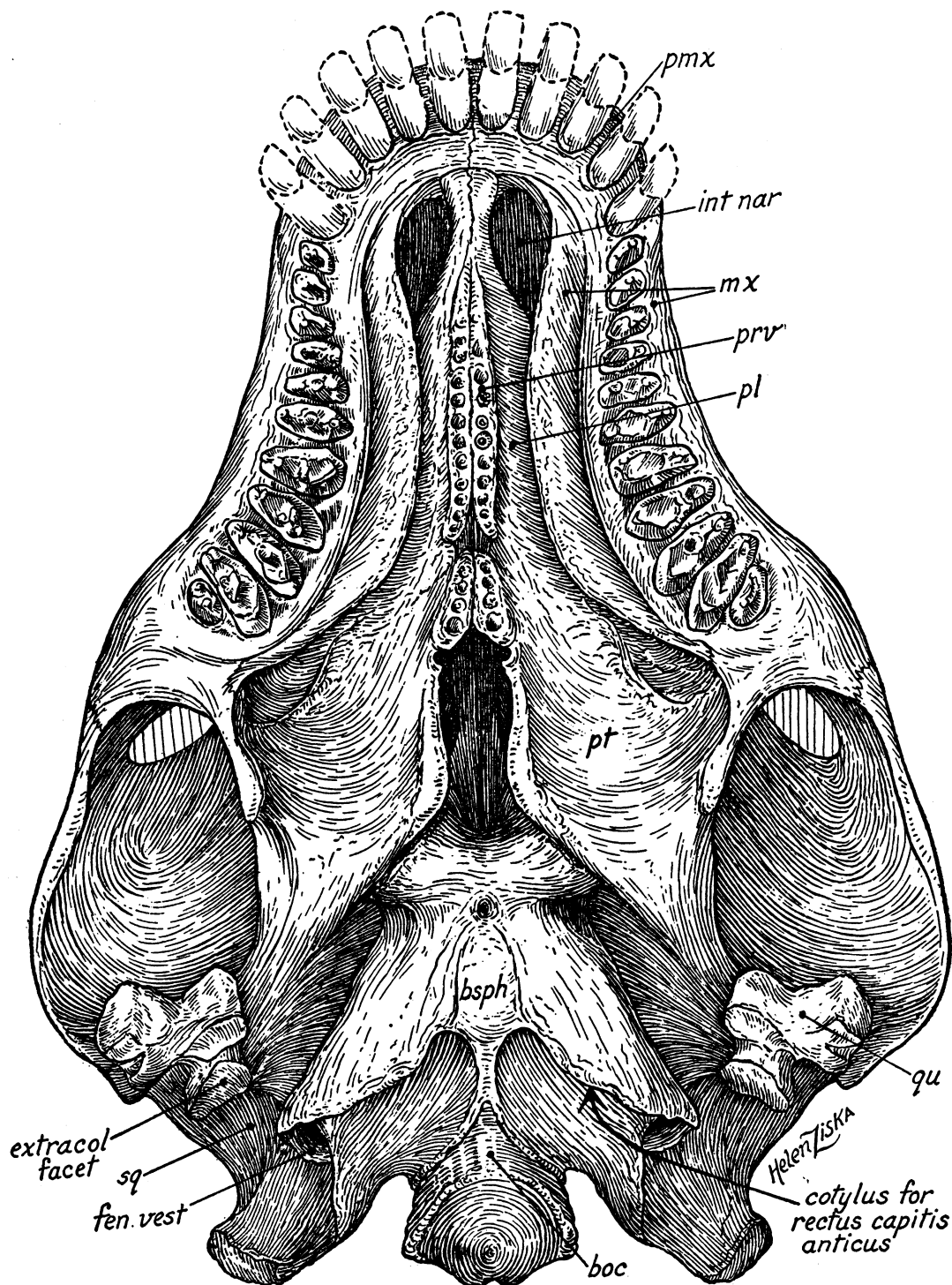


FIG. 6. Skulls of diadectid (A), pareiasaur (B), and chelonians (C, D). A, Mostly from A.M.N.H. No. 4839, mandible from A.M.N.H. Nos. 4684 and 4353 and Welles' figure (1941, p. 426); B, after Boonstra (1933a); C, after Jaekel; D, original.

However, it would presumably be easier to get rid of the small marginal teeth of pareiasaurs than of the large crushing teeth of *Diadectes*. And according to Jaekel (1918, pp. 172, 195) *Triassochelys* retained clear vestiges of small teeth in the maxillae and dentaries, while it still bore a median patch and four converging rows of small teeth on the pterygoids (*ibid.*, p. 172), together with a long median streak on the prevomers between the large choanae (fig. 8B), all agreeing

nearer to certain pareiasaurs than it was to *Chelone*. In *Diadectes* there are curved palatal ridges (fig. 7) on the maxillae and palatines, but nothing like the massive secondary palate of *Chelone* (composed of rolled-over flanges of the maxillae and palatines that arch over the choanae) is known either in the pareiasaurs or in *Triassochelys*. The massiveness and full development of these parts in *Chelone* (fig. 8C) may indeed be correlated with similar qualities of its beak and man-



Diadectes

FIG. 7. Palatal aspect of skull of *Diadectes*. Reconstructed from A.M.N.H. Nos. 4352, 4839, and 4370, with data from Case (1905, 1911, 1912) and von Huene (1913).

dible, as well as with the huge size of the jaw muscles. The secondary palate of most other fossil and recent chelonians is much less strongly developed than that of *Chelone*, and in some it may be lacking entirely.

muscles, which have pushed up the high median occipital crest (cf. L. A. Adams, 1919, pp. 88-89, and pl. 6, figs. 1, 2). In *Diadectes* the jaw muscles were confined to the dorsally shut-in temporal chamber (figs.

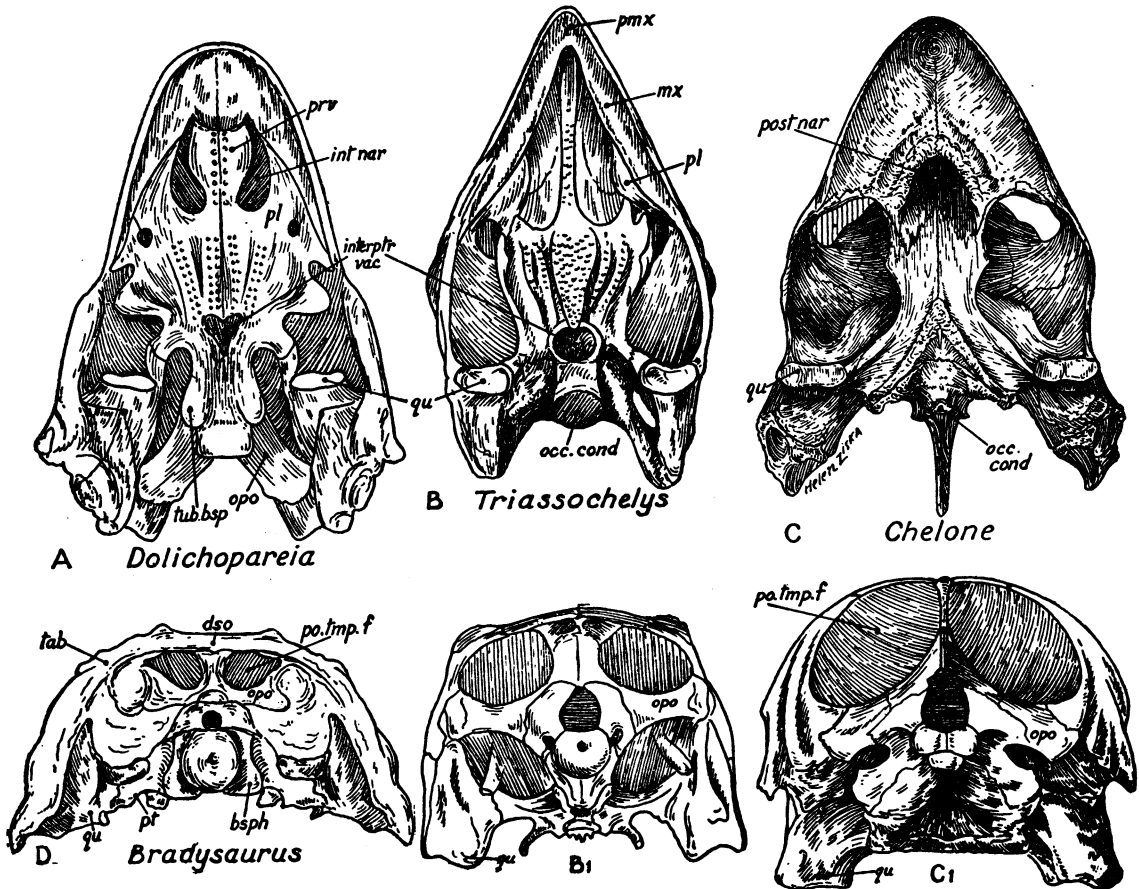


FIG. 8. Palatal and occipital aspects of skulls of Permian pareiasaur (A, D), Triassic chelonian (B, B 1) and recent sea turtle (C, C 1). A, D, After Boonstra; B, B 1, C 1, after Jaekel.

The occipital views (fig. 8) tell the same story. They also indicate that the tripartite condition of the occipital condyle in *Chelone* is a secondary feature, but that its paired posttemporal fenestrae have been inherited from those of *Triassochelys* and that they in turn are strictly homologous with those of the pareiasaurian. According to Sushkin (1928, p. 264) these fossae were already developed in the cotylosaur *Captorhinus*, but they were not present in *Diadectes*.

In all the turtles these posttemporal holes were invaded by the large temporal jaw

7, 9) both above and behind, and the rear wall of the occiput was occupied by nuchal muscles (Evans, 1939, p. 58). Thus with regard to these features of the occiput the pareiasaur (fig. 8D) more clearly foreshadowed the chelonian and was well advanced beyond *Diadectes*.

In all three forms (figs. 6, 8) the massive quadrates were monimostylic, that is, they were firmly fixed in place, medially by their attachments to the great pterygoids, laterally by the quadratojugals, and dorsally by the squamosals, especially by the massive paroc-

capital processes of the opisthotic bones.

The opisthotics in *Chelone* (figs. 8C, 12C) were suturally separate from the exoccipitals, as they were also in the pareiasaurs (Boonstra, 1933a, pp. 17, 18, and pl. 4, fig. 1) and *Captorhinus* (Sushkin, 1928, p. 264, figs. 1, 2), but the separateness of the opisthotic was less clear in *Diadectes*. According to White (1939, p. 345) the opisthotic was distinct

according to Boonstra (1933a, pl. 1), the otic notch in the side view is concealed by the backward growth of the squamosal and quadratojugal, but in the rear view (fig. 8A, D) the tympanic cavity was evidently medial to the squamosal and quadrate, the chief difference being that in *Chelone* (fig. 8C 1), owing to the expansion of the post-temporal fenestrae under the influence of the

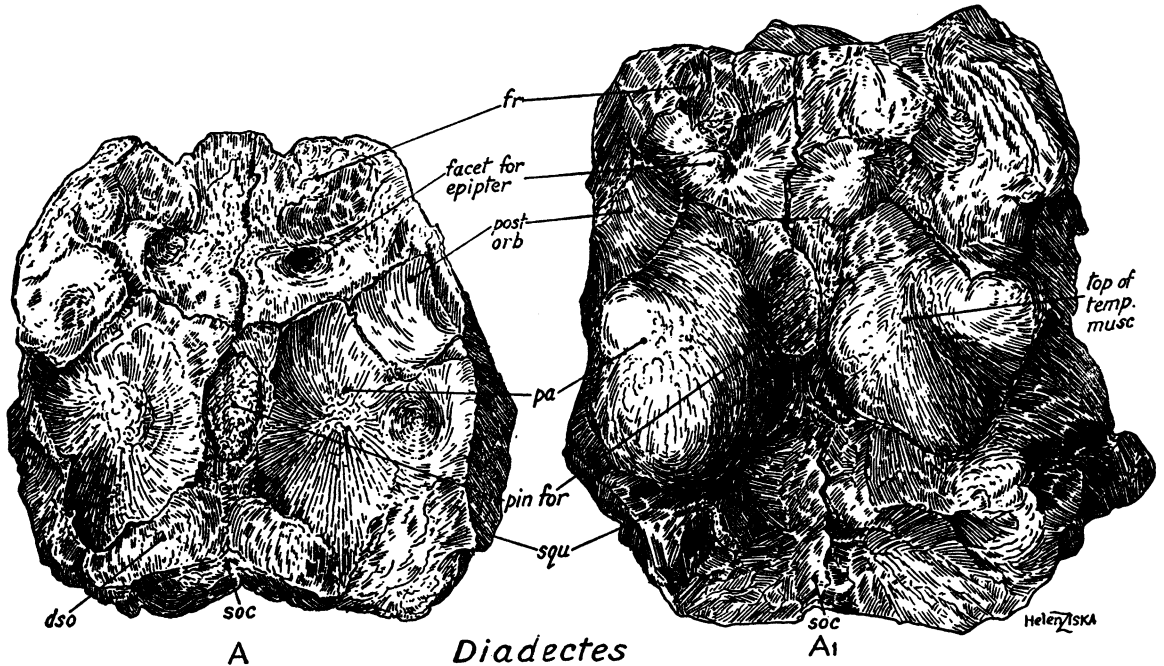


FIG. 9. Under side (A) of the temporal roof of *Diadectes*, with natural cast (A 1) or obverse of the same. The narrow braincase, indicated by the large pineal canal, lies between the large chambers that contained the temporal muscles.

in *Seymouria*, as it was also in *Kotlassia* (Bystrow, 1944, p. 385). In many later reptiles, on the contrary, the opisthotic and exoccipital were not separate, so that here as in other ways the turtles have inherited some very early reptilian features.

In *Chelone* and other Cryptodira the posterior side of the quadrate and the adjacent border of the squamosal (fig. 6C, D) were together curved into a G-shaped figure bordering the "meatal excavation" (Cope) or tympanic notch. In *Diadectes* (fig. 6A) this notch is essentially similar, except that the tabular (which is lost in modern turtles) forms the upper border (cf. von Huene, 1913, p. 334, fig. 17). In pareiasaurs (fig. 6B),

huge jaw muscles, the outer part of the tympanic cavity has, as it were, been pressed downward below the level of the occipital condyle. It would not indeed be surprising if part of the resemblance to *Diadectes* in the otic notch of *Chelone* were merely convergent, because the otic notch of *Triassochelys* was narrow and less G-shaped than that of *Chelone*. In either case the "meatal excavation" and all its bounding ridges were, so to speak, the work of the tubo-tympanic pouch, which, as in the mosasaurs, moulded the surrounding bones into a G (cf. Jaekel, 1918, p. 163, fig. 43).

The stapes (columella auris) of *Diadectes* is not known but to judge from the stoutness

of the surrounding bones and the large size of the crater-like depression which served instead of a true fenestra vestibuli, it must

"the stapes was thus probably a massive curved bone with two lateral processes and a medial process tapering nearly to a point

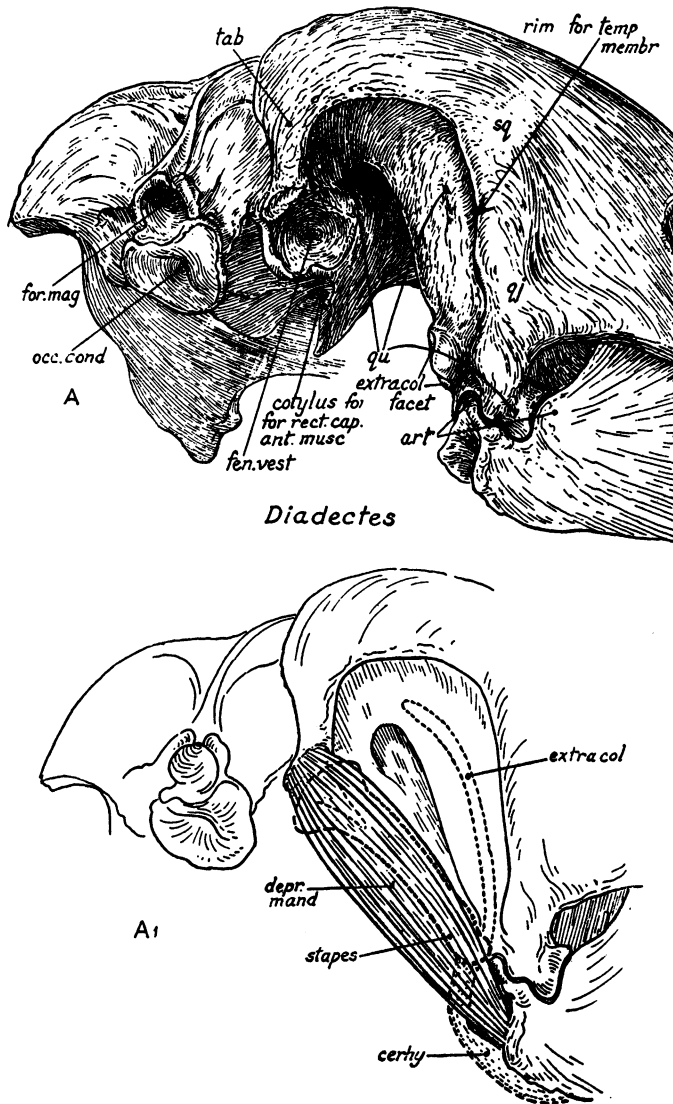


FIG. 10. Oblique rear view (A) of skull of *Diadectes*, with attempted restoration of middle ear parts and depressor mandibulae muscle. (In A, for *temp.*, read *tymp.*)

have had a large and thick shaft, as is further suggested by the large size of its extracolumellar contact with the quadrate (figs. 7, 10). The stapes of pareiasaurs is also unknown, but after his thorough studies of the skulls, Boonstra (1933a, p. 21) concludes that

at the fenestra ovalis." Probably the very large stapes which may thus be predicated for *Diadectes* and pareiasaurs retained its primitive piscine function of supporting the lower part of the hyoid arch and larynx. Moreover, although the rim for the tympanic

membrane was well defined in *Diadectes*, we may doubt whether this membrane served so much for transmitting sound waves through the stapes as for facilitating the adjustment of the pressure inside the tubotympanal canal to changes in pressure of the air or water. According to Jaekel (1918,

quadrate, but its evident homology with that of *Triassochelys* is another feature that tends to connect the turtles with the cotylosaurian stem.

Parts of the hyobranchial complex of two adult pareiasaurs, as described and named by Boonstra (1932b), differ conspicuously

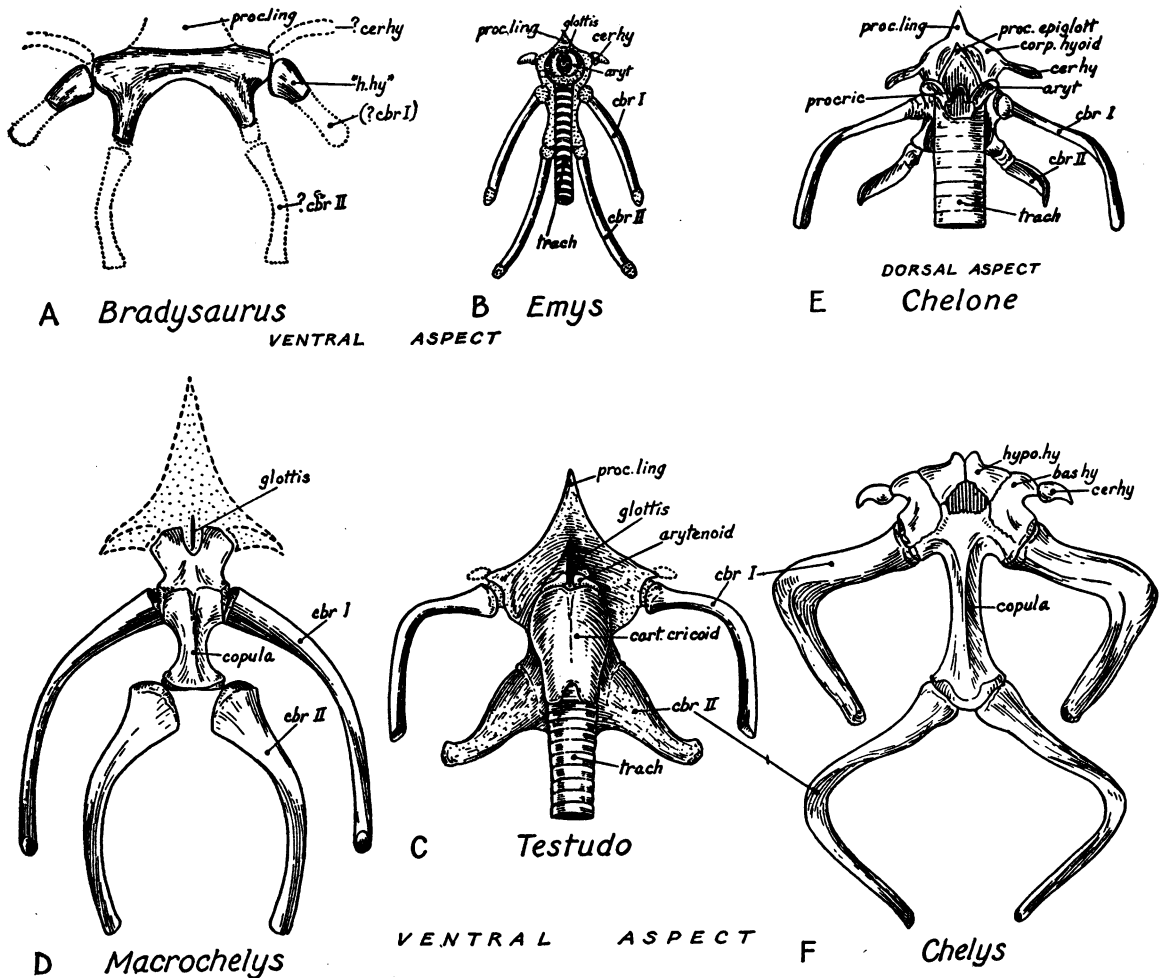


FIG. 11. Hyoid bones of pareiasaur (A) and recent chelonians (B-F). A, After Boonstra (1932b); B, after Wiedersheim (1907); C, D, F, from American Museum specimens; E, after Ihle, Van Kampen, et al.

p. 163) the columella auris of *Triassochelys* (*ibid.*, p. 164, fig. 44, *Hm*) likewise still served as a "hyomandibular." The columella of the adult *Chelone* has become a very thin curved rod, lodged partly in a special "incisura columellae" on the rear face of the

(fig. 11) from those of adult *Testudo*, *Emys*, *Macrochelys*, especially (1) in having an exceedingly short basihyal; (2) in apparently lacking an ossified processus lingualis (= "basihyal" of Parker, or hypohyal of later authors); and also (3) in lacking an ossified

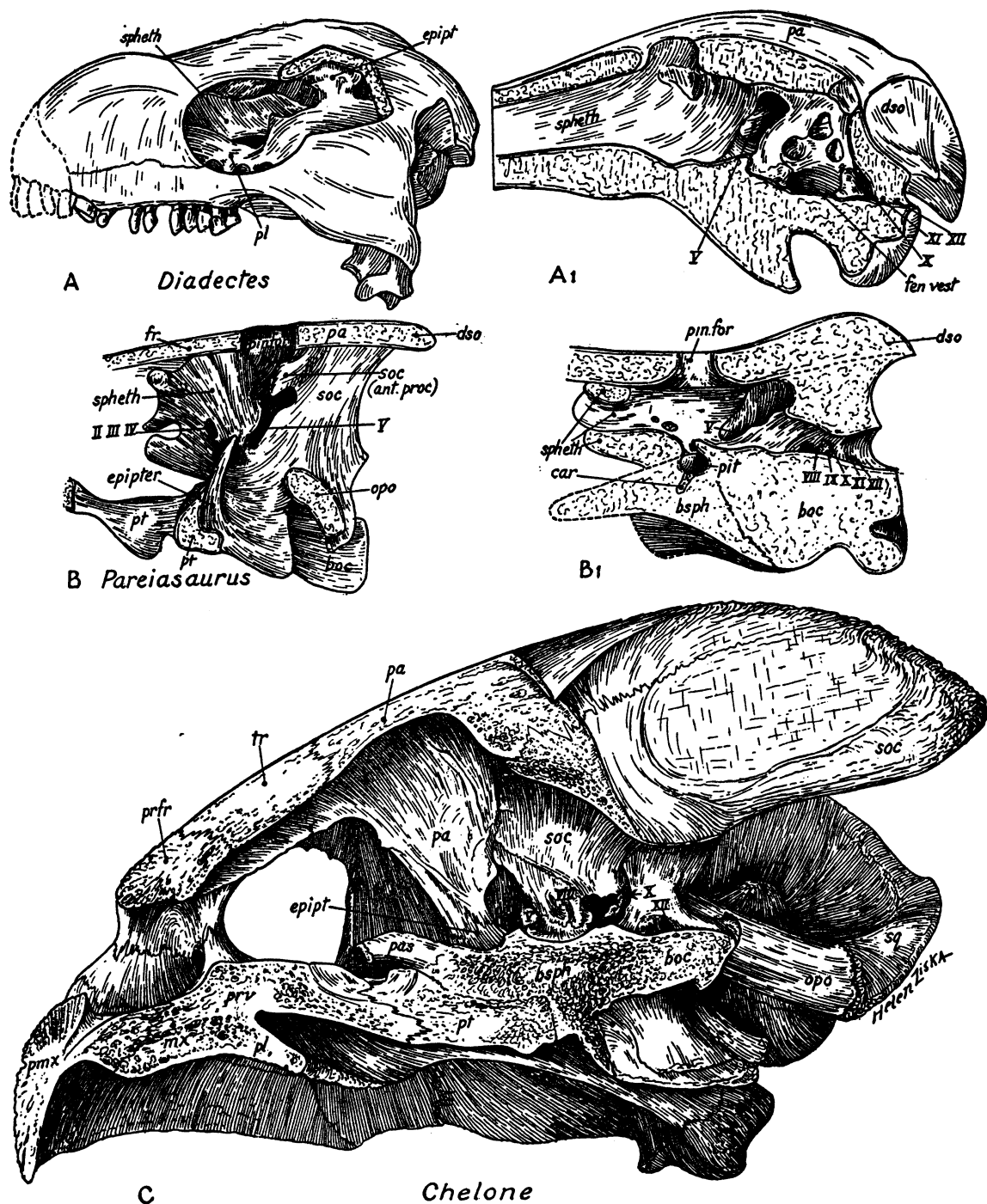


FIG. 12. The braincase of *Diadectes* (A, A 1), pareiasaur (B, B 1) and modern chelonian (C). A, Skull of *Diadectes* (A.M.N.H. No. 4839), with part of temporal roof cut away, showing large epipterygoid in contact with cranial roof. A 1, Paramesial section and right half of cranium of *Diadectes*. A.M.N.H. No. 4441, with data from Watson (1916). Shows the primitive sphenethmoid, large epiphyseal tube and low otic-occipital chamber. B, Lateral view of pareiasaur braincase, showing reduced epipterygoid. After Boonstra. B 1, Mesial section of pareiasaur braincase. After Watson. C, Paramesial section and right half of skull of *Chelone*, showing highly raised roof of braincase, great sagittal crest, and abortive epipterygoid.

second ceratobranchial. In an embryo *Chelone* figured by Parker his "basihyal" is relatively shorter and wider than it is in the adults of the other genera (fig. 11). Possibly these dif-

ferences may be associated with (1) the shortness and great width of the neck in pareiasaurs; (2) the narrowness and flexible tubular form of the neck in chelonians.

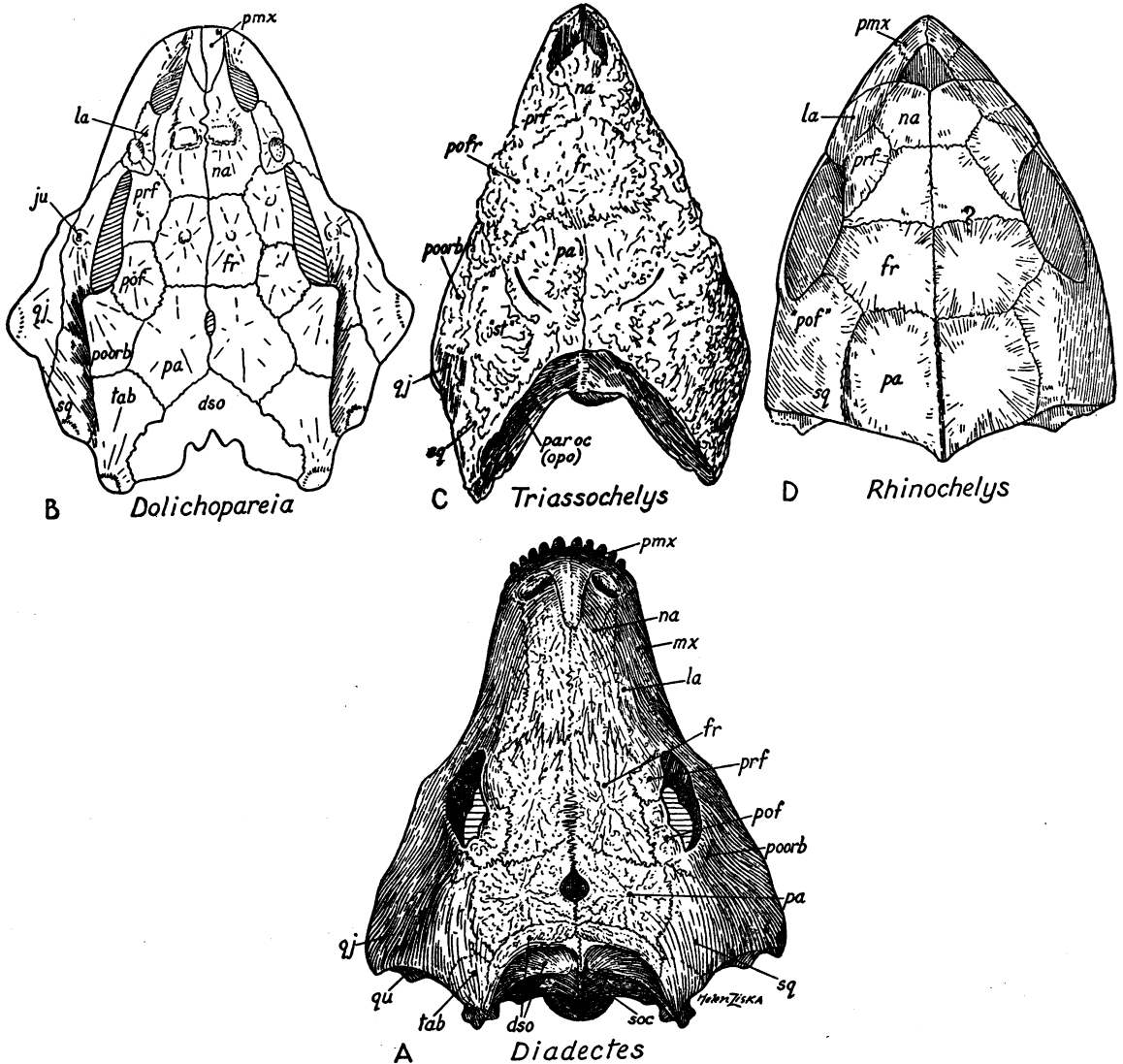


FIG. 13. Dorsal aspect of skulls of *Diadectes* (A), pareiasaur (B), *Triassochelys* (C), Jurassic amphichelydian (D). B, After Boonstra; C, after Jaekel; D, from Zittel.

ferences may be associated with (1) the shortness and great width of the neck in pareiasaurs; (2) the narrowness and flexible tubular form of the neck in chelonians.

Mesial sections of the skull (fig. 12) in *Diadectes*, pareiasaurs, and modern turtle again show that the turtle skull owes both its

cotylosaurian in its lack of cranial flexure and strong development of the median basi-parasphenoid rostrum. Through the hypertrophy of the jaw muscles, the roof of the turtle skull has been raised high above the low-roofed level of the diadectids and pareiasaurs. The epipterygoid, which in

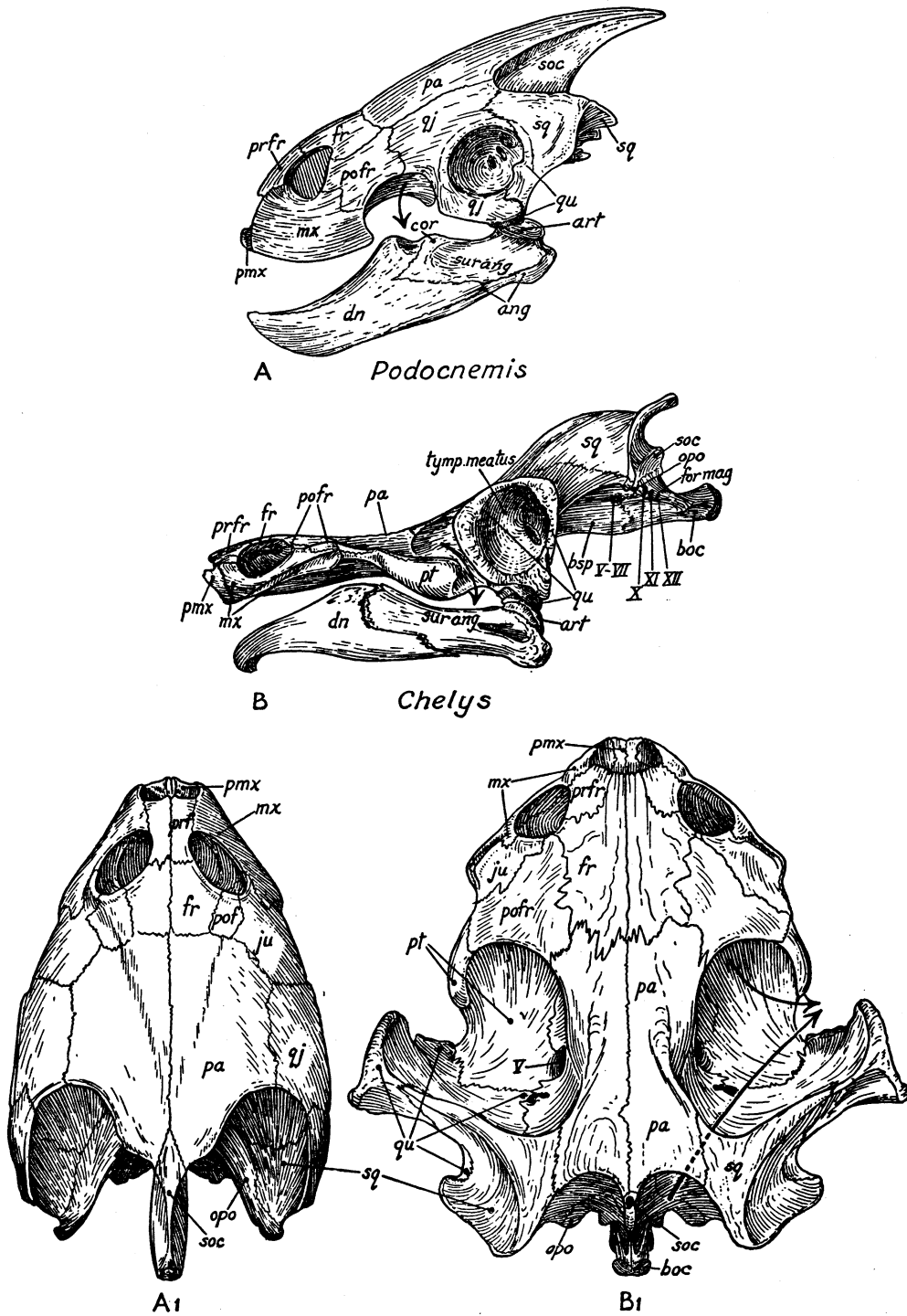


FIG. 14. Skulls of Pleurodira. *Podocnemis* (A, A 1), after Hay (1908, pl. 4); *Chelys* (B, B 1), from American Museum specimens.

diadectids is very large and helps support the skull roof, is reduced in pareiasaurs (fig. 12B) and nearly aborted in *Chelone*, and the large pineal opening of the cotylosaurs is completely closed.

In spite of the advanced stage represented by *Chelone* in the construction of its secondary palate and massive jaws, its dorsal skull pattern nevertheless retains the general type seen in *Triassochelys*, *Rhinochelys* (fig. 13D), and other Mesozoic amphichelydians, which are all presumably more primitive than any of the modern cryptodirans or pleurodirans. In the leathery turtles (*Dermochelys*, *Sphargis*) the skull is essentially like that of *Chelone*, but with secondarily enfeebled jaws and a marked tendency for the dried skull to fall apart easily, due to cartilaginous connections and poor sutures.

In the Chelonidae (fig. 6D) the shell of bone over the temporal region remains but little excavated from the rear and rather closely resembles that of *Triassochelys*. Conceivably this condition may be secondary, as the, in general, more primitive *Chelydra* has a more deeply embayed temporal roof, while the typical tortoises retain only a post-frontal-quadratojugal bar.

Fenestration of the temporal roof from the rear is also seen in various stages in the Pleurodira (fig. 14), from the relatively primitive condition in *Podocnemis*, which is essentially like that of *Chelydra*, to the excessively specialized stage in the Matamata (*Chelys fimbriata*), in which the emargination of the temporal region from the rear has been supplemented by extensive transverse emargination, so that the dorsal sides of the broad pterygoids are widely exposed. The skull in the trionychids is likewise specialized in still other ways from the primitive cryptodire pattern.

Thus there seems to be no great risk of serious error either in assuming a substantial unity of origin of the entire order or in taking the skulls of *Triassochelys* and other Amphichelydia as representative of a primitive chelonian type that was ancestral to those of modernized Cryptodira, Pleurodira, and related branches. The striking evidences of affinity of the skull of *Triassochelys* to the pareiasaurian type suggest that the origin of the chelonian order is to be sought some-

where within limits of the Pareiasauria, but not perhaps in any of the known gigantic forms of that group.

VERTEBRAE AND RIBS

In modernized turtles the expanded ribs, together with the bony neural plates, collectively form a single immovable carapace, which effectively prohibits either dorso-ventral or lateral flexure of the greater part of the vertebral column; thus the only parts of the column left free to move are the cervical and caudal vertebrae. Hence it is not surprising that the centra (pl. 34), especially of the mid-thoracic vertebrae, are greatly elongate besides being closely appressed to each other at both ends; or that the anterior and posterior zygapophyses, which permit dorso-ventral flexure in primitive reptiles, have here lost their transverse facets and have become merged with the anterior and posterior descending vertical prolongations of the neural plates above the spinal nerve exits. True neural spines seem to be absent except on the first and last thoracic and first sacral vertebrae. The latter, at least in *Chelydra*, retains a real neural spine and what appears to be a postzygapophysis. Meanwhile the tunnel for the spinal cord has increased considerably in relative size.

Each of the widely spreading thoracic ribs of *Macrochelys* is immovably fastened to the vertebral column by a sharply forking V-shaped proximal end; the thin lower branch (capitulum), resembling an inverted flying buttress (fig. 15C), is suturally united intercentrally with a wide lateral projection from the centra of two successive vertebrae and from the base of the neural arch; the upper costal branch (pseudo-tuberculum), which is continuous laterally only with the so-called dermal portion of the rib complex, makes an extended sutural contact with the neural plate.

In *Triassochelys* both the visceral surface and the cross section of the carapace, as figured by Jaekel (1918, pp. 103, 129), conform closely to the foregoing description, especially in the relations of the thoracic centra to each other and to the wide rib plates, so that in these features the Upper Triassic chelonians were almost as modernized as their surviving descendants.

The thoracic vertebrae and ribs of pareiasaurs (fig. 15A), while nearer to those of diadectids (fig. 16A), are also to some extent modified in the direction of *Triassochelys*, as shown in table 1.

wide, hinge-like joints, favoring dorso-ventral flexure but prohibiting lateral abduction or adduction. The zygapophyses favor the same flexures and are not radically different from the primitive types in their directions. In

TABLE 1
VERTEBRAL CHARACTERS

	<i>Diadectes</i>	<i>Pareiasaur</i> (<i>Bradysaurus</i>)	<i>Triassochelys</i>
Proportions of a mid-thoracic vertebra	Very high	Much lower, with very wide transverse processes	Low and elongate, with transversely short transverse processes
Anterior and posterior zygapophyses	Large, supported by massive buttresses	The same	Absent or fused with vertical flanges from neural plates
Hyposphenes and epiphyses	Highly developed	Reduced	Absent
Thoracic ribs	Curved downward around a somewhat deep, barrel-like thorax	Essentially as in <i>Diadectes</i> , but with very wide proximal ends connecting with wide transverse processes	Ribs arching upward, then outward and downward around a wide, relatively low carapace. Ribs greatly widened and flattened, connecting with horizontal transverse processes and with neural plates
Lateral flexibility of thoracic region	Marked	Reduced	None

In short, the thoracic region of pareiasaurs seems to afford a nearer source for that of the most primitive known chelonian, *Triassochelys*, than does that of *Diadectes*.

With regard to the numbers of presacral vertebrae: for *Diadectes*, Case (1911, pl. 14) figures 22; for the pareiasaur *Bradysaurus*, Boonstra (1933c, pl. 28) and Hartmann-Weinberg (1930) give 19; for *Triassochelys*, Jaekel gives 18 (if we subtract the pro-atlas) and in modern Chelonia also there are 18 (Gadow, 1920, pp. 315, 316).

The cervical vertebrae (figs. 17-19) of modern Cryptodira and Pleurodira differ profoundly and condition the well-known differences in the method of retracting the head. In the former the centra, especially of the sixth and seventh vertebrae, develop

the Pleurodira, on the other hand, the centra develop ball-and-socket joints, the opposite anterior zygapophyses and their supporting pedicels are drawn in near to the midline, while their articular facets have slipped around onto the front face of the zygapophysial process and there form a large, strongly convex turntable for the equally concave facet of the posterior zygapophysis of the preceding vertebra. This is a far higher specialization than that which is attained by the Cryptodira, but both are easily derivable from the conditions described by Jaekel for *Triassochelys*, while all the cervical vertebrae of the latter are not very far beyond those of the pareiasaurs.

In *Chelydra* and other Cryptodira the ninth vertebra (fig. 15C) forms the main pivot for

the sigmoid neck, from which it receives upward and backward thrusts. Its strong, forwardly produced neural spine, together

downwardly curved anterior zygapophyses and their pillars, while wrenching strains are neutralized by inverted flying buttresses

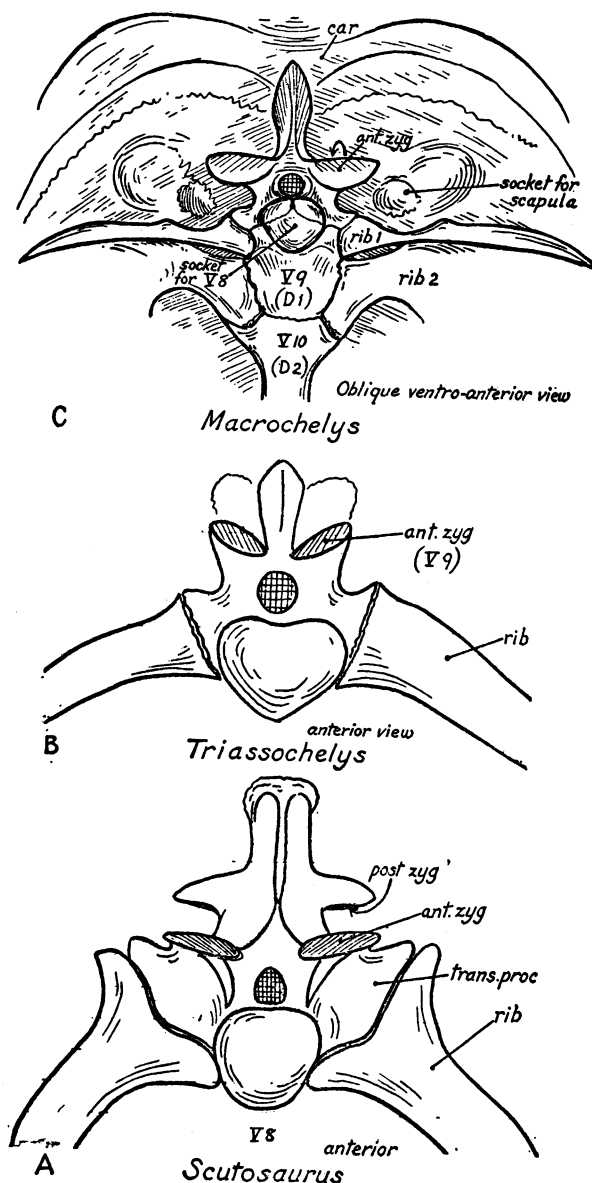


FIG. 15. Relations of anterior dorsal ribs and vertebrae in pareiasaur (A), Triassic (B), and modernized (C) chelonians. A, From American Museum specimen.

with the well-braced bowl at the front end of its centrum, resists upthrusts. Anteroposterior thrusts are met by its great smooth,

formed by the capitula of its own ribs and those of its neighbor, the tenth vertebra. These complexities are barely foreshadowed

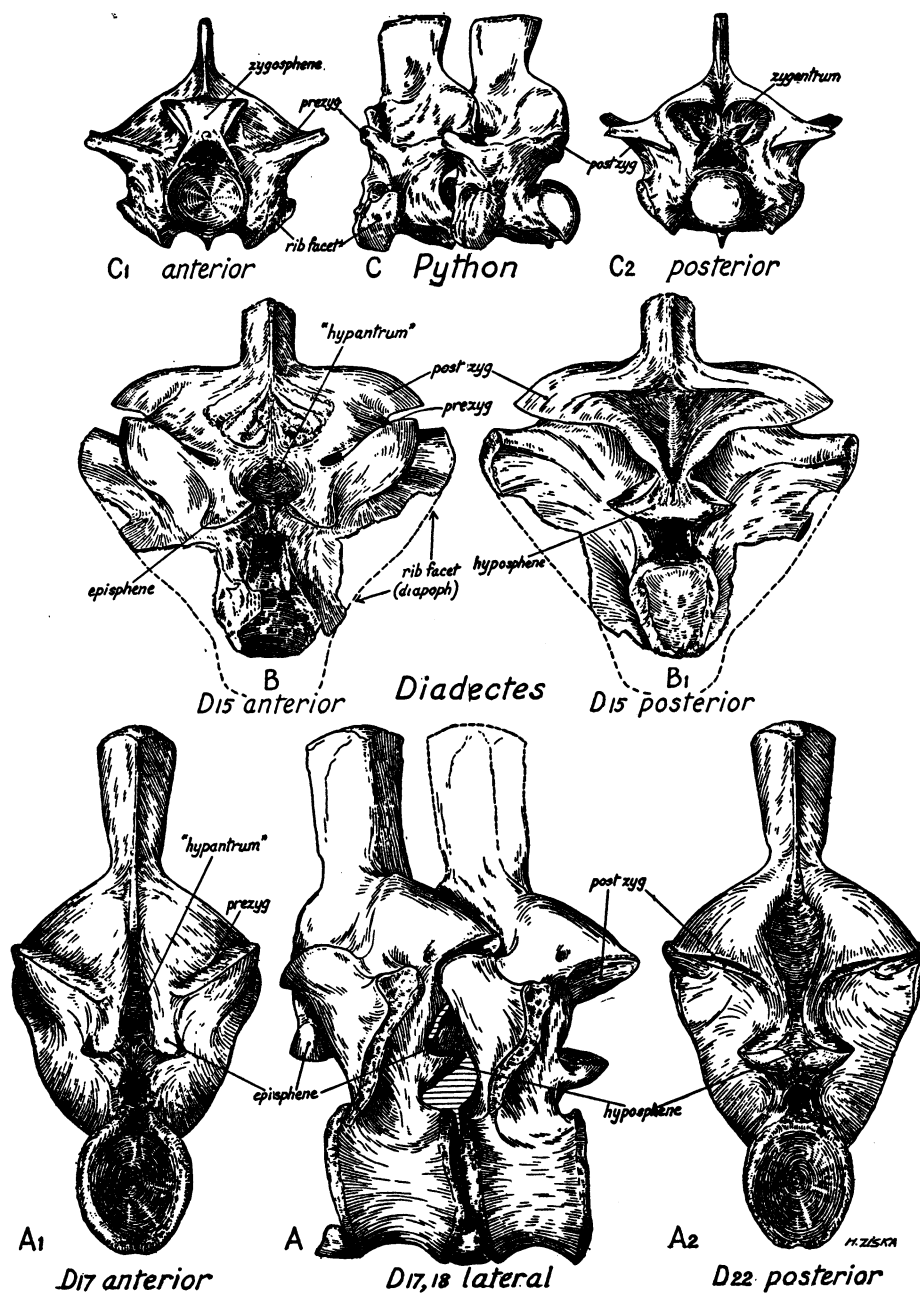


FIG. 16. Dorsal vertebrae of *Diadectes* (A, A 1, A 2, B, B 1) and python (C, C 1, C 2). A, A 1, A 2, From A.M.N.H. No. 4354. Shows the contrast between the zygosphenes-zygantrum articulations of serpents (C, C 1, C 2), which are dorsal to zygapophysial articular surfaces, and the hyposphenes-episphe articulations of *Diadectes*, which are ventral to them. The supposed "hypantrum" on the anterior face (Williston, 1925, p. 91) is indeed a single median depression but, contrary to long-accepted statements, it does not bear articular facets and probably lodged median ligaments or muscles. The true accessory articular surfaces are furnished by the paired dorsal faces of the zygosphenes and the paired ventral surfaces of the hitherto unnamed episphe.

in *Triassochelys* and are not to be expected in a pre-chelonian ancestor before the consolidation of the carapace.

PECTORAL GIRDLE AND LIMBS

The carapace of the Permian *Eunotosaurus* (Watson, 1914b) was already beginning to overlap the upper ends of the pectoral girdle

position. In embryonic stages of recent chelonians (fig. 20) the rudiment of the carapace appears well behind the root of the very large neck and gradually overspreads the pectoral girdle, raising the anterior ribs and swinging them far beyond the tops of the scapulae (Ruckes, 1929b, pp. 109-115, figs. 1-30).

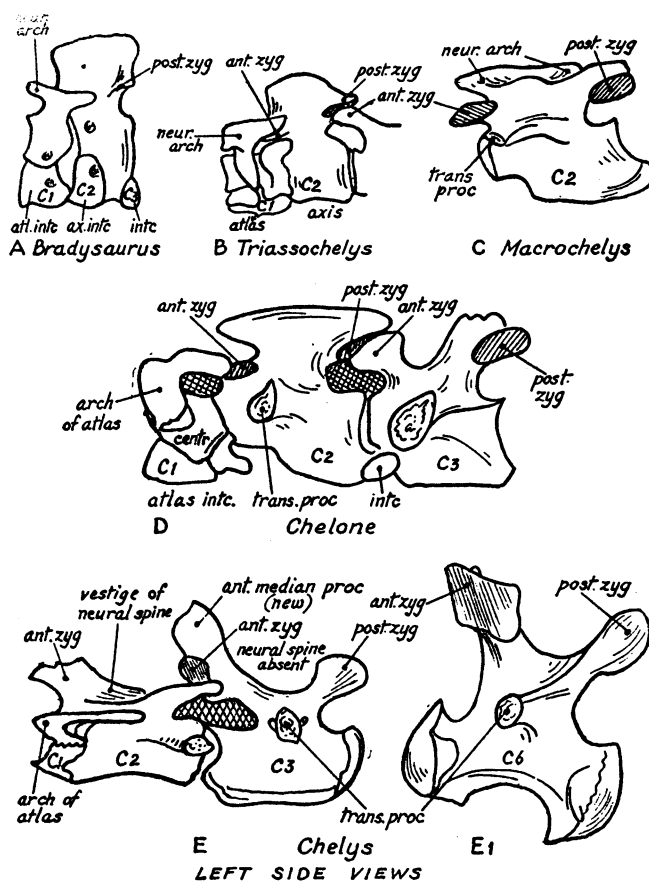
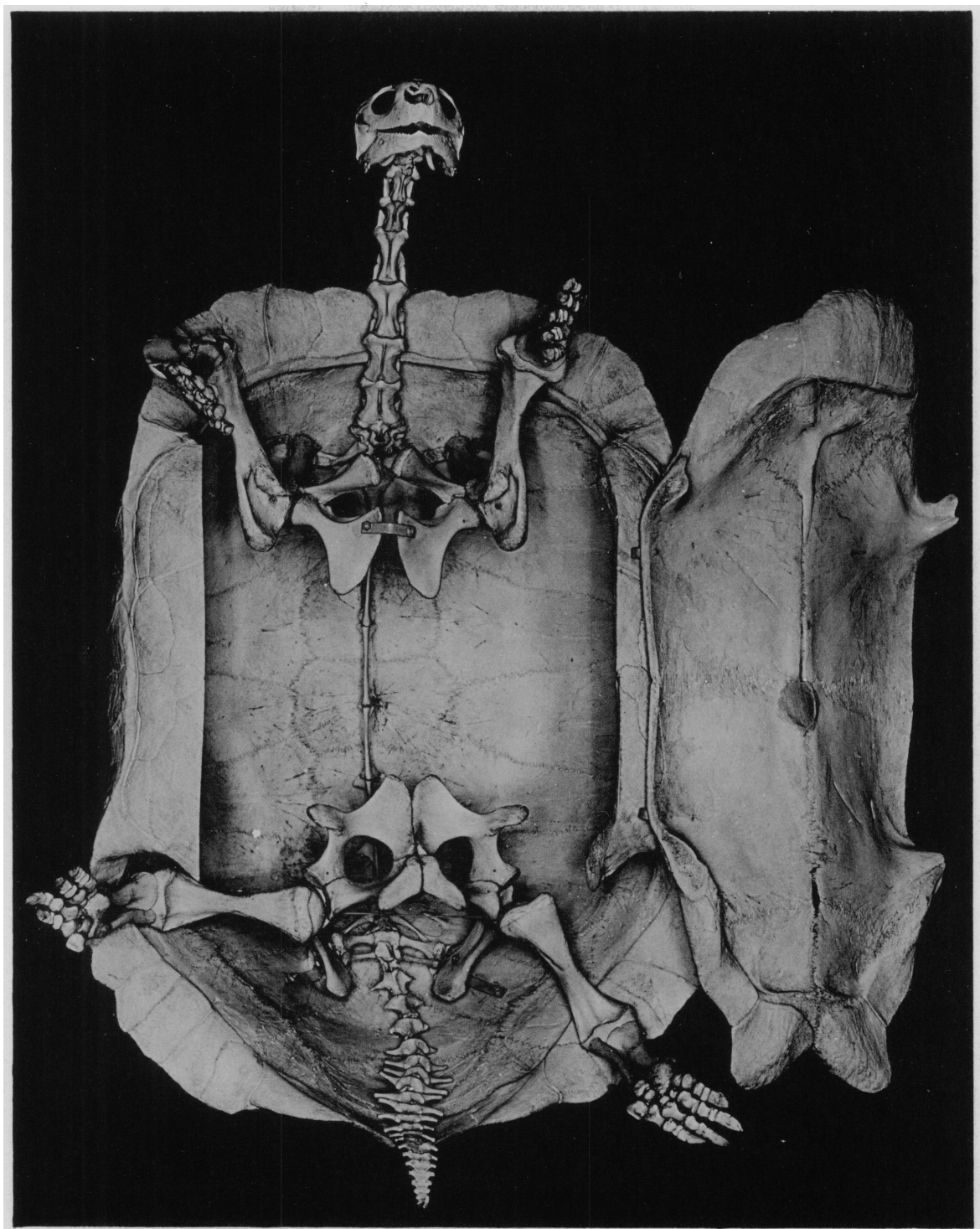


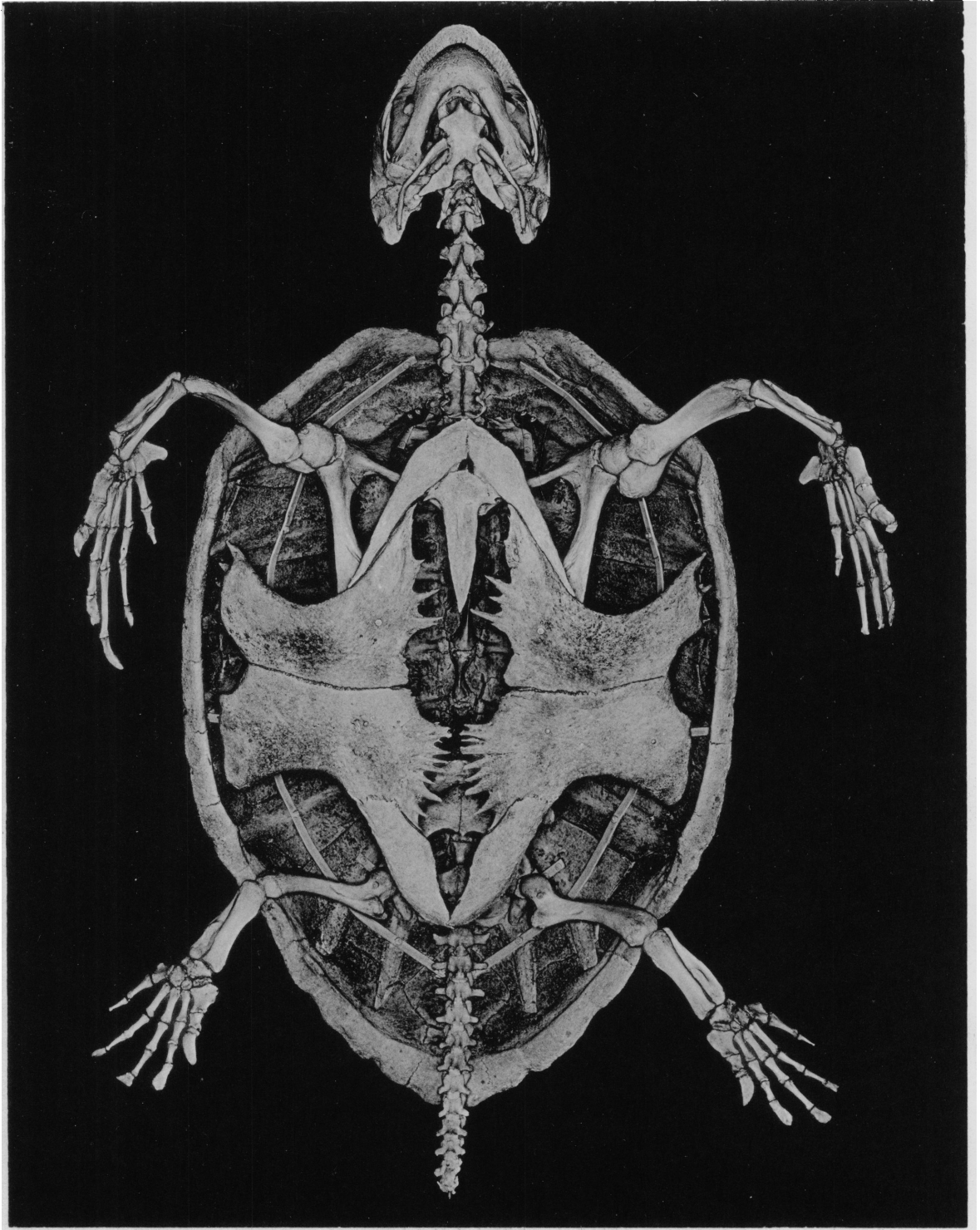
FIG. 17. Cervical vertebrae of pareiasaur (A), *Triassochelys* (B), and modernized chelonians (C, D, E, E 1). A, After Boonstra; B, after Jaekel; C, D, E, E 1, from specimens.

(fig. 4), and in *Triassochelys* it projected considerably above the cleithra (Jaekel, 1918, p. 116, fig. 17). The astonishing retraction of the root of the neck beneath the anterior ribs was made possible in part by an early transverse widening of the fore part of the carapace, involving the raising of the anterior thoracic ribs into a nearly horizontal

The plastron develops in the floor of the pectoral body wall, extending from beneath the heart to beneath the anterior end of the pelvis; it probably replaces an earlier parasternum. Even in the 6-mm. embryo of *Chelydra* (fig. 20A) the plastron ends sharply at the humeral and femoral notches. The former defines the sharp and ancient bound-



Skeleton of *Testudo pardalis*



Skeleton of *Chelone*

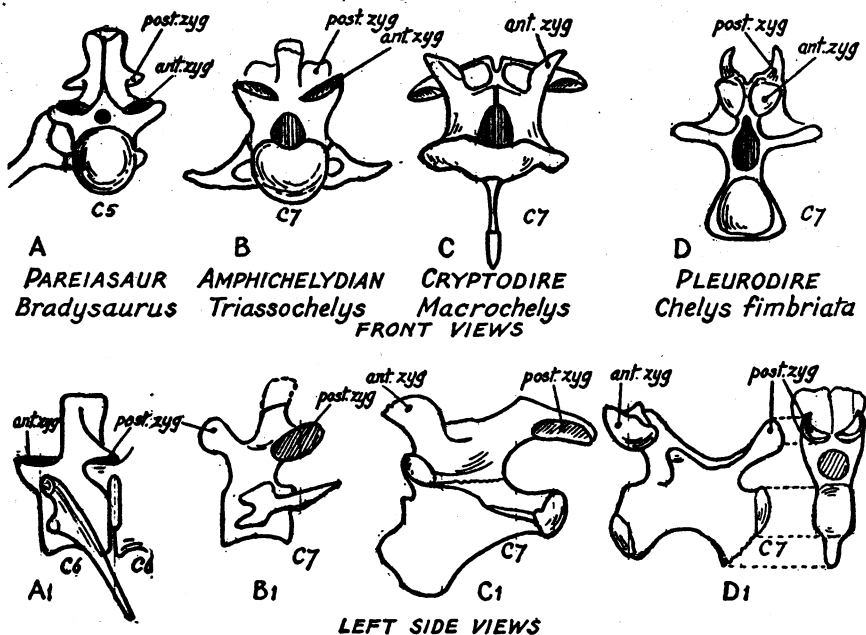


FIG. 18. Cervical vertebrae in pareiasaur (A, A 1), amphichelydian (B, B 1), cryptodiran (C, C 1), and pleurodiran (D, D 1). Side and front views. From specimens.

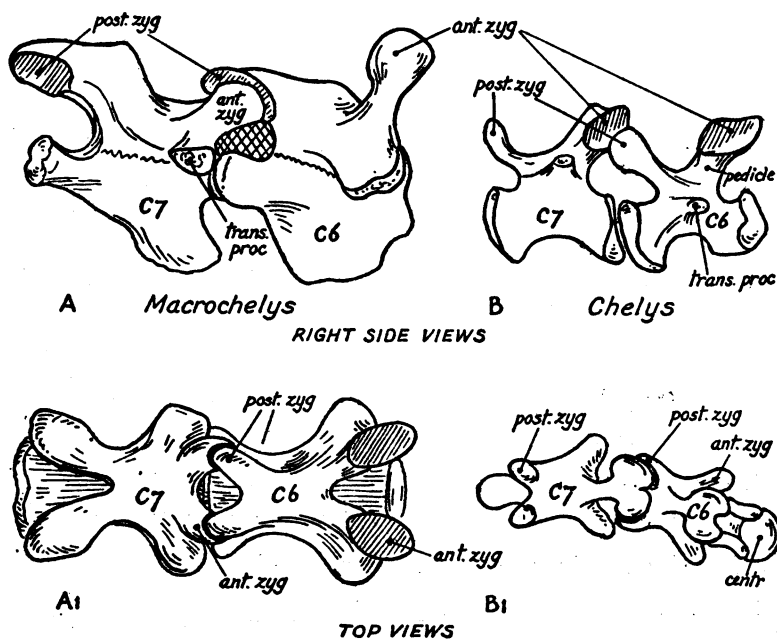


FIG. 19. Sixth and seventh cervical vertebrae of cryptodiran (A, A 1) and pleurodiran (B, B 1). Top views, showing different adaptations for bending the neck.

ary between the dermal pectoral girdle and the neck; the femoral notch marks the place where the pelvic limb bud has, as it were, burrowed inward and upward.

As the plastron surrounds the interclavicle and clavicles, it impresses them into itself and separates them from the coracoids, which

origin from the dorsum of the neck and thorax onto the outer sides of the deep scapular muscles (fig. 21). These and other factors cooperated in the piling up of the shoulder muscles into a pyramidal mass, which was supported at its core by the rod-like scapula, the sharply projecting acromion,

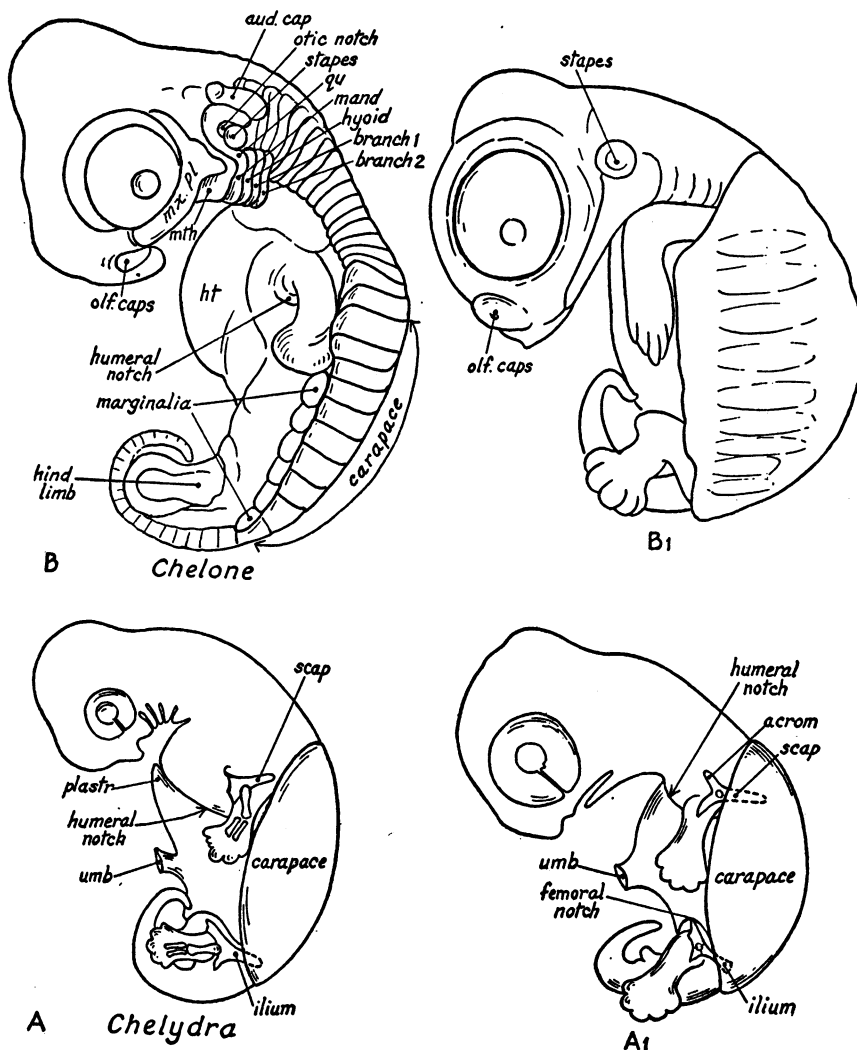


FIG. 20. Embryo turtles, showing the origin and spread of the carapace and plastron. A, A 1, After Ruckes (1929b); B, B 1, after W. K. Parker (1880).

thus appear as free blades in the dried skeleton (pl. 35).

The new spatial relations of the shoulder girdle to the enclosing shell accompanied radical changes in the movements of the limbs and a shift of the trapezius, latissimus dorsi, and other muscles that formerly took

and the inwardly directed, fan-like coracoid. The coracoid and acromion are tied together by a so-called episternal band (Huntington, 1918, p. 372). The changes in the musculature of the pelvic limbs were less radical (fig. 22).

The morphologic sequence of changes of the parts of the pectoral girdle indicated

	<i>Diadectes</i>	<i>Pareiasaur</i>	<i>Triassocheilus</i>	<i>Chelydra</i>
Scapula	Flattened, blade-like	Higher; shorter anteroposteriorly	High and very short	Tall and rod-like
Acromial process	Not developed	Conspicuous	Large	Very long, rod-like
Glenoid articular facet	Extended anteroposteriorly	Coracoid part oblique	Extended obliquely downward and backward	Nearly vertical
Coracoid	Plate-like, extended anteroposteriorly	Shorter anteroposteriorly	Very short; extended inward	Fan-like or spatulate

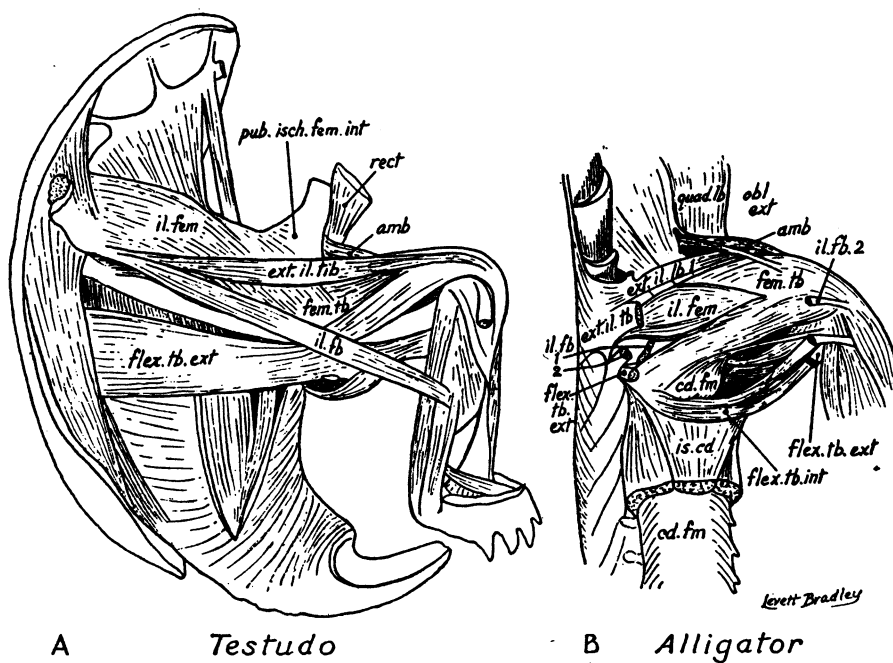


FIG. 22. Musculature of the pelvic limb in a chelonian (A) and a typical reptile (B). After Gadow. For key to lettering, see Gadow (1882).

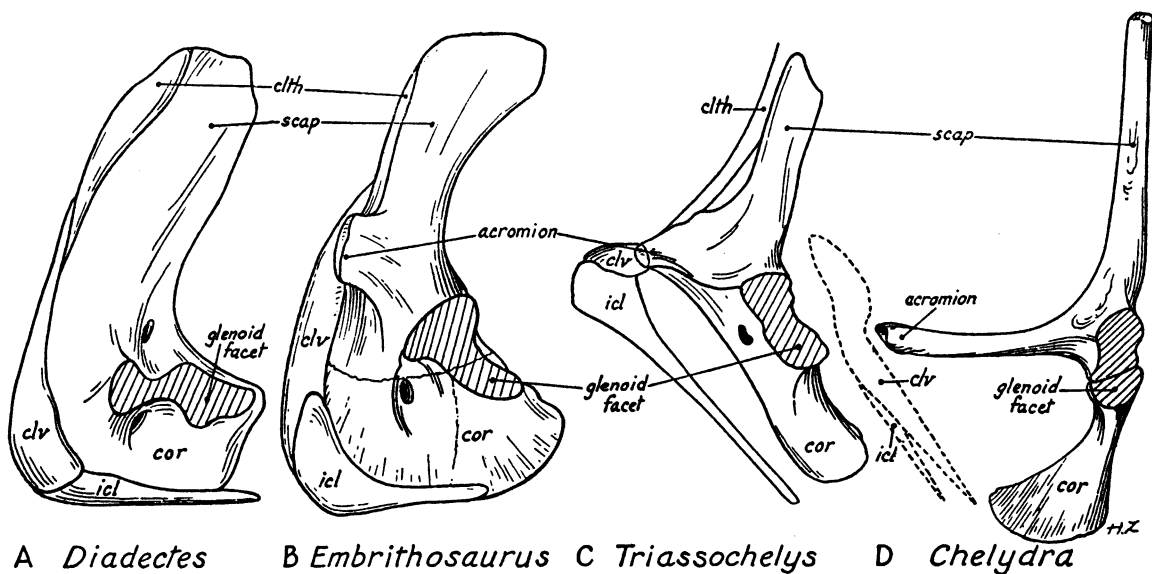


FIG. 23. Pectoral girdles of diadectid (A), pareiasaur (B), *Triassochelys* (C), and *Chelydra* (D). A, B, D, From American Museum specimens; C, after Jaekel.

in figure 23A-D may be summarized as in table 2.

The humerus of *Diadectes* has strongly emphasized all the marks of a primitive Permian tetrapod (Romer, 1922, pp. 554-559; Miner, 1925, fig. 19). For example, its shaft (fig. 24A) was very short, and the extremely wide proximal end bore a long, flattened, spirally warped capital facet; this permitted a limited twisting and rocking movement on the glenoid articular facet of the scapulo-coracoid. In accord with the

and other flexors of the forearm. The opposite, or ectocondyle, although much shorter than the entocondyle, was very massive and quite conspicuous. From its margin arose the extensor carpi and extensor digitorum longus muscles. Above the entocondyle was a conspicuous supinator process for the humero-radialis and supinator longus. On the huge deltopectoral crest were inserted the pectoralis, the dorsalis scapulae, and the clavicular portions of the deltoid. On the dorsal surface of the shaft of the humerus was

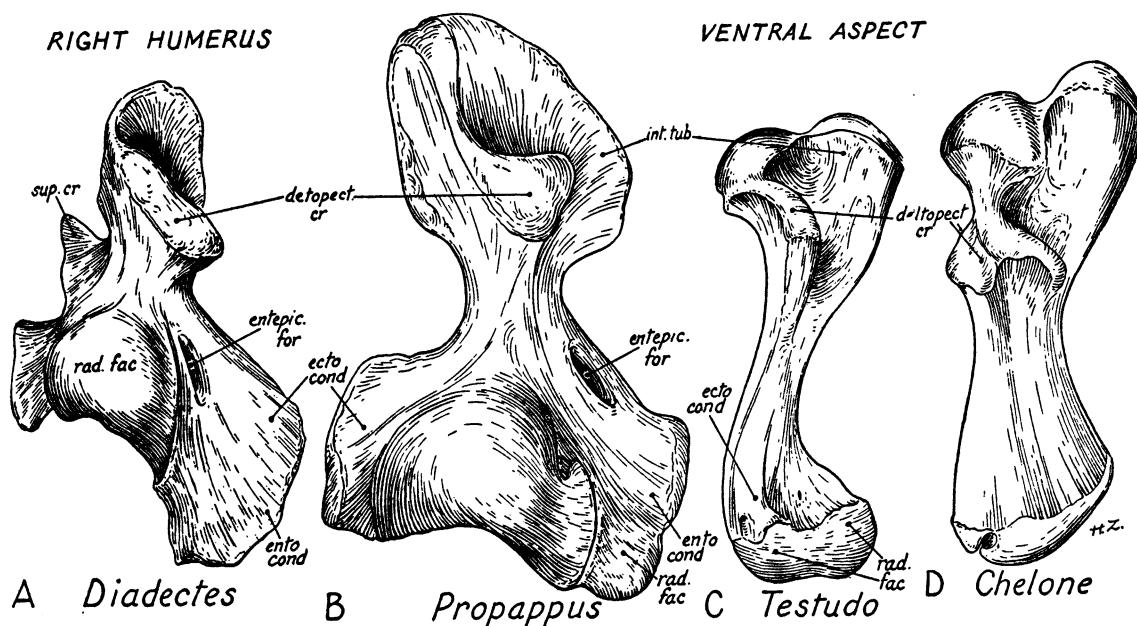


FIG. 24. Humeri of diadectid (A), pareiasaur (B), tortoise (C), and sea turtle (D). American Museum specimens.

sharply angulated forearm, the large capitulum or radial facet was on the front or ventral face of the shaft, facing downward, but was continuous medially and dorsoposteriorly with the facet for the ulna. The very large distal end of the humerus was produced into a huge, downwardly pointing entocondylar process, the general plane of which was twisted to about 80 degrees to the plane of the proximal end. Miner (1925) and Romer (1922) agree that on and near the proximal margin of this entocondylar process were inserted the great coracobrachialis muscles, a flexor of the upper arm; from its antero-ventral surface arose the flexor carpi radialis

inserted the powerful anconeus medialis (part of the triceps), while the ventral surface of the shaft gave rise to the brachialis internus. The entepicondylar foramen in primitive reptiles serves for the transmission and protection of the brachial nerve and artery (Huntington, 1918, p. 390); in *Diadectes* it is represented by a long and conspicuous fissure. The ectepicondylar foramen had not yet appeared but, as shown by earlier authors and confirmed by Romer (1922) and Miner (1925), arose later by the folding down of the supinator crest over the ectocondyle and the subsequent conversion of the groove into a canal.

In the humerus of the pareiasaur *Propap-pus* (fig. 24B) the primitive tetrapod characters noted above are somewhat modified by the further expansion of the radial capitellum into a huge, partly globose prominence and extension of the ulnar facet onto the dorsal surface of the olecranal depression, so that the forearm could be fully extended on the humerus. Moreover, the supinator crest has bent downward and joined the entocondyle, while the ventral process of the deltopectoral crest has grown into a roundly triangular protuberance.

movements by the pectoral and pelvic notches, the following changes have taken place:

1. Greater mobility at the shoulder was attained by developing the caput humeri into a ball-like protuberance *pari passu* with the above change in the glenoid facet of the scapulo-coracoid and with the increasing ability to raise the body well off the ground.

2. The length of the stride was increased by lengthening the shaft, while the retraction of the limb into the humeral notch was facilitated by the marked narrowing of the

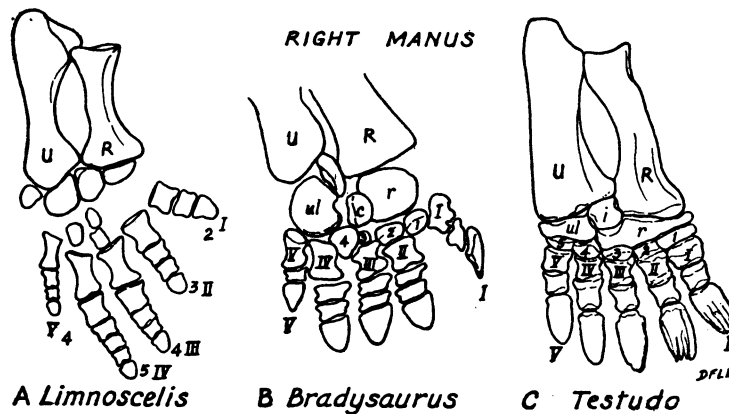


FIG. 25. Forearm and hand of cotylosaur (A), pareiasaur (B), and tortoise (C). A, C, After Williston; B, after Boonstra.

Although the humerus of *Triassochelys* itself is not known, von Huene (1926, p. 510, fig. 1) describes and figures a chelonian humerus from the uppermost Trias of Württemberg which he refers, on good evidence, to the Amphichelydia. This is already essentially chelonian in its sigmoid flexure of the shaft in lateral view, its dorsad turning of the globular caput humeri, the presence of an ectepicondylar foramen and canal, and in the general form of the distal end. But it is apparently more primitive than the humerus of *Testudo* (fig. 24C) in its notably smaller medial tuberosity ("median trochanter") and in the more globular form and smaller size of the radial capitellum.

The humerus of *Testudo* (fig. 24C) at first sight differs much more from that of *Propap-pus* than the latter does from that of *Diadectes*. Further comparison, however, suggests that with the fixation of the carapace and plastron and the limitation of the limb

distal end, with the elimination of both entepicondylar and ectepicondylar projections.

3. Still greater extension of the lower arm was obtained by widening the radial facet all across the distal end.

4. Acceleration of growth rates on the dorsal side of the distal half of the humerus shaft caused the latter to curve downward toward the top of the radius and ulna, while retardation of growth rates on the ventral side, just distal to the head, together with rapid increase of the lateral tuberosity and still greater growth of the medial tuberosity, and other anisomeral growth, all imparted a sigmoid curvature of the bone as a whole when viewed from either side. The result of these and similar modifications was to permit the opposite humeri to be swung forward in front of the humeral notches and parallel to the extended neck, and at the same time to twist distally down toward the ground,

so that in walking the elbows could be drawn forward like knees (fig. 5A and pl. 34).

Even greater changes have occurred during the evolution of the strange humerus of the sea turtles (fig. 24D), where, as part of the wing-like paddle (pl. 35), the humerus, losing its sigmoid curvature, has become secondarily flattened, the medial tuberosity has attained great size, while the deltopectoral crest has been greatly reduced. Thus the humeri of *Diadectes*, *Propappus*, the Upper Triassic amphichelydian *Testudo*, and *Chelone* fall into a well-knit morphological series which reinforces much other evidence that the chelonian order has been derived remotely from the basic cotylosaurs and more immediately from the stem pareiasaurs.

For the forearm and hand (fig. 25A) of a cotylosaur we may use Williston's figure of those parts in *Limnoscelis*. The radius and ulna are wide transversely, the distal end of the ulna extending well below that of the radius. The olecranon is large. Part of the carpals were cartilaginous. There were four bones in the first row, the radiale being rather small. By analogy with other primitive Permian tetrapods, Williston probably correctly arranged all the digits in a series converging toward the ulna. The wide metacarpals increased rapidly in length from Mtc I to Mtc III; Mtc IV was about equal to III. Mtc V was shorter and narrower than III and IV, and it diverged remarkably from Mtc IV. The primitive reptilian phalangeal formula was preserved intact, namely, 2, 3, 4, 5, 4. The distal phalanges indicate relatively small nail-like claws.

In the forearm and hand of pareiasaurs (fig. 25B), as figured from excellent material by Boonstra (1932b, pt. 8, pls. 42, 43) the olecranon is enormous, implying an extremely powerful triceps system. The radiale is very large and well ossified, the intermedium small. Probably two centralia were present. Some of the inner carpalia may have been small or cartilaginous, but carpal 4 was large and had contacts with Mtc IV and V. All the metacarpals were very short and wide, that of the pollex being extremely wide and massive. The first digit was very large and directed inward, the others diminished to the small fifth. The ungual phalanges were very large, the first digit decreasing gradually to

D IV and suddenly to D V. The phalangeal formula was reduced to 2, 3, 3, 3, 2.

The forearm and hand of *Testudo* (fig. 25C) are basically the same as in the pareiasaurs but with some anisomeral emphases, e.g., the radiale has become very wide and may have absorbed the centrals, the metacarpals are excessively short, all the claws are very large, and the phalangeal formula is reduced to 2, 2, 2, 2, 2. The manus as a whole is strikingly elephantine and adapted for a vertical position of the forearm of a heavy animal.

Thus, as here noted in regard to many other parts, the pareiasaur stage in the hand appears to be structurally ancestral to the chelonian.

The hands of the sea turtles have become transformed into wing-like flippers (pl. 35).

PELVIC GIRDLE AND LIMBS

The pelvis of *Diadectes* (fig. 26A) has its ventral, pubo-ischiadic plates well extended anteroposteriorly to give a long swing to the femora, while the dorsal border of its low ilium is extended anteroposteriorly for the longissimus dorsi and ilio-costalis muscles (Romer, 1922, pl. 44). The large acetabular depression has a cardiform rim, its axis pointing obliquely downward. It already permits considerable twisting and long anteroposterior swing of the caput femoris. All these and other features of the pelvis of *Diadectes* are associated with the sprawling movements, with strongly bent and everted posture of the thighs and with the inability to raise the pelvis high off the ground.

The pelvis of pareiasaurs (fig. 26B) is much shorter ventrally and higher dorsally than that of *Diadectes*, and the acetabulum has a shorter anteroposterior axis, is relatively higher dorsoventrally, and on the whole faces more obliquely downward, so that the head of the femur thrusts more upward against the overhanging dorsal rim of the acetabular depression. The space for the gluteal muscles on the outer blade of the ilium has greatly increased; this prevents sagging of the opposite side when its foot is raised from the ground (cf. White, T. E., 1939).

In *Triassochelys* (Jaekel, 1918) the well-fenestrated pelvis (fig. 26C) is anteroposteriorly shortened, the ilium both elevated and

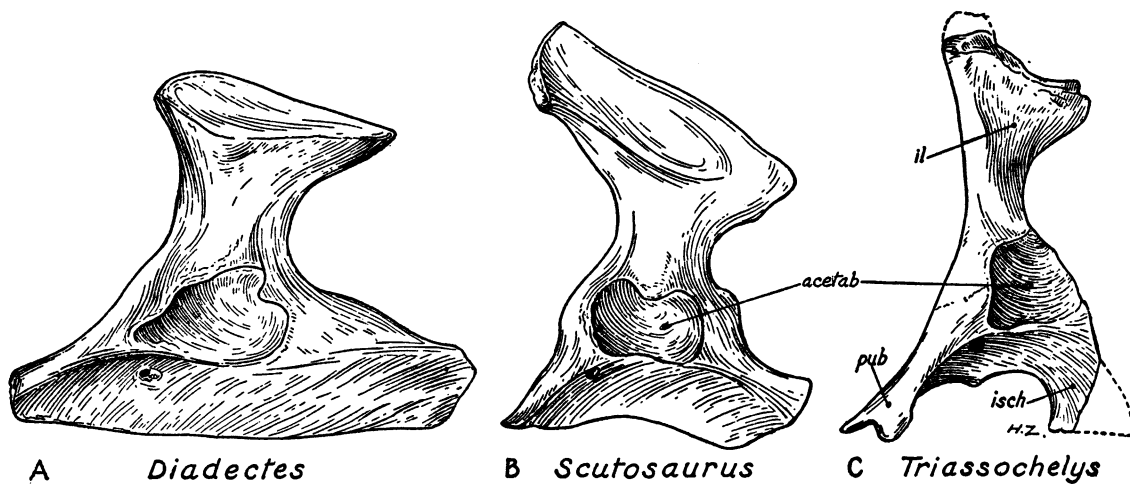


FIG. 26. Pelvis of diadectid (A), pareiasaur (B), and amphichelydian (C). A, B, From American Museum specimens; C, after Jaekel.

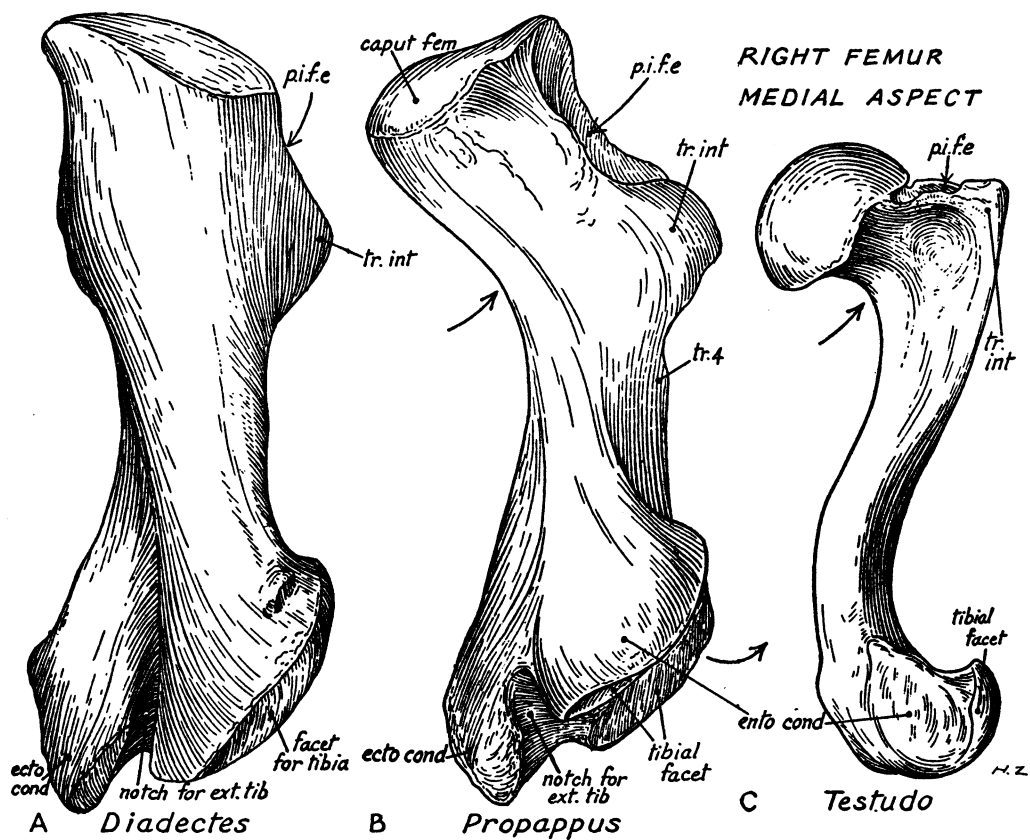


FIG. 27. Right femur, medial aspect, of diadectid (A), pareiasaur (B), and tortoise (C). From American Museum specimens.

shortened to support the dome of the carapace, while the acetabulum has been deepened dorsoventrally in accord with the globular development of the caput femoris and now faces partly backward as well as outward to permit a longer sweep of the femur and a more direct thrust from the rear.

The pelvis of *Testudo* is remarkably close to that of *Triassochelys*. In side view the three branches, ilium, pubis, ischium, form a truss or kingpost for the support of the

In the pareiasaur *Propappus* (fig. 27B) the head end is bent forward and upward on the shaft, the caput femoris is expanded into a wide oval, the prominent internal trochanter bounds a large concavity, presumably for the pubi-ischio-femoralis muscles, and the facets for the tibia are rounder, permitting wider extension of the tibia on the femur than was possible in *Diadectes*.

In *Testudo* the caput femoris (fig. 27C) has become globular, and its midpoint is inclined

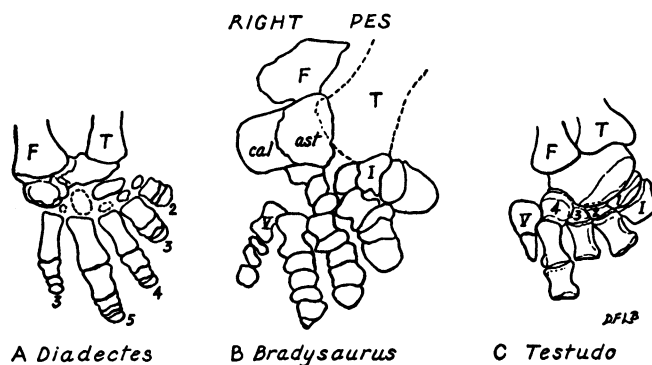


FIG. 28. Right foot of diadectid (A), pareiasaur (B), and tortoise (C). A, After Romer and Byrne; B, after Haughton; C, after Williston.

carapace (Ruckes, 1929a) especially in Pleurodira, where the pubis and ischium are solidly based on the plastron. In aquatic and marine turtles, as the carapace widens the ilium is directed backward as well as upward (Ruckes, 1929a). In the soft-shelled turtles (trionychids) the carapace becomes very broad and nearly flat, while the pubes send forward a pair of great anterior plates analogous with those of plesiosaurs and equally concerned with the protraction and retraction of the rear paddles.

The femur of *Diadectes* (fig. 27A) is adapted to the bent-kneed posture, in which the femur is directed outward and slightly upward. The caput femoris is an elongate oval of slight convexity; the shaft is nearly straight, the distal end with large protuberances and two wide facets for the tibia separated by a deep notch for the extensor tibialis. On the proximal ventral third there is a high internal trochanter and a median depression supported distally by a low, well-rounded stem.

nearly at a right angle to the axis of the upper half of the shaft. The sigmoid contour is due to the faster growth of the ventral side of the proximal half and of the dorsal side of the distal half. Through this sigmoid curve the lower leg and foot can be extended behind the carapace, and when the knee is drawn forward, the shank and foot can be turned downward around the edge of the femoral notch.

Thus the typical chelonian femur aligns itself with other parts in suggesting that the pareiasaur affords a structurally connecting stage on the path of its evolution from the diadectid cotylosaur.

The lower leg and foot of *Diadectes* (fig. 28A) conserve much of the primitive tetrapod condition (Romer, 1922; Romer and Byrne, 1931; Schaeffer, 1941, p. 428). Their principal specialization is the enlargement of the intermedium and fibulare to form an astragalus and a calcaneum, whose facets permit considerable rotation of the tibia on the astragalus. However, there was also a

mesotarsal joint as in pareiasaurs (Schaeffer, *ibid.*, p. 431). The primitive anisomerism of the metatarsals and convergence of the entire tarsus toward the fibula were retained, as was also the primitive reptilian phalangeal formula (1, 2, 3, 4, 5, 3).

The pareiasaur pes (fig. 28) has advanced beyond that of *Diadectes*, especially in the enlargement and consolidation of the astragalus and calcaneum and in the reduction of the phalangeal formula to 2, 3, 3, 4, 3. In

general it closely approaches the *Testudo* type.

In *Testudo* (fig. 28) the consolidation of the astragalus and calcaneum suggests derivation from massive pareiasaurs in which such consolidation had already taken place. Thus the primitive *Triassochelys* may be a dwarf derivative of a much heavier race. All the tarsals are now well ossified, and the phalangeal formula in chelonians is reduced to 2, 3, 3, 3, 3 (Williston, 1925, fig. 154, p. 188).

COMPARISON OF CAPTORHINOMORPH AND TURTLE SKELETONS

IN SOME FEATURES the smaller cotylosaurs, especially the Upper Pennsylvanian and/or Lower Permian captorhinomorphs, would seem at first sight to make a better starting point for the turtles than the diadectids, which already had a specialized dentition. For the most part, the captorhinomorphs were rather small and lizard-like, the excep-

advanced beyond the primitive reptilian type and might well be almost immediately ancestral to the diadectid, and more remotely ancestral to the pareiasaurian, and eventually to the chelonian type.

The entire palatal view of *Limnoscelis* (Williston, 1914) was also of primitive reptilian stamp, especially in so far as the

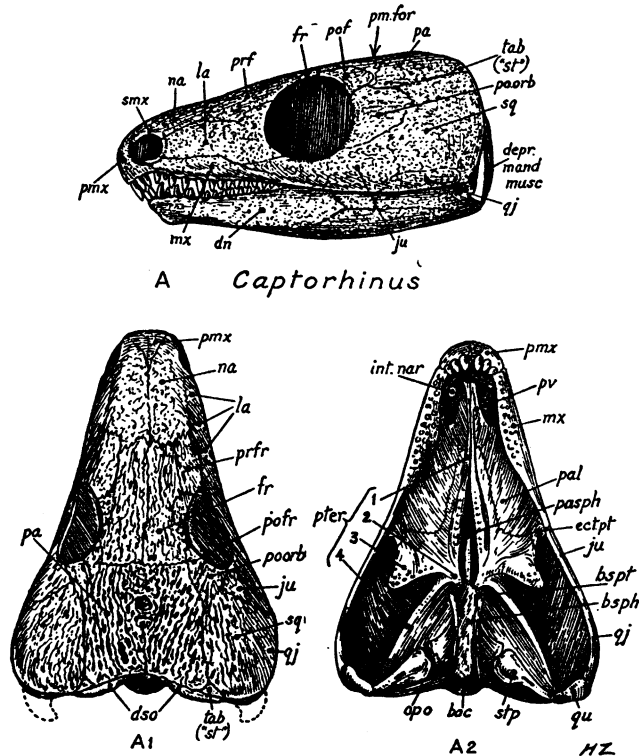


FIG. 29. Skull of a captorhinid cotylosaur. Composite from American Museum specimens. Sutural pattern after Case, Williston, Broom, von Huene, Sushkin, Romer, and Price.

tion being *Limnoscelis*; this reptile, as restored by Williston (1914, p. 20), was about 2 meters long. *Limnoscelis* had a far more primitive dentition than *Diadectes*, with simple conical-tipped cheek teeth, not modified into crushing ovals. Its rather large front upper teeth pointed downward and a little backward and were for catching and piercing. On the whole, the jaws and dentition, although perhaps on the way toward a snipe-billed, fish-catching stage, were not far

widening of the jaw muscles had bent the pterygoids sharply inward against the basi-ptyergoid processes of the parabasisphenoid; meanwhile under the influence of the same capiti-mandibularis muscle mass, the anterior processes of the pterygoid were: (1) bending outward and thus enlarging the interptyergoid vacuity; (2) developing sharply transverse tooth-studded bars; and (3) growing downward to form a descending process, or sliding surface, to guide the mandible

upward into correct occlusal relations with the upper jaw and teeth. Thus in *Limnoscelis* (Williston, 1911, fig. 4, p. 29) was perhaps the earliest known example of the so-called rhynchocephalian palate, which is more delicately constructed in the smaller captorhinomorphs and in the modern tuatara. The protean modifications of this pattern are manifest in the diadectids, pareiasaurs, chelonians, and in fact in all known reptilian orders, while other and still greater transformations are seen in the birds and mammals.

In the smaller captorhinomorphs (fig. 29) the upper front teeth were pointed downward and overhung the somewhat procumbent lower front teeth, essentially as in *Limnoscelis*, but the cheek teeth were small, numerous, and in clusters, and there were small teeth on the anterior branches of the pterygoids and prevomers. But secondary palatal plates from the maxillae and palatines, such as are seen in the primitive chelonians, had not developed.

The smaller captorhinomorphs (*Labidosauris*, *Captorhinus*), while sharing with *Limnoscelis* the elimination of the otic notch, have advanced beyond *Limnoscelis* in the loss of the supratemporals, in the reduction of the tabulars to vestiges, and in the turning downward of the whole of the dermosupraoccipitals onto the nuchal surface. Otherwise their skull and jaws retain such primitive reptilian features as an unperforated temporal roof and a lacrimal extending from the

anterior nares to the orbit. Thus the skull, jaws, and dentition of the captorhinomorphs are far more primitive than those of chelonians, but they do not show such convincing evidences of close relationship to the chelonians as do those of the pareiasaurs.

The vertebrae of *Limnoscelis* and the smaller captorhinomorphs were essentially like those of *Diadectes*, except that they had not developed hyposphenes and hypantra. They differed from those of pareiasaurs in having very short transverse processes. But in the absence of an immovable plastron, the vertebral column as a whole retained considerable flexibility, and the thoracic part had not begun to be immobilized as it was in the chelonians.

It can also be said of the captorhinid ribs, pectoral and pelvic girdles, and limbs, hands, and feet, that while they retained many primitive reptilian features, which at a remote period the ancestors of the chelonians must also have possessed, yet the captorhinids give no indubitable signs of being direct ancestors of the turtles. Moreover, it seems likely that if the captorhinomorphs had possessed a vigorously developed dermal skeleton of bony plates embedded in a leathery skin, some tokens of it would have been discovered. On the contrary, the captorhinids present more marks of relationship to the pelycosaurs and other forms that were becoming swifter and more agile predators (Romer and Price, 1940).

COMPARISON OF SEYMOURIAMORPH AND TURTLE SKELETONS

THE THOROUGH MONOGRAPHIC STUDIES of T. E. White (1939) on *Seymouria* from the Lower Permian of Texas and of Bystrow (1944) on *Kollassia* from the Upper Permian of Russia have shown that these animals, whether regarded either as primitive reptiles or as advanced amphibians, retain many primitive tetrapod characters intermingled with their own divergent specializations, but neither of them shows any definitely prechelonian tendencies.

In a general way *Seymouria* remotely approaches the diadectid cotylosaurs in its general habitus, especially in the vertebrae, which have large, high, transverse processes, large pre-zygapophysial and post-zygapophysial facets, rounded shoulder-like swellings above the posterior zygapophysial facets, and well-developed intercentra, which carry facets for the capitula of the ribs. But hyposphene-episphene articulations are wanting.

The entire vertebral column of *Seymouria* seems sufficiently primitive to have given rise to that of the chelonians, but the evidence from other parts of the skeleton indicates decisively that it did not do so.

In many other ways *Seymouria* remained on, or had drifted toward, an amphibian level and away from an immediately prechelonian stage. Thus, its muzzle was broad, with flat amphibian-like palate, which as yet showed little if any tendency toward the inrolling of palatal plates of the palatines and maxillae to form a secondary palate (see the cross sections figured by White, 1939, p. 340); nor was the occipital plate perforated

by posttemporal fenestrae (White, 1939, p. 334). The large otic notch and the consequent curvatures of the quadrate, squamosal, supratemporal, and tabular merely show that in both *Seymouria* and the chelonians this region was being moulded by a diverticulum of the tubo-tympanal canal to support a tympanic membrane.

Although its carapacial covering, if any, is unknown, in its girdles and limbs *Seymouria* was on the whole far more primitive than the chelonians and had already adopted the rocking, bent-legged gait which eventually contributed to the fixation of the column by the coalescence of the carapacial elements. On the whole the evidence suggests that *Seymouria* was a sort of contemporary great uncle to the diadectid cotylosaurs and perhaps through them could claim a remote connection with the chelonians.

Still further removed from the chelonians was the Upper Permian *Kollassia*, the habitus of which was tending in the direction of such secondarily aquatic urodeles as *Cryptobranchus*. Although it had a well-developed plated dorsal armor of flat quadrangular bony scutes, doubtless surfaced with a leathery skin, this armor was more nearly akin to that of the amphibian otocoelids than to the chelonian type. Its wide flattened skull, truncated posteriorly, suggested the larval *Branchiosaurus*, retaining the primitive intertemporals and supratemporals and dorsally exposed tabulars and dermo-supraoccipitals. Its mandible retained the amphibian intercoronoid and two splenials, while its tooth structure was also labyrinthodont.

COMPARISON OF PLACODONT AND TURTLE SKELETONS

AS NOTED ABOVE (p. 282), the view that the chelonians are nearly related to the turtle-like placodonts rested in part on the comparison of modern turtle skulls with Triassic

pattern than did the placodont. This is equivalent to saying that solely on the basis of skull pattern, the placodonts could more easily have been derived from the earliest

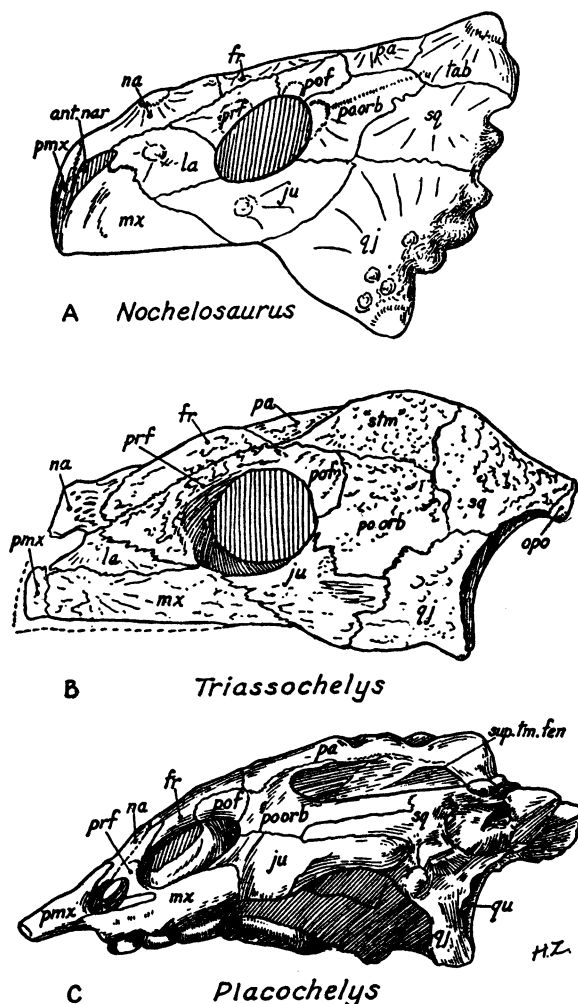


FIG. 30. Skulls of pareiasaur (A), *Triassochelys* (B), and *Placochelys* (C). A, After Boonstra; B, after Jaekel; C, after von Heune.

placodonts. But if we compare (fig. 30) the Triassic turtle skull with those of Triassic placodonts (Broili, 1912; von Huene, 1931) and a Permian pareiasaur, the turtle is seen to have retained a far older, less specialized

known chelonians than the chelonians from the placodonts! It is true that both placodont and chelonian quadrates and squamosals have been curved or hollowed out by a dorsal dilatation of the tubo-tympanal system. But

so have the quadrates of mosasaurs, phytosaurs, and crocodilians and the temporal complex of notoungulates, jerboas, and men.

It is also true that the Lower Jurassic

Henodus (fig. 31A 1) shows that one placodont at least got rid of most of its teeth and acquired a beak. But the beak of *Henodus* did not entitle it to claim close kinship either

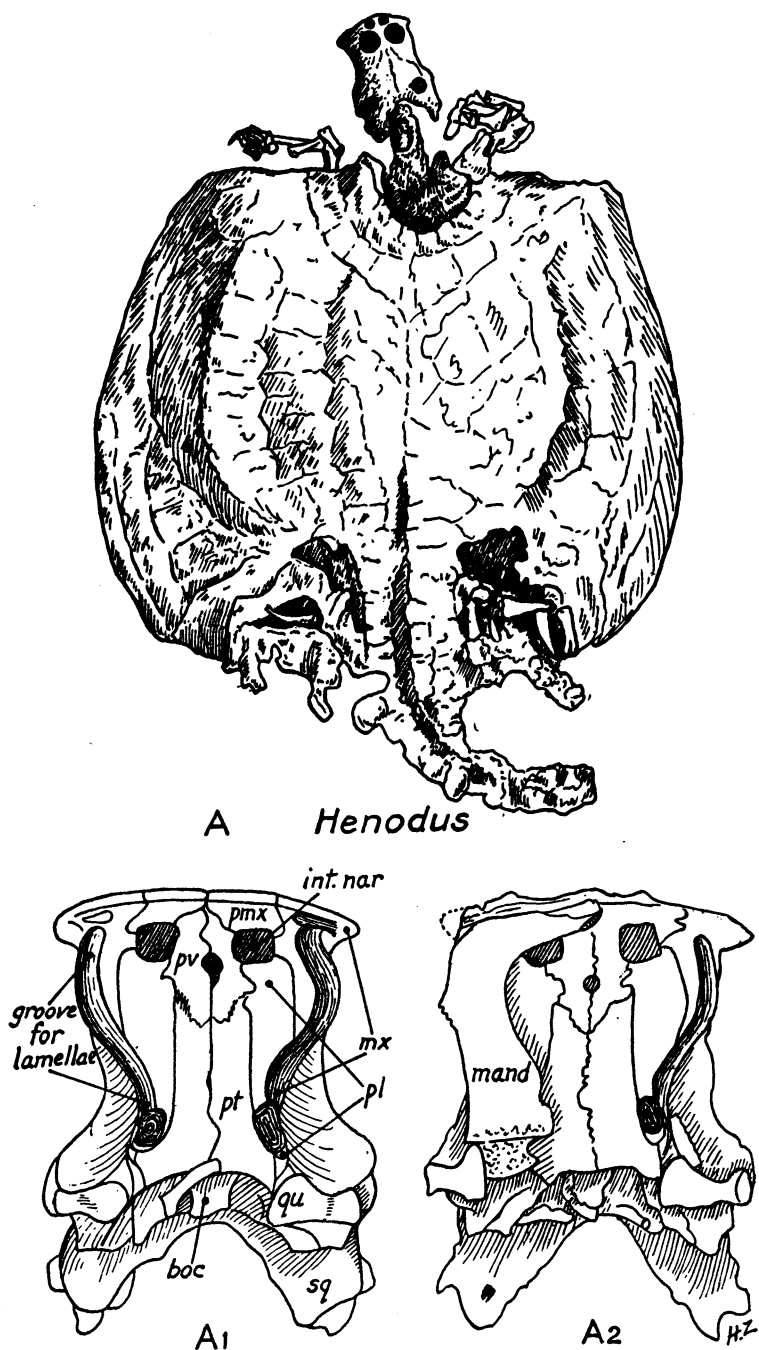


FIG. 31. The "false turtle," *Henodus chelyops* von Huene. A, Dorsal view; A 1, skull, palatal aspect; A 2, another specimen with one-half of mandible. After von Huene.

with shoveller ducks or the duck-billed platypus. In short, although there are several striking resemblances between placodont and chelonian skulls, the earliest chelonians still literally belonged in the Anapsida, along with the cotylosaurs and pareiasaurs, since neither the sides nor the top of their temporal roof had been perforated to form supratemporal or lateral temporal fenestrae; whereas in the placodonts the dorsal (supratemporal) fenestrae were well developed.

muscles worked their way backward through the posttemporal openings (fig. 8B 1), and great pressure was exerted on the anterior beaked part of the wide jaws.

In the palatal view, the skull of *Triassochelys* was extremely unlike those of placodonts, and such features as the latter do show in common with *Triassochelys* may safely be regarded as part of the common heritage from the Permian stem reptiles.

The carapace of *Placochelys* consisted of an

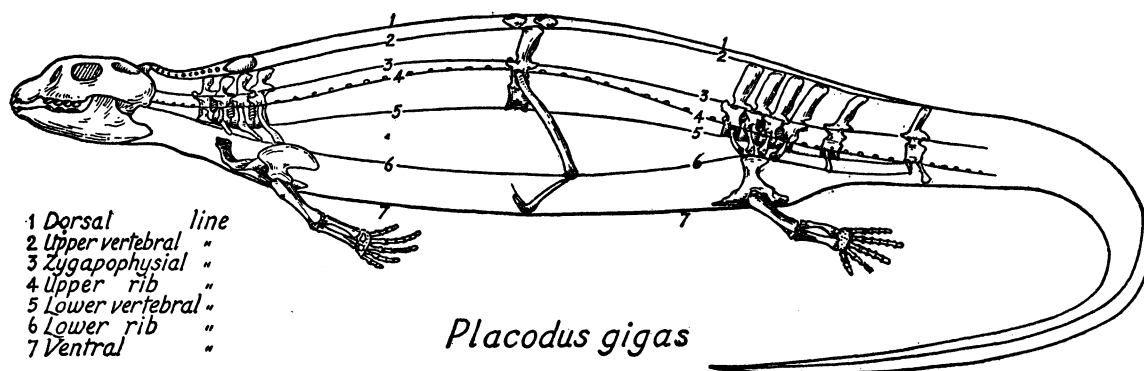


FIG. 32. The skeleton of *Placodus*. Diagram based chiefly on photographs of the mounted skeleton in the Senckenberg Museum, Frankfurt. With data from Drevermann (1933). Estimated total length about $7\frac{1}{2}$ feet.

The placodont skulls, even with their massive crushing teeth and appropriate bracing for the powerful jaw muscles and strong jaws, are generally recognized as being genetically related to the skulls of lariosaurs and nothosaurs. To these they were also functionally related, somewhat as the massive skull of the sheephead (*Archosargus*), with its crushing teeth and thick jaws, is related to the lightly built skull of the snappers (Lutianidae). The dentition of *Paraplacodus*, as described by Peyer (1935), is indeed strongly suggestive of the sheep-head type and like the latter may have been derived from an early predatory stage with caniniform marginal teeth.

In the lariosaurs, nothosaurs, plesiosaurs, and placodonts (fig. 30C) the main pull of the temporal muscles was evidently nearly directly dorsoventral, as it is in other lines with a "snipe-bill" or fish-snatching rostrum, often with narrow parallel rows of marginal teeth. In *Triassochelys*, on the other hand, the jaw

aggregation of large and small conical bosses, which, as restored by Jaekel (1907), were arranged in a more or less regular reticulate pattern. In *Henodus*, the last of the placodonts (fig. 31), the general configuration of the wide, low carapace (von Huene, 1936a, 1938) suggests that of the trionychids, but the secondary polyisomeres of the shell in *Henodus* were multitudinous, whereas in the far older *Triassochelys* the main units of the carapace were much fewer and essentially chelonian in pattern (fig. 5).

The postcranial skeleton of *Placodus*, as described by Drevermann (1933) and von Huene (1933) was profoundly different from that of any chelonian, and in general contour (fig. 32) it rather suggested a manatee. Lacking a chelonian type of carapace, its vertebrae, ribs, and gastralria were likewise un-turtle-like. In its very short neck the vertebrae did not even remotely foreshadow the amazing specializations of either the Cryptodira or the Pleurodira. Its pectoral

girdle was definitely nothosaurian: the clavicles formed a great transverse bar, in which the small interclavicle was incorporated, as in nothosaurs; the scapulae, low and recurved, contrasted widely with the tall rod-like scapulae of chelonians; the expanded, plate-like coracoids suggested the plesiosaur type. The humerus, completely nothosaurian

(fig. 33), had become reduced to a slightly curved rod and lacked the vigorous development of the lateral and medial tuberosities that is characteristic of chelonians. A similar contrast could be shown to be true of the pelvis and hind limbs.

In short, *Placodus* is as un-turtle-like in its girdles and limbs as it is in its dentition.

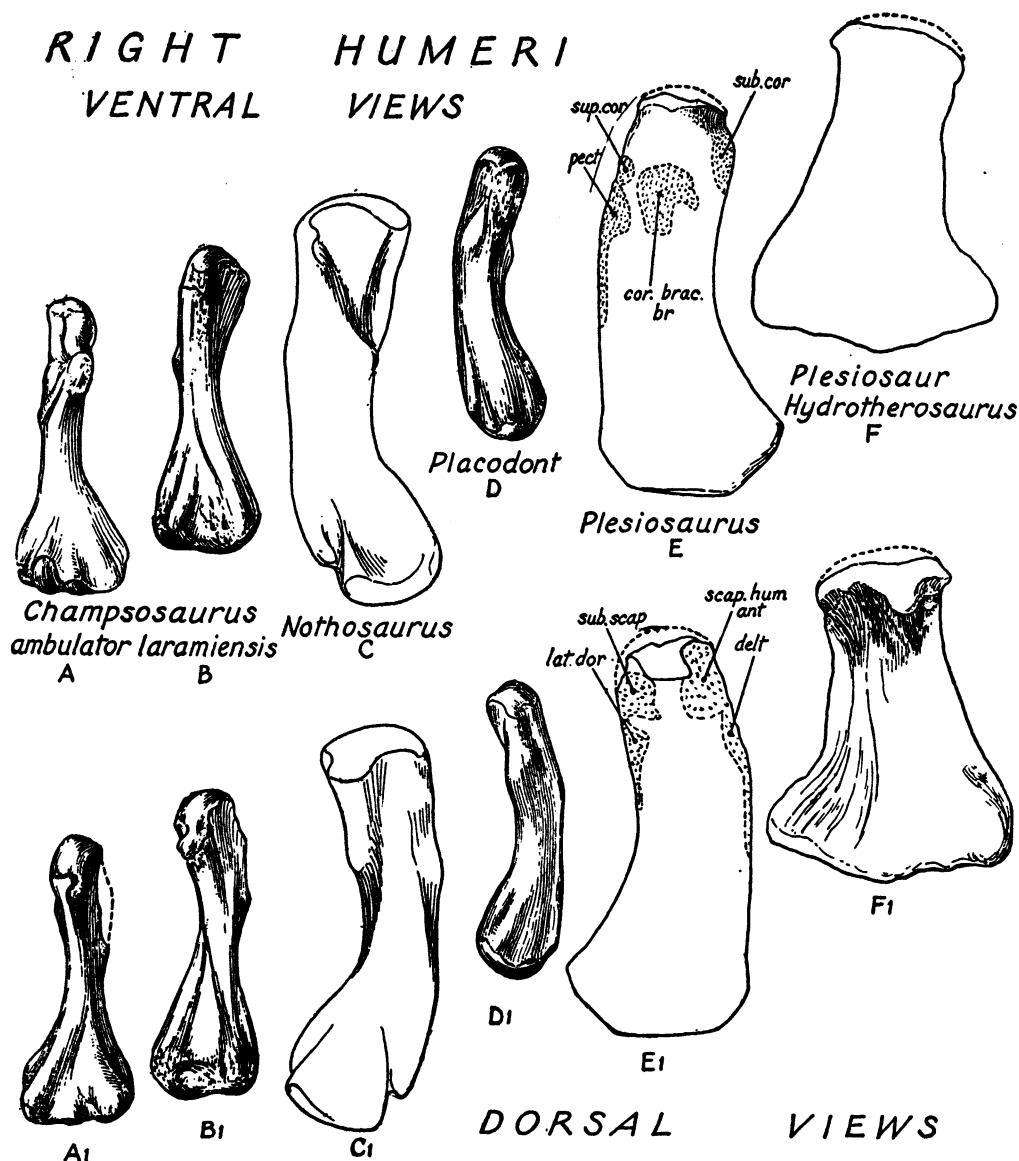


FIG. 33. Comparative series of right humeri, illustrating progression from a relatively primitive, semi-aquatic type, with little modified limbs (A, B) to highly specialized marine plesiosaurs. The placodont humerus (D) closely resembles that of the nothosaur (C). A, B, After Barnum Brown; C, D, after von Meyer; E, after Watson; F, after Welles.

And even when *Henodus*, the last of the placodonts (von Huene, 1936a, 1938) made, as it were, a belated attempt to become a turtle, the best it could do was to take on a very wide, round, flattened shell, remotely like that of a "soft-shelled" turtle (*Trionyx*) and suggesting the subcircular disc of *Potamotrygon*, with a stout long tail, not unlike that of *Macrochelys*, combined with a wide bill like that of a duck-billed dinosaur but very short (fig. 31A 2). Meanwhile, however, *Henodus* retained a substantially placodont heritage in its skull, vertebrae, ribs, girdles, limb bones, hands, and feet (von Huene, 1936a, p. 127; 1938, pp. 107-111).

Eunotosaurus, with its quite tortoise-like form (fig. 4), more nearly approached the later chelonian type in the Permian than did

Placochelys in the Upper Triassic.

According to Jaekel (1907, pl. 7), the stout "ventral ribs" of *Placochelys* were closely embraced by widened bony "gastralia," which were analogous with the plates surrounding the dorsal ribs of chelonians. Presumably then the bony plastron of the placodont *Saurosphargis* and its allies (von Huene, 1936a, p. 145) arose through the consolidation of the parasternum, or ventral rib system. But such a stage is unknown in any chelonian or pareiasaurian, and in the chelonians the plastron may be due to a new growth of the bone-producing integument. This may have replaced a precociously eliminated gastralia complex, which had been highly developed in many early tetrapods but was poorly developed, or unreported, in seymouriamorphs and cotylosaurs.

DISCUSSION: CONVERGENT EVOLUTION AMONG TESTUDINATE ANIMALS

THE SHELL OF ANY CHELONIAN is only a very special kind of armor, and whether made by man or produced in the laboratory of nature, armor is composed of polyisomeres. These are serially homologous or homogenous units (Gregory, 1934, 1935b) such as the links of chain armor or the bony polygons of the shells of glyptodonts, ankylosaurs, and *Dermochelys*. Such polyisomeres are often organized or integrated into larger units, and these complex pieces may be either fused together into a fixed test or carapace or movably articulated with each other, as the parts covering the arms and legs in mediaeval armor, or the plates on the abdominal segments of a lobster. Examples of polyisomeres belonging to non-homologous sets are the multitudinous conical bony pieces of the carapace of *Placochelys* and the conical horny shields that make up the surface armor of certain tortoises.

When the parts of an originally homologous series of polyisomeres undergo regional changes in dimension and contour, they are called anisomeres. Thus anisomeres are but modified polyisomeres, and one category grades into the other. Combinations of polyisomeres of different sets are called polyanisomeres.

In the animal kingdom the skeletal polyisomeres and/or polyanisomeres are deposited by membranous tissue, such as the shell-producing mantle of mollusks or the integument of vertebrates. In both cases the shell or exoskeleton may be composed of several layers, horny on the outside, calcareous or bony in the deep layers.

There are often many striking resemblances even in detail between the minute structure of the shells of such widely unrelated animals as the king crab, *Limulus*, and the Silurian ostracoderms (Patten, 1912, pp. 289-301). Patten indeed maintained that "the distinction between the epidermal skeleton of the arachnids and the dermal one in vertebrates is therefore only one of degree, not of kind." However that may be, it is a fact that in the oldest known verte-

brates, the Ordovician ostracoderms, the units of the cephalo-thoracic shield or test were polyanisomeres of extreme complexity, with stratified basal layer, trabeculated middle layer, and glass-like or "enamel" surface layer, all punctured by minute lymph or mucous canals and richly supplied with cells and blood vessels that deposited bone-like and dentine-like material.

With regard to external form, among some of the later gastropods the screw-like growth of the mantle became greatly accelerated on the outer side of the aperture, while the spire was variously reduced. In the cowries, *Cypraea caputserpentis* has developed a streamlined domed shell, flattened beneath, with bulging basal marginal angles, all curiously suggesting the shell of a high-backed tortoise. Thus an almost bilaterally symmetrical, tortoise-like shell has been evolved from a remote helicoid ancestor. And the shell of the tortoise itself has reached its modern forms only after passing through several major transformations.

All the available evidence suggests that the earliest vertebrates were bottom-living forms, more or less depressed, broadly tadpole-shaped, with an exoskeletal shield covering the head and shoulder girdle, followed by a locomotor system of many segments (cf. Heintz, 1935).

Free-swimming predatory fishes came later, through reduction in size of the head and multiplication of the locomotor segments. From the earliest of these, in turn, sprang the air-breathing fishes, one branch of which (the Crossopterygii) gave rise to the amphibians.

Among the latter the Upper Pennsylvanian and Lower Permian Otocoelidae were foreshadowing the turtles in developing a series of transversely wide bony scutes above the neural spines of the dorsal vertebrae, together with a circular tympanic membrane and "meatal concavity." At one time Cope regarded these forms, together with *Diadectes*, as possible ancestors of the Chelonia, but much additional collateral evidence

TABLE 3
CONVERGENT EVOLUTION AMONG TESTUDINATE VERTEBRATES

Name	<i>Bothriolepis</i>	<i>Otocoelus</i>	<i>Triassochelys</i>	<i>Henodus</i>	<i>Archelon</i>	<i>Ankylosaurus</i>	<i>Glyptodon</i>
Geologic age	Devonian	L. Permian	Up. Triassic	L. Jurassic	Up. Cretaceous	Up. Cretaceous	Pleistocene
Class	Placodermi	Amphibia	Reptilia	Reptilia	Reptilia	Reptilia	Mammalia
Order	Antiarchi	Labyrinthodontia	Chelonia	Placodontia	Chelonia	Dinosauria	Edentata
Local habitat	Fresh water	?Swamps	More terrestrial	Inshore; shallow water	Marine	?Swamps	Terrestrial
Contour of test or thorax in:							
Dorsal view	Oval	Oval	Oval	Wide oval	Wide oval	Oval	Oval
Lateral view	Domed	Flat	Low domed	Flat	Flat	Domed	Domed
Skull fastened to:							
Pectoral girdle	Yes	No	No	No	No	No	No
Free neck	No	Yes	Yes	Yes	Yes	Yes	Yes
Skull with helmet or scutes	Yes	?	Yes	Yes	No	Yes	Yes
Pectoral appendages as:							
Paddles	Yes	No	No	Partly yes	Yes	No	No
Feet	No	Yes	Yes	Partly yes	No	Yes	Yes
Carapace covering scapula	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Scutes above neural arches	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Bony scutes uniting with ribs	No ribs	No	Yes	Yes	Yes	Yes	No
Ventral surface with:							
Scales or tubercles	No	?No	No	Yes	No	?Yes	?No
Gaстрalia	No	Probably yes	No	Yes	No	?No	No
Flat bony plastron	Yes	No	Yes	Yes	Yes	No	No

shows that they were specialized amphibians, which were merely converging toward the turtles in certain features.

When in Upper Devonian or Lower Mississippian time certain air-breathing fishes succeeded in transforming their stout paddles into fore feet and hind feet, various lines of further evolution became open to them. Some of them, by multiplying the thoracic and caudal segments, rapidly diminished the ratio of limb length to total body length. The terminal stages of such lines were limbless serpentiform types, such as the Permo-Carboniferous *Aistopoda* and the

modern *Amphiuma*, *Proteus*, and others. Similar changes transformed the moderately short, well-limbed lizards into snake-like forms of several families. All these had very long and flexible bodies and are at the opposite end stage from that of the turtles and similar testudinate animals; the latter have reached their terminus after shortening and immobilizing the thorax, retaining stout and flexible limbs, and usually emphasizing the mobility of the neck. Similar end results have been attained in certain dinosaurs (*Ankylosaurus*) and among the mammals in the glyptodonts. (See table 3.)

CONCLUSIONS

1. COMPARATIVE ANALYSIS of chelonian skeletons by earlier authors are confirmed and extended, as indicating quite definitely that the Testudinata (Chelonia) are a very ancient group of reptiles without close relationship to other surviving orders.

2. The Triassic chelonian *Triassochelys*, as described by Jaekel, already possessed a truly chelonian carapace and plastron but retained many primitive reptilian features, especially in its cervical vertebrae and pectoral girdle.

3. The conclusion of earlier authors that the Chelonia were derived from the Upper Pennsylvanian and Lower Permian cotylosaurs is confirmed.

4. But the present comparative osteological study shows that, among the cotylosaurs, the Permian pareiasaurs approach nearer to the Triassic chelonians in many features than did the Upper Pennsylvanian and Lower Permian diadectids.

5. The smaller captorhinomorphs had already lost the otic notch and reduced the tabulars ("supratemporals") to a vestigial condition, whereas these elements, called supratemporals by Jaekel in *Triassochelys*, were apparently well developed in the stem chelonians, although lost in later chelonians. Moreover the captorhinids were relatively slender-limbed reptiles, and they have been generally recognized as suitable ancestors for the pelycosaurs and therapsids. They apparently lacked carapacial nodules and show nothing definitely chelonian in their vertebrae, girdles, limbs, hands, or feet.

6. Even the gigantic known pareiasaurs seem to present almost ideal conditions for the derivation of the primitive chelonian characters of the skull, carapace, vertebrae, ribs, girdles, limbs, hands, and feet. The stout girdles and limbs of pareiasaurs are well adapted to the lifting propulsion of their massive bodies; the vertebrae, girdles, and limbs of *Triassochelys* were also stoutly built. Perhaps the first turtles were both pygmies and pycnics, a pug-like branch of the pareiasaurs in which adolescence and maturity came on long before the normal height had

been reached but not before great strength, especially in the limbs, had been developed.

7. The stem chelonians may have been derived from some small pareiasaurs related to *Elginia*, which is known chiefly from a skull about 15 cm. long. This skull retains a pineal foramen and small marginal teeth and has several spikes projecting from its squamosal border; it is thus regarded as nearer to the typical pareiasaurs than to the primitive chelonian *Triassochelys*.

8. The placodonts, as clearly recognized by Drevermann and von Huene, were a progressively sluggish and finally turtle-like offshoot of the nothosaurian stem, as shown by their retention of many primitive sauropterygian features, including dorsal supratemporal fenestrae, monimostylic or fixed quadrates, an almost plesiosaur-like pectoral girdle, and a well-developed gastralia system. Their latest member, *Henodus chelyops*, had evolved a perfected carapace and plastron and was amazingly turtle-like in general appearance but retained numerous traces of a remote nothosaurian derivation, together with many significant differences from the contemporary true chelonians (von Huene, 1936a, 1938).

9. The Lower Permian *Seymouria*, whether regarded as a progressive labyrinthodont or a primitive cotylosaur, already possessed a well-developed carapace, consisting of numerous polygonal ossicles which were doubtless covered by a tough leathery integument, but neither the limbs nor girdles show nearly so much resemblance to those of turtles as do the corresponding parts of pareiasaurs. *Kotlassia* Bystrow (1944), the Russian relative of *Seymouria*, seems to be converging toward such modern urodeles as *Cryptobranchus* and has no evident claim for near relationship to the turtles.

10. Testudinate forms, that is, with a carapace, have been developed independently in the following vertebrate groups: Placodermi: Antiarchi (*Pterichthys*, *Bothriolepis*); Amphibia: Labyrinthodontia (*Otocoelus*); Reptilia: Chelonia, Placodontia (*Henodus*), Dinosauria (*Ankylosaurus*); Mammalia: Ed-

entata (*Glyptodon*). In such cases the survival value of a strong carapace has evidently been sufficient to compensate for its adverse effect on rapid locomotion.

11. Some of the disadvantages and limitations imposed by the carapace and plastron of turtles have been met and compensated in the following ways:

a. Fixation of the thoracic vertebrae and ribs by the plastron have been accompanied by remarkable differentiations in the cervical vertebrae. Among the Cryptodira, the ninth vertebra, firmly supported both by the carapace and by the tenth vertebra, serves as a base and pivot for the vertically retractable neck, its wide, rolling anterior zygapophysial facets permitting ample vertical and considerable lateral movements of the neck. In the Pleurodira, the anterior zygapophysial facets, especially of the sixth and seventh vertebrae, have grown forward and, together with the cup-and-ball articulations of the centra, form well-turned pivots for sharp lateral movements of the neck. Neither of these specializations was developed in *Triasosuchelys*, whose neck vertebrae remained much nearer to the pareiasaurian stage.

b. The pectoral girdle of chelonians, overshadowed by the anterior rim of the carapace, transmits part of the thrust of the fore limb to the under side of the carapace. It has lost its clavicles and interclavicle to the plastron and has assumed a triramous form, with a long columnar scapula, a strong rod-like acromial process, and a fan-like coracoid. These three form the frame of a muscular pyramid for the scapulo-humeral and subscapular coraco-brachial and other arm muscles. Every part of the chelonian pectoral girdle has evidently been derived from a pareiasaurian or pareiasaur-like ancestral stage.

c. The humerus of the typical chelonian

has acquired its sigmoid curvature, its globular head, and generally femur-like appearance partly to enable it to function as if it were an anterior knee, which can be directed sharply forward; the sigmoid flexure and other features also facilitate the withdrawal of the arm into the humeral notch between the carapace and plastron. Here again the *Pareiasaurus* humerus gives the necessary suggestions as to the rather complex way in which the humerus of the typical chelonian has been derived from a primitive reptilian type.

d. The pelvis of typical chelonians, although overgrown by the posterior border of the plastron, retains some of its primitive reptilian stamp, save for the fenestration of the pubo-ischiadic plate. The chelonian pelvis is foreshadowed in that of the pareiasaurian, which shows an early stage in the shortening of the pubo-ischiadic plate, the elevation of the ilium and the enlargement and obliquely dorsoventral direction of the acetabulum. The more posterior direction of the acetabulum in the chelonian gives the femur a more direct thrust from the rear.

e. The sigmoid femur of chelonians has raised the head above the plane of the shaft and is likewise readily derivable from the pareiasaurian stage.

f. The almost elephant-like hands and feet of land tortoises are directly derivable from those of pareiasaurs.

g. The plastron of chelonians appears to be an entirely unique development within the chelonian order and is not foreshadowed by the sternum and parasternum or gastralia complex of lower reptiles, which was presumably lost before the origin of the order, but is due to the spread of the process of ossification across the wide ventral integumental zone between the pectoral girdle and the pelvis.

REFERENCES

- ADAMS, LEVERETT ALLEN
1919. A memoir on the phylogeny of the jaw muscles in recent and fossil vertebrates. *Ann. New York Acad. Sci.*, vol. 28, pp. 51-166, figs. 1-5, pls. 1-13.
- BAUR, GEORGE
1887a. On the morphogeny of the carapace of the Testudinata. *Amer. Nat.*, vol. 21, p. 89.
1887b. On the phylogenetic arrangement of the Sauropsida. *Jour. Morph.*, vol. 1, no. 1, pp. 93-104. [*Stereosternum*, Proganosauria, p. 103; turtles related to stem of plesiosaurs, pp. 97-99.]
- BOONSTRA, LIEUWE D.
1929-1933. Pareiasaurian studies. (See Houghton, Sidney H., and Lieuwe D. Boonstra.)
1930. A contribution to the cranial osteology of *Pareiasaurus serridens* (Owen). *Ann. Univ. Stellenbosch*, vol. 8, sect. A, no. 5, pp. 1-18, figs. 1-3, pl. 1.
1932a. The phylogenesis of the Pareiasauridae: a study in evolution. *South African Jour. Sci.*, vol. 29, pt. 1, pp. 480-486, 1 fig.
1932b. A note on the hyoid apparatus of two Permian reptiles (pareiasaurians). *Anat. Anz.*, vol. 75, nos. 4, 5, pp. 77-81, 3 figs.
- BROILI, FERDINAND
1912. Zur Osteologie des Schädels von *Placodus*. *Palaeontographica*, vol. 59, pp. 147-155, figs. 1-4, 1 pl.
- BROOM, ROBERT
1924. On the classification of the reptiles. *Bull. Amer. Mus. Nat. Hist.*, vol. 51, pp. 39-65, figs. 1-13.
- BYSTROW, A. P.
1944. *Kotlassia prima* Amalitsky. *Bull. Geol. Soc. Amer.*, vol. 55, no. 4, pp. 379-416, figs. 1-22.
- CASE, ERMINE COWLES
1905. The osteology of the Diadectidae and their relations to the Chelydosauria. *Jour. Geol.*, vol. 13, no. 2, pp. 126-159, figs. 1-20.
1911. A revision of the Cotylosauria of North America. *Carnegie Inst. Washington Publ.*, no. 145, pp. 1-121, figs. 1-52, pls. 1-14.
- COLBERT, EDWIN HARRIS
1946. *Hypsognathus*, a Triassic reptile from New Jersey. *Bull. Amer. Mus. Nat. Hist.*, vol. 86, pp. 225-274, figs. 1-20, pls. 25-33.
- COPE, EDWARD DRINKER
1880. The skull of *Empedocles*. *Amer. Nat.*, vol. 14, p. 304. [First use of name "Cotylosauria."]
1896a. The ancestry of the Testudinata. *Ibid.*, vol. 30, pp. 398-400.
1896b. The reptilian order Cotylosauria. *Proc. Amer. Phil. Soc.*, (for the year 1895), vol. 34, pp. 436-457, pls. 7-9.
1896c. Second contribution to the history of the Cotylosauria. *Ibid.*, vol. 35, pp. 122-139, pls. 7-10.
1898. Syllabus of lectures on the Vertebrata. Philadelphia, University of Pennsylvania, pp. 1-135, figs. 1-66.
- DREVERMANN, FR.
1924. Schädel und Unterkiefer von *Cyamodus*. *Abhandl. Senckenbergische Naturf. Gesellsch.*, vol. 38, pp. 291-309, pl. 23.
1933. Die Placodontier. 3.—Das Skelett von *Placodus gigas* Agassiz im Senckenberg Museum. *Ibid.*, vol. 38, pp. 323-364, pls. 1-16.
- ELFTMAN, HERBERT
1929. Functional adaptations of the pelvis in marsupials. *Bull. Amer. Mus. Nat. Hist.*, vol. 58, pp. 189-232, figs. 1-12, pls. 9-14.
- EVANS, FRANCIS GAYNOR
1939. The morphology and functional evolution of the atlas-axis complex from fish to mammals. *Ann. New York Acad. Sci.*, vol. 39, art. 2, pp. 29-104, figs. 1-15.
- FÜRBRINGER, MAX
1922. Das Zungenbein der Wirbeltiere insbesondere der Reptilien und Vögel. *Abhandl. Heidelberger akad. Wiss., math. naturw. Kl., div. B*, no. 11, xii + 164 pp., 12 pls.
- GADOW, HANS
1882. Beiträge zur Myologie der hinteren Extremität der Reptilien. *Morph. Jahrb.*, vol. 7, pp. 329-466, figs. 1-4, pls. 17-21.
1920. Amphibia and reptiles. In *Cambridge natural history*, eds. S. F. Harmer and A. E. Shipley. London, vol. 8, xiii + 668 pp., 181 figs.
- GOETTE, A.
1899. Über die Entwicklung des Knöchernen Rückenschildes (carapax) der Schild-

- Kröten. Zeitschr. Wiss. Zool., vol. 66, pp. 407-434, figs. 1-3, pls. 27-29.
- GREGORY, WILLIAM KING
 1910. The orders of mammals, parts I, II. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1-524, figs. 1-32.
 1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Amer. Phil. Soc., vol. 23, art. 2, vii+481 pp., figs. 1-302, pls. 1, 2.
 1934. Polyisomerism and anisomerism in cranial and dental evolution among vertebrates. Proc. Natl. Acad. Sci., vol. 20, no. 1, pp. 1-9, figs. 1-3.
 1935a. On the evolution of the skulls of vertebrates with special reference to heritable changes in proportional diameters (anisomerism). *Ibid.*, vol. 21, no. 1, pp. 1-8, figs. 1-3.
 1935b. Reduplication in evolution. Quart. Rev. Biol., vol. 10, no. 3, pp. 272-290, figs. 1-12.
 1936. The transformation of organic designs: a review of the origin and deployment of the earlier vertebrates. Biol. Rev., Cambridge Phil. Soc., vol. 11, no. 3, pp. 311-344, figs. 1-10.
- GREGORY, WILLIAM KING, AND LEVERETT ALLEN ADAMS
 1915. The temporal fossae of vertebrates in relation to the jaw muscles. Science, new ser., vol. 41, no. 1064, pp. 763-765.
- GREGORY, WILLIAM KING, AND CHARLES LEWIS CAMP
 1918. Studies in comparative myology and osteology, no. III. Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 447-563, figs. 1-16, pls. 39-50.
- GREGORY, WILLIAM KING, ROY WALDO MINER, AND GLADWYN KINGSLEY NOBLE
 1923. The carpus of *Eryops* and the structure of the primitive chiropterygium. Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 279-288, figs. 1-4.
- GREGORY, WILLIAM KING, AND GLADWYN KINGSLEY NOBLE
 1924. The origin of the mammalian alisphenoid bone. Jour. Morph. Physiol., vol. 39, no. 2, pp. 435-463, figs. 1-13, 1 pl.
- GREGORY, WILLIAM KING, AND HENRY CUSHIER RAVEN
 1941. Studies on the origin and early evolution of paired fins and limbs, parts I-IV. Ann. New York Acad. Sci., vol. 42, art. 3, pp. 273-360, figs. 1-34, pls. 1-5.
- HARTMAN-WEINBERG, A.
 1930. Zur Systematik der Nord-Düna-Pareiasauridae. Palaeont. Zeitschr., vol. 12, pp. 47-59, figs. 1-9.
- HAUGHTON, SIDNEY H.
 1929-1933. Pareiasaurian studies. (See Haughton, Sidney H., and Lieuwe D. Boonstra.)
- HAUGHTON, SIDNEY H., AND LIEUWE D. BOONSTRA
 1929-1933. Pareiasaurian studies, parts I-XI, as follows:
 1929a. Part I.—An attempt at a classification of the Pareiasauria based on skull features. Ann. South African Mus., vol. 28, pp. 79-87.
 1929b. Part II (Haughton, S. H.).—Notes on some pareiasaurian brain-cases. *Ibid.*, vol. 28, pp. 88-96, figs. 21-26.
 1929c. Part III (Boonstra, L. D.).—On the pareiasaurian manus. *Ibid.*, vol. 28, pp. 97-112, figs. 27, 28, pls. 6-8.
 1929d. Part IV (Boonstra, L. D.).—On the pareiasaurian pes. *Ibid.*, vol. 28, pp. 113-122, fig. 29, pls. 9-12.
 1930a. Part V (Haughton, S. H., and L. D. Boonstra).—On the pareiasaurian mandible. *Ibid.*, vol. 28, pp. 261-289, figs. 4-16, pls. 32-36.
 1930b. Part VI (Haughton, S. H., and L. D. Boonstra).—The osteology and myology of the locomotor apparatus. A—Hind limb. *Ibid.*, vol. 28, pp. 297-366, figs. 1-60, pl. 38.
 1932a. Part VII (Boonstra, L. D.).—On the hind limb of the two little-known pareiasaurian genera: *Anthodon* and *Pareiasaurus*. *Ibid.*, vol. 28, pp. 429-435, figs. 1-7.
 1932b. Part VIII (Boonstra, L. D.).—The osteology and myology of the locomotor apparatus. B—Fore limb. *Ibid.*, vol. 28, pp. 437-503, figs. 1-41, pls. 42-44.
 1933a. Part IX (Boonstra, L. D.).—The cranial osteology. *Ibid.*, vol. 31, pp. 1-38, figs. 1-5, pls. 1-22.
 1933b. Part X (Boonstra, L. D.).—The dermal armour. *Ibid.*, vol. 31, pp. 39-48, pls. 23-27.
 1933c. Part XI (Boonstra, L. D.).—The vertebral column and ribs. *Ibid.*, vol. 31, pp. 49-66, figs. 1-7, pl. 28.
- HAY, OLIVER PERRY
 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, figs. 1-5.
 1908. The fossil turtles of North America.

- Carnegie Inst. Washington Publ., no. 75, pp. 1-568, figs. 1-704, pls. 1-113.
- HEINTZ, ANATOL
1935. How the fishes learned to swim. Smithsonian Rept. (for the year 1934), publ. 3316, pp. 223-245, figs. 1-12.
- HUENE, FRIEDRICH VON
1913. The skull elements of the Permian Tetrapoda in the American Museum of Natural History, New York. Bull. Amer. Mus. Nat. Hist., vol. 32, pp. 315-386, figs. 1-57.
1920. *Sclerosaurus* und seine Beziehungen zu anderen Cotylosauriern und zu den Schildkröten. Zeitschr. f. induktive Abstammungs- und Vererbungslehre, vol. 24, pp. 163-166, 1 fig.
1926. Einige Schildkrötenreste aus der obersten Trias Württembergs. Centralbl. f. Min., div. B, no. 14, pp. 509-514, figs. 1-4.
1931. Ergänzungen zur Kenntnis des Schädels von *Placochelys* und seiner Bedeutung. Geol. Hungarica, ser. palaeont., fasc. 9, pp. 1-18, pls. 1-3.
1933. Die Placodontier. 4. Zur Lebensweise und Verwandtschaft von *Placodus*. Abhandl. Senckenbergische Naturf. Gesellsch., vol. 38, pp. 365-382, figs. 1-5.
1936a. *Henodus chelyops*, ein neuer Placodontier. Palaeontographica, vol. 84, div. A, pp. 99-148, figs. 1-37, pls. 9-13.
1936b. Kurze übersicht über die Geschichte der Vertebraten. Eine graphische Darstellung. Palaeont. Zeitschr., vol. 18, pp. 198-201, pl. 10.
1938. Der dritte *Henodus*, Ergänzungen zur Kenntnis des Placodontiers *Henodus chelyops* Huene. Palaeontographica, vol. 89, div. A, pp. 105-114, figs. 1-6, pls. 3, 4.
1940. Die stammesgeschichtliche Gestalt der Wirbeltiere-ein Lebensablauf. Palaeont. Zeitschr., vol. 22, pp. 55-62, figs. 1, 2.
- HUNTINGTON, GEORGE S.
1918. Modern problems of evolution, variation and inheritance in the anatomical part of the medical curriculum. Anat. Rec., vol. 14, no. 6, pp. 359-445, figs. 1-18, pls. 1-17. [Shoulder girdle of *Chelydra*, fig. 6, p. 372; morphology of the entepicondylar foramen, pp. 390-392.]
- IHLE, J. E. W., P. N. VAN KAMPEN, H. F. NIERSTRASZ, AND J. VERSLUYS
1927. Vergleichende Anatomie der Wirbeltiere. Berlin, viii+906 pp., 987 figs.
- JAEKEL, OTTO
1902. Ueber *Placochelys* n.g. und ihre Bedeutung für die Stammesgeschichte der Schildkröten. Neues Jahrb. Min., vol. 1, pp. 127-144, pl. 2.
1907. *Placochelys placodonta* aus der Obertrias des Bakony. Resultate der wissenschaftl. Erforschung des Balatonsees, vol. 1, pt. 1, palaeont. suppl., pp. 1-90, figs. 1-50, pls. 1-10.
1914. Über die Wirbeltierfunde in der oberen Trias von Halberstadt. Palaeont. Zeitschr., vol. 1, pp. 155-215, figs. 1-34, pls. 3-5.
1918. Die Wirbeltierfunde aus dem Keuper von Halberstadt. Serie 2. Testudinata. Teil 1. *Stegochelys dux*, n.g., n.sp. *Ibid.*, vol. 2, pp. 88-214, figs. 1-62, pls. 2-7.
- MINER, ROY WALDO
1925. The pectoral limb of *Eryops* and other primitive tetrapods. Bull. Amer. Mus. Nat. Hist., vol. 51, pp. 145-312, figs. 1-104.
- OWEN, RICHARD
1849. On the development and homologies of the carapace and plastron of the chelonian reptiles. Memoirs from the Trans. Geol. Soc. London, vol. 11, pp. 151-171, figs. 1-9, pl. 13.
- PARKER, WILLIAM KITCHEN
1880. On the development of the green turtle (*Chelone viridis*, Schneid.). Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873-1876. Zoology. London, vol. 1, pt. 5, pp. 1-58, pls. 1-13.
- PATTEN, WILLIAM
1912. The evolution of the vertebrates and their kin. Philadelphia, xxi+486 pp., 309 figs.
- PEYER, BERNHARD
1931. Die Triasfauna der Tessiner Kalkalpen. III. Placodontia. Abhandl. d. Schweizerischen Palaeont. Gesellsch., vol. 51, pp. 1-25, pls. 15-17.
1934. Die Triasfauna der Tessiner Kalkalpen. VII. Neubeschreibung der Saurier von Perledo. *Ibid.*, vols. 53, 54, pp. 1-130, figs. 1-14, pls. 31-41.
1935. Die Triasfauna der Tessiner Kalkalpen. VIII. Weitere Placodontierfunde. *Ibid.*, vol. 55, pp. 1-26, pls. 42-46.
- ROMER, ALFRED SHERWOOD
1922. The locomotor apparatus of certain primitive and mammal-like reptiles. Bull. Amer. Mus. Nat. Hist., vol. 46, pp. 517-606, figs. 1-7, pls. 27-46.
1933. Vertebrate paleontology. Chicago, Uni-

- versity of Chicago Press, vii + 491 pp., 359 figs.
1945. Vertebrate paleontology. Second edition. Chicago, University of Chicago Press, viii + 687 pp., 377 figs.
- ROMER, ALFRED SHERWOOD, AND FRANK BYRNE
1931. The pes of *Diadectes*: notes on the primitive tetrapod limb. *Palaeobiologica*, vol. 4, pp. 24-48, figs. 1-9.
- ROMER, ALFRED SHERWOOD, AND L. W. PRICE
1940. Review of the Pelycosauria. *Geol. Soc. Amer. Special Papers*, no. 28, x + 538 pp., figs. 1-71, pls. 1-46, tables 1-8.
- RUCKES, HERBERT
1929a. Studies in chelonian osteology. Part I. Truss and arch analogies in chelonian pelves. *Ann. New York Acad. Sci.*, vol. 31, pp. 31-80, figs. 1-14, pls. 4-7.
1929b. Studies in chelonian osteology. Part II. The morphological relationships between the girdles, ribs and carapace. *Ibid.*, vol. 31, pp. 81-120, figs. 1-30.
- SCHAEFFER, BOBB
1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. *Bull. Amer. Mus. Nat. Hist.*, vol. 78, pp. 395-472, figs. 1-21.
- SEELEY, HARRY GOVIER
1887-1895. Researches on the structure, organization and classification of the fossil Reptilia. Parts I-IX. *Phil. Trans. Roy. Soc.*, London, vols. 178-186.
- SUSHKIN, PETER P.
1928. Contributions to the cranial morphology of *Captorhinus* Cope (Reptilia, Cotylosauria, Captorhinidae). *Palaeobiologica*, vol. 1, pp. 263-280, figs. 1-10.
- WATERMAN, HARRIET CUTLER
1929. Studies on the evolution of the pelvis of man and other primates. *Bull. Amer. Mus. Nat. Hist.*, vol. 58, pp. 585-642, figs. 1-10, pl. 22.
- WATSON, DAVID MEREDITH SEARES
1914a. On the skull of a pariasaurian reptile, and on the relationship of that type. *Proc. Zool. Soc. London*, pp. 155-180, figs. 1-7.
1914b. *Eunotosaurus africanus* Seeley and the ancestry of the Chelonia. *Ibid.*, pp. 1011-1020, fig. 1, pl. 7.
1916. On the structure of the brain-case in certain Lower Permian tetrapods. *Bull. Amer. Mus. Nat. Hist.*, vol. 35, pp. 611-636, figs. 1-11.
1924. The elasmosaurid shoulder-girdle and fore-limb. *Proc. Zool. Soc. London*, pp. 885-917, figs. 1-12.
- WELLES, SAMUEL PAUL
1941. The mandible of a diadectid cotylosaur. *Univ. California Bull. Dept. Geol. Sci.*, vol. 25, pp. 423-432, figs. 1, 2.
1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. *Mem. Univ. California*, vol. 13, no. 3, pp. 125-254, figs. 1-37, pls. 12-29 and frontispiece.
- WHITE, THEODORE E.
1939. Osteology of *Seymouria baylorensis* Broili. *Bull. Mus. Comp. Zool. Harvard Coll.*, vol. 85, no. 5, pp. 325-409, figs. 1-30, pls. 1-3.
- WIEDERSHEIM, ROBERT
1907. Einführung in die Vergleichende Anatomie der Wirbeltiere. Jena, Gustav Fischer, xxii + 471 pp., 334 figs.
- WILLISTON, SAMUEL WENDELL
1904. The temporal arches of the Reptilia. *Biol. Bull.*, vol. 7, no. 4, pp. 175-192, figs. 1-17.
1907. The skull of *Brachauchenius*, with observations on the relationships of the plesiosaurs. *Proc. U. S. Natl. Mus.*, vol. 32, pp. 477-489, pls. 1-4.
1911. American Permian vertebrates. Chicago, University of Chicago Press, 145 pp., 38 pls., 32 figs. [*Limnoscelis*, forelimb and hand, fig. 13, p. 39; skull, fig. 4, p. 29.]
1914. Water reptiles of the past and present. Chicago, University of Chicago Press, 251 pp., 131 figs. [*Limnoscelis*, restored skeleton, fig. 3, p. 20.]
1917. The phylogeny and classification of reptiles. *Jour. Geol.*, vol. 25, no. 5, pp. 411-421, figs. 1-5.
1925. The osteology of the reptiles. [Ed. William K. Gregory.] Cambridge, Harvard University Press, xiii + 300 pp., 191 figs.

