informs us (personal communication) that these measurements were actually made at 1300 μm (236 GHz).

4. The JCMT is operated jointly by the United Kingdom Science and Engineering Research Council, the Netherlands Organizations for the Advancement of Pure Research, the Canadian National Research Council, and the University of Hawaii.
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7. The positions of the PCS were determined from ephemerides in the *Astronomical Almanac for the Year 1993* (Government Printing Office, Washington, DC, 1993).
8. Our pointing sources were taken from a recent submillimeter catalog [G. Sandell, in preparation]. The Uranus and Jupiter calibration measurements are referenced from the work of M. J. Griffin and co-workers [*Icarus* **65**, 244 (1986)] and G. S. Orton and colleagues [*ibid.* **67**, 289 (1986)].
9. L. M. Trafton and S. A. Stern. *Astrophys. J.* **267**, 872 (1983).
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11. Estimates of the vertical scale length of the diurnal thermal wave on Pluto are between 50 and 1000 times the wavelength of our measurements (*1, 9*). Because these values are thick compared to the $\sim$10 wavelength penetration of common dielectrics in the millimeter wave regime [B. L. Ulich, J. R. Dickel, I. De Pater, *Icarus* **60**, 590 (1984)], it is reasonable to conclude that our measurements sample the thermally relevant skin temperature.
12. The radius of Charon is known to lie between 600 km and 640 km (*1*). The 620-km value used here is intermediate and can introduce no more than a 6% error in Charon's flux contribution, corresponding to no more than 1 to 2% of the total PCS flux. The radius of Pluto is uncertain at the ±3% level, owing to discrepancies between mutual event and stellar occultation data (*1*). The range of solutions falls between 1151 km and 1220 km. A radius of 1180 km is a conservatively small value, on the basis of the most complete analysis [R. L. Millis *et al.*, unpublished data].
13. T. Owen *et al.*, *Science* **261**, 745 (1993).
14. If either Pluto or Charon has a radius at its upper limit (642 and 1220 km, respectively), as opposed to the 1180- and 620-km values used above, solutions up to 3 to 4 K colder would be indicated. Similarly if Pluto or Charon had a radius at its lower limit (602 and 1151 km, respectively), then solutions 2 to 3 K warmer would be indicated. If the surface emissivity on Pluto is as low as 0.5, the surface temperature would be driven into the 55- to 60-K range of the IRAS-derived results. However, this temperature is not consistent with pressure data on Pluto's atmosphere (*15*).
15. J. L. Elliot and L. A. Young, *Astron. J.* **103**, 991 (1991).
16. If Pluto is cold (30 to 43 K) and Charon is warm (53 to 59 K) as predicted by our model, then the PCS would have been below the IRAS detection limits.
17. It is also possible that there is some contribution from a rotationally variable thermal flux from Charon.
18. The total column abundance (N_{tot}) is derived from the total pressure, with the use of the perfect gas law and the scale height measured during the 1988 occultation, giving $N_{\mathrm{tot}} = 0.6 \times 10^{15}$ to 1.8×10^{15} cm^{-2}. The small CH_4 mixing ratio suggested by the low surface temperature may be at odds with the popular methane-induced atmospheric thermal gradient model [R. V. Yelle and J. I. Lunine, *Nature* **339**, 288 (1989)].
19. On the basis of laboratory data, the visible-wavelength CH_4 bands on Pluto appeared to require a much higher atmospheric column than those that early thermal models indicated were present (*1*). This problem motivated some early suggestions (*9*) for a very low emissivity, high-temperature surface that would support a relatively dense atmosphere (compared to the established, 1- to 3-μbar pressure). The cold Pluto results found here bolster previous evidence [M. W. Buie and U. Fink, *Icarus* **70**, 483 (1987)] concerning this old quandry by demonstrating that the visible-wavelength CH_4 absorptions must be formed by the solid-state frost rather than by an overlying gas column.
20. The spherical albedo, *A*, is the ratio of total radiative flux emitted by a spherical object in all directions to the incident flux on it. By definition, $A = pq$, where *p* is the geometric albedo and *q* is the so-called phase integral. The geometric albedo is the ratio of the brightness of an object to that of a perfectly diffusing disk of the same size, under the same illumination conditions. The phase integral is a numerical coefficient describing the integral behavior of the object's phase function over its surface.
21. The range of 0.44 to 0.59 in Pluto's geometric albedo [D. J. Tholen and M. W. Buie, *Astron. J.* **96**, 1977 (1989)] is dominated by Pluto's 25% lightcurve amplitude and uncertainties in Pluto's radius; strict measurement errors are less than 1%.
22. Accurate polynomial fits to laboratory vapor pressure data taken over a number of cosmogonically important ices at temperatures of 30 to 80 K are given by G. N. Brown, Jr., and W. T. Ziegler [*Advances in Cryogenic Engineering* (Plenum, New York, vol. 25, 1980), p. 662].
23. We obtained additional JCMT observations of Pluto and Charon on 22 May 1993 UT with significantly improved observation times yield 15 ± 4.8 mJy at 1300 μm. This value confirms our previous results.

24. We thank the staffs of the JCMT and IRAM observatories for their assistance with the observations and M. Buie, I. De Pater, L. Lebofsky, J. Spencer, M. Sykes, and D. Tholen for useful discussions.

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The Origin of the Turtle Body Plan: Bridging a Famous Morphological Gap

Michael S. Y. Lee

A restudy of pareiasaurs reveals that these primitive reptiles are the nearest relatives of turtles. The two groups share numerous derived characters, such as a reduced presacral count, an acromion process, and a trochanter major, which are absent in other basal amniotes. Many traits long thought specific to chelonians also occur in pareiasaurs and must have evolved before the distinctive turtle shell appeared. Evidence uniting captorhinid or procolophonoids with turtles is shown to be weak. The phylogeny proposed here also suggests that certain features of the earliest turtle (*Proganochelys*) that have been interpreted as specializations, such as the large supratemporal and robust metacarpals, are primitive for turtles. In pareiasaurs, the osteoderms represent the precursors of the chelonian shell and the morphology of the anterior region is consistent with the idea that the shoulder girdle in turtles has migrated posteriorly into the rib cage.

Turtles, mammals, and birds differ greatly from their primitive reptilian ancestors. However, although the mammal and bird origins are both documented by numerous transitional fossils, turtles appear abruptly. Distinctive chelonian features such as the carapace, plastron, and the location of the shoulder girdle within the rib cage are already well developed in the earliest known turtles (*1*). Attempts by morphologists to understand how the turtle body plan arose have been hindered by the apparent absence of intermediate forms (*2*). In this report, I demonstrate that pareiasaurs are the closest relatives of turtles and are intermediates between turtles and generalized reptiles.

Pareiasaurs (*3*) are large anapsid reptiles that flourished briefly and achieved a cosmopolitan distribution during the Late Permian (*4*). These ponderous, heavily armored herbivores appear to form a monophyletic group, characterized by several derived traits such as crenulated ("iguanodont") teeth, large descending cheek flanges that cover the posterior region of the lower jaw, a prominent ventral boss on the mandible, four or more sacral vertebrae, a forwardly directed ilium, a reduced pubis, and a wide, flattened femoral shaft. Because new information from a thorough reexamination of these poorly known creatures was expected to shed light on their relations with other reptiles, a cladistic analysis of pareiasaurs and other basal amniotes was undertaken (*5*).

Pareiasaurs were found to share 16 derived features with turtles (Figs. 1 to 4): (A1) a choana located far medially from the alveolar ridge of the maxilla, largely separating the palatine from the vomer; (A2) a large, circular, medially located foramen palatinum posterius (the suborbital foramen of diapsids is more laterally located and of a different shape); (A3) a massive horizontal paroccipital process firmly sutured to the squamosal (also sutured to the supratemporal in pareiasaurs and to the quadrate in turtles); (A4) a long lateral flange of the exoccipital on the posterior face of the paroccipital process; (A5) a basisphenoid and basioccipital solidly ossified together, resulting in the loss of the ventral otic fissure that

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normally exists between these bones; (A6) a fully ossified medial wall of prootic, separating the inner ear cavity from the brain cavity and pierced by foramina for acoustic nerves (this area is partially ossified in *Diadectes* but remains unossified dorsally); (A7) the transverse flange of the pterygoid is reduced and forwardly directed (convergently acquired in bolosaurs and some diadectomorphs); (A8) the supraoccipital forms a long, high, narrow, solid median ridge, sutured to the skull roof along its entire length; (A9) the entire palate, including the transverse flange of the pterygoid, is raised well above the ventral margin of the upper jaw, with the palatine contacting the maxilla far above the alveolar ridge; (A10) prominent lateral projections present on at least the first 14 caudal vertebrae (primitively these are present on only the first five to nine vertebrae); (A11) the chevrons are not wedged between adjacent centra, each chevron instead articulating one caudal vertebra by way of distinct posteroventral facets on the centrum (also present in some mesosaurs in association with pachyostotic haemal arches); (A12) an acromion process on the anterior margin of the scapula; (A13) a humerus with an ectepicondylar foramen [also present in some early synapsids and diapsids but primitively absent in both these groups (*6*, *7*)]; (A14) a femur with the major (greater) trochanter on the posterior (postaxial) margin; (A15) a reduced fifth pedal digit that is much more slender and no longer than the first pedal digit; and (A16) a prominent dorsal buttress, V-shaped in ventral view, overhanging the acetabulum. These traits are present in all pareiasaurs and either occur in all turtles or represent the primitive condition in turtles (*8*–*10*). Thirteen of these synapomorphies are particularly significant because they are absent in all other basal amniotes [*Westlothiana*, diadectomorphs, pelycosaurs, millerosaurs, lanthanosuchids, *Acleistorhinus*, bolosaurs, mesosaurs, captorhinids, protorothyridids, primitive diapsids (*11*), nyctiphruretids, nycteroleterids, and procolophonoids] and in reptiliomorph amphibians (anthracosauroids and seymouriamorphs).

Nine more derived traits diagnose a more inclusive group of chelonians, pareiasaurs, and *Sclerosaurus* (Fig. 1): (B1) 20 or fewer presacral vertebrae [convergently acquired in *Eunotosaurus*, an aberrant caseid pelycosaur (*12*)]; (B2) a tall and narrow scapula blade, with a height that is over four times as high as wide (present in derived pelycosaurs and *Tseajaia* but absent in primitive pelycosaurs and diadectomorphs); (B3) the glenoid is not screw-shaped but bipartite, consisting of two flat surfaces (formed by the scapula and the coracoid) that meet at a right angle; (B4) when the scapula is restored to its life position, the long or major axis of the glenoid is orientated anterodorsally, not horizontally; (B5) a reduced manual phalangeal formula (23332, convergently acquired in some caseid pelycosaurs); (B6) the astragalus and calcaneum are completely fused; (B7) a reduced pedal phalangeal formula (≤23343, convergently acquired in some caseid pelycosaurs); (B8) thick dermal armor over the dorsal region (also present in the seymouriamorph *Kotlassia*); and (B9) the loss of the gastralia (a

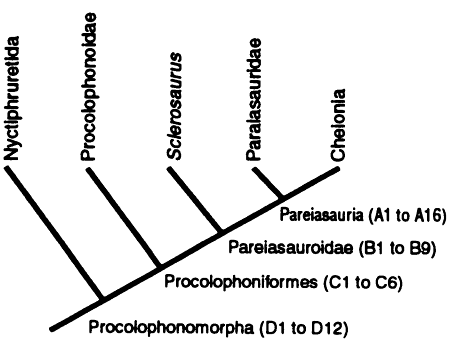

Fig. 1. A cladogram depicting chelonian relationships, based on a cladistic analysis of basal amniotes (*5*). Numbers refer to derived traits diagnosing each grouping. Traits A1 to A16 and B1 to B9 are discussed in the text and (except A16) illustrated in Figs. 2 to 4. Nyctiphruretia includes both Nyctiphruretidae and Nycteroleteridae. C1, the quadratojugal is enlarged, with a long dorsoventral dimension; C2, the cultriform process is shortened; C3, the pineal foramen is located anteriorly, near the fronto-parietal suture (the pineal is usually absent in chelonians but is present in this location in atavistic mutants); C4, the fifth distal tarsal is lost. D1, the stapes is imperforate and rodlike; D2, there is a palatine-prefrontal buttress that encloses the foramen orbito-nasale; D3, the quadrate ramus of the pterygoid is short; D4, there is an enlarged cranio-quadrate space, because the paroccipital process and quadrate ramus of the pterygoid are parallel and do not converge distally; D5, the postparietals are located on the skull roof rather than on the occiput (not applicable to turtles); D6, the anterior border of the splenial is notched; D7, the foramen intermandibularis caudalis is located posteriorly; D8, the posterodorsally directed spine (epipophysis) on the atlas neural arch is reduced; D9, there are paired depressions on the anterior and posterior faces of the neural arches of the dorsal vertebrae (not applicable to chelonians); D10, there is a third sacral rib (only present in some chelonians); D11, the interclavicle is T-shaped, with an anterior groove and long lateral arms, and the fourth trochanter on the femur is lost; D12, the pedal centralia are lost.

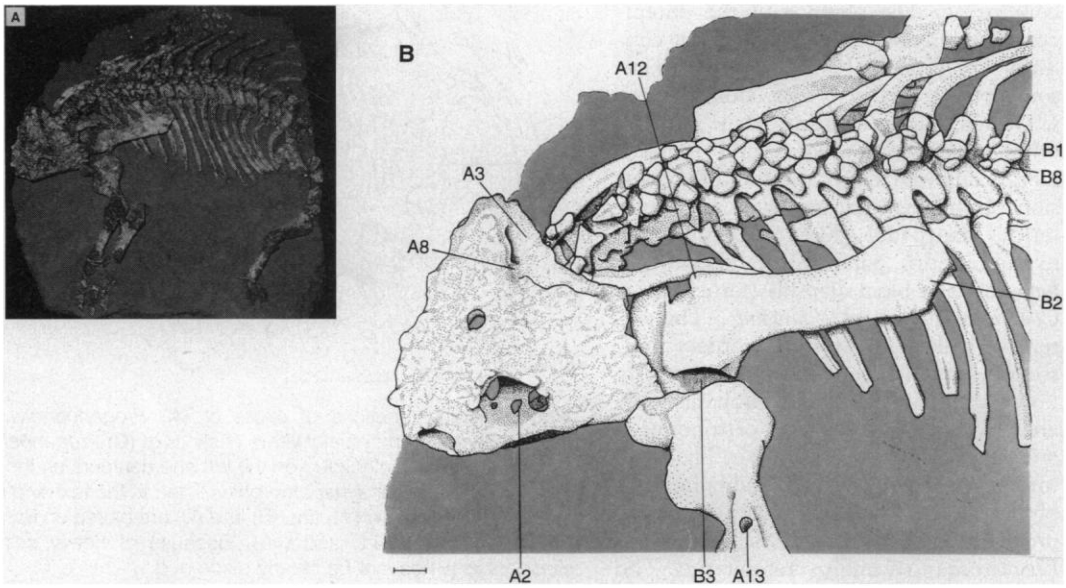

Fig. 2. (**A**) Articulated specimen of *Deltavjatia vjatkensis*, a pareiasaur from the Upper Permian Zone IV (Tatarian) of Russia (Cambridge University Museum of Zoology T1321). The rib cage is flat but undisturbed. The dermal armor is feebly developed in this small individual: osteoderms are small and present only in the anterior dorsal region, a condition similar to that found in juvenile temnospondyl amphibians such as dissorophids. In adult pareiasaurs the armor is more extensive. (**B**) Drawing of the anterior region of (A). Labels are as in Fig. 1; scale bar, 2 cm.

character difficult to determine in chelonians). The *Sclerosaurus* genus has been identified as a procolophonoid by some workers (*13*) and a pareiasaur by others (*8*). On the basis of these traits, *Sclerosaurus* appears more closely related to pareiasaurs and chelonians than to procolophonoids. Apart from transversely broadened marginal teeth, there are no convincing features uniting *Sclerosaurus* with procolophonoids. Similar dentition has evolved repeatedly in other herbivorous lineages. Contrary to early reconstructions (*13*), *Sclerosaurus* does not exhibit the posteriorly enlarged orbit found in all procolophonoids (*14*).

It has often been assumed that the highly modified postcranial skeleton of chelonians reveals little about their affinities with more generalized tetrapods (*1, 2, 8, 15*). However, 16 of the 25 derived traits that link turtles to pareiasaurs (and *Sclerosaurus*) are postcranial. Previous suggestions that pareiasaurs and turtles are closely related (*16, 17*) have not been substantiated by such convincing evidence. Support for alternative views of chelonian relationships is weak. Of the five characters usually cited as evidence for captorhinid affinities (*18*), three—the absence of the tabular bone and supinator process and the presence of the foramen orbitonasale—are exhibited by many other primitive amniotes (*15, 19*), including pareiasaurs. The remaining two traits—the loss of the ectopterygoid and the presence of a medial flange of the jugal—are correlated. Similarly, of the 11 characters corroborating the recently proposed sister-group relationship between turtles and procolophonoids (*15*), only one appears valid: the otic notch bordered by an enlarged quadratojugal. [Even this condition is approached in some millerosaurs (*20*).] The other synapomorphies are less convincing. The absence of the entepicondylar foramen is not the general condition in procolophonoids; furthermore, some pareiasaurs also lack this foramen (*21*). The remaining traits occur in many other primitive amniotes and reptiliomorph amphibians. The anterior expansion of the maxilla occurs in nycteroleterids, lanthanosuchids, *Acleistorhinus*, nyctiphruretids, pareiasaurs, and many pelycosaurs and basal diapsids (for example, *Coelurosauravus* and *Youngina*). The extensive palatine-prefrontal contact rod-shaped, imperforate stapes, and anteriorly notched splenial are present in pareiasaurs and nyctiphruretids and so corroborate a more inclusive group (Fig. 1). The splenial is excluded from the mandibular symphysis in millerosaurs, nyctiphruretids, protorothyridids, early diapsids (such as *Petrolacosaurus*), and nycteroleterids. The shortened cultriform process occurs in pareiasaurs, nyctiphruretids, nycteroleterids, *Acleistorhinus*, and lanthanosuchids, and the postparietals are extremely reduced or lost in lanthanosuchids, nyctiphruretids, bolosaurs, some pelycosaurs, and many primitive diapsids (for example, *Coelurosauravus* and *Youngina*). Similarly, the edentulous transverse flange of the pterygoid occurs in seymouriamorphs, bolosaurs, *Diadectes*, and some pareiasaurs (*22*), while the ventral ridge in this area occurs in pareiasaurs, lanthanosuchids, nyctiphruretids, nycteroleterids, and some millerosaurs (such as *Broomia*). Finally, the large retroarticular process with a dorsal surface formed by the articular, "angular" (presumably the authors meant surangular), and prearticular is absent in all early Mesozoic and most later turtles (*9*); the relevant sutures in *Proganochelys* are not determinable (*1*).

Even at their earliest appearance in the fossil record (*Proganochelys* in the Upper Triassic), chelonians differ from typical reptiles in many traits apart from their characteristic carapace and plastron (*1, 2, 8, 15*). Thus, most of these features were thought to have evolved approximately simultaneously with the turtle shell, and the origin of turtles was consequently seen as a huge evolutionary leap. The evidence that pareiasaurs, *Sclerosaurus*, procolophonoids, and nyctiphruretians are the successive out-groups to turtles bridges the morphological gap between turtles and generalized reptiles and sheds light on the sequence of acquisition of chelonian traits. Many of the specializations often thought to be uniquely chelonian (*1, 2, 8*) are present in other procolophonomorphs (Fig. 1), making the morphological gap between turtles and their nearest relatives less dramatic than previously thought. Some of these traits occur in all procolophonomorphs (Fig. 1), as well as in a few other basal amniotes, and so must have evolved at the base of the Procolophonomorpha or earlier. These characters include the large posttemporal fenestrae, reduced interpterygoid vacuities, the long jugal-quadratojugal contact, the small fenestra ovalis, the shortened cultriform process, and the small, medially enclosed adductor fossa of the mandible. Similarly, nine of the twelve procolophonomorph

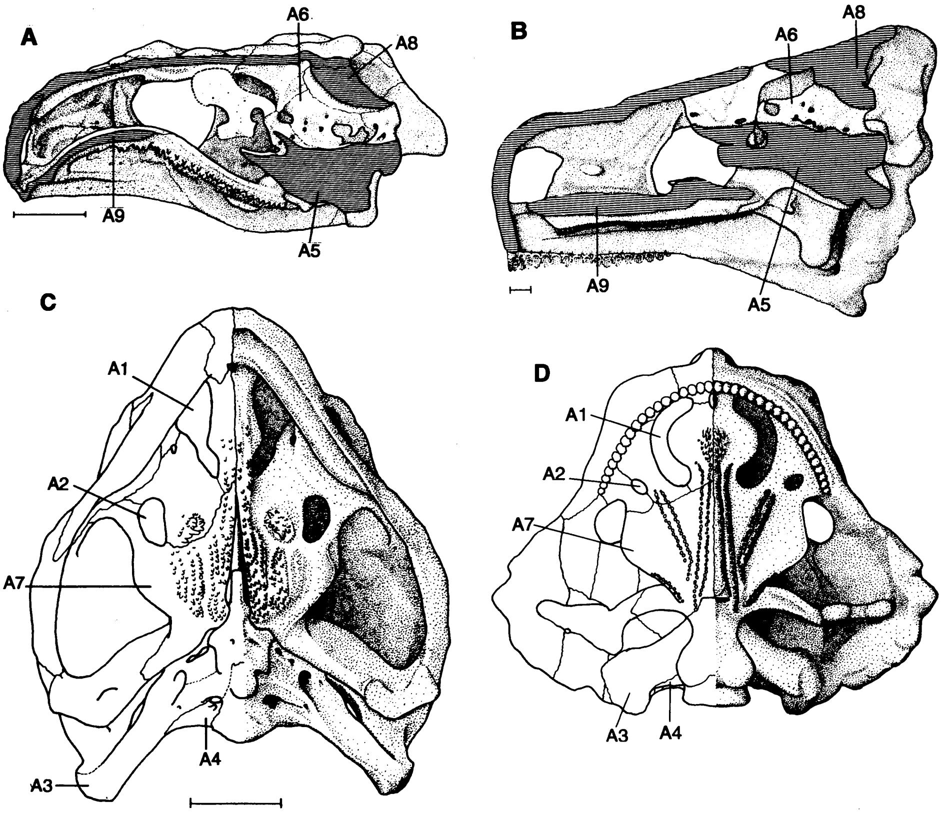

Fig. 3. Sagittal sections of skulls of (**A**) *Proganochelys* (Chelonia) and (**B**) *Embrithosaurus* (Pareiasauridae) and palatal views of skulls of (**C**) *Proganochelys* and (**D**) *Bradysaurus* (Pareiasauridae), with sutures depicted on the left and contours on the right. Scale bars, 2 cm; labels denote chelonian-pareiasaur synapomorphies listed in the text and in the legend of Fig. 1. (A) and (C) are modified from Gaffney (*1*), and (B) and (D) are based on British Museum of Natural History (BMNH) R7782, BMNH R1971, and (*40*). Because of heavy ossification, sutures between braincase elements in (B) cannot be clearly discerned.

synapomorphies (all except D5, D9, and D10 in Fig. 1), three of the four procolophoniform synapomorphies (all except C3), seven of the nine pareiasauroid synapomorphies (all except B4 and B9), and 14 of the 16 pareiasaurian synapomorphies (all except A5 and A9) have been described as chelonian specializations (*1*, *2*, *8*). Thus, at least 39 apparent chelonian traits actually diagnose more inclusive groups and must have evolved before the carapace and plastron appeared. Furthermore, many features characteristic of modern turtles are not present in *Proganochelys* and so must have evolved after the shell appeared. Examples of such traits are the loss of the lacrimal, enclosure of the middle ear region, fusion of the vomers, and specializations of the jaw musculature (*1*). The results of this study demonstrate that in chelonians, as in mammals and birds, features characteristic of an apparently discrete and highly integrated Bauplan were accumulated gradually and in a precise order. The paleobiological aspects of the origin of turtles can now be investigated in much the same way as the origins of mammals and birds.

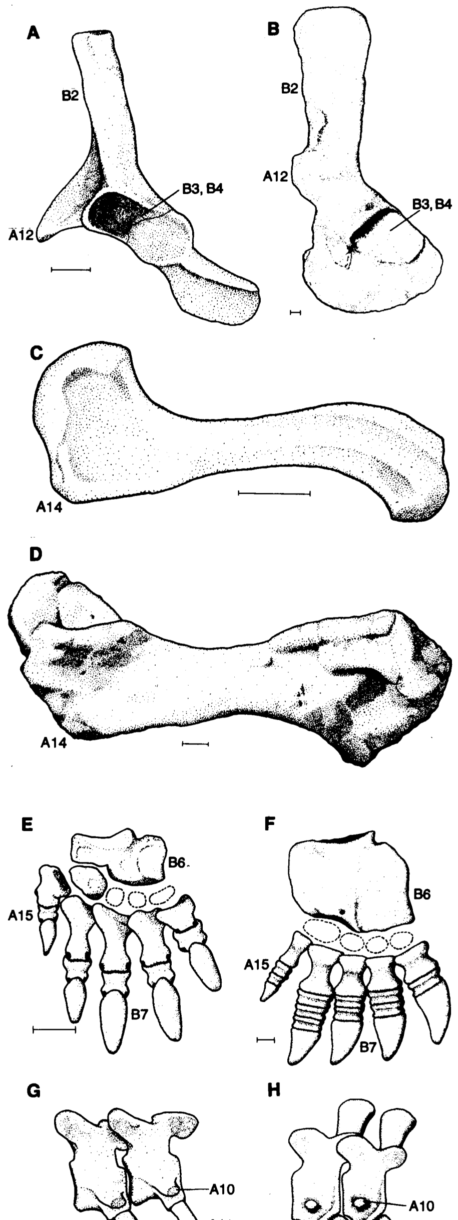

Fig. 4. Lateral views of left scapulocoracoid of (**A**) *Proganochelys* (Chelonia) and (**B**) *Scutosaurus* (Pareiasauridae). Posterior (postaxial) views of the right femur of (**C**) *Proganochelys* and (**D**) *Scutosaurus*. Dorsal views of right pes of (**E**) *Proganochelys* and (**F**) *Bradysaurus* (Pareiasauridae). Left views of the middle caudal vertebrae of (**G**) *Proganochelys* and (**H**) *Bradysaurus*. Scale bars, 2 cm; (A), (C), (E), and (G) are redrawn from Gaffney (*1*); (B) is after BMNH R4025; (D) is after BMNH 4030; (F) is after BMNH 1971 and (*41*); and (H) is after BMNH 1971 and (*42*). Labeled features are described in the text and in Fig. 1.

The phylogeny in Fig. 1 helps to bridge the gap between turtles and generalized reptiles in another way. The earliest known turtle, *Proganochelys*, although intermediate between all other turtles (casichelydians) and generalized amniotes in many respects, also appears to exhibit many specializations that preclude it from being ancestral to all other chelonians (*1*). However, at least four of the apparent autapomorphies of *Proganochelys* are also present in pareiasaurs, *Sclerosaurus*, procolophonoids, and nyctiphruretians. Therefore, these traits—the foramen jugular anterius almost as large as the foramen magnum, the quadrate flange of pterygoid extending only half the distance to the quadrate condyle, the absence of the medial process of jugal (Fig. 3, C and D), and the supratemporal that forms most of the posterior margin of the skull roof—should be reinterpreted as primitive for chelonians, being retained in *Proganochelys* but lost in all other turtles. Similarly, the robust metacarpals and metatarsals characteristic of *Proganochelys* are also found in pareiasaurs (Fig. 4), *Sclerosaurus*, and some procolophonoids and are probably primitive for chelonians rather than autapomorphic. Furthermore, many other apparent autapomorphies of *Proganochelys* (*1*)—for example, frontals excluded from the orbital margin, bosses above orbits and nares (*23*), the thick braincase floor, the "pleurosphenoid" ossification, a prootic foramen enclosed by bone, the anterodorsally directed dorsum sellae, the loss of the prootic-opisthotic suture, and the dorsal lump at the apex of the retroarticular process (*23*)—are also present in pareiasaurs (Figs. 2B and 3, A and B) but not in more distant out-groups (*Sclerosaurus*, procolophonoids, and nyctiphruretids). These traits either evolved convergently in pareiasaurs and *Proganochelys* or arose once at the base of the pareiasaur-turtle clade, persisting in pareiasaurs and *Proganochelys* but being lost. The latter hypothesis implies that these apparent specializations of *Proganochelys* are primitive for turtles, putting it even closer to the main line of chelonian evolution. Although *Proganochelys* does exhibit a few unequivocal autapomorphies, notably the tail club and the hypoischia (*1*), it resembles the expected ancestor of all later chelonians more closely than previously thought.

The phylogenetic arrangement proposed here sheds light on the homologies of the chelonian carapace. In pareiasaurs, the dorsum, flanks, and sometimes the belly were covered in longitudinal rows of bony plates (*24*). No other primitive reptile has such extensive dermal armor; among reptiliomorph amphibians this condition is approached only in the seymouriamorph *Kotlassia*. Because dermal armor has evolved independently so many times in reptiles (*8*), its occurrence in pareiasaurs and turtles is not by itself conclusive evidence of a relationship. However, because many other features suggest that pareiasaurs and turtles form a clade and because both groups have heavy dermal armor, the most reasonable assumption is that the dermal ossifications in these animals are homologous. The precursors of the chelonian carapace and plastron can now be seen in the osteoderms of pareiasaurs. These osteoderms are often suturally united. There is a longstanding debate (*25*) over whether the neural and costal elements of the chelonian carapace arose through the expansion of the neural arches and ribs (*26*) or through the fusion of unmodified neural arches and ribs with dermal ossifications (*27*). The intimate association of the dermal plates with the vertebrae and ribs in all pareiasaurs (*24*, *28*) supports the second hypothesis. A similar process has been demonstrated to have occurred elsewhere in the body of some pareiasaurs: the superficial supernumerary bone between the interparietal and the supratemporal in *Elginia mirabilis* (*29*) and *Nanopareia luckhoffi* (*30*) almost certainly represents an osteoderm that has been incorporated into the skull.

The scapulocoracoid in turtles lies under the carapace, within the rib cage. How this unusual arrangement arose remains unclear, and numerous evolutionary scenarios have been proposed to explain it (*2*, *31*, *32*). Watson (*32*) suggested that a broad, flat carapace composed of laterally flaring ribs and heavy dermal armor first evolved behind the scapulocoracoid (*33*), which then migrated posteriorly. This hypothesis, which is not widely accepted (*32, 34*), is supported by the results of this study. The long ribs of pareiasaurs project laterally from the vertebral column and are only slightly curved. Most pareiasaurs are preserved with their dorsal sides up, indicating that this was the preferred orientation of the carcass, and the rib cage is usually undisturbed despite dorsoventral compression (*35*) (Fig. 2). These morphological and taphonomic features suggest that the bodies of pareiasaurs were broader and flatter than previously thought. However, the shoulder girdle is much more narrow than the rib cage because the clavicles and coracoids do not form wide ventral plates (*36*). Therefore, it appears that pareiasaurs had almost the exact morphology predicted by Watson for "*Archichelone*" (*32*)—a narrow shoulder girdle anterior to a wide, flat carapace.

Vertebral counts also support Watson's hypothesis. Most basal amniotes, including nyctiphruretians and procolophonoids, have approximately five cervical and 20 dorsal vertebrae (*37*). The *Sclerosaurus* genus and pareiasaurs possess five cervicals and 14 or 15 dorsals, whereas all turtles possess eight cervicals and 10 dorsals. The most parsimonious evolutionary scenario is that five or six dorsals were lost in the lineage leading to *Sclerosaurus*, pareiasaurs, and turtles (resulting in the arrangement found in *Sclerosaurus* and pareiasaurs). This hypothesis also holds that in the lineage leading to turtles, a further modification increased the number of cervicals and reduced the number of dorsals. These changes suggest that the shoulder girdle in chelonians has shifted posteriorly approximately three vertebrae, which would mean that cervicals six to eight in chelonians are modified dorsals. The major line of neck flexion in both pleurodiran and cryptodiran turtles is between cervicals five and six (perhaps the old cervical-dorsal boundary); cervicals six, seven, and eight usually work as a single rigid unit (*38*). In pareiasaurs, the transverse processes on the five cervical centra are ventral; on the first three dorsals they gradually assume a more dorsal position. In the earliest turtle, *Proganochelys* (*4*), this change occurs at cervicals six, seven, and eight. The dorsal tip of the scapula lies adjacent to cervical seven in *Proganochelys* but behind cervical eight in later turtles (*1*). This change might represent the final stages in the posterior migration of the scapulocoracoid. Furthermore, the scapulocoracoid in turtles undergoes an ontogenetic migration that recapitulates the phylogenetic changes suggested above: The somitic tissue destined to develop into the scapulocoracoid originates in the posterior cervical region and migrates posteriorly during early embryogenesis (*2*). However, it is not clear if this condition is unusual for reptiles (*2*). A similar phylogenetic shift has occurred in the pelvic girdle. In *Proganochelys* (*1*) and most other turtles, the dorsal end of the ilium lies behind the tenth dorsal (thoracic) rib. In certain pleurodires, however, the pelvic girdle comes to lie within the rib cage by migrating forward to contact the last two dorsal vertebrae, whose ribs develop thickened "sacral" contacts, and the two original sacral vertebrae become incorporated into the caudal series (*8, 10, 39*). The evidence for Watson's scenario is inconclusive, but it remains the only plausible hypothesis proposed to date.

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