THE COMPARATIVE OSTEOLOGY OF THE TRIASSIC TURTLE *PROGANOCHELYS*

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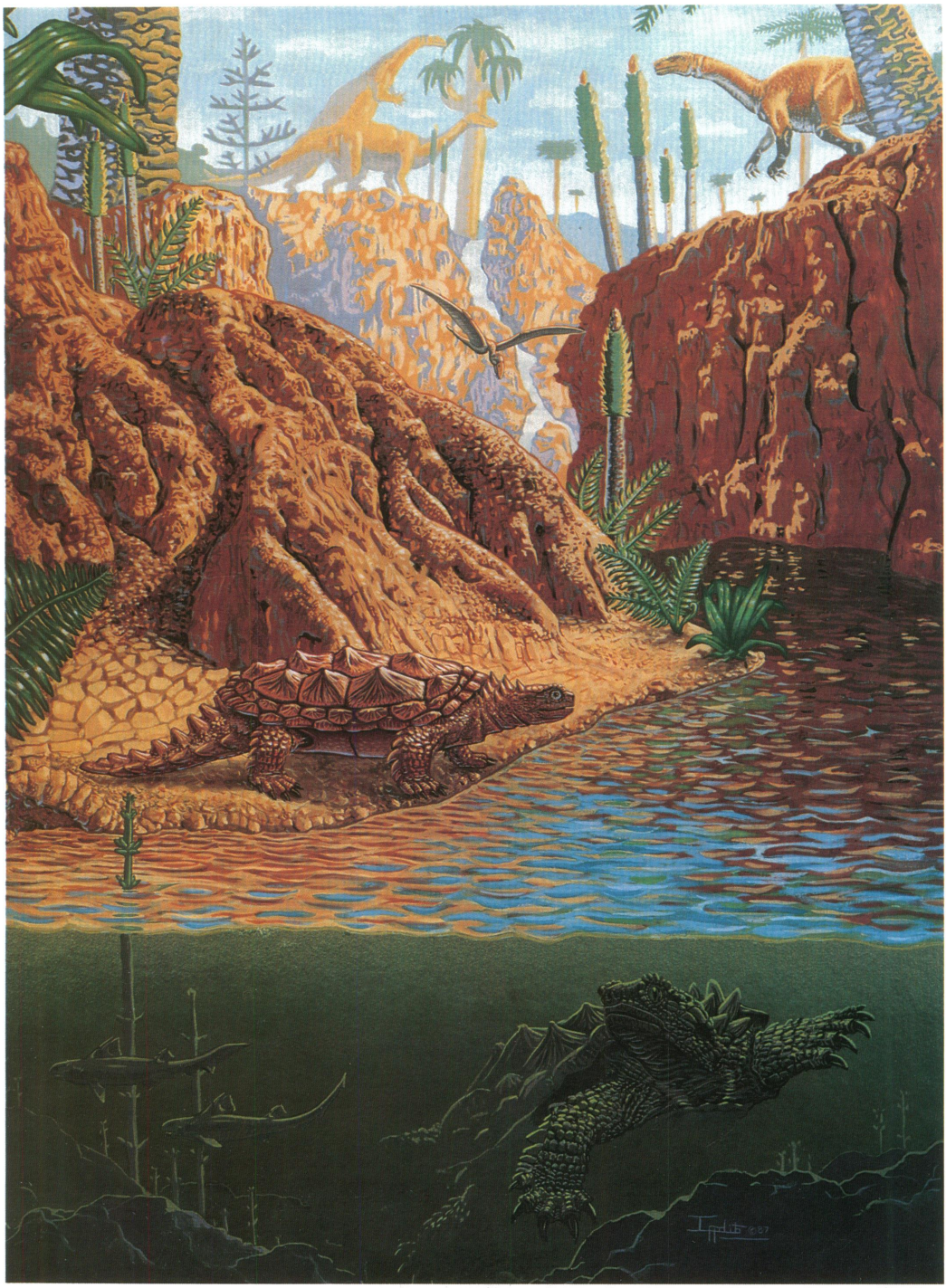

Fig. 1. Restored environment of *Proganochelys* during the Late Triassic in West Germany. This scene is based on fossils and taphonomic studies of the Trossingen *Plateosaurus* quarry. The deposition site is thought to have been formed by mud flows on the edge of a lake. Besides the turtle, *Proganochelys* (center), and the prosauropod dinosaur, *Plateosaurus* (rear), small hybodont sharks (lower left) found associated with *Proganochelys* and *Plateosaurus* at Halberstadt are shown.

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ABSTRACT

Proganochelys quenstedti Baur (= *Triassochelys dux* Jaekel, *Stegochelys dux* Jaekel) from the Late Triassic Norian of Germany is the oldest well-preserved turtle. This paper describes the complete osteology of *Proganochelys* for the first time. The skull, shell, cervical vertebrae, caudal vertebrae, girdles, and limbs of *Proganochelys* are compared with primitive amniotes exemplified by *Captorhinus,* and with more advanced turtles, the pleurodires and cryptodires. The descriptions of *Proganochelys* are based on seven specimens, including three skull-shell associations. One of these specimens is an almost complete skeleton of what is hypothesized to be a young adult. Another skeleton is interpreted as a younger juvenile, while the remainder are interpreted as older adults.

Proganochelys has the following chelonian synapomorphies: (1) Bony shell consisting of a carapace formed from costal bones with fused ribs, neural bones with fused thoracic vertebrae, and marginal bones; a plastron formed from interclavicle, clavicle, and five paired bones sutured together; carapace and plastron enclosing shoulder girdle and pelvic girdle. (2) Quadrate concave posteriorly and exposed laterally on cheek. (3) Postparietals and postfrontals absent. (4) Lacrimal bone small. (5) Maxilla, premaxilla, and dentary edentulous. (6) Stapes solid, rodlike, without foramen or processes.

Proganochelys is hypothesized as the sister group to all other turtles. It retains the following primitive amniote characters absent in other turtles. (1) Supratemporal bone. (2) Lacrimal bone and duct. (3) Moveable basipterygoid articulation. (4) Middle ear without bony lateral wall. (5) Vomer paired. (6) Paroccipital process of opisthotic attached to braincase only at its distal end.

Proganochelys has the following characters that are interpreted as autapomorphies. (1) Ventral tubercle on basioccipital. (2) Tail club. (3) Phalangeal formula (manus and pes) of 2-2-2-2-2.

Interpretations of the depositional environment of *Proganochelys* combined with features of the limb morphology suggest that *Proganochelys* occupied fresh water as a bottom walker but was not exclusively aquatic or terrestrial.

INTRODUCTION

Turtles are sometimes considered to be "living fossils," i.e., structurally conservative throughout their history. Although turtles do appear superficially similar because they have a shell, fundamental changes in many organ systems have taken place during their history. *Proganochelys,* the oldest turtle known from complete skeletons, has a typical chelonian shell but is more generalized in the other parts of the skeleton. *Proganochelys* thus provides an unusual opportunity to make extensive comparisons among turtles and generalized amniotes. The purpose of this paper is to fulfill this opportunity and to present a comparative osteology of generalized amniotes, *Proganochelys,* and more advanced turtles.

This paper is organized so that the descriptive material in general follows the order of treatment in Romer's (1956) *Osteology of the Reptiles.* The skull section follows the order of treatment in Gaffney (1979a), which should also be seen for terminology. I have tried to describe the material available of *Proganochelys* and then to compare it with the generalized amniote condition, usually as seen in captorhinids on the one hand, and then with more advanced turtles, pleurodires and cryptodires on the other hand. Comparisons with pleurodires and cryptodires rely on previously described cladograms (Gaffney and Meylan, 1988) with particular attention to the Early Jurassic cryptodire *Kayentachelys* (Gaffney et al., 1987). In order to provide a summary and outline of the descriptive and comparative features used, a series of tables is included for each of the morphologic regions.

The determination of the closest outgroup of turtles is based on Gaffney and McKenna (1979) and Gaffney and Meylan (1988) and their hypothesis that captorhinids are the sister group of turtles. However, even if this hypothesis is incorrect, comparisons with captorhinids are not in vain. Although there are certainly autapomorphies in *Captorhinus* and its close relatives, a great deal of its morphology is primitive at the level of Amniota. More important, however, captorhinids are the best preserved and best described of all the possible candidates for "most generalized amniote." I have relied on literature descriptions of captorhinids, but I have also reexamined much of the original material. A restudy by Ms. Meeker and myself of the specimens described by Heaton (1979) as *Eocaptorhinus laticeps* has resulted in modifications to his restorations of the skull. Nearly all the drawings of captorhinid osteology have been checked and/or modified by examination of specimens.

Heaton (1979) adopted a stratophenetic view of the Captorhinidae: "The sequence of *Romeria–Protocaptorhinus–Eocaptorhinus–Captorhinus* is interpreted as a single continuous phylogenetic lineage . . ." (p. 81). A general criticism of this methodology is developed in Gaffney and McKenna (1979). The problem is distinguishing *Eocaptorhinus* and *Captorhinus.* The only relatively consistent morphologic distinction between the two genera is the presence in *Eocaptorhinus* of a single row of teeth in the marginal dentition and in *Captorhinus* of two or three rows of marginal teeth. Bolt and DeMar (1975) have shown that at one locality, specimens identifiable as *Captorhinus* are known that have a single row of teeth on one side and a double row on the other side. Gaffney and McKenna (1979) accepted the use of *Eocaptorhinus* but in this paper I have synonymized *Eocaptorhinus laticeps* with *Captorhinus aguti.* The specimens ascribed to *Eocaptorhinus* by Heaton appear to be morphologically indistinguishable from *Captorhinus* except in the tooth row number, and for the purposes of comparisons with turtles are best considered one taxon. Nonetheless, the sources for the specific morphologic features are usually particular specimens and these are referred to in the text.

ACKNOWLEDGMENTS

The long-term usefulness of this paper relies on the quality and accuracy of the figures. I have been very fortunate in having three collaborators whose skills and dedication as scientific illustrators have produced figures that will stand among the best. These artists, Lorraine Meeker, Frank Ippolito, and Ches-

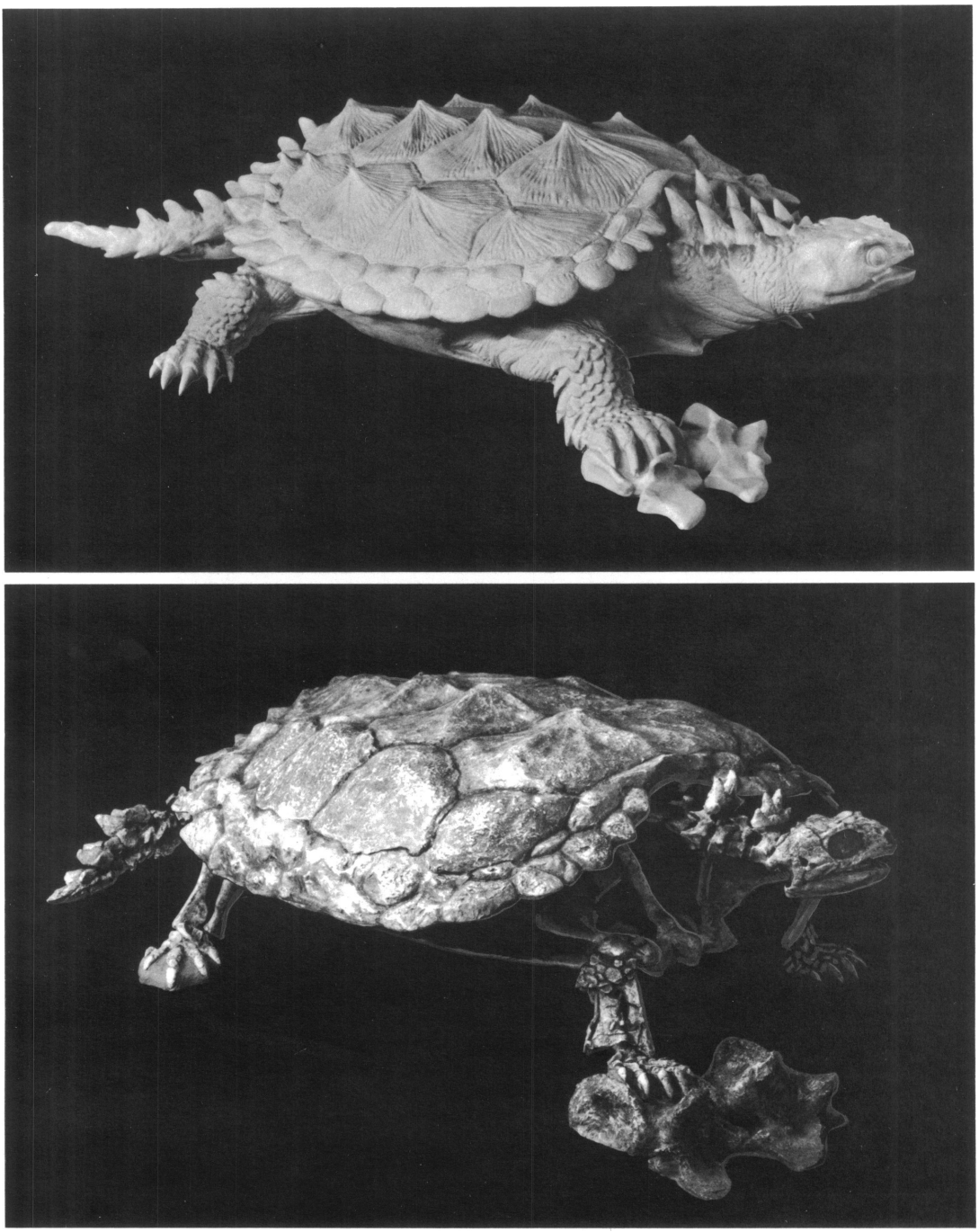

Fig. 2. *Proganochelys quenstedti,* anterolateral views. Upper, life restoration; lower, cast of articulated skeleton, SMNS 16980. Restoration made ½ size by David Dann. Right forelimb resting on *Plateosaurus* vertebrae, based on the Trossingen quarry association.

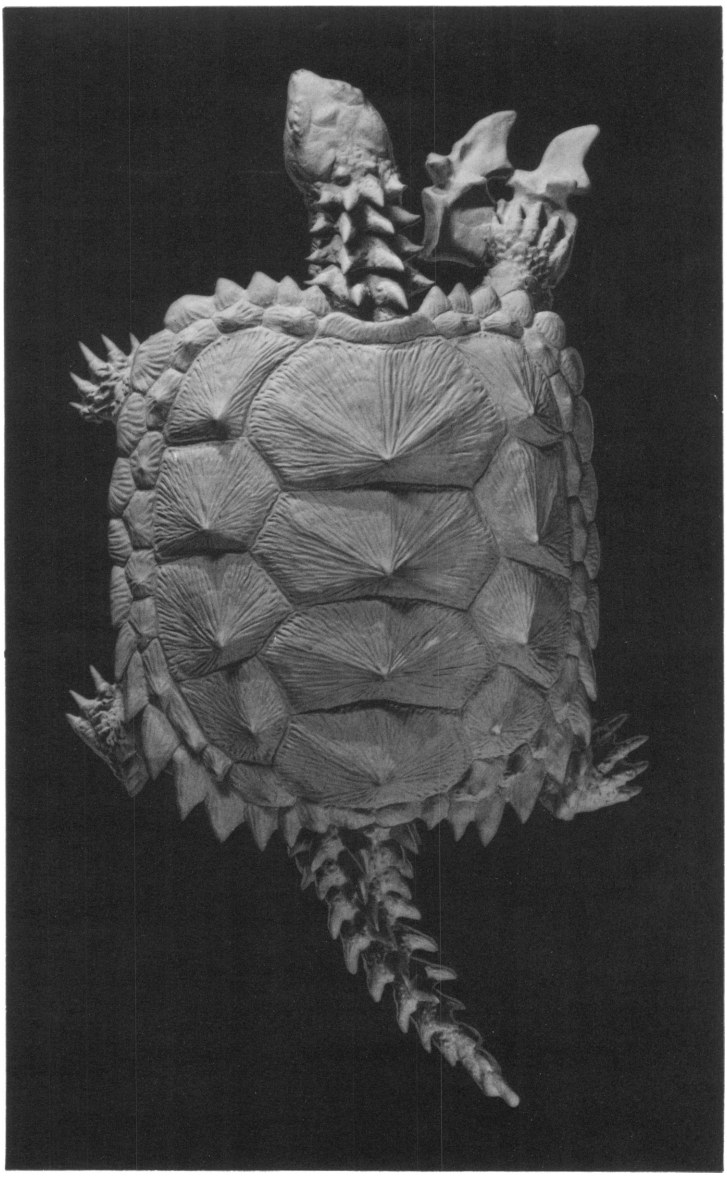

Fig. 3. *Proganochelys quenstedti.* Dorsal view of life restoration made at ½ natural size.

ter Tarka, contributed equally to the figures illustrating this paper. Ms. Meeker and Mr. Tarka traveled to Stuttgart to prepare and draw the shells and other postcrania that could not be taken to the American Museum.

The opportunity to study the Triassic turtles in Stuttgart was possible because of the encouragement and support of Dr. Rupert Wild, Curator, and Professor Dr. Bernhard Ziegler, Director, Staatliches Museum für Naturkunde in Stuttgart. Dr. Wild spent a great deal of time and effort helping me and my colleagues and I am very grateful for his support and hospitality. He found crucial notes and photographs from the Trossingen excavation and took me to the *Proganochelys* localities in southern Germany. I thank Dr. Wild and the SMNS for allowing me to use these photographs here. Dr. Karl-Heinz Fischer and Dr. Hermann Jaeger, Museum

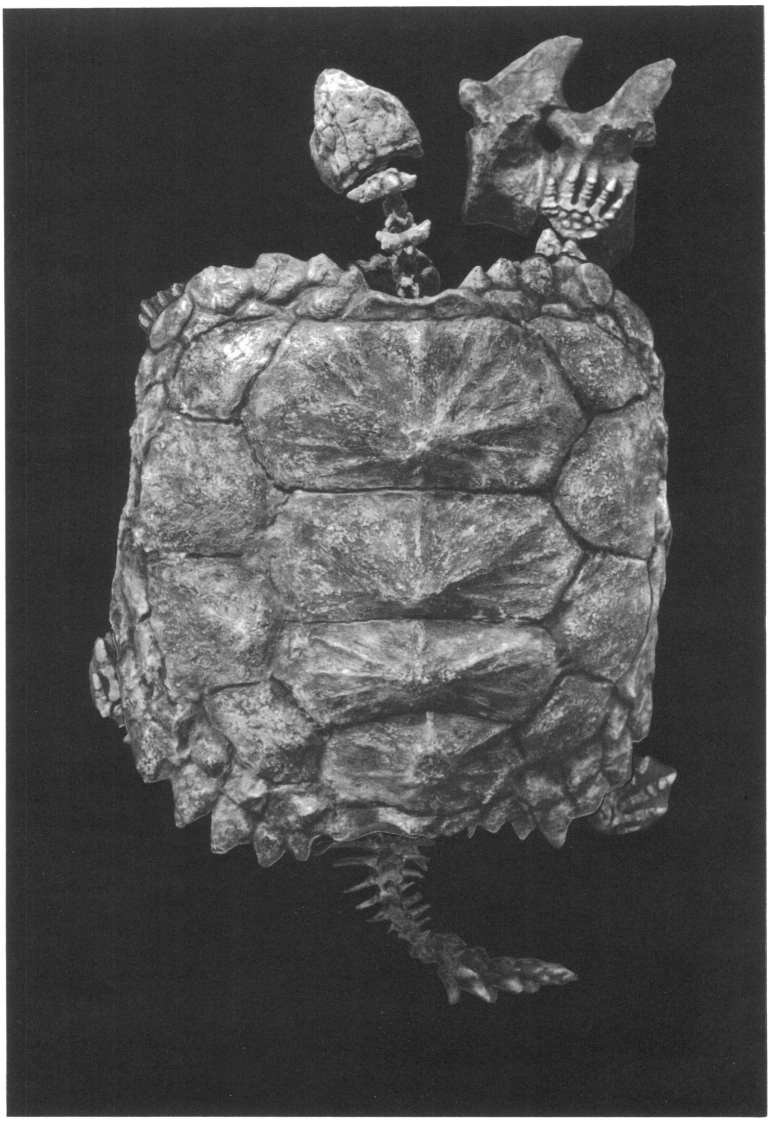

Fig. 4. *Proganochelys quenstedti.* Dorsal view of mounted skeleton. Cast of SMNS 16980.

für Naturkunde, Berlin, very kindly made available to us the Jaekel specimens in their care. Professor Frank Westphal and Dr. Wolfgang Reif, Tübingen Universität, helped with the type of *Proganochelys quenstedti.*

The extremely difficult preparation of the skull of SMNS 16980, in which the endocranium and middle ear were cleared of matrix, was the work of Otto Simonis, formerly of the AMNH. In addition to Mr. Simonis, Ann Burke, Jeanne Kelly, Frank Ippolito, Lorraine Meeker, and Chester Tarka all worked on preparation of the *Proganochelys* material. The casting of SMNS 16980 was done by Jeanne Kelly, Jane Shumsky, and Frank Ippolito, assisted by M. Brandmark and B. Sternberg. The reconstructed model of *Proganochelys* was the work of David Dann.

This project benefited greatly from the support of NSF grant DEB 8002885 for the initial travel, preparation, and illustration sup-

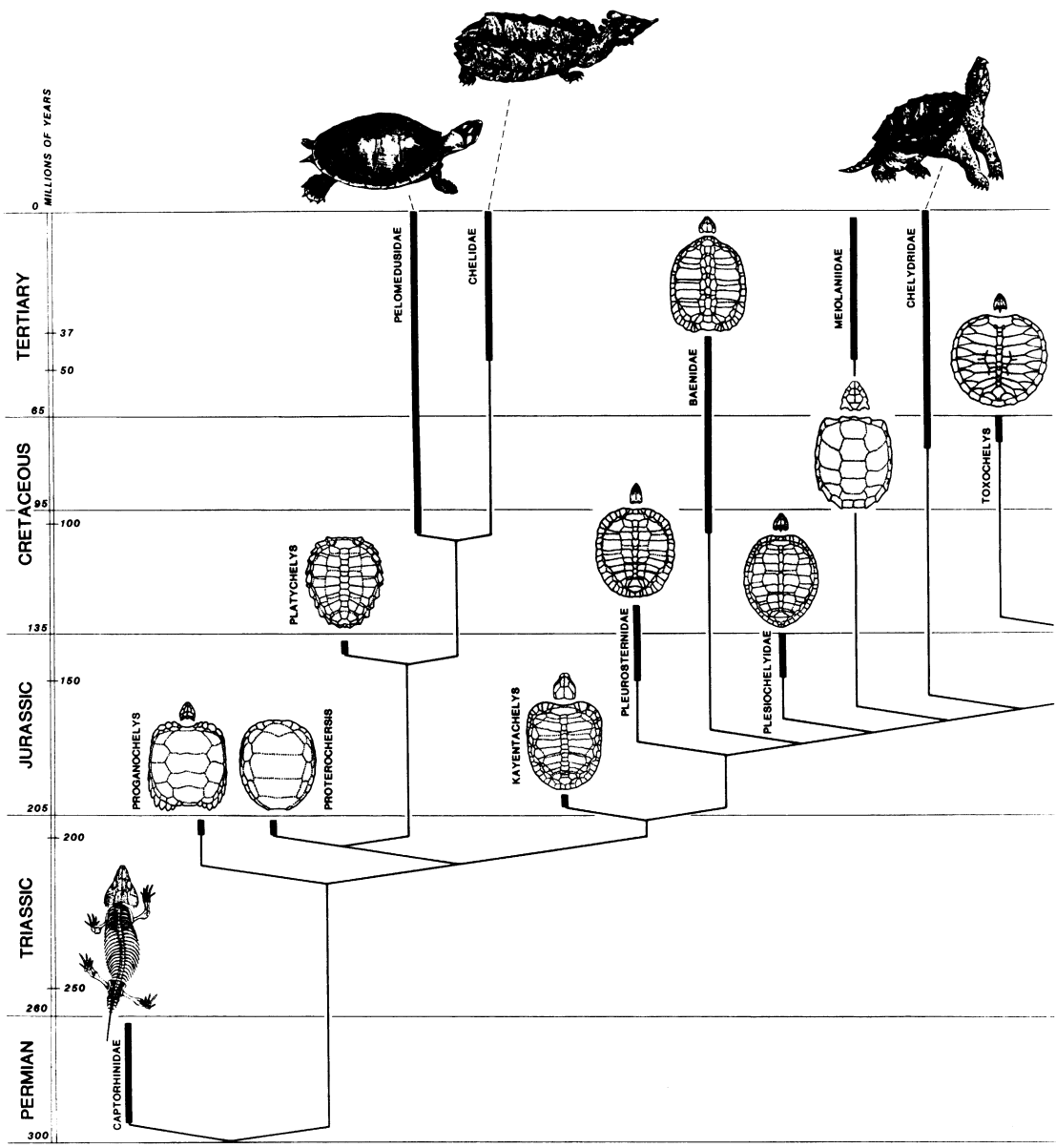

Fig. 5. The relationships of the main groups of turtles placed in a stratigraphic perspective. This is based on a cladogram described in detail in Gaffney and Meylan (1988). Ranges are shown by thick lines. Recent groups are represented by drawings of living turtles while extinct taxa are represented by skeletons.

port, and BSR 8314816 for the extensive comparative work on turtle postcranial anatomy and primitive turtles, particularly *Kayentachelys.*

Barbara Werscheck significantly aided me in manuscript and bibliographic work, and carried some of the *Proganochelys* specimens from SMNS to AMNH. The project would

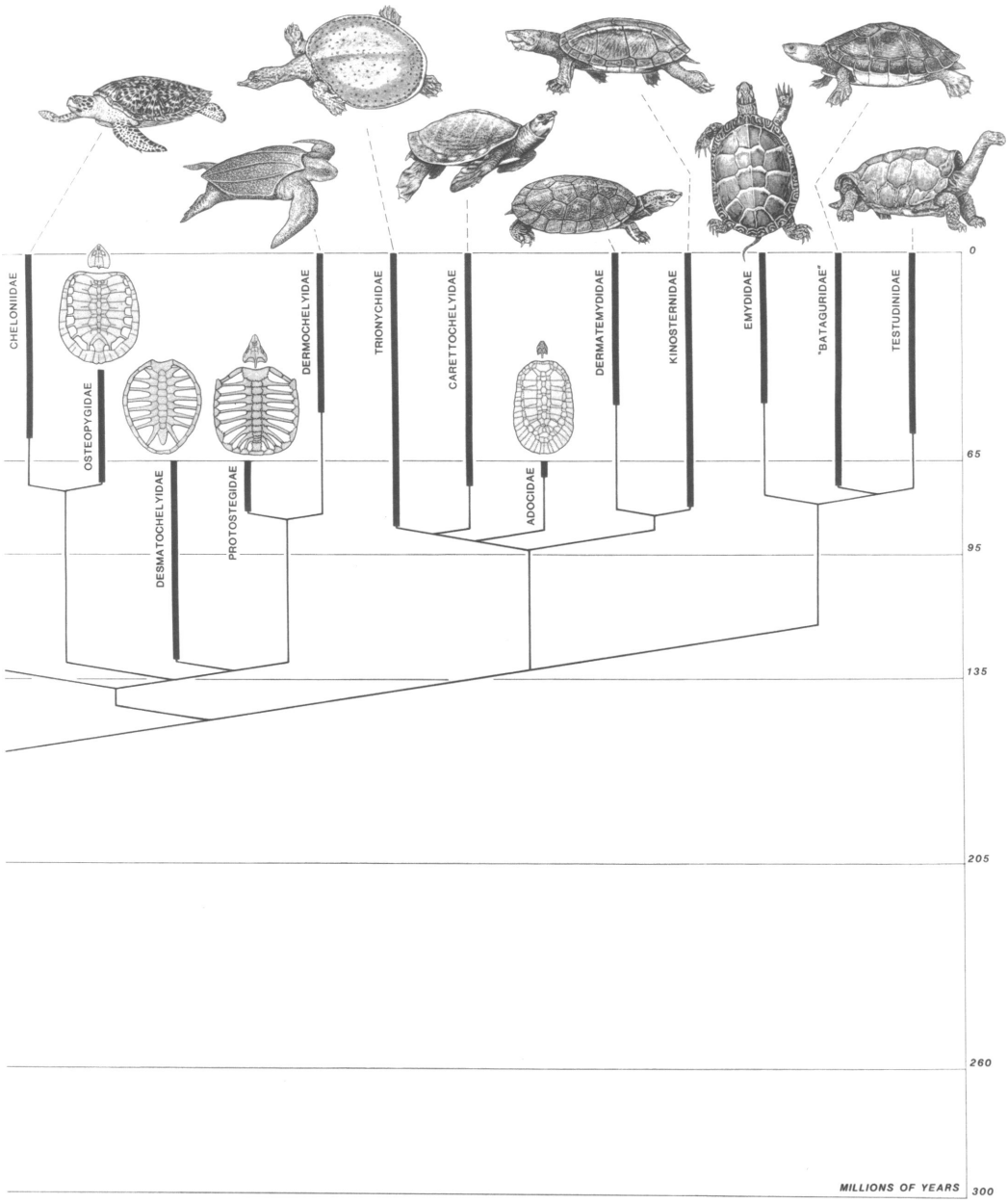

Fig. 5. Continued.

not have been completed without her help and encouragement.

Reviewing a manuscript of this size is an onerous task and I am fortunate to have colleagues that would do it. I am very grateful to Sam McDowell, Peter Meylan, Ann Burke, and Rob Voss for improving the paper.

Abbreviations

AMNH	American Museum of Natural History
DDR	German Democratic Republic (East Germany)
FRG	Federal Republic of Germany (West Germany)
MB	Museum fur Naturkunde, Berlin, DDR

SMNS Staatliches Museum für Naturkunde, Stuttgart, FRG

Anatomical

(for skull figures only; see captions for all other abbreviations)

ang	angular
art	articular
bo	basioccipital
bs	basisphenoid
cor	coronoid
den	dentary
epi	epipterygoid
ex	exoccipital
fr	frontal
ju	jugal
mx	maxilla
na	nasal
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pra	prearticular
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sp	splenial
sq	squamosal
sur	surangular
vo	vomer

PREVIOUS WORK

The first mention of a specimen identifiable as *Proganochelys* was a reference by Cope (1884: 114) to a Triassic turtle from Württemberg in the hands of the German paleontologist, Quenstedt. In 1887, Baur named a new taxon on the basis of this specimen in a footnote to an article on ichthyosaur limbs. The footnote is repeated here (in translation):

> The darkness that surrounds the origin of the turtles yet intensifies when one realizes that the oldest known turtle (at this time), from the Stubensandstein of the Keuper, has a completely closed carapace and plastron; and might possibly belong to the "Pleurodira" since the pelvis seems to be fused with the carapace and plastron. This just mentioned turtle is in the Mineralogy Museum in Tübingen and was found by Mr. Tscherning. Cope mentions it in his important work: The Vertebrata of the Tertiary Formation of the West, Book I, 1883, p. 114 in the following way: "The older (Testudinata) makes its appearance in the Triassic period, for I am assured by Dr. F. Endlich of Eading, Pa. that the species obtained by Professor Quenstedt in Württemberg, belongs undoubtedly to the Testudinata." I will discuss this fossil in more detail in another paper. However, briefly: No bones were preserved, all the animal left behind were the internal mold of the shell and pelvic bones. Eight costals can be identified, the plastron was completely closed; however, the individual elements cannot be separated. We cannot tell whether or not it had a mesoplastron. However, there is no doubt that plastron and carapace were fused laterally without a fontanelle. The measurements are as follows: Longest length: 570 mm, widest width: 566 mm, highest height: 354 mm.
>
> I have to thank Prof. Quenstedt in Tübingen for the data and analyses of this interesting fossil. *Chelytherium,* H. v. Meyer (Palaeontolographica, vol. XIV, 1865) from the same horizon might be generically the same as the Tübingen example. Until we have further finds, I would like to call the Tübingen specimen—genus: *Proganochelys,* species: *quenstedtii.*

This specimen, an uncataloged steinkern in the paleontological museum at the University of Tübingen (fig. 104), is the type of *Proganochelys quenstedti.* Zakrszewski, also in 1888, referred to this specimen and substantiated its chelonian nature and its age. He indicated the locality as "Schönbuch" near Hafner-Neuhausen (now Neuenhausen). In 1889, Quenstedt finally described and figured the specimen, naming it *Psammochelys keuperina,* a synonym of Baur's *Proganochelys quenstedti.* The poor nature of the steinkern prevented further work on *Proganochelys* but another discovery in Aixheim-Neuhaus in 1897 of a shell (SMNS 10012) retaining much of the bone of the carapace, allowed Fraas (1899) to restore the shell of *Proganochelys.* Unfortunately, sutures are not readily visible on this specimen and Fraas's reconstruction (1899: fig. 1) has many serious errors. Nonetheless, he figured and described the new shell and also published new figures of the Tübingen specimen. (Hennig, 1923: fig. 56, also has a photograph of the Tübingen specimen.) Ballerstedt (1921) reexamined the material described by Fraas and Quenstedt and came up with a new reconstruction of the new plastron. A description of this specimen with new figures is provided below.

Although the 19th century work on *Proganochelys* (and also *Proterochersis*) showed the presence in the Triassic of turtles, the material was not sufficiently well preserved to develop convincing ideas about relation-

ships of these specimens to other turtles and to amniotes in general. The discovery of a better preserved Triassic turtle specimen in the pre-Harz mountains during excavations for *Plateosaurus* skeletons in 1909–11 provided new information on the skull, neck, and limb girdles of *Proganochelys.* The locality, fauna, and first description of this turtle was published by Jaekel (1914) with a more intensive description following (1918a). Jaekel (1914) first named the turtle *Stegochelys dux* but when he became aware that *Stegochelys* was preoccupied (by *Stegochelys* Lydekker, 1889) he renamed it *Triassochelys dux* (Jaekel, 1918b). Nonetheless, as discussed below and in Gaffney (1985a), I have concluded that this name is a junior synonym of *Proganochelys quenstedti.* Jaekel's description and figures of *Triassochelys,* however, have been very influential. His figures of the carapace have proven to be roughly accurate but the skull of his specimen was laterally crushed, causing very misleading interpretations.

In 1927 another Aixheim-Neuhaus *Proganochelys* came to light (SMNS 15759), a partial shell with some limb and vertebral elements, and, most importantly, a skull. Although this specimen has never been described, figures of the skull have appeared casually in Berckhemer (1931: fig. 3; 1951: 36), and Kuhn (1956: fig. 59).

The most important Triassic turtle find to date is a series of three skeletons found in 1932 in Trossingen about 4.5 km southwest of Aixheim-Neuhaus but higher in the section, during *Plateosaurus* excavations. The quarry geology was described by Seemann (1933) and is discussed below. The turtles were placed in the hands of F. Berckhemer in Stuttgart where preparation was undertaken. A note with the figures appeared (Berckhemer, 1938: pl. 4) and Staesche later began a study of the material. However, the only information on these specimens to reach publication was a short discussion accompanied by figures of the skull of SMNS 16980 in Parsons and Williams (1961). These figures and the earlier ones of Jaekel, Fraas, and Quenstedt have been repeated in many review works, sometimes with reinterpretations of dubious significance. These need not be dealt with here; the earlier ones are listed in Kuhn (1941). Two recent papers (Gaffney, 1983; Gaffney and Meeker, 1983) have appeared on the skull of SMNS 16980, and Gaffney (1985a) described much of the shell morphology.

PROGANOCHELYS SPECIMENS USED IN THIS STUDY
(See table 1)

University of Tübingen (uncataloged, fig. 108)

Consists of: Internal mold (steinkern) of shell, showing dorsal epiplastral processes but lacking posterior margins of carapace and anterior and posterior margins of plastron.

Locality: Neuenhaus (formerly Häfner-Neuhausen in the district of Schönbuch); Zakrszewski (1888), Quenstedt (1889), FRG (Federal Republic of Germany).

Horizon: Late Triassic, Keuper, Stubensandstein (Quenstedt, 1889).

Literature: The first reference to this specimen was made by Cope (1884); Baur (1887) named it *Proganochelys quenstedti,* but Quenstedt described it in detail (also naming it *Psammochelys keuperina*). Quenstedt's drawings are somewhat stylized but still useful. Photographs of the specimen appear in Fraas (1899: pl. 8) and Hennig (1923: fig. 56) while Ballerstedt (1921) discussed and restored the plastron.

Comments: The specimen has no bone remaining, it is an internal mold of the shell in a relatively coarse sandstone. See section below.

MB.1910.45.2 (figs. 28, 73)

Consists of: Skull with lower jaws, carapace, plastron lacking most of anterior lobe but with dorsal portions of epiplastral processes ("cleithra"), cervical vertebrae, left scapula, coracoid, and dermal ossicles (a pelvis and right femur head from the same locality but apparently not from the same individual, has the number MB.1910.45.3).

Locality: Baerecke and Limpricht Quarry, Halberstadt, DDR (Jaekel, 1914; Fischer, 1975). Collected in 1910.

Horizon: Late Triassic, Keuper (Jaekel, 1914; Kuhn, 1939; Fischer, 1975).

Literature: The Berlin specimen was de-

TABLE 1
Preserved Material of *Proganochelys*

	SMNS 16980	SMNS 17203	SMNS 17204	SMNS 15759	MB 1910.45.2
Skull	+	–	–	+	+
Lower jaws	+	–	–	+	+
Carapace	+	+	+	+ (part)	+
Plastron	+	+	+	+ (part)	+
Cervical vertebrae	+	–	+ (part)	+ (part)	+
Caudal vertebrae	+	+	+	–	–
Scapula-coracoid	R, L	L	–	–	L
Ilium	R, L	R, L	?	–	*
Pubis	R, L	R, L	R, L	R, L	*
Ischium	R, L	R, L	R, L	R, L	*
Hypoischium	+	+	+	+	–
Humerus	R, L	L	R, L (part)	–	–
Radius	R, L	L	R	?	–
Ulna	R, L	L	R	–	–
Carpus	R, L	?L	–	R (part)	–
Manus	R, L	–	R (part)	R	–
Femur	R, L	R, L	R, L	L (part)	*
Tibia	L, R (part)	R, L	R, L	–	–
Fibula	L, R (part)	R, L	R, L	–	–
Tarsus	R, L (part)	R (part)	R, L	–	–
Pes	R, L	–	R, L	–	–
Neck osteoderms	+	?	–	–	+
Tail osteoderms	–	+	+	–	–

* A pelvis and femur head are preserved as MB 1910.45.3, a different individual.

scribed in detail by Jaekel (1918a). The skull restorations are seriously in error and there are some inconsistencies in the shell restorations but the shell photographs (Jaekel, 1918a: figs. 1, 3, pl. 2) are accurate and useful. Figure 1 in this paper is interesting as it is the only photograph showing the plastron still attached to the carapace. Other figures of the skull may be found in Gaffney (1979a).

Comments: The bone of the Berlin specimen is harder and retains a better surface than the Trossingen specimens, but there are minute fractures, breaking the bone into small trapezoids, that obscure sutures and other fine details. I have been unable to confirm most of Jaekel's (1918a) sutures, in either the shell or the skull. The bridge areas of the carapace are extensively restored with plaster and lateral crushing has distorted the original curvature.

SMNS 10012 (fig. 62)

Consists of: Partial carapace, with internal surface and external surface preserved in separate pieces; partial natural mold of internal surface of plastron; separate piece with natural internal mold of left posterior carapace section.

Locality: Quarry in Aixheim-Neuhaus, FRG. Collected by Haug in 1897 (see also Fraas, 1899).

Horizon: Late Triassic, Keuper, Stubensandstein.

Literature: This specimen was described and figured by Fraas (1899) with futher comments by Ballerstedt (1921). The figures by Fraas (1899: pls. 5 and 6) of the carapace as preserved are accurate and useful but the restoration of the carapace (Fraas, ibid.: fig. 1) has serious errors (discussed below). Unfortunately this figure has been repeated frequently.

Comments: The specimen was found in a quarry by blasting and the carapace was split through the bone. Preparation took place by embedding each section in plaster and removing the matrix. The results are confusing; the internal bone surface of the carapace (fig. 64) is preserved in a thick plaster bed and the

external bone surface of the same carapace (fig. 62) is separated and embedded in its own plaster piece, yet they are part of the same carapace.

SMNS 15759 (= SMNS 15782 and 15783, fig. 66)

Consists of: Laterally crushed skull and lower jaws; right half of carapace lacking lateral and posterior margins; plastron fragments including right epiplastron; right manus with dermal armor; fragment of left forearm armor with distal end of radius, distal end of left femur; ventral plate of pelvis with paired hypoischia attached; fragment of medial section of carapace with two thoracic centra; three articulated cervicals; dermal armor with four articulated tubercles; and various fragments.

Locality: Quarry at an old mill consisting of two buildings, Aixheim-Neuhaus, FRG. Skull found a few centimeters above shell (from label written by Berckhemer). This site was relocated in 1983 by Wild and Gaffney (fig. 7). Collected by Hugger, 1927.

Horizon: Late Triassic, Keuper, Stubensandstein.

Literature: The skull has been casually figured (by Berckhemer, 1951: fig. 36; Kuhn, 1956: fig. 59) but never described.

Comments: Photographs, taken before World War II (fig. 67) indicate that a plastron and more of the carapace was originally present but these were destroyed during the war (R. Wild, personal commun.). The preservation of the specimen is good but all elements have been distorted by crushing to some extent.

SMNS 16980 (figs. 2, 4)

Consists of: A nearly complete skeleton, with skull, jaws, carapace, plastron, cervicals (lacking 6 and 7), caudals, tail club, fore- and hindlimbs (lacking part of right tibia and fibula), both shoulder girdles, pelvis, hypoischia, and numerous dermal osteoderms.

Locality: *Plateosaurus* quarry in Trossingen, FRG (figs. 8–12). Collected by R. Seemann in 1932 (see below for more data).

Horizon: Late Triassic, Keuper. Originally described as Knollenmergel but now thought to be upper Stubensandstein (see discussion below).

Literature: An important figure showing the anterior half of the specimen, articulated but lacking the shell, was published in Berckhemer (1938: pl. 4, shell also figured). The skull has appeared in Parsons and Williams (1961) and Gaffney (1979a) but the best study to date is in Gaffney and Meeker (1983) and Gaffney (1983).

Comments: SMNS 16980 is the best preserved and most complete skeleton of a Triassic turtle known to date. The shell is more complete than any other *Proganochelys* shell and seems to be the least distorted.

SMNS 17203 (fig. 100)

Consists of: Carapace and plastron, both lacking right anterior quadrant; right humerus, radius, and ulna; right and left femur, tibia and fibula; right tarsus, hypoischium, pelvis, left scapula, caudal vertebrae and tail club.

Locality and Horizon: Same as SMNS 16980

Literature: None.

Comments: SMNS 17203 is the smallest of the available specimens and provides nearly all of the information on sutures in the carapace and much of the data on plastral sutures. The entire specimen is crushed dorsoventrally with parts of the left shoulder girdle protruding through the carapace.

SMNS 17204 (figs. 85, 87)

Consists of: Carapace and plastron with nearly complete right forelimb, both hindlimbs, pelvis, cervicals 6 and 7, caudal vertebrae, and tail club.

Locality and Horizon: Same as SMNS 16980.

Literature: None.

Comments: SMNS 17204 is the largest of the three Trossingen *Proganochelys* and is about the same size as the Berlin specimen (MB.1910.45.2). The preservation of the specimen is peculiar: the right forelimb, both hindlimbs, and tail are nearly complete and articulated, but the carapace is badly crushed and has a large *Plateosaurus* bone, probably a fibula, within the shell cavity. The plastron is intact but the carapace has been crushed so that the right side is displaced ventrally and lies on the plastron. Most of the dorsal surface of the carapace is poorly preserved and not completely prepared, but the left lat-

Fig. 6. Map of Germany showing *Proganochelys* localities indicated by asterisks (*).

eral and posterior margins are well preserved and useful scute information has been obtained from this region. A plaster block has been attached to the dorsal surface of the carapace to facilitate turning the shell over without damage.

GEOLOGIC AND GEOGRAPHIC DISTRIBUTION OF *PROGANOCHELYS*

There are only three areas where *Proganochelys* specimens have been found: Halberstadt, in the western part of the DDR; near Tübingen in the FRG; and the vicinity of Trossingen in Baden-Württemberg in the FRG. The turtle specimens in these areas are from Late Triassic exposures, in the Keuper, of Norian age. The rocks are a complex series of sandstones, shales, and some limestone concretions. Current consensus indicates that all of the *Proganochelys*-bearing rocks in Germany are between 220 and 205 million years old. Based on the relative positions of the Trossingen specimens near the contact of the Upper Stubensandstein, it is likely that at least those specimens are in the middle of the Norian, around 210 million years old, but this is really just a guess. Correlation between Halberstadt and the Trossingen localities is not dependable enough to determine the relative stratigraphic positions of the specimens from these two regions.

The Halberstadt quarry and its fauna is described in Jaekel (1914, 1918a) and summarized in Fischer (1975). Although Jaekel (1914) prepared a quarry map, I have been unable to determine the position of the turtle in the quarry. In his section of the quarry (Jaekel, 1914: 162–163) the turtle and the

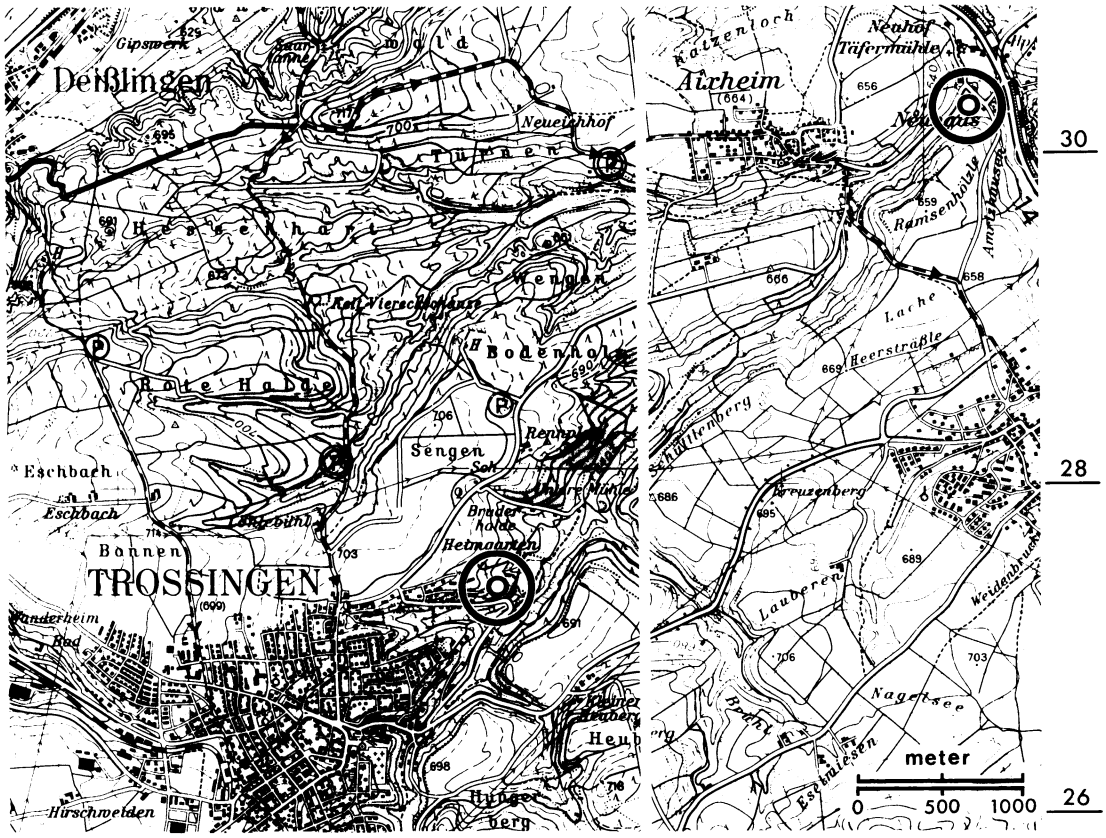

Fig. 7. Map of Trossingen-Aixheim region of southwestern Germany showing *Proganochelys* localities indicated by circles. The Trossingen quarry (lower center) was the source for SMNS 16980, SMNS 17203, and SMNS 17204. Neuhaus (upper right) was the source for SMNS 15759. SMNS 10012 also came from the Neuhaus area but the exact location is not known. The map is from the Landesvermessungsamt Baden-Württemberg topographical series 1:50,000; Spaichingen, L7918 (left half), and Villingen-Schwenningen, L7916 (right half).

plateosaurs were apparently found together in layer 7 ("g"), a greenish gray and red clay. Forty *Plateosaurus* specimens were found in the quarry along with the turtle, phytosaurs, labyrinthodonts, and fishes. The general geologic situation is presumed to be a freshwater deposit near a sea margin. As in southern Germany, the Keuper in this region is characterized by alternating sandstones, clays, and shales that are not easily correlated over long distances by lithologic sequence and composition.

The *Proganochelys* specimens from the Trossingen area are probably from two horizons: a higher level, formerly considered to be in the Knollenmergel but now argued to be correlated with the upper Stubensandstein (Brenner and Villinger, 1981) and a lower level that appears to be in the middle Stubensandstein. SMNS 10012 and SMNS 15759 are also from Aixheim-Neuhaus and are labeled as coming from the "Stubensandstein" but no more precise stratigraphic data has survived. Brenner and Villinger (1981) have a section of the Stubensandstein in "N.E. Aixheim," which must be very close to the Neuhaus localities. This section suggests that there are only outcrops of the middle Stubensandstein in the immediate vicinity of Neuhaus. The two specimens from Aixheim-Neuhaus, SMNS 10012 (collected 1897), and SMNS 15759 (collected 1927), and the Tübingen type (collected before 1884) from Neuenhausen in the Schönbuch, have the

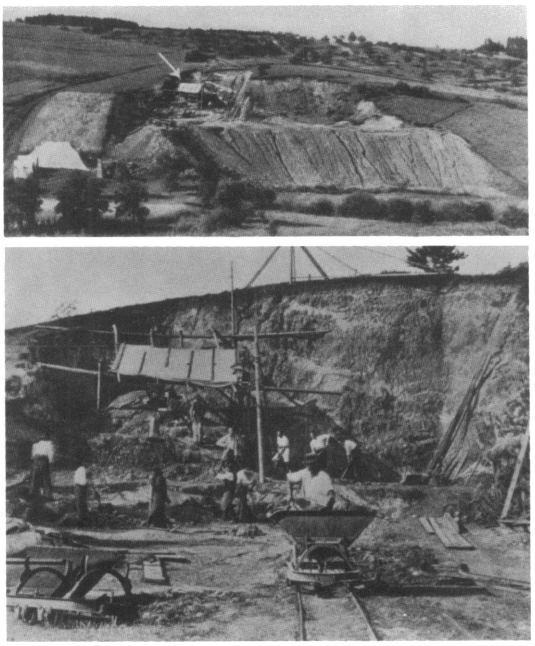

Fig. 8. Trossingen *Plateosaurus* quarry in August 1922 during the excavation by Tübingen University under the direction of F. von Huene. View in upper photo is looking north with the valley of the Trosselbach in the foreground. Lower photo is a close-up of the area indicated by arrow in upper photo. From von Huene (1928).

white bone and clean quartz sand matrix typical of Stubensandstein fossils so there is no reason to doubt that they all came from the Stubensandstein type lithology. The Neuhaus area has yielded a number of vertebrate fossils from the Stubensandstein but the exact position of most is no longer known. In 1983 Rupert Wild of the SMNS took me to Neuhaus where we spoke with an elderly resident who remembered the collecting in 1927 of "crocodiles (= phytosaurs) and turtles" in a small quarry, now an orchard, southwest of the main street and southeast of the Trosselbach (fig. 7). This orchard is presumed to be the source of SMNS 15759.

The type and first discovered specimen of *Proganochelys* is the Tübingen steinkern (fig. 108) from Neuhausen (now Neuenhausen, fide R. Wild, personal commun.) in the Schönbuch district north of Tübingen (Zakrszewski, 1888; Quenstedt, 1889). It is from the Stubensandstein but more precise stratigraphic and locality data is unavailable.

THE TROSSINGEN *PROGANOCHELYS*

The Trossingen quarry was first opened in 1911 by Eberhard Fraas who collected remains of *Plateosaurus* (Fraas, 1913) during two field seasons for the Königliches Naturalienkabinett, Stuttgart (now the Staatliches Museum für Naturkunde, SMNS). A second, more ambitious operation (fig. 8) was run in 1921–1923 by Friedrich von Huene of the Institut und Museum für Geologie und Paläontologie in Tübingen. Von Huene (1923, 1929, 1944) collected the better known but composite *Plateosaurus* specimens now mounted in Tübingen and the American Museum of Natural History.

In 1932 the Württembergische Naturaliensammlung decided to reopen the Trossingen quarry in the last and most extensive excavation (figs. 9, 14). The work was done under the direction of Curator Reinhold Seemann, colleague of Fritz Berckhemer, Chief Curator of the SMNS. Twenty-five unemployed workers were acquired to do the labor of excavating, with lodging provided by the Matthias Hohner firm, a muscial instrument company still prominent in Trossingen. Times were hard in Germany in 1932 and at least part of the rationale in reopening the Trossingen quarry was to provide work for unemployed men in the Freiwilliger Arbeitsdienst using public assistance funds. Seemann ran the quarry operation with the assistance of chief preparator Max Böck, who also did at least the initial preparation of the turtles (fig. 15). The quarry was opened in the early summer of 1932 (Seemann's notebook begins on May 9, 1932) and was worked until October 22, 1932, enlarging the original excavation by nearly 400 percent (D. Weishampel, personal commun.), and collecting more than 50 partial skeletons of *Plateosaurus*.

The *Proganochelys* skeletons were discovered during the last phases of excavation in the lower portion of the quarry. Seemann's surviving photographs and fieldnotes allow a partial reconstruction of the circumstances and positions of the turtles but some questions still remain. The first indication of the turtle discovery is a note on October 1 that

Fig. 9. Trossingen *Plateosaurus* quarry in 1932, taken about halfway through the field season. View is looking north. Photo by R. Seemann.

the broken edge of what appeared to be a turtle shell plate was found in "Felsenmergel" (very hard marl). This was given the field number "Fund 54." On October 5 collection of the turtle was begun. They soon discovered that the skull, shell, and forelimbs were in natural articulation, even though most of the breaks were through the skeleton. A number of photographs (figs. 10–13) were taken during collection and Seemann sketched the position of the specimen. Based on this material, the first turtle discovered "Fund 54" can be identified as SMNS 16980 because it is the only one of the three with a skull. The specimen was lying right side up with the anterior-posterior axis of the shell oriented WSW-ENE (anterior to the west). As in the Berckhemer (1938) photograph (reproduced here as fig. 98), the skull is bent over to the right of the main axis of the shell. Seemann indicated the skull and both forelimbs in his sketch and in the series of photographs. The specimen came out in irregular blocks broken across the bone elements. One of the more interesting of the series of photographs taken on October 5, 1932, shows a section right through the anterior third of SMNS 16980 (fig. 13) with shell and limb bones in situ. The outline of the carapace and plastron can be seen with forelimb and shoulder girdle elements inside.

On October 6, during the collecting of the rest of Fund 54 (SMNS 16980), another specimen "resembling a turtle" was found northwest of Fund 54. This second specimen is shown in Seemann's quarry map, both the published version (figs. 11, 12) and the original working map. In the published map and in his notes he referred to this as "Fund 54a" but on the working version it is "54b" and the original Fund 54 is "54a." This was presumably a lapsus. Unfortunately, in the list of field numbers in Seemann's notebook there is no 54a or 54b and the only reference interpretable as a turtle is Fund 54, which clearly is SMNS 16980, at least in the photographs. It is very likely that the Fund 54a, shown on Seemann's published map as almost lying in contact with Fund 54 but directly due west (in contrast to "northwest"

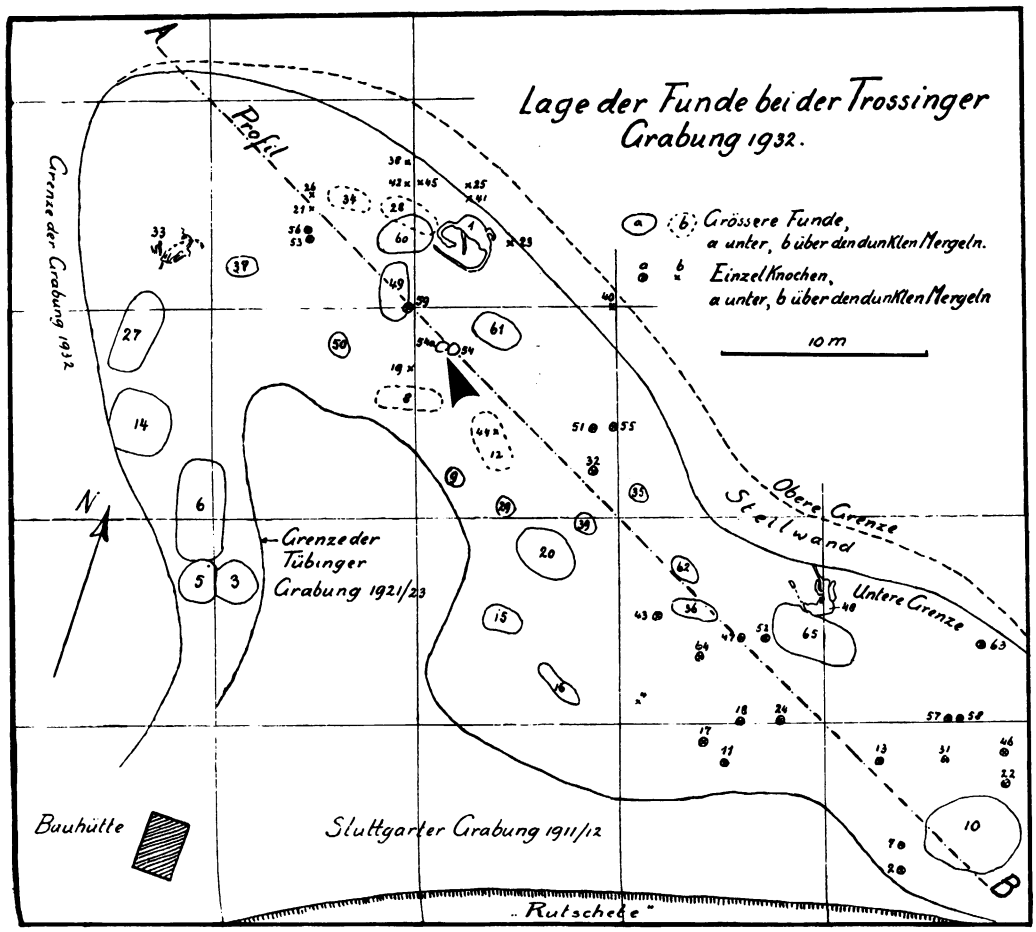

Fig. 10. Map of Trossingen *Plateosaurus* quarry. Triangle points to Funde 54 and 54a, the position of the *Proganochelys* specimens. See text for discussion. From Seemann (1933).

in the notes), is either SMNS 17203 or SMNS 17204. On October 7 there is reference to indeterminable bones just east of, and a little higher than, Fund 54, but they are not described or given a field number. The most likely scenario at present is that Fund 54a (on Seemann's published map) is the larger SMNS 17204 and that the indeterminable bones nearby are SMNS 17203, the juvenile turtle. Oral tradition in the SMNS has it that all three turtle specimens were found very close together (R. Wild, personal commun.), supporting this guess. Nonetheless, it is remarkable that two specimens (SMNS 17203 and SMNS 17204) that were so unique and well preserved rated only casual notice in an otherwise meticulous record of specimen positions and identifications. One possible explanation is that due to the proximity of the three turtles and the irregular breaks in the rock the workers did not realize that more than two specimens were present until they were prepared.

Seemann and his workers had planned to end operations the week following the collection of the turtles, but the collapse of the western quarry face in the vicinity of Fund 48 resulted in the death of one man and injuries to others. They continued work despite the shock of this tragedy but Seemann's notes in this period are not very detailed. During the week of October 17–22 work was done on only three specimens, one of which was Fund 54. Again, it is likely that the workers

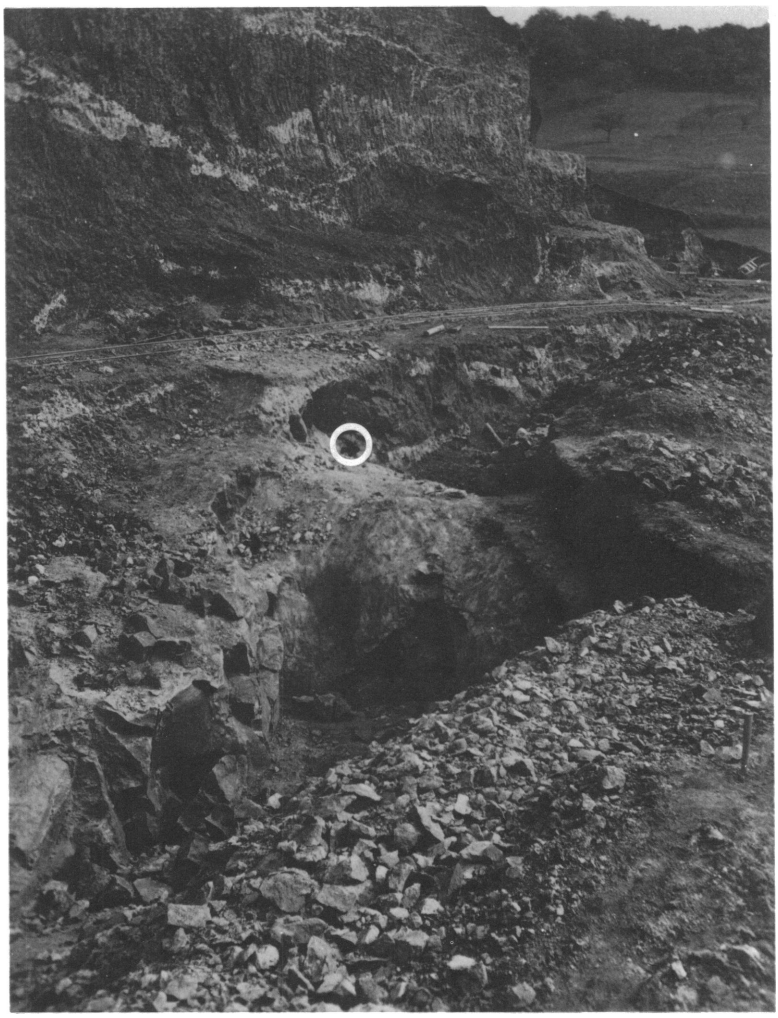

Fig. 11. Photo of Trossingen *Plateosaurus* quarry, September 29, 1932. Circle shows position of Fund 54 (*Proganochelys* specimens) as indicated on original print. Photo by R. Seemann.

were unable to distinguish among the three turtles and this reference probably relates to SMNS 17203 or SMNS 17204, or portions of both, rather than specifically to SMNS 16980.

At this point we might examine the available taphonomic data on *Proganochelys,* as it rests almost entirely on the Trossingen collection and Seemann's work. Von Huene (1928) thought that the plateosaurs traveled in herds around an arid landscape and were trapped by a drying waterhole at Trossingen. Seemann showed that most of von Huene's evidence was mistaken and was not consistent with the sedimentology. Instead, Seemann argued that the Trossingen quarry contained a mud flow that had buried many of the plateosaurs. The quarry section had been divided by von Huene and Seemann into three units (using Seemann's terms for convenience) from bottom to top: Liegende Mergel or lower marl, Dunkel Mergel or dark marl, and Hangende Mergel or upper marl (fig. 12). Most of the better plateosaur specimens and the three turtles were found in the Liegende Mergel. The intermediate Dunkel Mergel is interpreted as the mud flow burying the animals found in the underlying Liegende Mer-

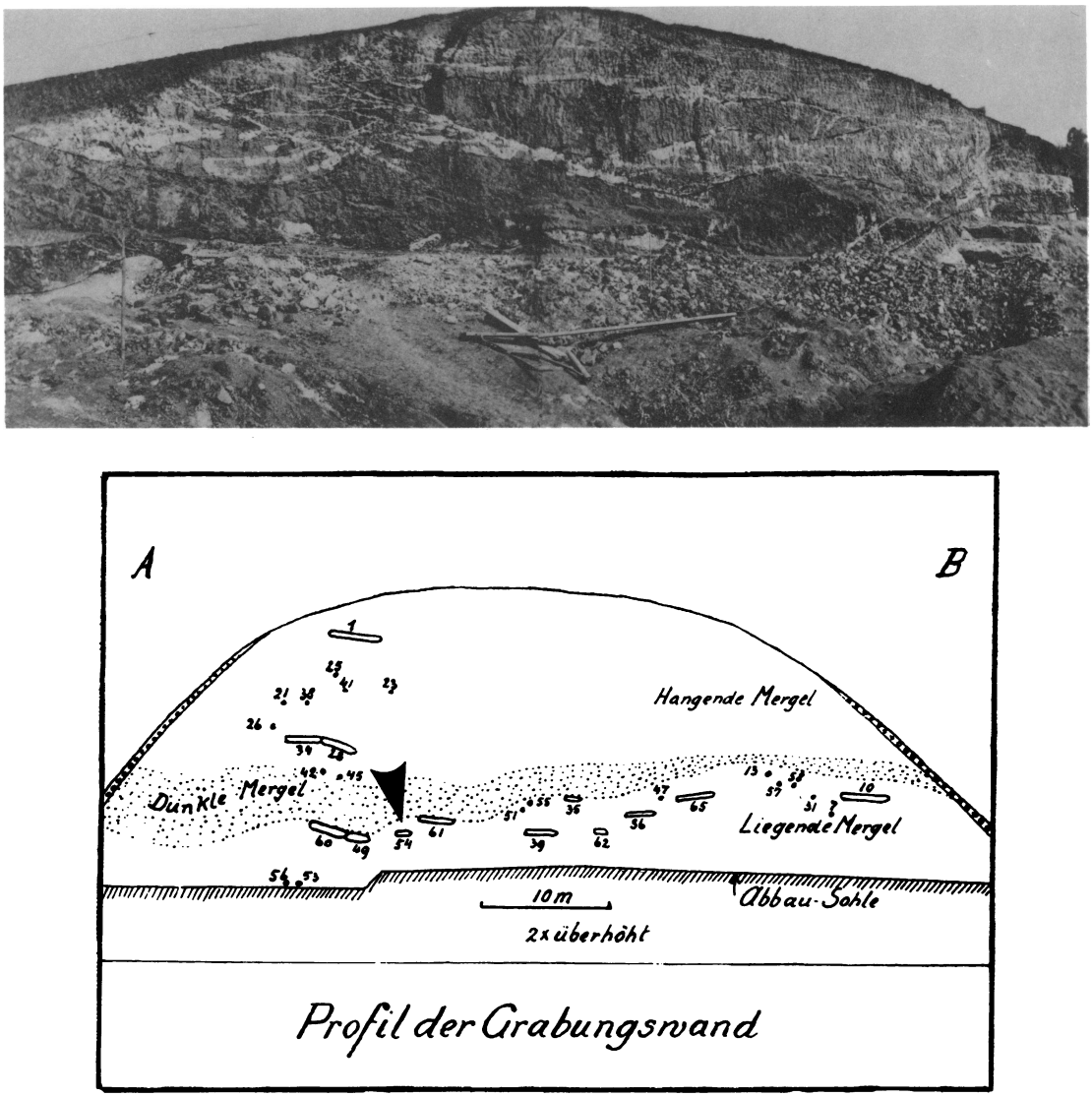

Fig. 12. Section of the Trossingen *Plateosaurus* quarry. Upper, photo taken near end of field season, 1932, by R. Seemann. Lower, profile from Seemann (1933) showing same section. Triangle points to Fund 54 (*Proganochelys* specimen, see text).

gel. Weishampel (1984) has analyzed the taphonomy of the *Plateosaurus* specimens and Seemann's data and came to similar conclusions. Using both Weishampel and Seemann, we can describe the quarry profile as follows:

The lower unit, Liegende Mergel, is a dark red mudstone, lacking obvious bedding and is exposed for about 2 m in the quarry. About 50 *Plateosaurus* specimens and the three *Proganochelys* specimens were found in the upper meters, some very close to the contact. The Dunkel Mergel varies in thickness from less than half a meter to more than 2 m in thickness, has irregular boundaries with the other two units, and consists of a brecciated mudstone, darker than the surrounding units. It contains only bone fragments that are graded from higher concentrations at the bottom to lower concentrations at the top. The upper unit, Hangende Mergel, is similar lithologi-

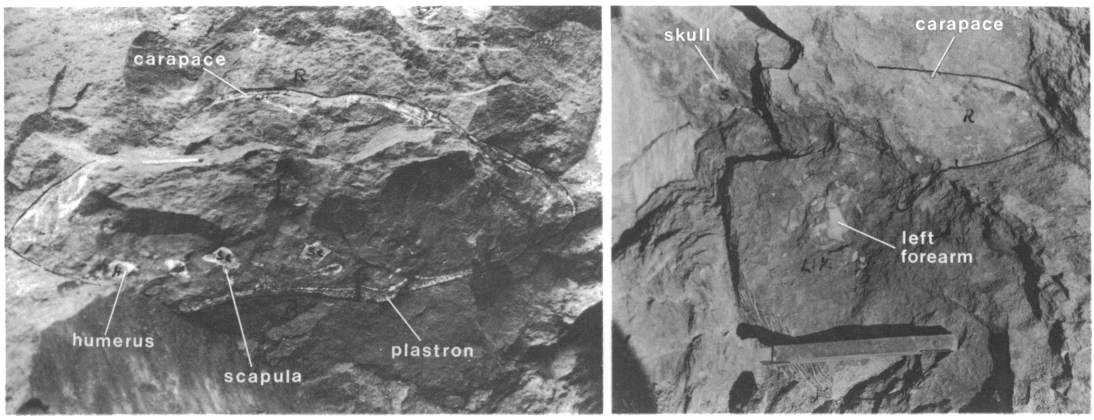

Fig. 13. *Proganochelys quenstedti,* SMNS 16980, during collection from Trossingen *Plateosaurus* quarry. Identifications are based on lettering (barely visible here) on the original print, presumably made by Seemann. Both prints are identified on the back as Fund 54, October 5, 1932. Photos by R. Seemann.

cally to the Liegende Mergel and has a maximum thickness of 9 m with a small amount of Liassic exposed at the top. There are some very complete *Plateosaurus* skeletons in the Hangende Mergel but there is no concentration as in the uppermost part of the Liegende Mergel. Weishampel (1984) interpreted a "background" deposition of plateosaur carcasses with the mudslide producing a concentration superimposed on it. The turtles clearly lay in the upper part of the Liegende Mergel and therefore were presumably buried by the mudslide if one accepts this scenario. The specimens themselves provide a little more information. SMNS 16980 was found right side up, fully articulated with very little postmortem disturbance except for slight dorsoventral distortion. The orientations of the other two specimens are not known but they are less complete, both lacking skulls. One of them, SMNS 17204, however, does have features consistent with the rapid mud flow catastrophe. This specimen has three limbs fully articulated, the tail is complete, all are covered with osteoderms, and yet part (but not all) of the carapace is crushed ventrally with a *Plateosaurus* fibula pushed down inside it.

Seemann published three papers (1932, 1933, 1941) relating to the Trossingen excavation. He primarily concerned himself with the geological aspects of the work. Fritz Berckhemer, the Chief Curator and paleontologist at SMNS during the 1930s and 1940s, initiated the preparation and scientific study of the *Proganochelys* specimens. Berckhemer is credited with saving the Triassic turtles and most of the vertebrate fossils at SMNS during World War II. The German government proclaimed any evacuation of collections to bombproof shelters as defeatist and imposed severe penalities but Berckhemer was able to have most of the collections safely removed to other locations. This was fortunate because the Stuttgart Museum building was completely destroyed by bombing (see Crumly, 1984, for the fate of other German collections during WW II). After the war, the collections were moved at first to the museum's ruins in Stuttgart, and later to Ludwigsburg, on the outskirts of Stuttgart. The collections and research offices were installed in a complex of buildings that were originally cavalry barracks and later an arsenal. Karl Staesche succeeded Berckhemer as curator of the fossil reptiles and began an investigation of the Triassic turtles which was never completed. In 1984 the SMNS moved to a new exhibition and research facility where the collections and exhibition of the Trossingen dinosaurs and turtles are finally combined.

SIZE AND ONTOGENETIC VARIATION AMONG THE *PROGANOCHELYS* SPECIMENS

The *Proganochelys* specimens used as the basis for this study (tables 1, 8, 11) exhibit

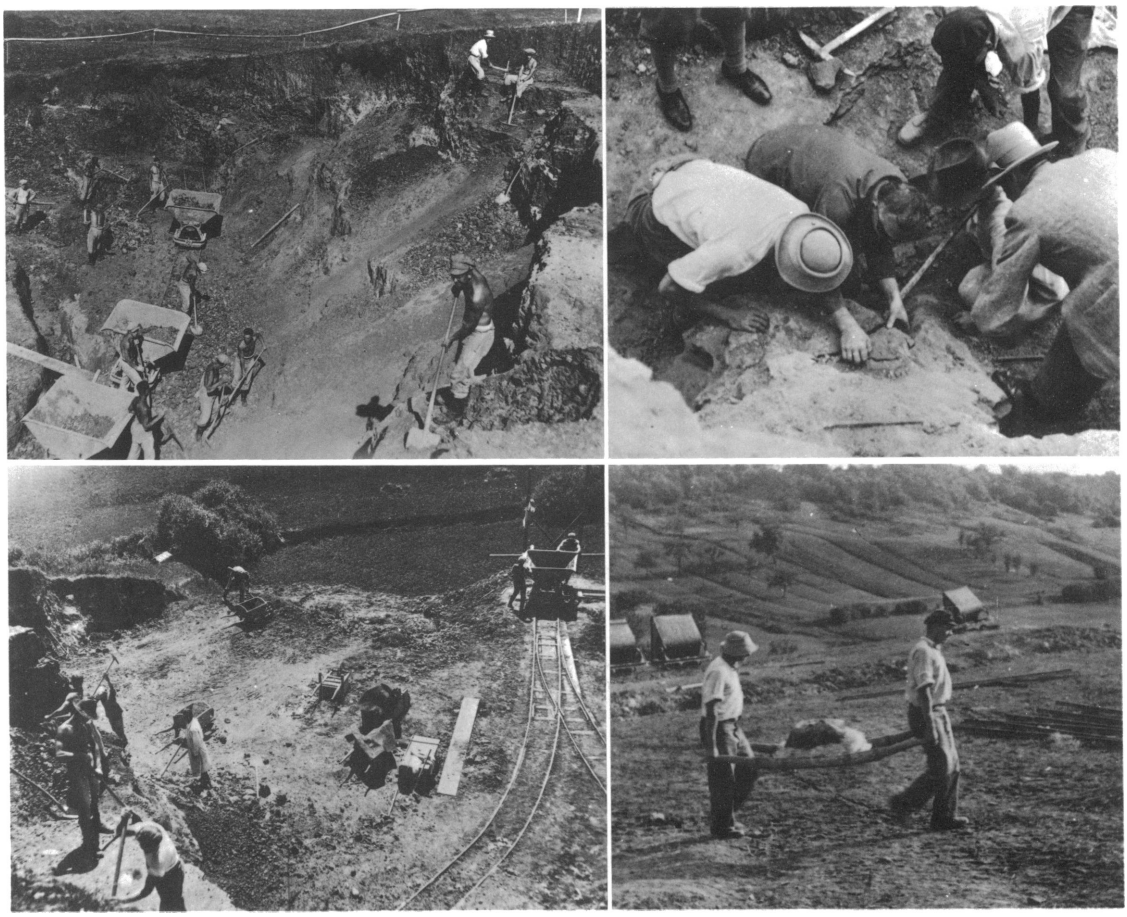

Fig. 14. Excavation in progress in Trossingen *Plateosaurus* quarry. Upper left, quarrying operation looking along quarry working face, August 1932. Upper right, discovery of *Proganochelys* specimen, probably SMNS 16980. Man with eye patch lifting rock is R. Seemann, October 5, 1932. Lower left, quarrying operation looking away from working face, August 1932. Lower right, removing *Proganochelys* specimen, October 5, 1932. Photos by R. Seemann.

variation in size and morphology. I interpret some of this variation as the result of relative growth differences. Because we refer to it repeatedly in the description, it is convenient to present the evidence for this interpretation early in the paper. Possible systematic implications of variation among the specimens is discussed after the morphologic descriptions.

It must be kept in mind that any analysis of relative growth in *Proganochelys* is hampered by the very small sample size and the varying degrees of preservation of the specimens. To a certain extent this is balanced by the fact that turtles as a group are still living and their development and variation are relatively well known.

Criteria for determining relative age of fossil vertebrates are far from unequivocal but there has been some standardization (see Brinkman, 1988, and references). In addition to size, which must remain as the most important criterion, the degree of ossification on articular surfaces, presence/absence of processes, and the extent of finished bone separating areas of cartilage-covered bone may be used to distinguish relative stages of maturity. Turtles additionally have the shell, which offers many criteria for estimating relative age. Zangerl (1969) in a review of turtle

shell morphology gave references to shell growth literature, while Dobie (1971) provided a study of *Macroclemys temmincki,* a living turtle roughly comparable to *Proganochelys* in size, possible habitat, and some morphologic features.

In looking at possible growth relations among *Proganochelys* specimens, the three Trossingen turtles form the best source of information. These specimens, SMNS 16980, 17203, 17204, were all found close together, at the same horizon (see discussion in preceding section) and are interpreted as having been living close to one another near the burial site. One of the specimens, SMNS 16980, is well preserved, almost complete, and is the most important element in the following description.

The size comparisons among these three specimens do not provide a completely straightforward and unambiguous guide to their relative age. Table 11 presents the most obvious measurements and it is clear that SMNS 17203, despite having an incomplete shell, is the smallest of the three. The morphology (discussed below) strongly supports the interpretation of this individual as being relatively younger than the other two specimens. SMNS 16980 and SMNS 17204 have measurements that are roughly similar. However, SMNS 17204 has a very poorly preserved carapace. The plastron, which is relatively well preserved in both specimens, is slightly smaller in SMNS 17204 than in SMNS 16980. For reasons given below, I think that SMNS 16980 is actually a younger individual than SMNS 17204. The size criteria show one specimen that is about 15 percent smaller than the other two.

The long bones are preserved in all three Trossingen specimens and most are well enough preserved to apply the criteria used by Brinkman (1988) and others for estimating relative age. Additionally, I have examined a series of *Macroclemys, Chelydra,* and various emydids in the AMNH collections to aid in comparison. Consistent with the size criterion, SMNS 17203 has a greater degree of unossified articular surfaces than the other two specimens. SMNS 16980 is distinctly better ossified than SMNS 17203, but not to the degree seen in SMNS 17204. Based on subjective comparison, I would judge the degree of this difference to be about twice as great between SMNS 17203 and SMNS 16980 than between SMNS 16980 and SMNS 17204.

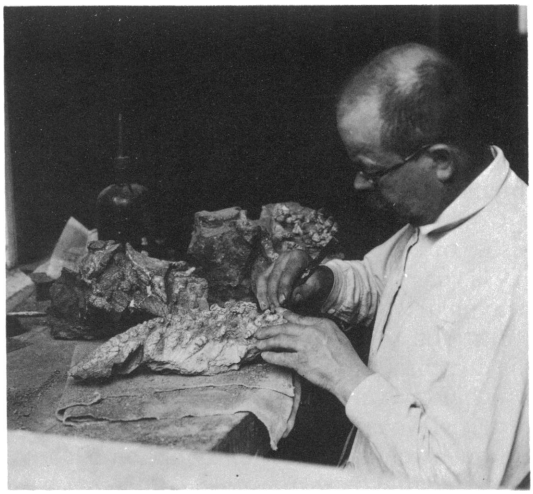

Fig. 15. Preparation of tail of SMNS 17204 by Max Böck.

The shell of turtles provides another useful source of features to judge relative age in turtles. Dobie (1971), Zangerl (1969), and others have examined the annuli often seen on vertebral, pleural, and other scales to compare numbers of growing seasons (not strictly equivalent to years; see these papers and references listed). Although I have tried to make use of these markings, I have not seen any that are consistent enough to use in comparisons. Virtually none is preserved in SMNS 17203 and 17204, while SMNS 16980 has been prepared to the extent that the remaining annuli are ambiguous.

A better series of comparisons, however, can be made using the degree of ossification in the shell. Again, SMNS 17203 has fontanelles in the carapace and plastron (figs. 99–102) that are closed in SMNS 17203 and SMNS 16980. This is a feature characteristic of juvenile turtles and agrees with the other criteria indicating a younger growth stage of SMNS 16980. Although all the fontanelles are closed in SMNS 16980, it has open sutures in the plastron that are much more tightly closed in SMNS 17204. The carapace of SMNS 17204 is very poorly preserved and hard to compare with that of SMNS 16980.

Another indication that SMNS 17204 may be older than SMNS 16980 is the slightly larger bones of the hind foot and the better ossified and larger osteoderms on the limbs and tail. This is also somewhat subjective, but it does parallel conditions in some specimens of *Chelydra* that I have seen.

Could some of the these differences be the result of sex differences—because, as Dobie (1971) has shown, males tend to be larger and heavier in *Macroclemys*? The only possible control on this is the postpelvic ossification, the hypoischium (see description sections), which is known only in *Proganochelys* among turtles. Two specimens have a single hypoischium, two have a double one, and I have suggested that these may reflect different sexes. In the absence of any analogies among living turtles, it is not possible to identify a particular sex with a particular hypoischium condition. However, SMNS 16980 and SMNS 17204 both have the single hypoischium, suggesting that they may be the same sex, and further supporting the interpretation of variation between them as involving relative growth.

Of the Trossingen specimens, only SMNS 16980 has a skull. Two other *Proganochelys* specimens also have skulls (although crushed) as well as partial or complete carapaces. Comparative measurements among these specimens (table 8) show an interesting relationship. If the largest skull, MB 1910.45.2, is put at 100 percent, then SMNS 15759 is 86 and SMNS 16980 64 percent of the size of the largest skull. The carapace lengths for the same three specimens are 100, 92, and 83 percent. Although there is no complete agreement, these figures are consistent with other criteria that would place SMNS 16980 as a not fully grown individual. Dobie (1971) has shown that carapace length in *Macroclemys* tends to level off at sexual maturity, and SMNS 16980 may be a sexually mature individual.

Based on the above discussion, I would interpret SMNS 17203 as being the most immature of all known *Proganochelys* specimens, but certainly beyond hatchling stage. It is unlikely to have reached sexual maturity. SMNS 16980 is an older individual, probably at the lower limits of the average size at sexual maturity, and not fully grown. SMNS 17204 is older than SMNS 16980, probably at or near the average size for adults of the species. Although comparable measurements are scarce, the other three specimens, MB 1910.45.2, SMNS 10012, and SMNS 15759, are probably also at or near the average size for adults. The skull measurements (also not clearly comparable due to preservational distortion; see descriptions), show a greater degree of size differences but this may be the result of differential growth in the skull and shell, a condition seen in living turtles (Dobie, 1971, and references).

SKULL MORPHOLOGY

(Figures 16–61 refer to skull morphology; fig. 16 is a general one of *Proganochelys*; figs. 21–39 document the material used, and figs. 18–20 are for comparison with other taxa.)

SCALE AREAS
(table 2, fig. 17)

The three *Proganochelys* skulls all show some indication of scale areas distinguished by broad grooves or protuberances. SMNS 15759 has the scale areas best defined, the margins have definite grooves, but the sutures are not visible and the crushing causes lateral distortion of the scale relationships. Some scale areas are interpretable in the Berlin skull but the generally poor preservation of the bone surface makes it the least satisfactory for seeing scale areas. The best preserved skull, SMNS 16980, does not have the best scale markings. Some areas are visible but the grooves and protuberances are not expressed to the degree seen in SMNS 15759, with the overall result that a complete scale system for *Proganochelys* cannot be developed at present.

The one set of scale areas that can be clearly identified in all three skulls is the four supraorbital bosses formed by the prefrontal and postorbital bones (numbers 1–4 in fig. 17). These scales form conical projections with 1 being the smallest and increasing in size to 3, the largest, while 4 is low but broader than the others. This scale set is best de-

TABLE 2
Comparison of Head Scalation in the Three *Proganochelys* Skulls (see Fig. 17)

	SMNS 15759	MB 1910.45.2	SMNS 16980
Four supraorbital scales (1–4)	Well developed, high protuberances	Low bosses	Low bosses
Midline scale 5	Present, high protuberance, well-defined margins	Low, possibly absent	Present, low boss, poor definition
Midline scale anterior to scale 5	Present	Apparently absent	Apparently absent
Scale 6	Longer than wide	Longer than wide	Wider than long
Nasal-frontal scale	Present	Present	Absent
Degree of expression of scale sulci and protuberances	Well developed	Poorly developed	Poorly developed

veloped in SMNS 15759, which has distinctive points while the other two skulls exhibit lower and more obtuse projections. The scale set in the Berlin skull is slightly better developed than in SMNS 16980 but very close to it in development. Scales 1 and 2 are formed by the prefrontal, scale 3 is formed by both prefrontal and postorbital, and scale 4 is formed by the postorbital. All three skulls have a midline, unpaired scale, the one labeled 5 is the most consistent. In SMNS 16980 this is formed on the frontal and is roughly pentagonal. In SMNS 15759 this pentagonal scale is very well delimited by distinct grooves and a high, raised area in the center, while in SMNS 16980 the scale is poorly delimited and may even be divided into more than one scale, although this is not clear. In the Berlin skull there appears to be a midline scale, possibly two, in this region, but there are no distinctive grooves nor a large raised area to identify it. The presumed margins of this possible scale area are not bilaterally symmetrical and may be the result of postmortem damage. In SMNS 15759 scale 5 has a curved, triangular scale anterior to it, well formed, with a median boss, but there is no sign of this scale in SMNS 16980 or the Berlin skull.

In SMNS 16980 the posterior quadrant of the skull roof, formed by parts of the frontal, parietal, and postorbital are covered by two paired scales, numbered 6 and 7 (fig. 17). Scale 6 is flat, but 7 has a raised area laterally where it extends onto the squamosal. SMNS 15759 may be interpreted as having both scales but their shapes are quite different. In SMNS 16980 these scales are wider than long while in SMNS 15759 scale 6 is longer than wide and scale 7 barely exists on the dorsal surface of the skull. I interpret these differences, however, as a result of the strong lateral compression that has deformed the skull roof of SMNS 15759. Nonetheless, there are real differences between the two skulls: scale 6 in SMNS 16980 reaches the supraorbital series but in SMNS 15759 there is another set of scales intervening which also narrows scale 6. The area of scale 6 can be interpreted in the Berlin skull as being more similar to that scale in SMNS 15759 than in SMNS 16980, but the region does not have clear scale markings.

Along the posterior margin of the skull roof, between the margin and scale 7 in SMNS 16980, are two paired bosses defined by broad grooves. The medial scale, number 8, is formed by the parietal while the lateral scale, 9, is formed mostly by the supratemporal. Both are wider than long. In SMNS 15759 these two bosses are recognizable, particularly 8, but they are elongate rather than wide, a result of lateral compression. In the middle of the parietal on the midline is a small, unpaired scale, 10, that in SMNS 16980 is contacted by scales 6, 7, and 8. In SMNS 15759, there is an unpaired scale but it lies at the posterior margin of the skull rather than separated from the margin by the meeting of scale 8 as in SMNS 16980. In the Berlin skull there may be a median scale in this region but its margins are doubtful.

Anteriorly the Berlin skull and SMNS 15759 both have a long, narrow ridge on the midline that runs from the apertura narium externa to the midline scale anterior to scale 5 (in SMNS 15759). This scale appears to be

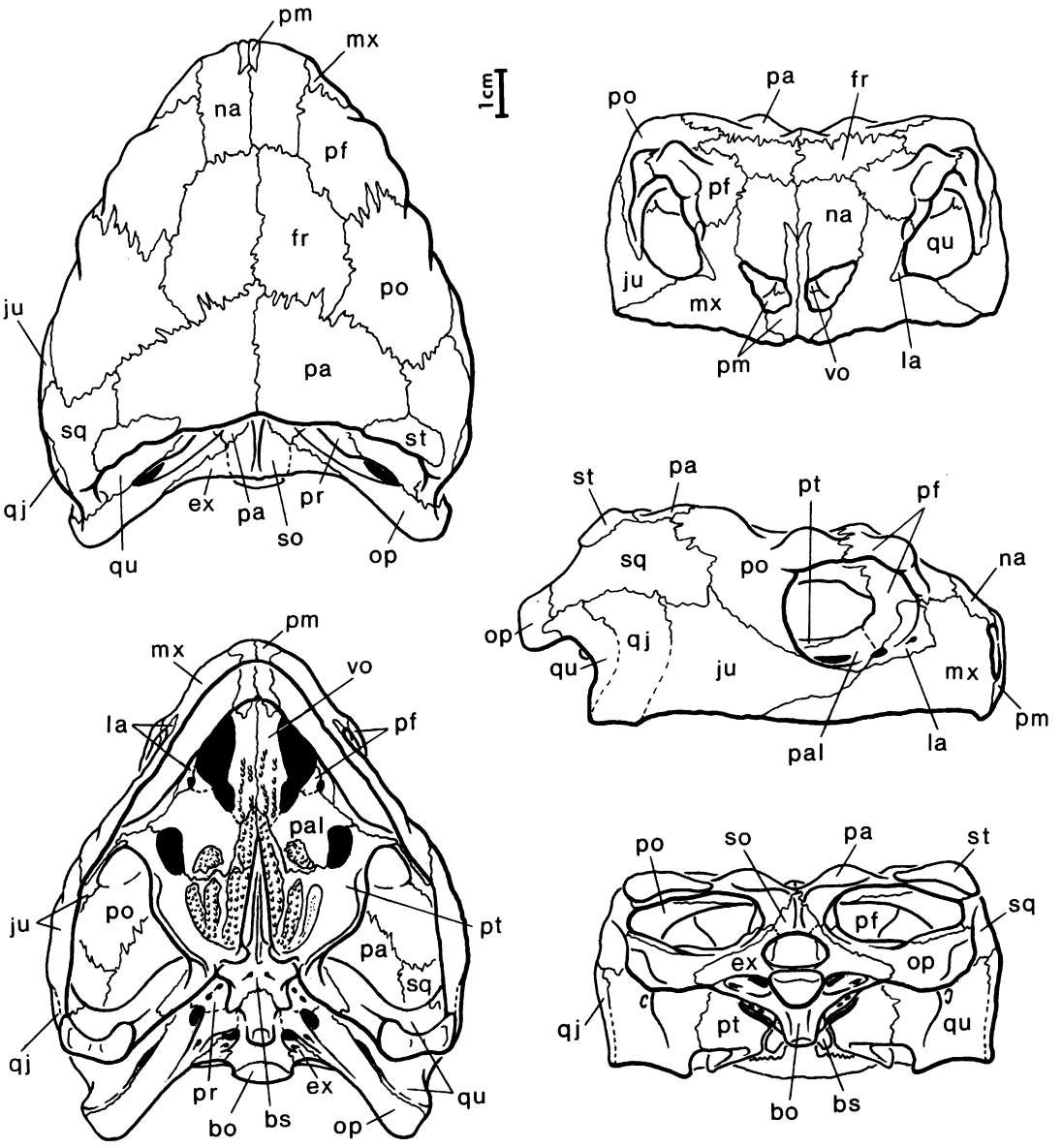

Fig. 16. *Proganochelys quenstedti,* SMNS 16980. Line drawings of skull. These drawings differ from earlier figures in Gaffney and Meeker (1983) and Gaffney (1983).

formed on the nasal and frontal bones and is clearly delimited in SMNS 15759 by distinct lateral grooves and a prominent raised ridge down the midline. SMNS 16980 has no indication of this scale and only one vague scale groove of any kind in the snout region.

The significance of the scale differences among the three *Proganochelys* skulls is difficult to assess. SMNS 15759 and the Berlin skull agree in having a longer than wide scale 6 and a nasal-frontal scale, in SMNS 16980 scale 6 is wider than long and there does not appear to be a nasal-frontal scale. SMNS 15759 differs strongly from the other two skulls in its distinct scale expression and prominent development of bosses and pro-

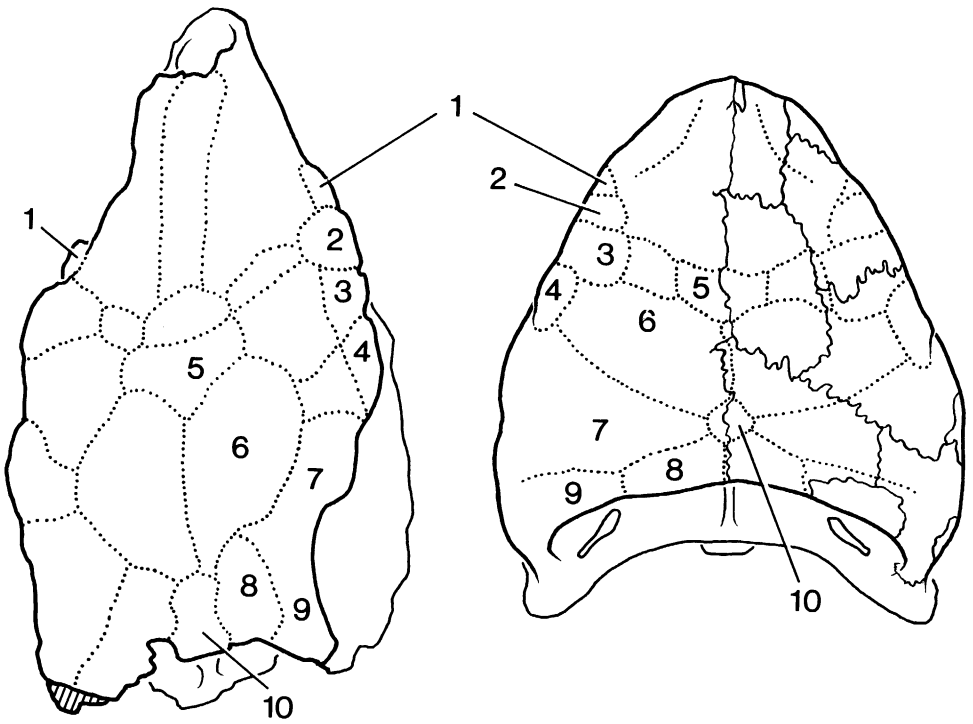

Fig. 17. *Proganochelys quenstedti,* scale areas of skulls in dorsal view. SMNS 15759 (left) and SMNS 16980 (right).

tuberances in the center of many scale areas. SMNS 15759 and SMNS 16980 agree in the definitive midline scale 5. Some of these conditions may be the result of postmortem changes or growth differences. At the present time no pattern of systematic significance emerges.

Comparison with other amniotes suggests that head scalation is a turtle synapomorphy; captorhinids and other generalized amniotes lack it. Comparison within turtles is difficult because there have been no comparative studies published. Among the few published descriptions, *Meiolania* (Gaffney, 1983) is perhaps the most similar to *Proganochelys* because both have median and paired scutes, often with projections and bosses. This condition, however, is probably primitive for turtles; baenids and pleurodires have head scalation but pleurosternids do not. Close comparison of the pattern in *Proganochelys* with that in *Meiolania* reveals few, if any, scales that could be considered homologous. The large A scale of *Meiolania* (Gaffney, 1983) appears similar to the scale 8 of *Proganochelys* but the former lies on the squamosal and supraoccipital while the latter is on the parietal. The large D scale of *Meiolania* is perhaps the 6 plus 7 of *Proganochelys* and the central median scale X of *Meiolania* might be compared with 5 of *Proganochelys.* Although *Meiolania* is characterized by prominent horns and bosses, these are in quite different positions than the protuberances of *Proganochelys.* There are no particular patterns that show a close similarity in the two genera.

DERMAL ROOFING ELEMENTS
(table 3, figs. 16, 43, 49)

NASAL

The nasal bones are preserved in all three *Proganochelys* skulls, but they are crushed and indistinct in the Berlin skull and SMNS 15759 while SMNS 16980 has them well preserved and clearly delimited.

TABLE 3
Comparison of Dermal Roofing Elements

	Captorhinus	*Proganochelys*	Casichelydia
Nasals partially separated anteriorly by dorsal process of premaxillae	Yes	Yes	No
Apertura narium externa orientation	Faces laterally	Faces primarily anteriorly	Faces primarily anteriorly
Fissura ethmoidalis	Very wide	Very wide	Wide to narrow; < *Proganochelys*
Vomer-prefrontal contact	No	Probably no	Yes, cryptodires; no, pleurodires
Palatine-prefrontal contact	No	Yes	Yes
Fossa nasalis	Large	Intermediate	Small
Lacrimal bone	Large, extends from orbit to apertura narium externa	Small, restricted to anterior orbital margin by extensive prefrontal-maxilla contact	Absent
Lacrimal duct	Formed by lacrimal bone from orbit to nose	Partially formed by maxilla as a trough extending anteriorly from lacrimal bone	Absent
Frontal enters orbital margin	Yes	No, separated by broad prefrontal-postorbital contact	Variable but primitively yes
Proportions of horizontal plate of parietal	Longer than wide	Wider than long	Longer than wide
Pineal foramen	Present	Absent	Absent
Processus inferior parietalis	Absent	Present	Present; more extensive than in *Proganochelys*
Ossified foramen nervi trigemini	Absent	Only partially formed in bone	Present and fully formed in bone
Postfrontal and postparietal bones	Present	Absent	Absent
Foramen palatinum posterius	Formed by jugal and palatine	Formed by pterygoid and palatine	Formed by pterygoid, palatine, maxilla, and jugal
Quadratojugal shape	Horizontally elongate	Vertically elongate	Vertically elongate
Quadratojugal reaches posterior margin of skull	Yes	No	No
Quadratojugal/quadrate position	Quadratojugal lateral to quadrate	Quadratojugal anterior to quadrate	Quadratojugal anterior to quadrate
Quadratojugal/jugal contact	≪ height of jugal	= height of jugal	= height of jugal
Antrum postoticum	Absent	Absent	Present
Medial flange on occiput	Present	Absent	Absent
Jugal-squamosal contact	Present	Present	Absent
Squamosal-quadratojugal contact	Almost as long as squamosal	Less than half length of squamosal	Variable; usually shorter than *C* or *P*
Squamosal-opisthotic contact	Absent	Present	Present
Supratemporal	Relatively small, fits in parietal notch	Relatively large; on top of parietal	Absent

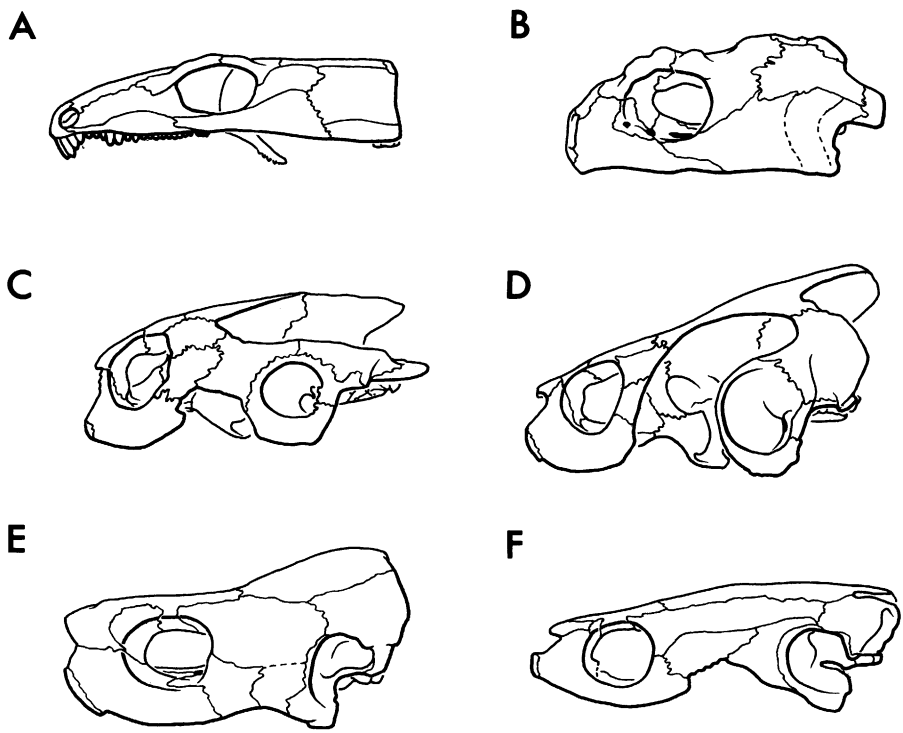

Fig. 18. Lateral views of skulls. **A,** *Captorhinus* sp., Early Permian, from Heaton (1979) and specimens. **B,** *Proganochelys quenstedti,* Late Triassic. **C,** *Pelomedusa subrufa,* Recent, from Gaffney (1979a). **D,** *Emydura macquarri,* Recent, from Gaffney (1979a). **E,** *Kayentachelys aprix,* Early Jurassic, from Gaffney et al. (1987). **F,** *Pleurosternon* (*Mesochelys*) sp., Early Cretaceous, from Evans and Kemp (1975).

The nasal of *Proganochelys* is a rectangular, nearly flat element, forming a conspicuous portion of the snout region. The nasals contact each other for most of their length but are partially separated anteriorly by the dorsal processes of the premaxillae, a condition unknown in other turtles but found in captorhinids. The nasal in *Proganochelys* forms roughly one-third of the skull roof along the midline, as in captorhinids but different from that in Casichelydia, which is proportionally smaller.

Posteriorly the nasal has a nearly transverse contact with the frontal, and there is a posterolateral contact with the prefrontal. Anterolaterally the nasal contacts the dorsal process of the maxilla. Although modified by the differing shapes of the nasal, these contacts are also seen in *Kayentachelys,* chelids, and *Pleurosternon* (= *Mesochelys*) and may be considered primitive for Casichelydia.

The anterior edge of the nasal in *Proganochelys* forms the dorsal margin of the apertura narium externa as in other turtles with nasals. In captorhinids, however, the nasal usually forms the medial margin of the apertura which is separated from the other apertura by the width of both nasals. Also, the apertura narium externa of *Proganochelys* faces anteriorly rather than laterally as in captorhinids. The *Proganochelys* condition appears to be a chelonian synapomorphy.

The ventral surface of the nasal in *Proganochelys* has a low, parasagittal ridge defining the lateral limits of the sulcus olfactorius. This ridge is similar in position and degree of development to that in *Captorhinus* (Heaton, 1979: figs. 16, 17) but it is slightly more acute in *Proganochelys.* The sulcus olfactorius in *Captorhinus* and *Proganochelys* is relatively broad and ill-defined when compared with the sulcus in most casichelydians which is usually much narrower with higher and better developed parasagittal ridges. Furthermore,

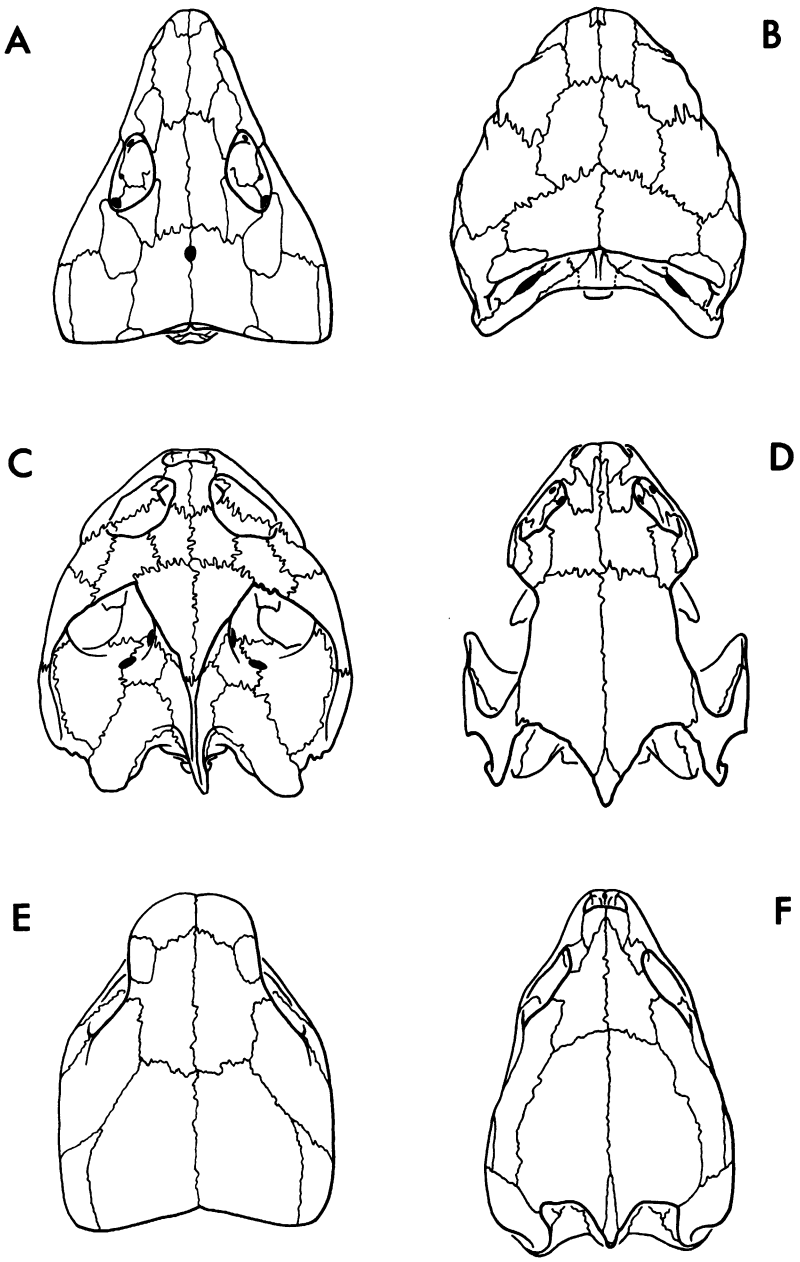

Fig. 19. Dorsal views of skulls. A–F, as in Figure 18.

in casichelydians these ridges are not developed on the nasals but rather on the frontals which occupy the general area occupied by the nasals in *Proganochelys* and captorhinids. *Kayentachelys* agrees with other casichelydians in this feature.

The Berlin skull and SMNS 15759 do not contribute significantly to understanding the nasal in *Proganochelys* due to crushing and ambiguous sutures. Jaekel's description (1918a: fig. 35) of the nasal sutures is in error and seems to show scale sulci rather than sutures. His identification of the dorsal premaxillary processes as part of the nasals is

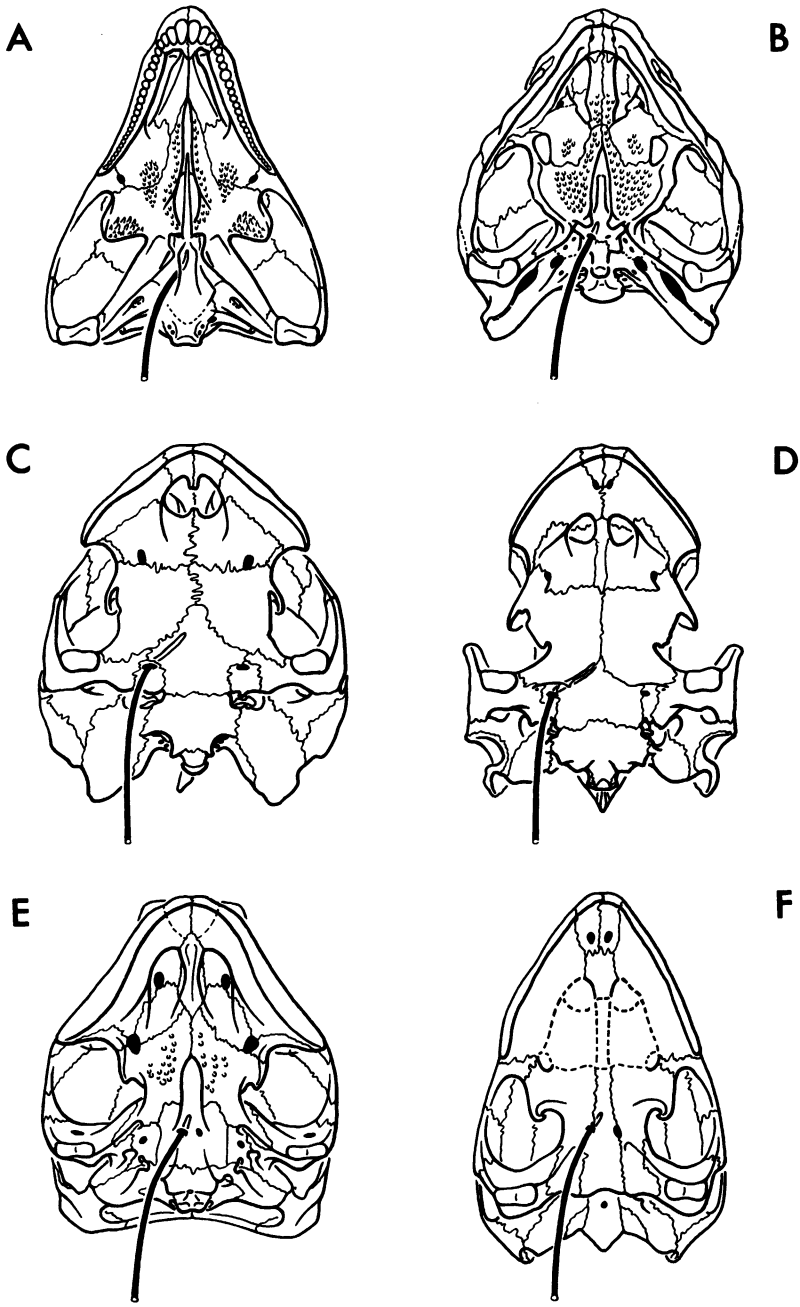

Fig. 20. Ventral views of skulls. On the right side the pathway of the internal carotid artery is indicated. A–F, as in Figure 18.

incorrect. Nonetheless, this skull and SMNS 15759 differ from SMNS 16980 and require comment. The Berlin skull and SMNS 15759 are crushed laterally so that the snout region is high and narrow rather than broad and wide as in SMNS 16980. The nasal apertures are also much narrower in the two crushed skulls, presumably due to postmortem dam-

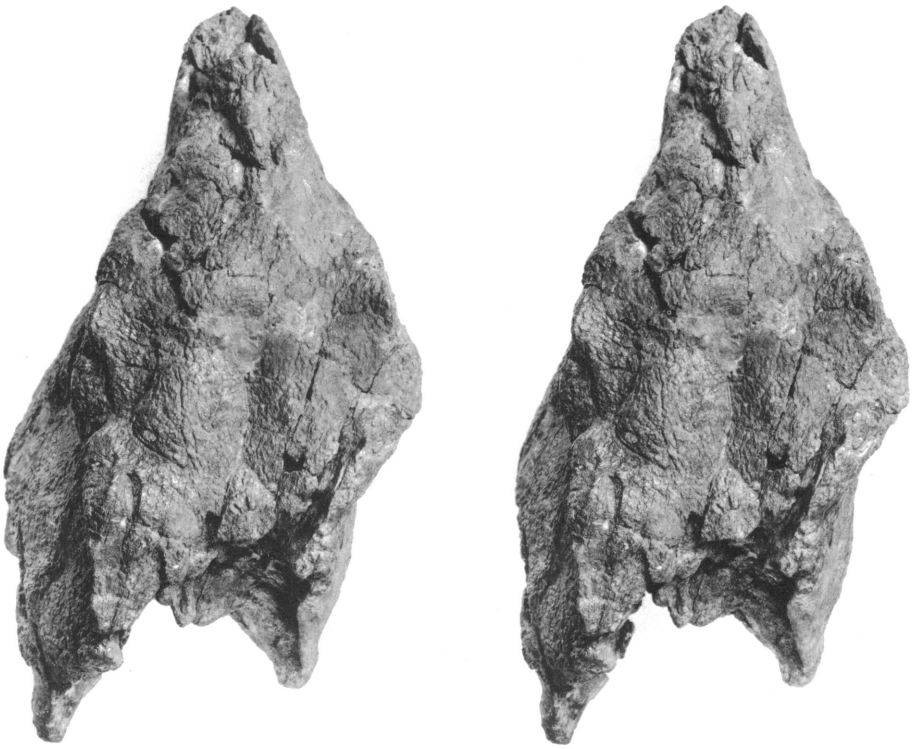

Fig. 21. *Proganochelys quenstedti,* MB 1910.45.2. Stereophotographs of dorsal view of skull.

Fig. 22. *Proganochelys quenstedti,* SMNS 16980. Stereophotographs of dorsal view of skull.

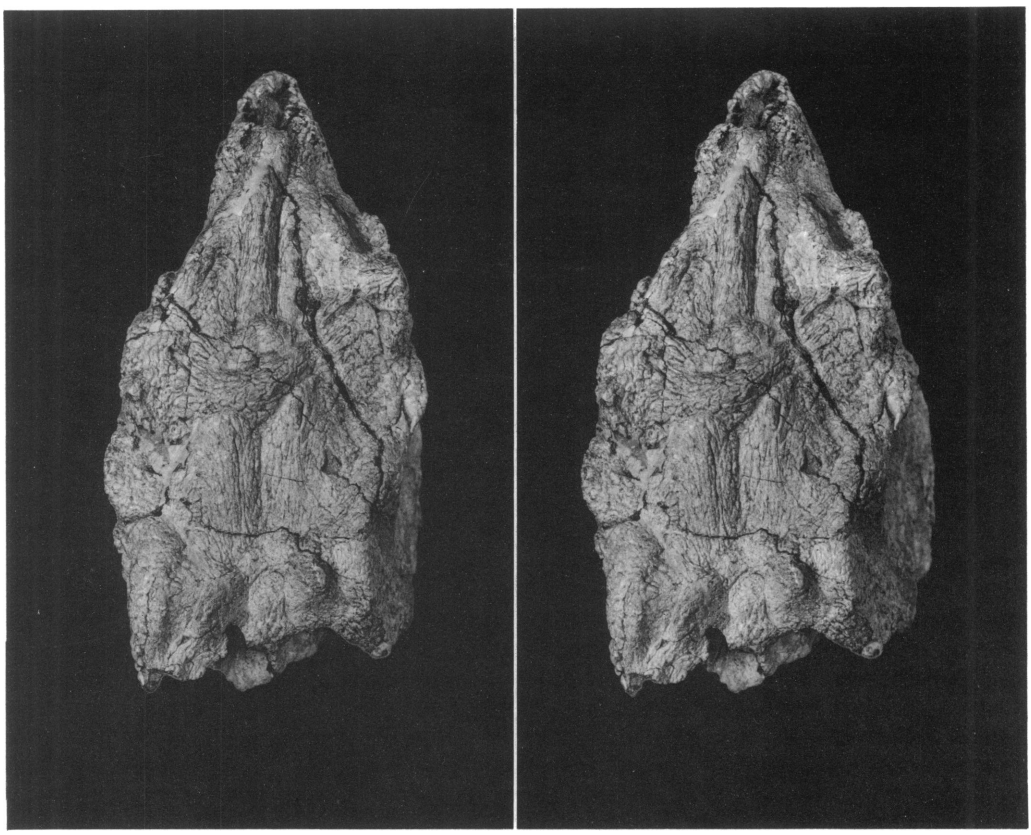

Fig. 23. *Proganochelys quenstedti,* SMNS 15759. Stereophotographs of dorsal view of skull.

age. There is, however, a difference that I do not feel can be interpreted as preservational. Both the Berlin skull and SMNS 15759 have a pitted, rugose surface on the nasal at its anterior margin, particularly clear in SMNS 15759. In this area in SMNS 16980 there is a slight pitted, raised area but it does not match the condition seen in the other two skulls. I interpret this difference as being due to growth and/or age; SMNS 16980 is interpreted as a small and presumably younger individual with these features yet undeveloped.

The ventral surface of the nasal can be seen best on the right side of SMNS 16980. Although sutures are somewhat obscured by the extensive network of cracks in the skull, it appears to me that the nasal extends posteriorly on the ventral surface to underlie part of the frontal and form an anteromedially trending suture with the frontal that ends on the midline. Laterally the nasal forms most of the ridge along the sulcus olfactorious but part of the prefrontal extends onto the ridge posteriorly. Anterolaterally, the nasal-maxillary suture on the ventral surface seems to follow the position of that suture on the dorsal surface.

PREFRONTAL
(figs. 16, 40, 43)

The prefrontal is present in all three skulls but it is best seen in SMNS 16980 where it is preserved on both sides of the skull. The dorsal portion of the prefrontal is clearly delimited by sutures but the ventral region is obscured to some extent by breakage.

The prefrontal of *Proganochelys* can be divided into two portions: a dorsal, horizontal plate on the skull roof and a ventral, descending process forming part of the anterior wall of the fossa orbitalis. The dorsal plate contacts the nasal anteromedially in a parasag-

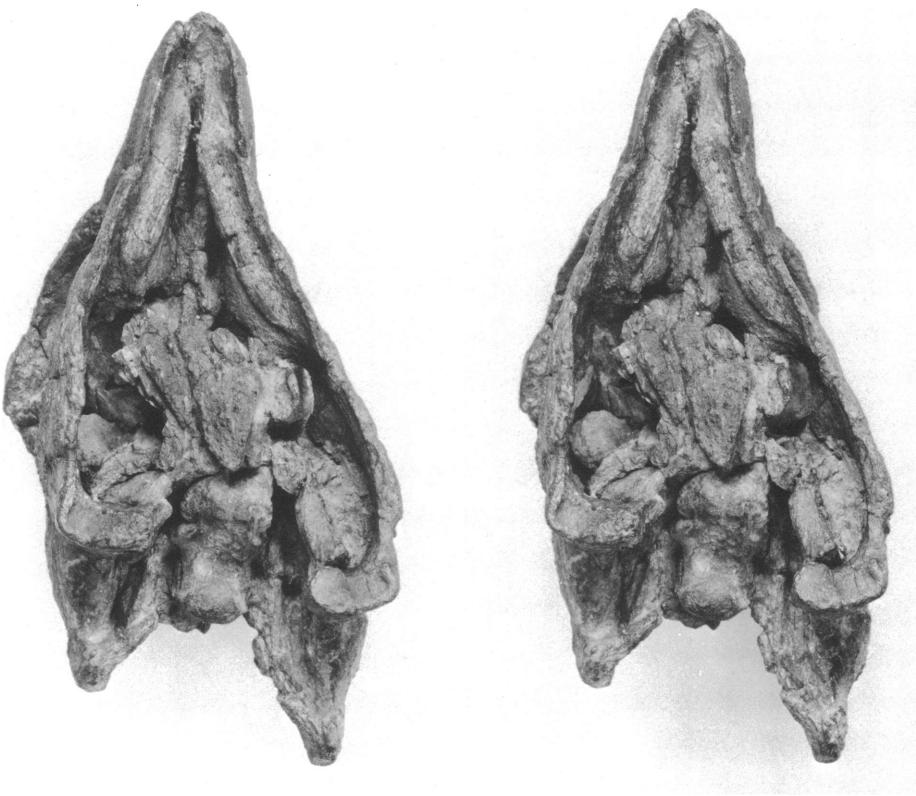

Fig. 24. *Proganochelys quenstedti,* MB 1910.45.2. Stereophotographs of ventral view of skull.

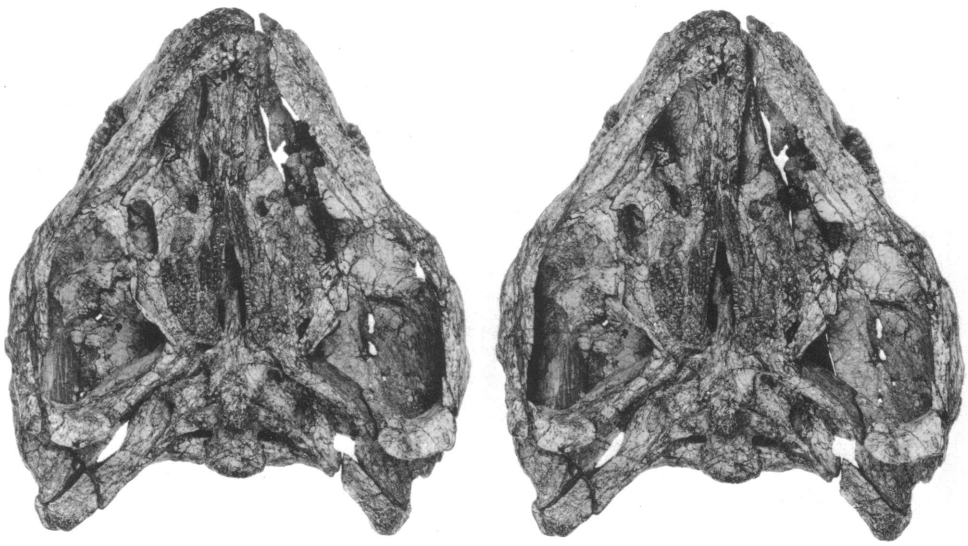

Fig. 25. *Proganochelys quenstedti,* SMNS 16980. Stereophotographs of ventral view of skull.

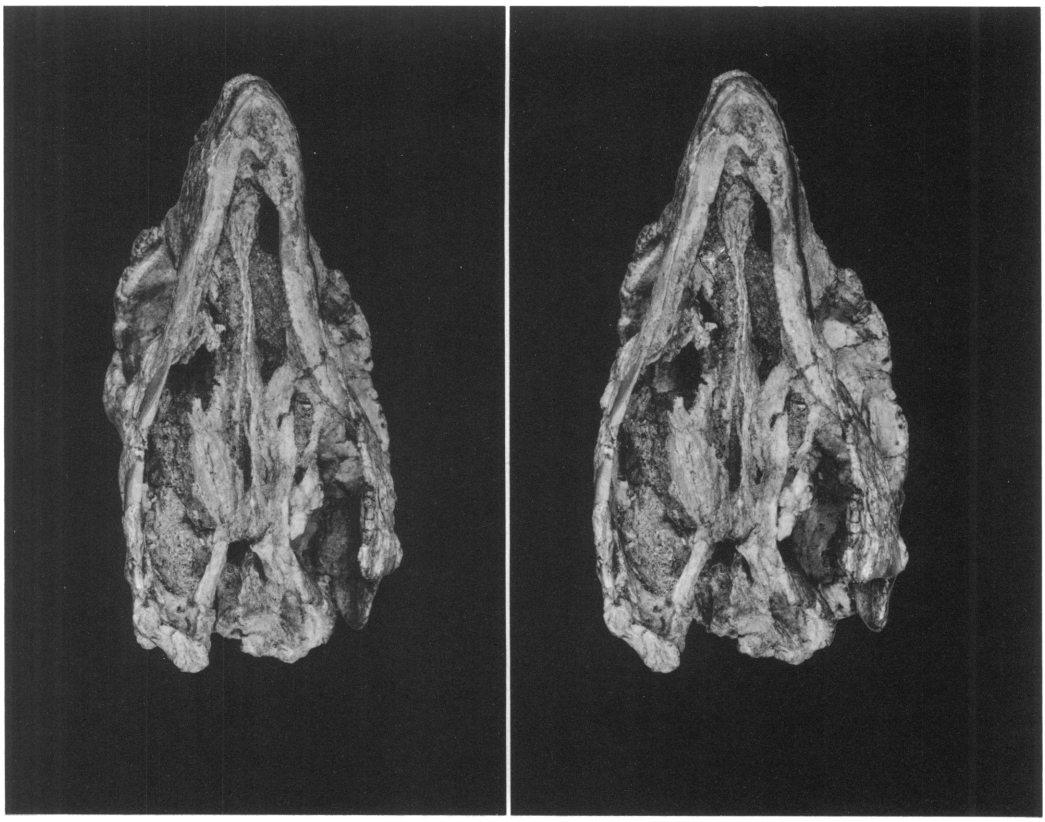

Fig. 26. *Proganochelys quenstedti,* SMNS 15759. Stereophotographs of ventral view of skull.

ittal suture running half the length of the prefrontal. Posteromedially there is a suture with the frontal that trends somewhat posterolaterally. The postorbital forms the posterior limits of the prefrontal in a transverse suture that enters the dorsal margin of the fossa orbitalis.

The sutures on the ventral surface are not clear but as I interpret them the prefrontal-postorbital suture trends medially to reach the frontal in the vicinity of the fissura ethmoidalis. In this interpretation the prefrontal reaches the nasal on the posterior part of the ridge forming the sulcus olfactorius. Anteriorly the prefrontal has a parasagittal suture with the nasal, similar in position to the suture on the dorsal surface. The maxilla-prefrontal suture is slightly more dorsal on the internal surface than on the external surface of the skull.

The ventral process of the prefrontal is not as well preserved as the dorsal plate. It is best seen in SMNS 16980, although it is present in the other two skulls. The ventral process of the prefrontal forms the anterodorsal wall of the fossa orbitalis and contacts the lacrimal ventrolaterally. Because of the presence of the lacrimal in *Proganochelys* the extent of the prefrontal in this area is less than in other turtles. The descending process of the prefrontal reaches the palatal elements ventrally. Although this region is broken and damaged, in the right side of SMNS 16980 part of the palatine contact can be seen. At this point the prefrontal curves ventrally and somewhat posteriorly as in other turtles. Laterally a small foramen orbito-nasale appears to be present. The area is broken but the anterior and lateral margins of a foramen can be seen in the lacrimal-prefrontal suture. Participation of the palatine, in the margin of this foramen as in most other turtles, is uncertain but likely.

The medial margin of the descending process of the prefrontal is best seen in SMNS

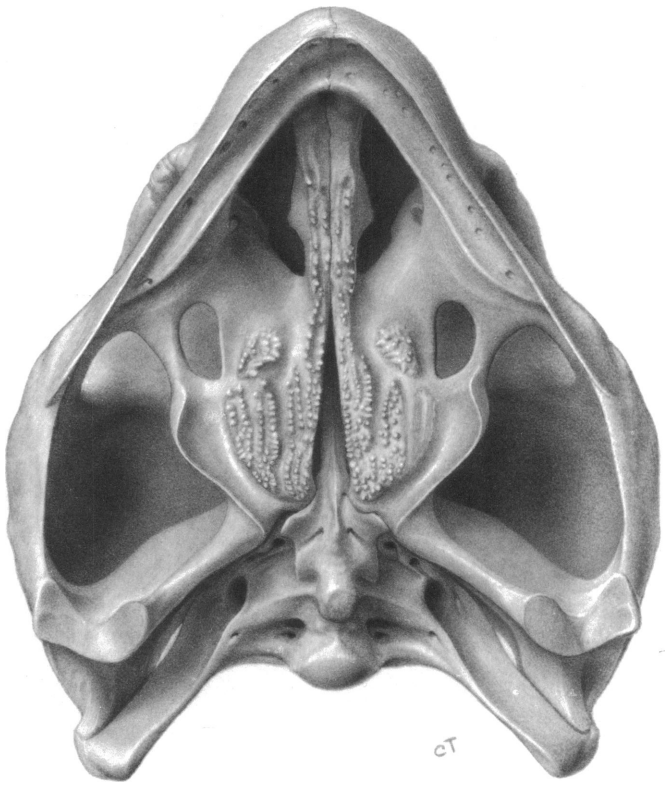

Fig. 27. *Proganochelys quenstedti,* SMNS 16980. Ventral view of skull, partially restored by transposing from one side to the other.

16980 but it is incomplete being demarcated by broken edges. Nonetheless, it does not appear that much bone is missing resulting in a fissura ethmoidalis that is wider than in any other turtle. Contact of the prefrontal with the vomer, a condition characteristic of cryptodires but not of pleurodires, is not present in any of the *Proganochelys* skulls. The relative positions of these bones make such a contact unlikely but due to the apparently incomplete bone margins, a prefrontal-vomer contact is not impossible.

Although the nasal region of *Proganochelys* is made up of a number of bones, the prefrontal is an integral part of the area, and, in view of the ambiguity of some of the sutures, it is convenient to describe the entire region here. The entire preorbital region of *Proganochelys* is relatively longer than in most other turtles. Those turtles, such as *Trionyx* and protostegids, which have long preorbital regions, have large premaxillary and maxillary extensions but still have a relatively short nasal area. In *Proganochelys* the paired apertura narium externa is relatively small when compared with the single apertura of the Casichelydia but it opens into a fossa nasalis that is quite large compared with that in other turtles. The nasal and the frontal form the roof of the fossa nasalis, as in *Captorhinus* but in contrast to more advanced Casichelydia in which the prefrontal dominates the roof of the fossa nasalis. *Kayentachelys, Pleurosternon,* and chelids, however, have relatively small prefrontals and this is presumed to be the primitive casichelydian condition. On the ventral surface of the nasal, and on part of the prefrontal, is a parasagittal ridge

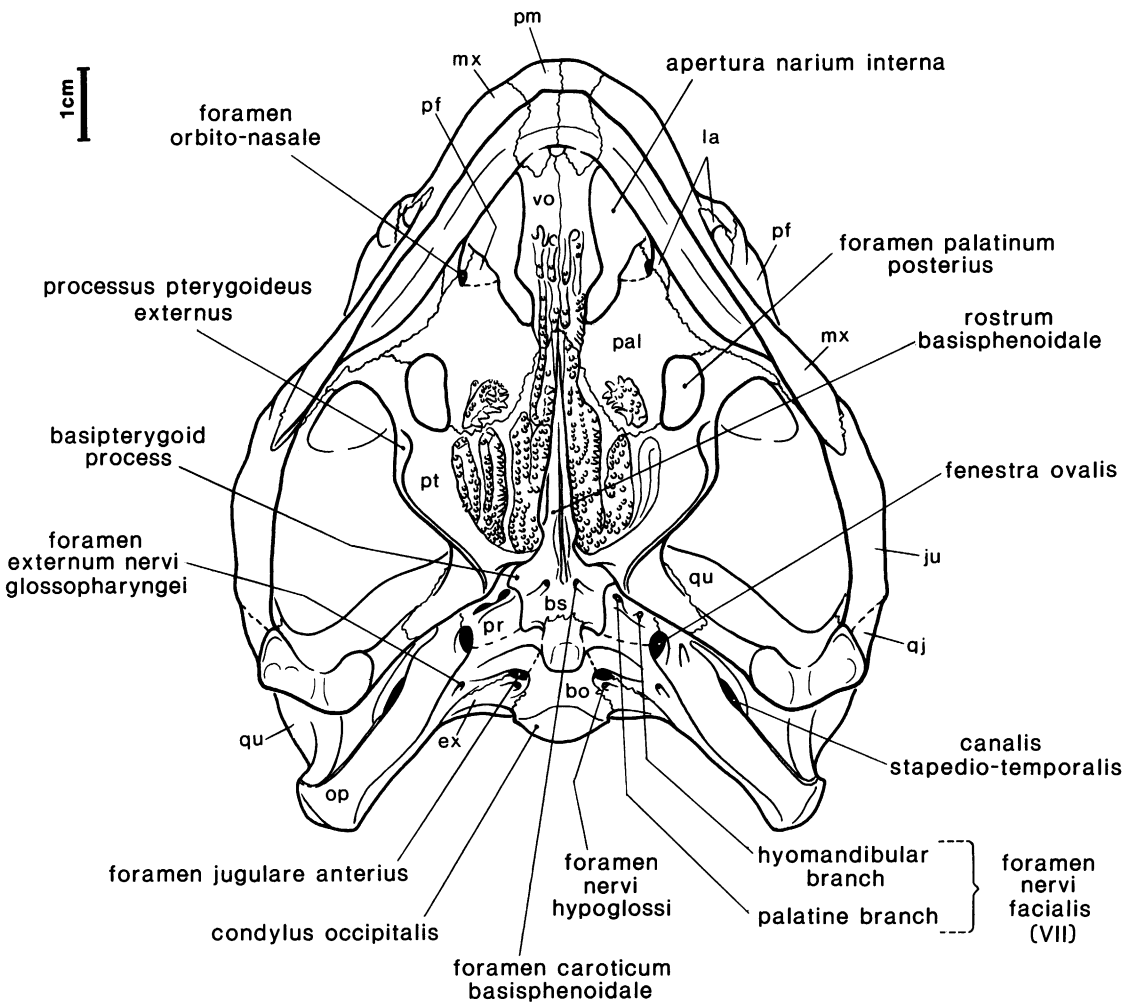

Fig. 27. Continued.

in *Proganochelys* running from the dorsal margin of the apertura narium externa posteriorly to the region of the fissura ethmoidalis which forms a midline trough dividing the fossa nasalis into lateral chambers. Anterolaterally, the fossa nasalis is formed by the dorsal process of the maxilla. Posterolaterally, the prefrontal forms most of the lateral chamber of the fossa nasalis. The descending process of the prefrontal separates the fossa orbitalis from the fossa nasalis, as in other turtles, but it also forms an extension of the fossa nasalis that is unusual for turtles. As can be seen best on the left side of SMNS 16980, the prefrontal defines a cavity that extends the fossa nasalis posteriorly and posteroventrally into the prefrontal and within the bony area forming the orbital margin. I have not found this cavity in other turtles and the homologous space appears to be obliterated by the telescoping of the snout in Casichelydia. In *Captorhinus* the space exists but it is not defined by bone to the extent seen in *Proganochelys*. Whether this condition in *Proganochelys* is autapomorphic for the taxon or whether it is structurally intermediate between the captorhinid and chelonian condition cannot be determined at present.

The size of the fossa nasalis in *Progan-*

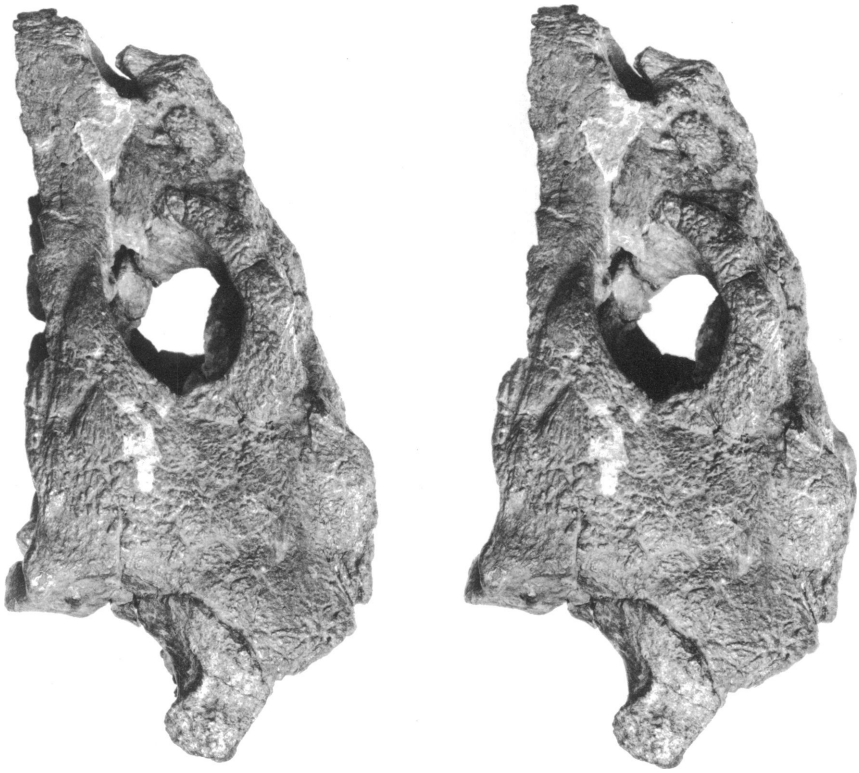

Fig. 28. *Proganochelys quenstedti,* MB 1910.45.2. Stereophotographs of left lateral view of skull.

Fig. 29. *Proganochelys quenstedti,* SMNS 16980. Stereophotographs of left lateral view of skull.

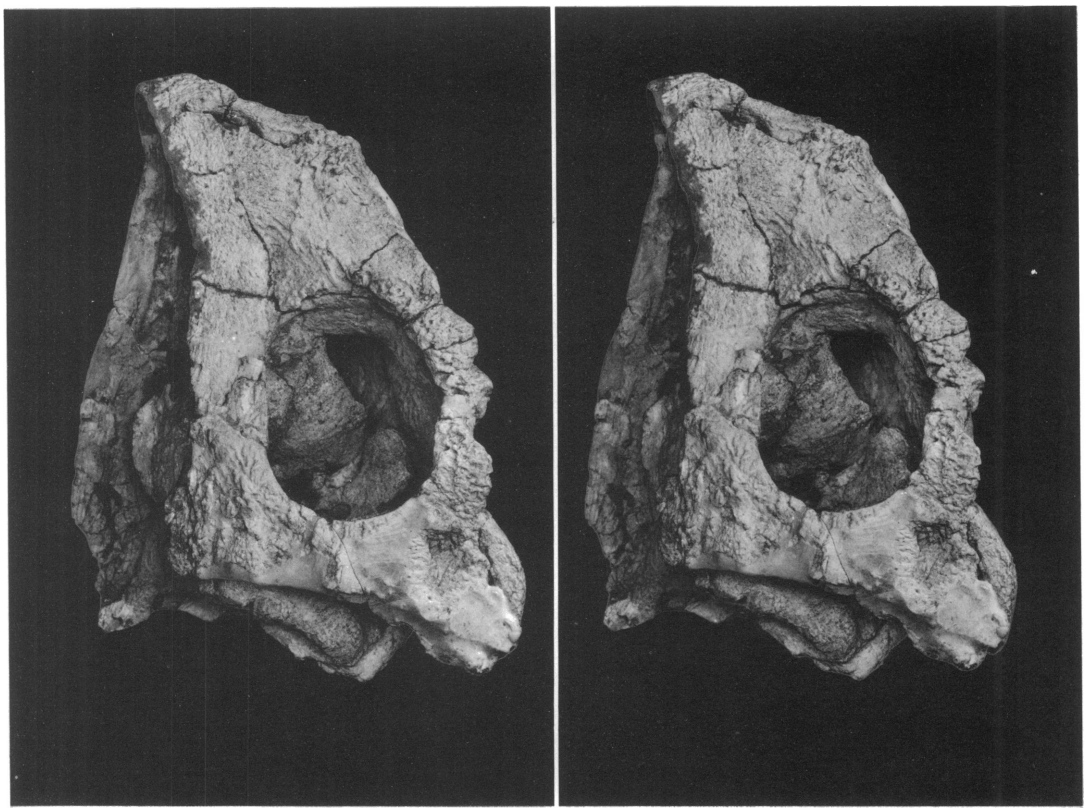

Fig. 30. *Proganochelys quenstedti,* SMNS 15759. Stereophotographs of left lateral view of skull.

ochelys is intermediate between the large nasal area of *Captorhinus* and the small area of Casichelydia. The differences involve both the length and the width of the fossa, but *Proganochelys* is advanced over *Captorhinus* in having much of the snout telescoping seen in Casichelydia but retaining the width of the fossa nasalis seen in *Captorhinus.*

LACRIMAL
(figs. 16, 40, 43)

Proganochelys is the only turtle known to have a lacrimal bone. Although the area is preserved in all three skulls, clear sutures are best seen in SMNS 16980.

The lacrimal is a roughly triangular element lying in the anteroventral corner of the orbit. Anteriorly and ventrally it contacts the maxilla; dorsally and medially it contacts the prefrontal; and posteroventrally it probably has a short contact with the jugal. Ventromedially, the lacrimal may have reached the palatine but this area is ambiguous in all specimens. On the internal surface of the skull the limits of the lacrimal are similar to those on the outside. In SMNS 16980, a single, large lacrimal foramen opens anteriorly into a lacrimal canal. The foramen and canal are approximately in the center of the lacrimal bone and are formed entirely by it. The canal is short and penetrates the bone, opening on the internal surface of the lacrimal bone in the posterolateral part of the fossa nasalis. The internal lacrimal foramen leads into a trough that extends anteriorly onto the maxilla and appears to have continued the structure contained in the lacrimal canal. This trough is best seen on the right side of SMNS 16980.

In SMNS 15759 two distinct lacrimal foramina can be seen on each side of the skull in the anteroventral orbital margin. Internal information is lacking and it cannot be de-

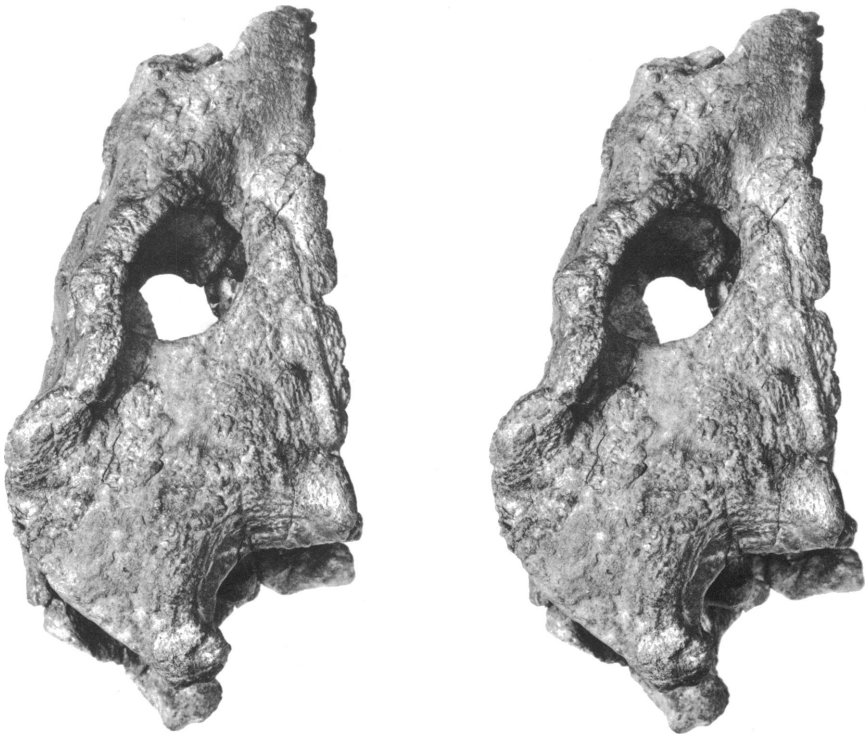

Fig. 31. *Proganochelys quenstedti,* MB 1910.45.2. Stereophotographs of right lateral view of skull.

Fig. 32. *Proganochelys quenstedti,* SMNS 16980. Stereophotographs of right lateral view of skull.

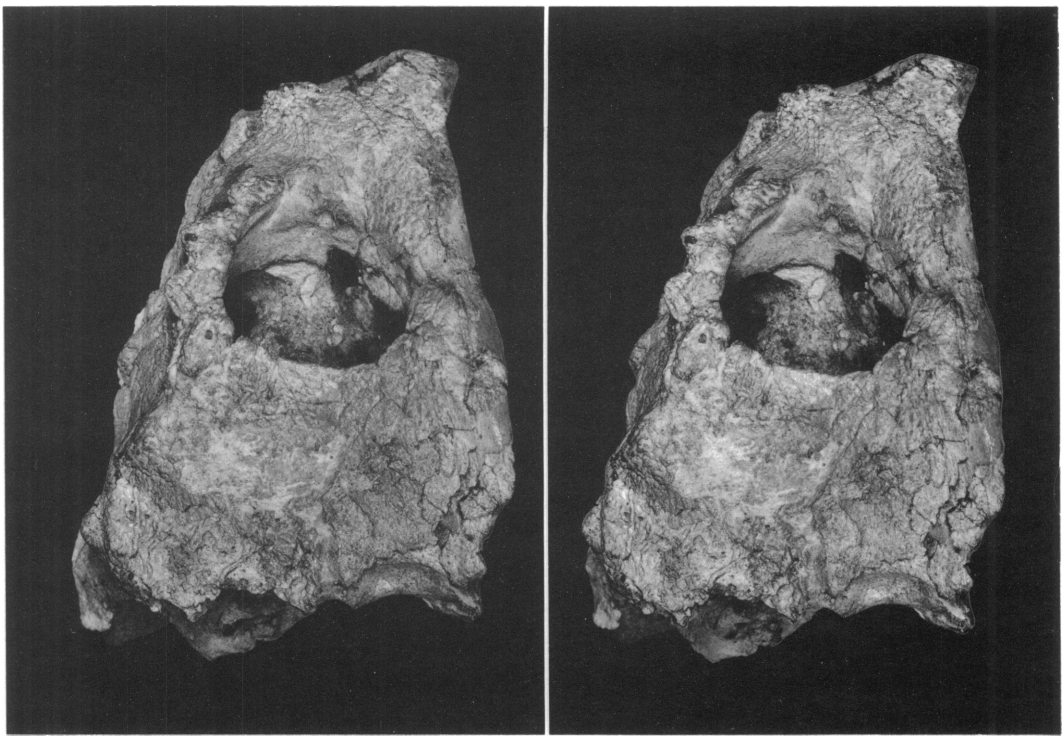

Fig. 33. *Proganochelys quenstedti,* SMNS 15759. Stereophotographs of right lateral view of skull.

termined whether or not these foramina joined a common canal or whether two canals were present. In *Captorhinus* (Heaton, 1979: fig. 15) more than one foramen is present in this position.

All other turtles lack the lacrimal bone and the lacrimal duct. In *Captorhinus* and generalized amniotes, the duct penetrates the bone and extends most of its length. The reduction of the bone in *Proganochelys,* however, may not correspond with the reduction of the soft tissue lacrimal duct because a clearly defined trough can be seen in the fossa nasalis that runs along the lateral wall of the fossa nasalis.

The primitive amniote condition of the lacrimal is one in which that bone extends from the apertura narium externa along the side of the skull to the anterior margin of the orbit. It is a large element with more lateral exposure than the maxilla. In many amniote groups, however, the extent of the lacrimal is reduced and it comes to be associated primarily with the orbital margin. In *Proganochelys* the anterior portion of the primitive amniote lacrimal is absent, being replaced by broad contact of the dorsal maxillary process with the nasal and prefrontal. In Casichelydia the area occupied by the lacrimal in *Proganochelys* is formed by the maxilla and prefrontal which meet in the anterior orbital margin. The morphologic telescoping of the snout in turtles is clearly related to many of the differences in the lacrimal but snout reduction can be seen in other amniote groups that have also retained the lacrimal bone.

FRONTAL
(figs. 16, 43)

The frontal is preserved in all three *Proganochelys* skulls but sutures can be clearly seen only in SMNS 16980. The frontal is a flat, paired element lying in the middle of the skull roof, between the orbits. Anteriorly the frontal contacts the nasal; laterally there is a long prefrontal contact followed by an equally long postorbital contact. This lateral suture trends laterally to a slight extent so that the frontal is wider posteriorly than anteriorly.

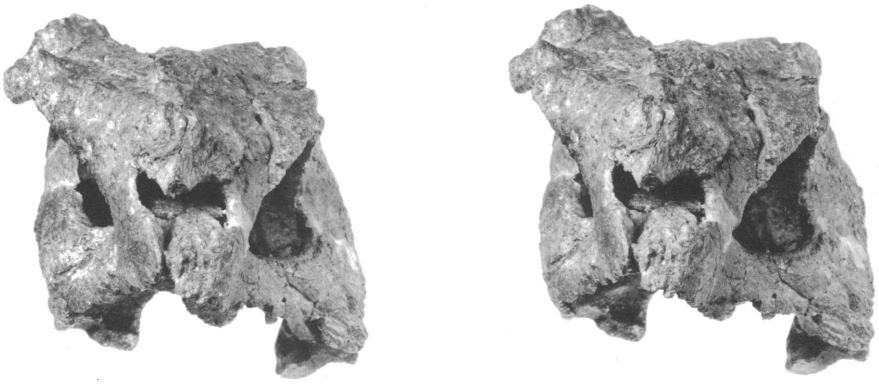

Fig. 34. *Proganochelys quenstedti,* MB 1910.45.2. Stereophotographs of anterior view of skull.

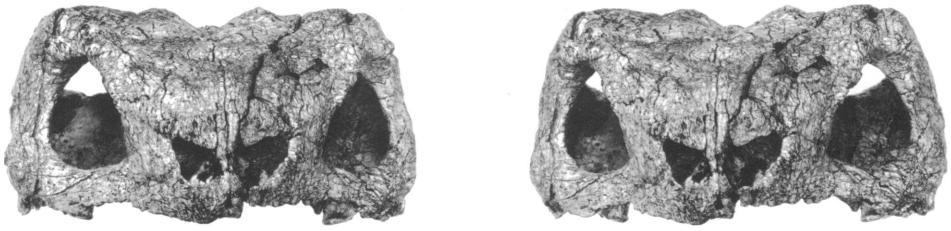

Fig. 35. *Proganochelys quenstedti,* SMNS 16980. Stereophotographs of anterior view of skull.

The posterior margin of the frontal is a transverse suture with the parietal except for the posterolateral corner where the postorbital curves posteromedially. Orbital exposure of the frontal is prevented by broad contact of the prefrontal and postorbital.

On the ventral surface the nasal underlies the anterior portion of the frontal so that the nasal-frontal suture trends posterolaterally from the midline. The prefrontal-frontal suture is not entirely clear but the prefrontal also seems to underlie the frontal laterally. The frontal lacks a well-developed sulcus olfactorius but that structure is nonetheless delimited by a low, parasagittal ridge that is highest anteriorly and virtually disappears as it approaches the parietal.

In *Captorhinus* and most turtles the frontal enters the orbital margin. Primitive cryptodires, such as *Kayentachelys* and pleurosternids, also have this condition and it is presumably primitive for Casichelydia, although it is highly variable in turtles as a group. *Meiolania* has a broadly meeting nasal and prefrontal similar to that of *Proganochelys* but the condition in *Meiolania* appears to result from the distal enlargement of both bones to overhang the nose and orbit to form the accessory nasal sinus. The broad nasal-prefrontal contact in *Proganochelys* is, therefore, interpreted as an autapomorphy.

PARIETAL
(figs. 16, 43, 49)

The parietal is preserved in all three *Proganochelys* skulls, but it is complete and delimited by clear sutures only in SMNS 16980.

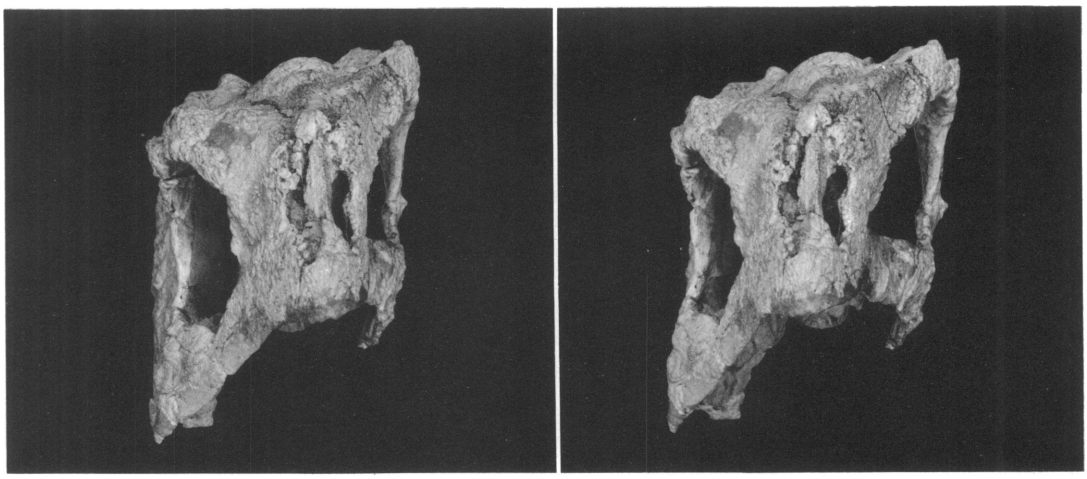

Fig. 36. *Proganochelys quenstedti,* SMNS 15759. Stereophotographs of anterior view of skull.

The parietal of *Proganochelys* has a horizontal plate on the skull roof and a vertical, parasagittal plate extending ventrally. The dorsal plate is wider than long and contacts the frontal anteromedially and the postorbital anterolaterally. The short, parasagittal margin of the parietal contacts the squamosal and the supratemporal lies on the parietal's posterolateral corner. Posteriorly the parietal forms the dorsal margin of the fossa temporalis superior and medially it meets the other parietal in a suture extending the length of the bone.

The skull roof portion of the parietal in *Proganochelys* differs from that bone in *Captorhinus* in being wider than long; in *Captorhinus* it is longer than wide. In other turtles the condition varies a great deal but it would seem from an examination of *Kayentachelys,* pleurosternids, and pleurodires that a long parietal is primitive for Casichelydia. In *Meiolania* the parietal is equidimensional. It would appear that the broad parietal is autapomorphic for *Proganochelys.* In comparison with *Captorhinus,* the postfrontal and postparietal contacts are absent, the frontal and postorbital contacts are tranversely long, and the squamosal contact is short. In comparison with the generalized casichelydian condition, such as is seen in *Kayentachelys* and *Pleurosternon,* the parietal of *Proganochelys* has the same contacts in about the same positions, once the differing lengths of the parietal are accounted for. The supratemporal contact found in *Proganochelys* is absent in casichelydians.

A pineal foramen is present in *Captorhinus* but absent in *Proganochelys* and nearly all other turtles (except as a variation in some testudinids and protostegids).

The ventral surface of the horizontal parietal plate has much the same relations to the other skull roof elements as the dorsal surface. The principal exception being the parietal-squamosal contact beneath the supratemporal, the latter bone having no exposure on the ventral surface of the skull roof. No vestige of a parietal foramen is visible.

The processus inferior parietalis is a very distinctive feature of turtles, extending from the skull roof ventrally to form much of the side wall of the braincase. The parietal of *Captorhinus* and other generalized amniotes is a flat, horizontal plate, entirely lacking a ventral process and a bony side wall to the braincase. In *Proganochelys* the processus inferior parietalis is present and well developed, but it is not as extensive as in casichelydians. The ventral contacts of the processus are best seen on the left side of SMNS 16980. The anteriormost contact is with the processus clinoideus of the basisphenoid (discussed below). Behind the foramen located between parietal and basisphenoid is a long parietal-prootic contact, as in other turtles. Posterior to the prootic the opisthotic appears to contact the parietal. The prootic-opisthotic suture is not clear on the left side but on the

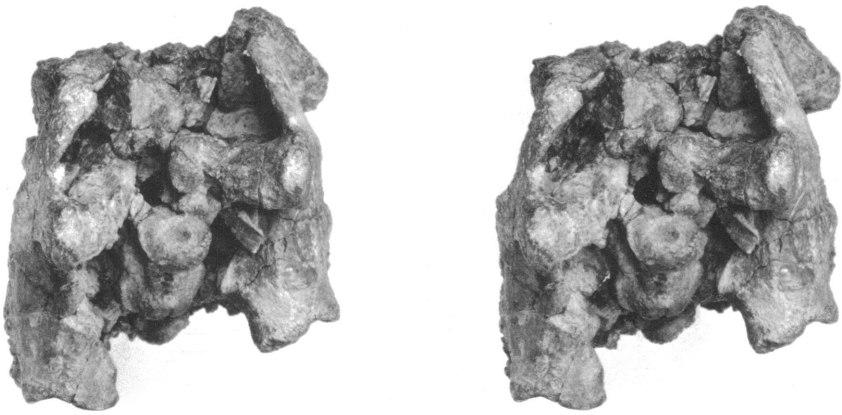

Fig. 37. *Proganochelys quenstedti,* MB 1910.45.2. Stereophotographs of occipital view of skull.

Fig. 38. *Proganochelys quenstedti,* SMNS 16980. Stereophotographs of occipital view of skull.

right side it seems to extend dorsomedially along the line of the foramen stapedio-temporalis. A parietal-opisthotic contact does not usually occur in Casichelydia (nor in *Captorhinus*) and in most turtles the supraoccipital lies between these bones. The supraoccipital of *Proganochelys,* as interpreted on the basis of one ambiguous specimen, is very small, but it is quite possible that this interpretation is in error. Posteriorly the parietal is exposed on the midline just below the skull roof margin. The supraoccipital forms the parietal margin below and lateral to this exposure but the exoccipital does not appear to reach the parietal (contrary to the figure in Gaffney, 1983; Gaffney and Meeker, 1983) being prevented by a supraoccipital-opisthotic contact as seen in Casichelydia.

Even relatively generalized turtles like *Kayentachelys* and *Pleurosternon* have a recognizable crista supraoccipitalis, most turtles being characterized by a very large one. *Proganochelys,* however, is barely advanced over *Captorhinus* in the development of this feature. In *Proganochelys,* as I interpret the sutures, the parietal and supraoccipital form the midline between the skull roof and the foramen magnum. In all Casichelydia the supraoccipital forms the midline reaching the parietal only at the margin of the skull roof (the exoccipitals may meet between the foramen magnum and the supraoccipital). In

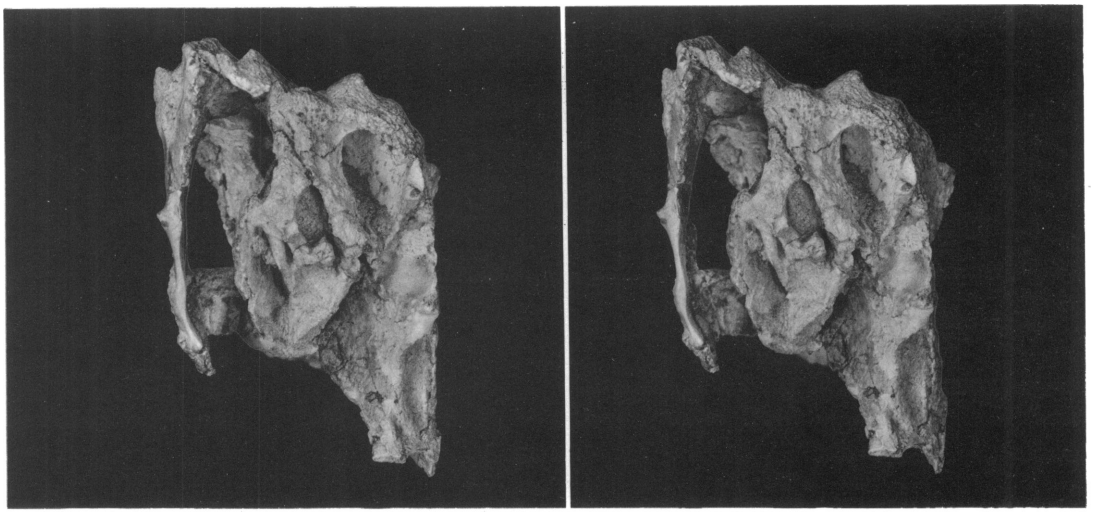

Fig. 39. *Proganochelys quenstedti,* SMNS 15759. Stereophotographs of occipital view of skull.

Casichelydia the parietals do not meet in the midline on the occiput; in view of the absence of any ventral parietal portion in *Captorhinus* the unique presence of this feature in *Proganochelys* is difficult to evaluate. In any case, the parietal and supraoccipital of *Proganochelys* bear a low, sagittal ridge that is similar in extent to that seen on the supraoccipital in *Captorhinus* and may be the homolog of at least a portion of the crista supraoccipitalis of casichelydians.

The anterior margin of the processus inferior parietalis in *Proganochelys* forms the posterior margin of the foramen interorbitale, which is very large in *Proganochelys* when compared with Casichelydia. In *Proganochelys* the processus inferior parietalis does not extend anteriorly very much beyond the position of the trigeminal ganglion, and a completely formed foramen nervi trigemini does not occur in *Proganochelys.* In casichelydians, the processus inferior parietalis has an extensive portion anterior to the foramen nervi trigemini (except in *Dermochelys*), a distinct advance over *Proganochelys* in the formation of an ossified cavum epiptericum (see Gaffney, 1979a).

A short process extends from the anteroventral margin of the processus clinoideus of the basisphenoid. Above and lateral to this process is a shelf formed by both the parietal and prootic that I interpret as the homolog of the foramen nervi trigemini of casichelydians. This foramen in casichelydians is external (i.e., lateral) to the cranioquadrate space. The parietal-prootic shelf of *Proganochelys* is extended ventrally by the quadrate to form the posterior and ventral margins of the foramen nervi trigemini. The parietal-basisphenoid contact is an ossification in the pila prootica, even though it produces a foramen; this foramen is internal to the cranioquadrate space and not homologous with the foramen nervi trigemini of Casichelydia. A contact with the processus clinoideus via a process of the parietal has been reported in *Plesiochelys* (Gaffney, 1976). It is possible that such a feature is primitive for turtles, although it is absent in captorhinids and nearly all other turtles. At present, an ossified pila prootica is best interpreted as an autapomorphy of *Proganochelys.*

The internal surface of the parietal is visible only in SMNS 16980 and the sutures limiting the processus inferior parietalis are not clear. However, the supraoccipital can be seen to underlie much of the posterior portion of the parietal, in contrast to its apparent limited external exposure. On the midline the supraoccipital ends abruptly about midway along the length of the parietal in an anteriorly facing facet that represents the change

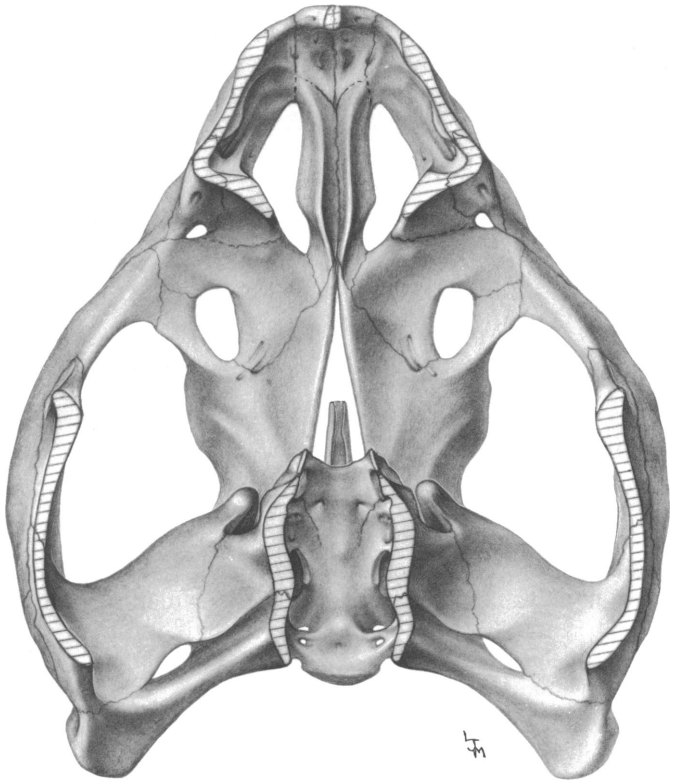

Fig. 40. *Proganochelys quenstedti,* SMNS 16980. Dorsal view of horizontally sectioned skull.

from bone to cartilage in the tectum synoticum (see Gaffney, 1979a: 10). Laterally, the supraoccipital extends ventrally beneath the parietal but the contacts with other bones are unclear.

JUGAL
(figs. 16, 40, 43)

The jugal is present in all three *Proganochelys* skulls but sutures are clearly seen only in SMNS 16980. The jugal is a flat element, roughly triangular in outline, forming much of the cheek, with a small medial process articulating with the palate.

Posteriorly, where the jugal is tallest, it articulates with the quadratojugal. Ventrally it forms the ventral margin of the cheek with no indication of emargination. Posterodorsally, the jugal contacts the squamosal; anterodorsally it contacts the postorbital. Anteriorly the jugal enters the ventral part of the orbit and forms the orbital margin at that point. Below the orbit the jugal has a suture with the maxilla that begins in the orbit and extends posteroventrally to the ventral cheek margin.

The jugal of *Proganochelys* is relatively large for a turtle and it is also relatively large when compared with the *Captorhinus* jugal. The size may be autapomorphic, but it may also be interpreted as correlated with the "telescoping" of the skull in comparison to *Captorhinus* and could be considered primitive for turtles. *Proganochelys* retains the jugal-squamosal contact seen in *Captorhinus*; the absence of this contact is a casichelydian synapomorphy. In *Captorhinus* the jugal extends forward under the orbit to reach the lacrimal and maxilla at the level of the anterior margin

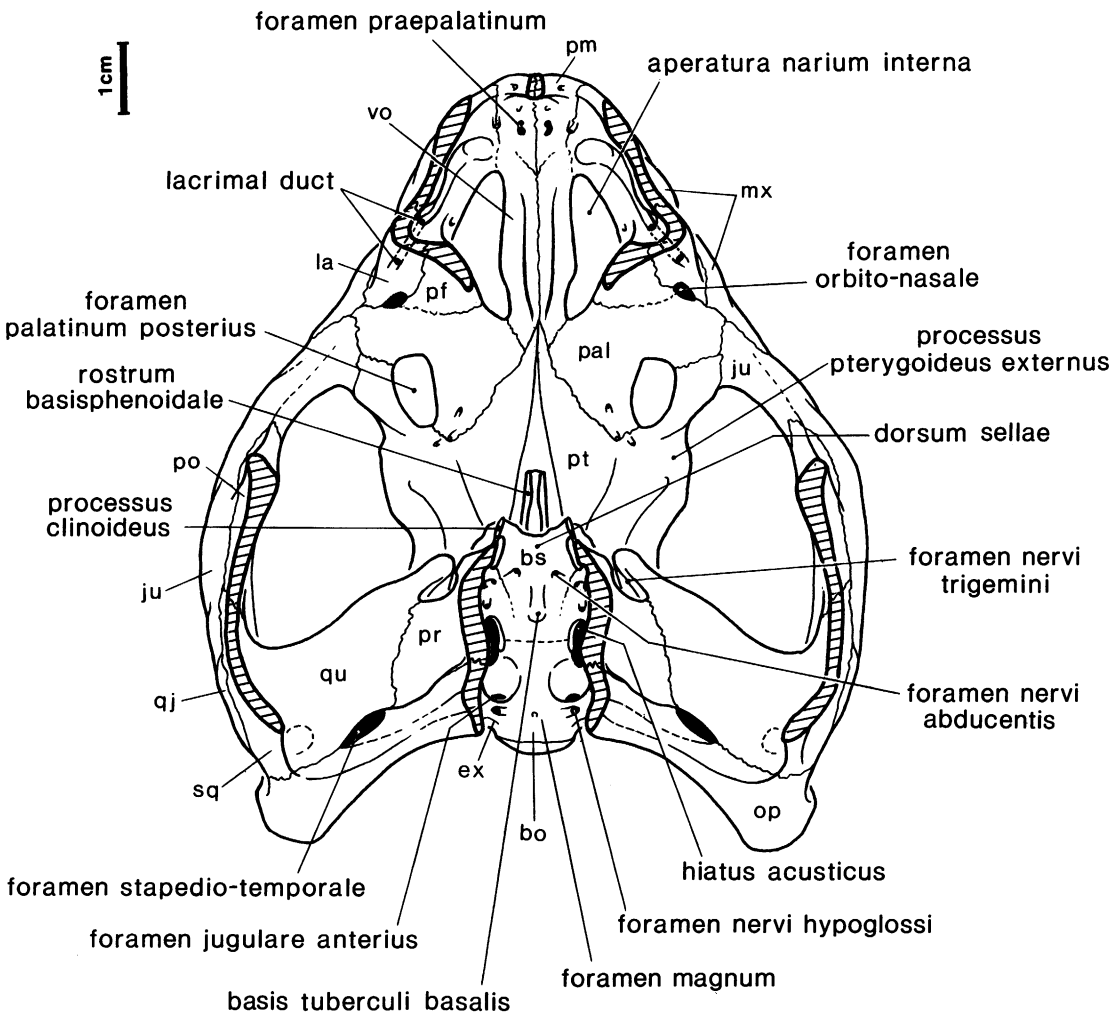

Fig. 40. Continued.

of the orbit. In *Proganochelys* the jugal does not extend anteriorly as far as in *Captorhinus,* and does not appear to reach the lacrimal. The area is preserved on both sides of SMNS 16980, and on both sides matrix fills a space between jugal and lacrimal. Nonetheless, the anterior extension of the jugal is greater in *Proganochelys* than in most Casichelydia. Thus the lack of an anterior jugal process reaching the anterior orbital margin is a chelonian synapomorphy.

In *Captorhinus* the jugal forms the ventral cheek margin for nearly its entire length. In *Proganochelys* and other turtles the maxilla sends a process posteriorly below the jugal to separate the jugal from the cheek margin for the anterior half or more of the length of the jugal. There are numerous modifications of this condition in more advanced chelonian groups.

The medial process of the jugal is best seen on the right side of SMNS 16980, but its relations are somewhat obscured by breakage. In ventral view the process seems to be nearly absent; only a short spur extending anteromedially along the anterior margin of the fossa subtemporalis. The process contacts the pterygoid anteriorly and medially and the maxilla anterolaterally. Dorsally, however, the jugal overlies the pterygoid and extends

farther anteriorly and medially. On the ventral surface, the above-described sutures are also breaks along which slight displacement seems to have occurred. Thus there is some possibilility for error. On the dorsal surface the jugal has what appears to be a relatively straight sutural margin medially that contacts the pterygoid. The anterior jugal contacts are in doubt but it appears to reach the palatine anterior to the pterygoid contact. The jugal does not border the foramen palatinum posterius nor the foramen orbitonasale, although the latter is separated from the jugal by a block of matrix.

Proganochelys has a medial jugal process comparable in size to that seen in *Captorhinus* but less visible in ventral view and not forming part of the foramen palatinum posterius (= suborbital foramen) as in *Captorhinus.* Although the jugal rarely forms part of this foramen in most turtles, it does reach it in *Kayentachelys* and *Pleurosternon,* suggesting that a jugal contribution to the foramen palatinum posterius is primitive for the Casichelydia. Its absence in *Proganochelys* is interpreted as an autapomorphy.

Quadratojugal
(fig. 16)

The quadratojugal is present on both sides of the Berlin skull, on the right side of SMNS 15759, and on both sides of SMNS 16980. Sutures are clearest in the latter specimen. The quadratojugal in *Proganochelys* is a vertically elongate sheet of bone in the posterior part of the cheek. Dorsally, the quadratojugal meets the squamosal, anterior the jugal, and posteriorly the quadrate. The quadratojugal is a thin element and even in SMNS 16980 it is incomplete on both sides. The posterior contact with the quadrate is curved concave posteriorly and forms the anterior margin of the cavum tympani, as in Casichelydia. The quadratojugal-quadrate suture is tight and seems to be fused, at least ventrally. The quadrate underlies the quadratojugal for most of this contact. Anteriorly the quadratojugal is broken on both sides of SMNS 16980 so that there is a small space (on the left side) and a large space (on the right side) between the quadratojugal and the jugal. Both the Berlin skull and SMNS 15759 are solid in this area, and I feel that the spaces in SMNS 16980 are the result of breakage. The quadratojugal-jugal contact seems to have been a squamous one, as in Casichelydia.

The quadratojugal of *Proganochelys* is clearly more similar to that in casichelydians than to that in *Captorhinus,* but this situation is probably closely related to the structure of the quadrate. In turtles the quadrate has a funnel-shaped cavum tympani with lateral exposure of the quadrate while in *Captorhinus* the quadrate is smaller, lacks a cavum tympani, and has no lateral exposure. The quadratojugal of *Captorhinus* is a horizontally elongate element lying lateral to the quadrate with much of the quadrate attached to its medial surface. In *Captorhinus* the quadratojugal forms part of the posterior margin of the skull, has a long dorsal suture with the squamosal, and has a short anterior contact with the jugal. In *Proganochelys* and in other turtles, the presence of a laterally exposed and vertically elongate quadrate is correlated with a different position of the quadratojugal. *Proganochelys* agrees with other turtles and is distinct from *Captorhinus* in the following features: vertically elongate quadratojugal, quadrate prevents posterior margin of quadratojugal from reaching posterior margin of the skull, C-shaped suture with quadrate along margin of cavum tympani, and extensive suture with jugal. *Kayentachelys* differs from *Proganochelys* and most other turtles in lacking a C-shaped quadratojugal-quadrate suture. This is related to the relatively small size of the quadratojugal in *Kayentachelys,* a presumed autapomorphy of this taxon.

As discussed under postorbital, *Proganochelys* differs from Casichelydia and agrees with *Captorhinus* in lacking a postorbital-quadratojugal contact, a presumed synapomorphy of Casichelydia.

Squamosal
(figs. 16, 40, 52)

The squamosal is preserved at least to some extent in all three *Proganochelys* skulls. In SMNS 15759 the bone is largely missing on the left side while on the right the posteroventral portion is missing. In the Berlin skull most of the squamosal is missing on the right

side, but it is nearly complete on the left. In neither of these skulls are most of the sutures clear; the position of the bone is based primarily on comparisons with SMNS 16980. In SMNS 16980 the squamosal is preserved complete on both sides with most of the sutures distinct.

The squamosal of *Proganochelys* is a plate-like element, curving ventrally from the skull roof to form part of the posterolateral skull area. In casichelydians the squamosal is conspicuously different; it is cone-shaped and contains a space, the antrum postoticum, that communicates with the cavum tympani. There is no indication whatever of this structure in *Proganochelys* and the squamosal is a simple, curved plate. This condition in *Proganochelys* is also different in *Captorhinus.* The squamosal in *Captorhinus* is a flat curved plate in the skull roof, much as in *Proganochelys,* but curves at the occiput to form a medially directed flange that forms a posterior wall for much of the temporal fossa and constricts the posterior temporal opening. This flange is absent in *Proganochelys*; there is no posterior wall for the temporal fossa, and the posterior temporal opening is very large.

In SMNS 16980 the squamosal contacts the postorbital anteriorly in an irregular, roughly transverse suture. There is a parasagittal contact with the parietal medially, and the supratemporal posteromedially. Anteroventrally the squamosal contacts the jugal, ventrally it contacts the quadratojugal, and posteroventrally the quadrate. Posteriorly the squamosal reaches the opisthotic.

The relations of the squamosal to the other dermal roof elements are not drastically different among captorhinids, *Proganochelys,* and casichelydians. The parietal and postorbital contacts are similar, except in those casichelydians that have well-developed pos-

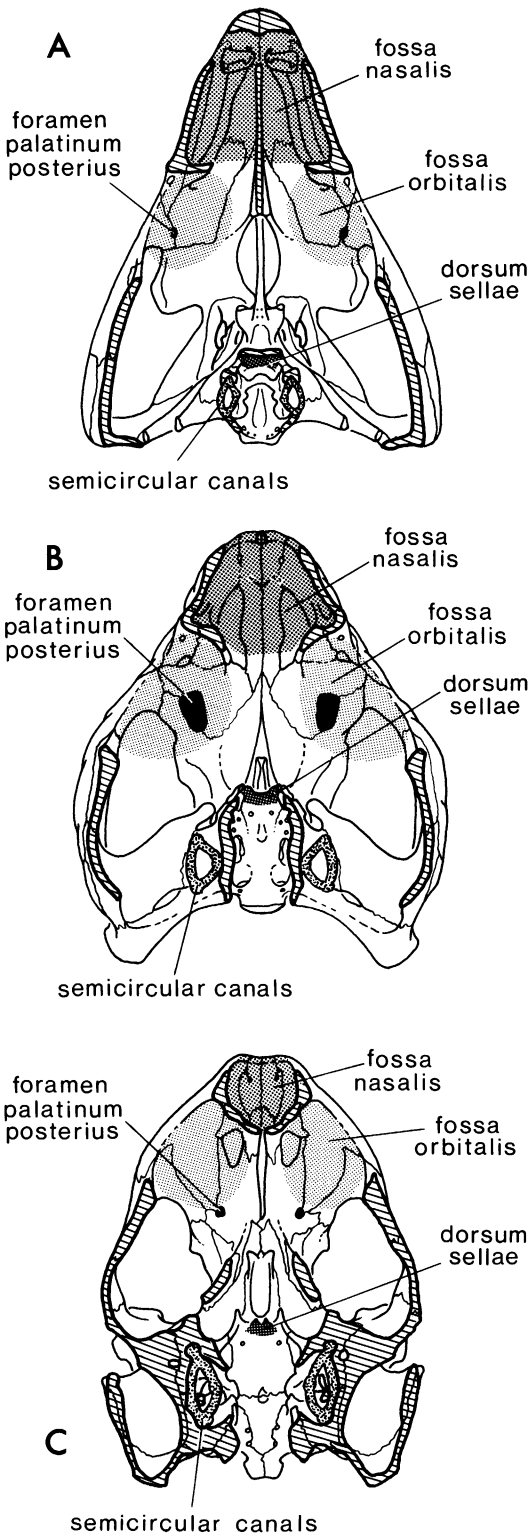

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Fig. 41. Comparison of horizontally sectioned skulls. Fossa nasalis, fossa orbitalis, dorsum sellae, and semicircular canals shown in different patterns for reference. **A,** *Captorhinus* sp., from Heaton (1979) and specimens. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Pseudemys concinna,* from Gaffney (1979a).

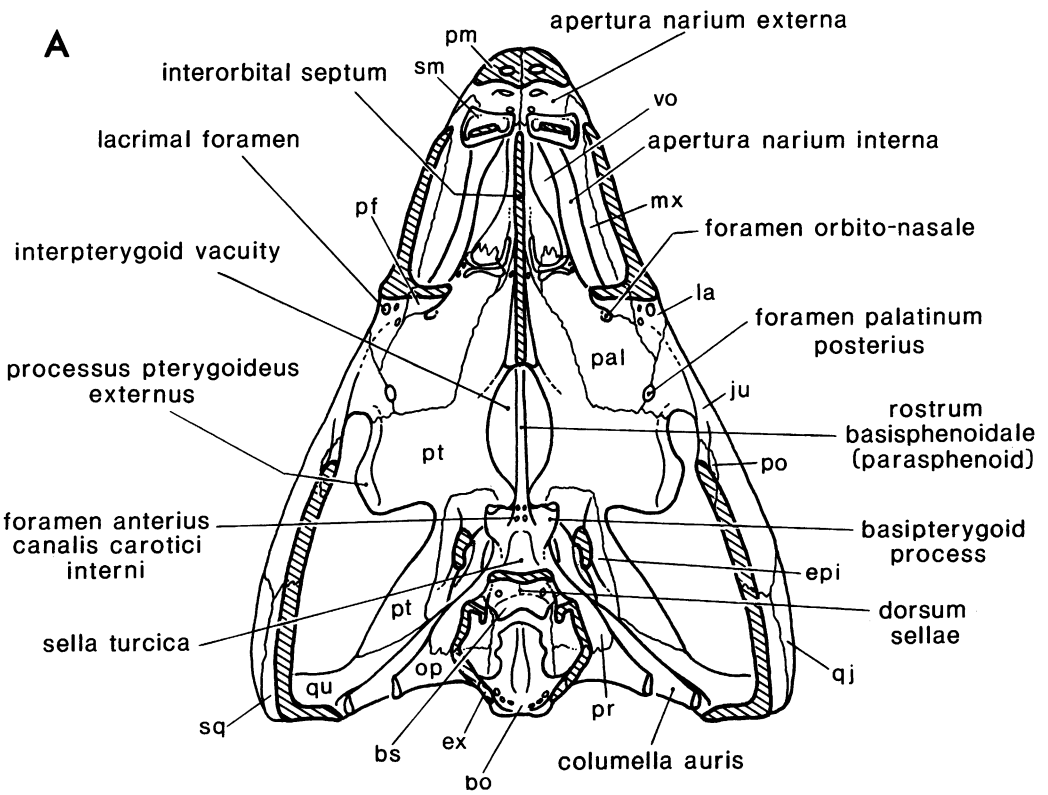
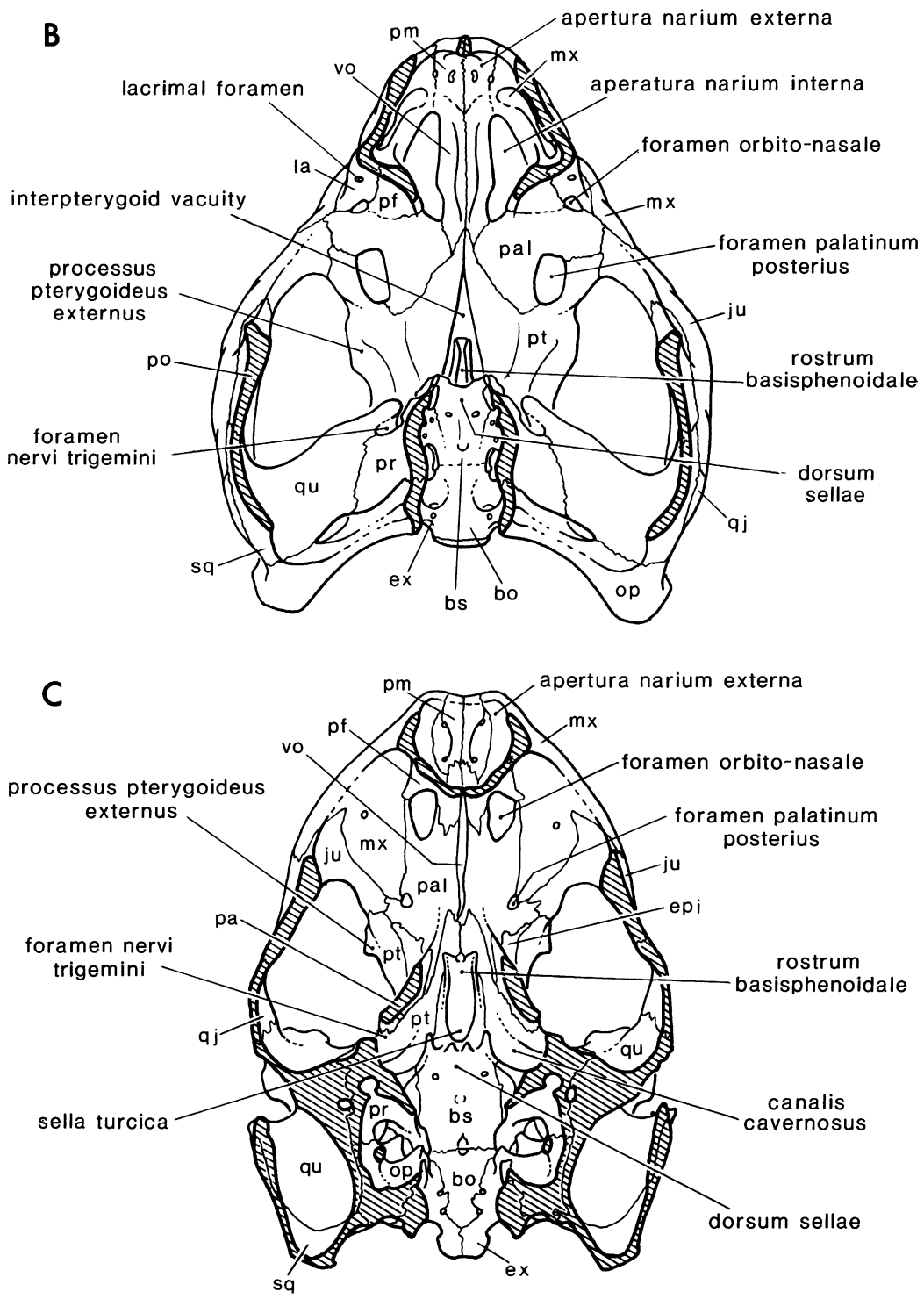


Fig. 42. Comparison of horizontally sectioned skulls. **A,** *Captorhinus* sp., from Price (1935), Heaton (1979) and specimens. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Pseudemys concinna,* from Gaffney (1979a).

terior temporal emargination, in which case the parietal contact may be absent and the postorbital contact reduced or absent. Casichelydians, however, lack a jugal-squamosal contact, present in captorhinids and *Proganochelys,* and this appears to be related to the smaller size of the jugal and the comparatively longer cheek in casichelydians. In captorhinids the squamosal has a long suture with the quadratojugal that runs for most of the length of the squamosal while this contact is much less in *Proganochelys.* Casichelydians are quite variable in this regard but would generally appear to be similar to *Proganochelys.* The lateral half of the supratemporal of captorhinids lies on the squamosal and this is the case in *Proganochelys,* although the supratemporal is a relatively larger element in the latter taxon. The bone is absent in casichelydians.

Significant differences involving the quadrate-squamosal contact can be seen among the three forms being compared. In captorhinids the quadrate is not visible or just barely visible in lateral view and the large squamosal forms nearly all of the posterior margin of the skull in lateral view. In *Proganochelys* the squamosal is much smaller and the quadrate is exposed laterally forming a significant part of the posterior skull margin in lateral view. In casichelydians the quadrate is developed into a typical cavum tympani so that instead of the limited quadrate-squamosal contact in *Proganochelys* there is a more extensive contact between the bones. Also in *Proganochelys* the squamosal-quadrate contact is virtually two-dimensional, the meeting of two curved plates, while in casichelydians the presence of the conical antrum postoticum, formed by the squamosal fitting on top of a well-developed cavum tympani, is a complex three-dimensional contact.



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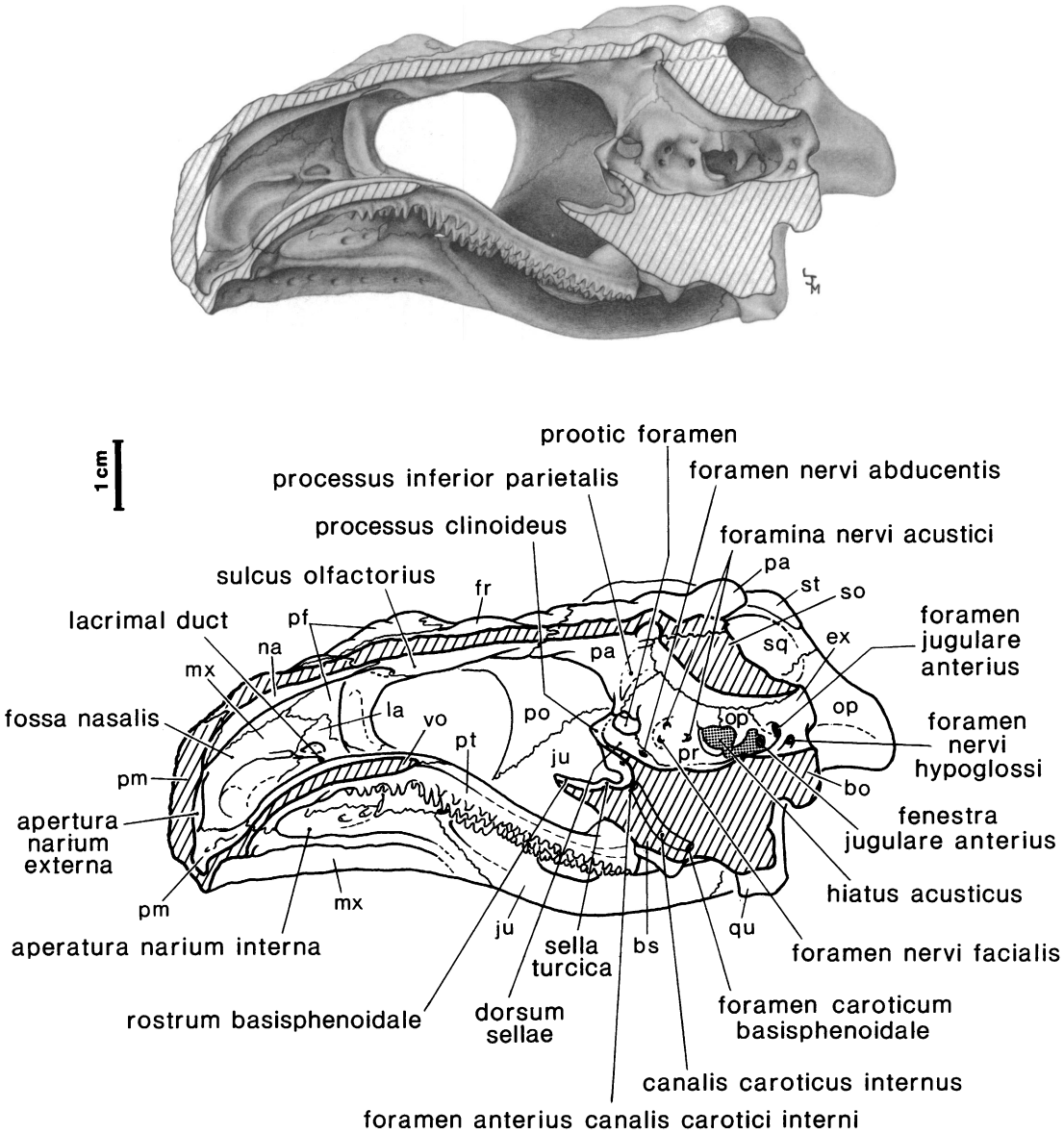


Fig. 43. *Proganochelys quenstedti,* SMNS 16980. Sagittally sectioned skull.

Posteriorly, the squamosal-opisthotic relations also differ among the three compared forms. In captorhinids the medial flange of the squamosal comes close to but does not (apparently) meet the paroccipital process of the opisthotic. In turtles, however, the paroccipital process has an extensive contact with the squamosal. In *Proganochelys* this contact is clear on the lateral and posterior surface of SMNS 16980 but less distinct on the internal surface. It is apparent, however, that the position of the contact is well lateral to its position in casichelydians due to the medial expansion of the squamosal in that group.

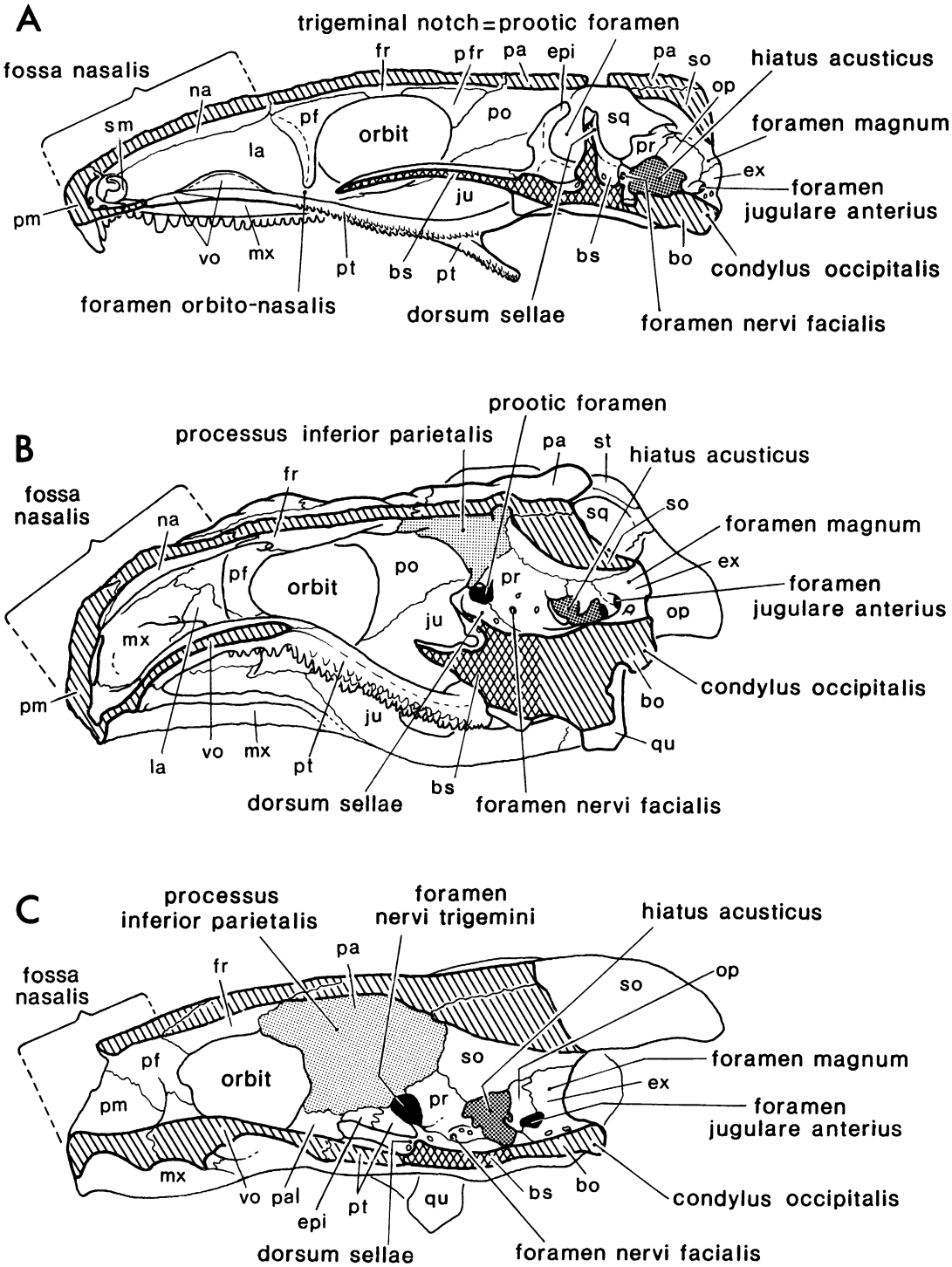


Fig. 44. Comparison of sagittally sectioned skulls. Different patterns are used for basisphenoid, hiatus acusticus, and processus inferior parietalis. **A,** *Captorhinus* sp., from Price (1935), Heaton (1979), and specimens. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Pseudemys concinna,* from Gaffney (1979a).

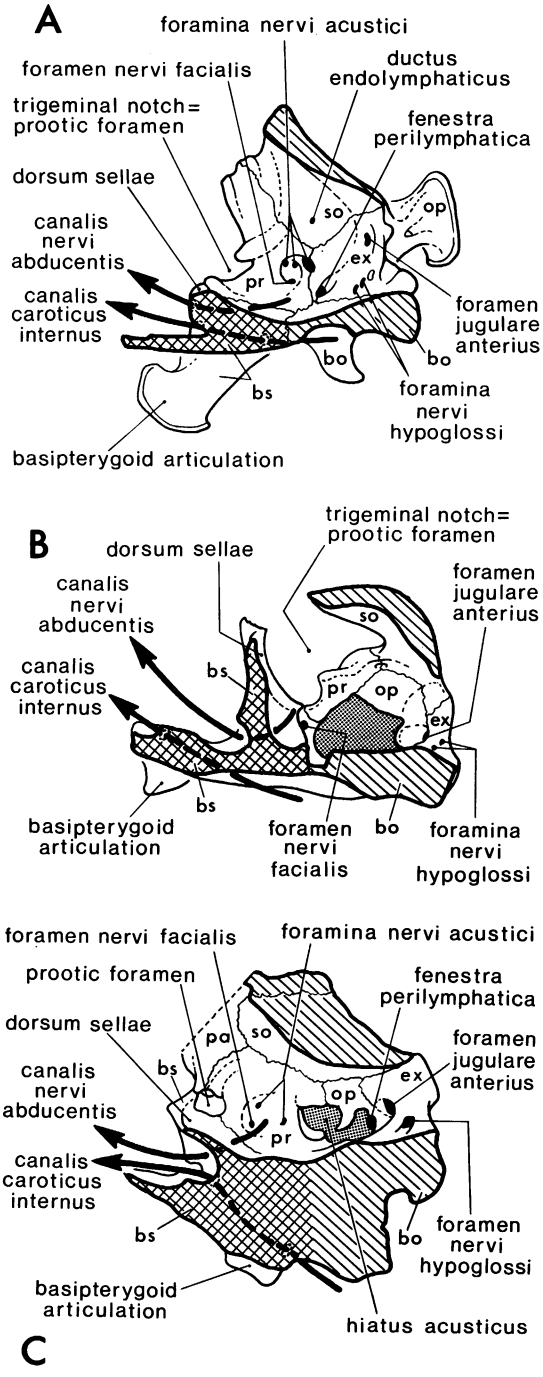


Fig. 45. Comparisons of neurocranial ossifications, sectioned sagittally. Anterior to the left, basisphenoid indicated by cross-hatching. **A,** *Ctenosaura,* from Oelrich (1956). **B,** *Captorhinus,* from Price (1935), Heaton (1979), and specimens. **C,** *Proganochelys* (SMNS 16980).

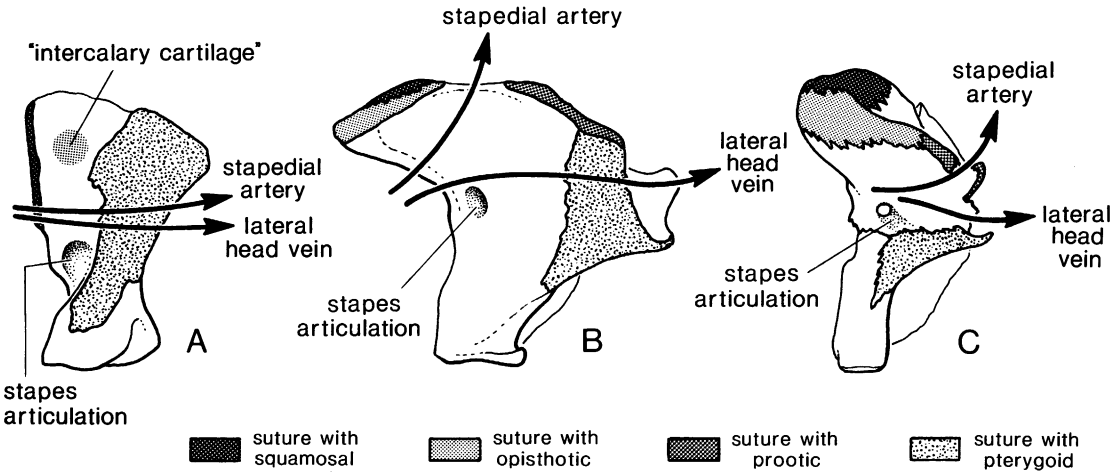


Fig. 46. Comparisons of the internal surface of left quadrates showing attachments and positions of various associated structures. Anterior to the right. **A,** *Captorhinus* sp., from Heaton (1979) and specimens. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Chelydra serpentina,* from Gaffney (1979a, fig. 10; note error in opisthotic suture in this figure) and AMNH 10786.

Postorbital
(fig. 16)

The postorbital of *Proganochelys* is present in all three skulls but sutures can be seen clearly only in SMNS 16980. The postorbital is a sheet of bone that lies posterodorsal to the orbit and forms part of the skull roof and part of the cheek. On the skull roof the postorbital contacts the prefrontal anteriorly, the frontal medially, the parietal posteromedially, and the squamosal posteriorly. Ventrally the postorbital has a long suture with the jugal beginning on the posteroventral orbital margin and rising dorsally to meet the squamosal. On the internal surface the contacts differ only slightly. The postorbital is thick where it forms the orbital margin and thins as the sheet extends away from the orbit.

The postorbital of *Proganochelys* occupies the area made up of postorbital plus postfrontal in *Captorhinus.* There is no trace of a postfrontal in *Proganochelys.* In Casichelydia the postorbital usually has a prominent contact with the quadratojugal, absent in *Proganochelys* and *Captorhinus.* The postorbital-quadratojugal contact takes place in casichelydians, preventing the jugal-squamosal contact seen in *Proganochelys* and *Captorhinus.* This condition in Casichelydia, i.e., the presence of a postorbital-quadratojugal contact and the absence of a squamosal-jugal contact, is hypothesized as a synapomorphy of Casichelydia.

Supratemporal
(figs. 16, 52)

Although the area is present, at least in part, in all three skulls, sutures delimiting the supratemporal are visible only in SMNS 16980. The supratemporal of *Proganochelys* is a small, paired element positioned at the posterolateral corner of the skull roof. The supratemporal contacts the parietal medially and the squamosal laterally and lies above both bones which meet beneath the supratemporal. There is no exposure of the supratemporal on the internal surface of the skull.

Casichelydia lack the supratemporal but it is characteristic of primitive amniotes. In *Captorhinus* the supratemporal fits into a notch in the parietal; *Proganochelys* does not seem to have this notch, the supratemporal seems to lie on the parietal. The size of the supratemporal in comparison to the rest of the skull is smaller in *Captorhinus* than in *Proganochelys,* a condition hypothesized here as autapomorphic for *Proganochelys.*

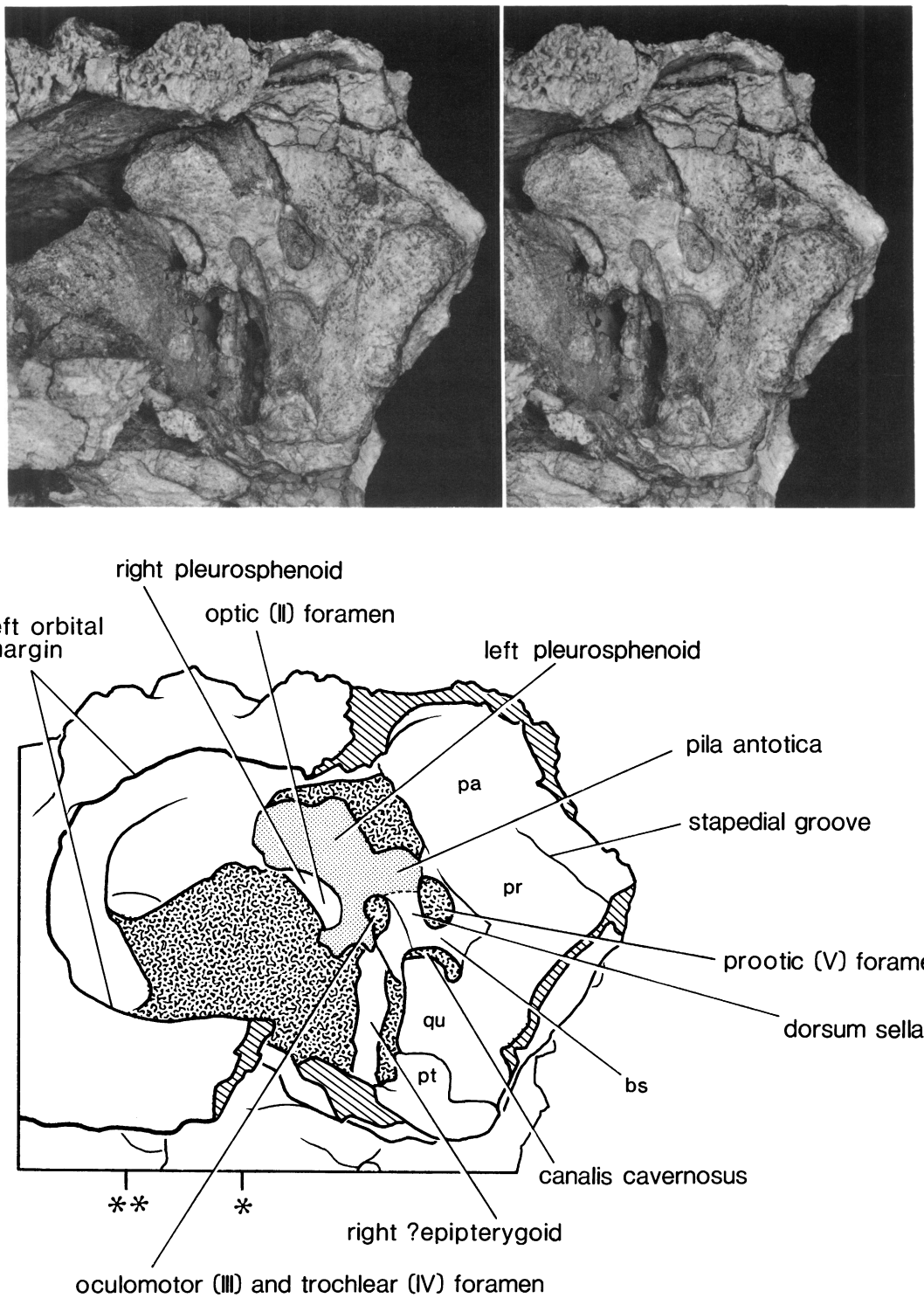


Fig. 47. *Proganochelys quenstedti*, SMNS 15759. Left ethmoid region with check removed. See also Figure 48.

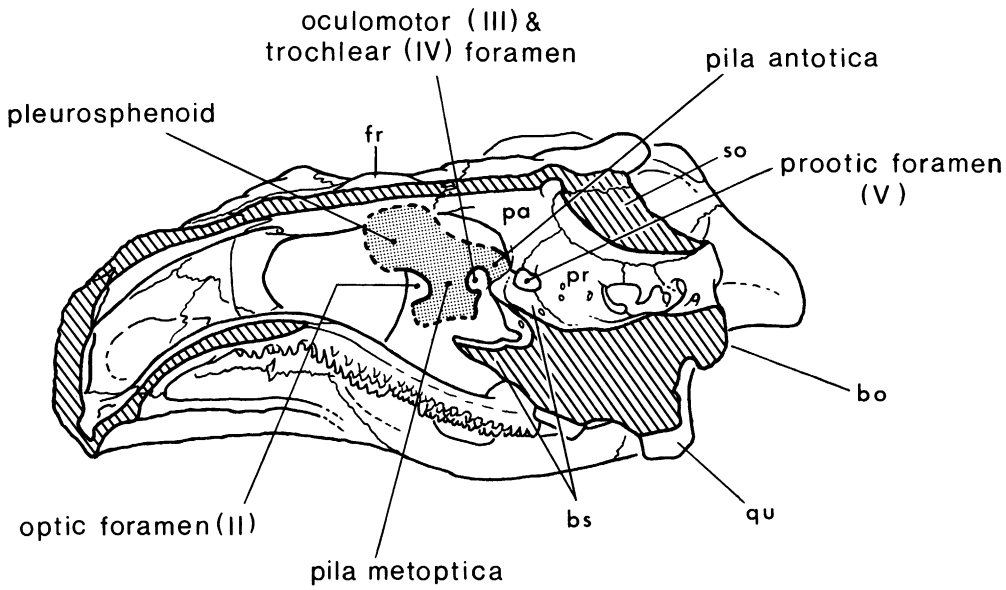


Fig. 48. *Proganochelys quenstedti,* SMNS 16980. Sagittal section with right laterosphenoid added from SMNS 15759. See Figure 47.

PALATAL ELEMENTS
(table 4, figs. 16, 27, 40, 43)

Premaxilla

The premaxilla is preserved in all three *Proganochelys* specimens but sutures are seen clearly only in SMNS 16980. The premaxilla is a relatively small, paired element lying at the front of the skull with a dorsal portion between the nares and a ventral portion of the triturating surface.

The dorsal process of the premaxilla forms the medial margin of the apertura narium externa and articulates dorsally with the nasal which has an indentation to receive the premaxilla on the midline. A dorsal process of the premaxilla which fits into the nasal occurs in *Captorhinus* but not in Casichelydia. Known casichelydians, which have separated external nares, i.e., *Meiolania,* have a nasal contribution to the septum. *Kayentachelys,* pleurosternids, and pleurodires lack divided nares, and it seems best to consider confluent nares as a synapomorphy at the level of all casichelydians with the *Meiolania* condition as autapomorphic.

Medially the premaxilla meets the other premaxilla. Posterolaterally the premaxilla contacts the maxilla beneath the apertura narium externa and on the triturating surface. The premaxilla forms only a small portion of the triturating surface, just on the midline. The labial ridge is quite prominent but is broken along its edge in SMNS 16980 and the Berlin specimen. SMNS 15759, however, has it intact and demonstrates that the ridge line is relatively straight with no pronounced protuberance or emargination. The labial ridge is higher in the Berlin skull and SMNS 15759 than in SMNS 16980 (see discussion below under Maxilla). The medial portion of the premaxilla, posterior to the labial ridge, is poorly preserved in the Berlin skull and SMNS 15759. In SMNS 16980 there are some foramina and rugosities but it is not clear whether or not these have been intensified by postmortem damage. Comparisons of the triturating surfaces with *Captorhinus* shows the chelonian edentulous synapomorphy of *Proganochelys.* There are no traces of teeth, alveoli, or any other structures not found in casichelydians. It is interesting that comparisons (Heaton, 1979: fig. 7) with the premaxilla of *Captorhinus* show that the basic shape of the premaxilla in *Proganochelys* is unchanged, except for the absence of teeth and the addition of a labial ridge.

Posterodorsally the premaxilla sends a short

Fig. 49. *Proganochelys quenstedti,* SMNS 16980. Lateral view of skull with left cheek region removed. Compare with Figure 50.

process to meet the vomer, which is paired in *Proganochelys.* The posterolateral margin of this process forms part of the margin of the apertura narium interna. In SMNS 16980, the only *Proganochelys* specimen in which these sutures are visible, the vomerine process on each side appears to be more or less displaced along the suture. As preserved, there is a midline cavity, irregular in shape, formed at the quadruple junction of vomers and premaxillae. This cavity appears to be natural but it could have resulted from bone displacement. In any event, a similar one does not occur in *Captorhinus* or other turtles. The vomerine process in Casichelydia is not generally as distinct as in *Proganochelys.*

In or near the vomer-premaxilla suture, casichelydians usually have paired foramina praepalatina that penetrate the bone from palate to fossa nasalis. Heaton (1979: fig. 7) identified the presumed homolog of this structure in *Captorhinus* as the prepalatal foramen and it is contained entirely within the premaxilla (as it is in some turtles). Although there are asymmetrical foramina in the premaxilla of *Proganochelys,* I have been unable to find a clearly identifiable foramen praepalatinum. This may be due to poor preservation rather than natural absence.

Maxilla
(figs. 16, 27, 40, 43)

Large parts of the maxilla are preserved in all three *Proganochelys* skulls, but the bone is entirely complete in none. Sutures and internal structures are best seen in SMNS 16980 while the triturating surfaces are best preserved in the Berlin skull and SMNS 15759.

The maxilla is a large element forming much of the anterolateral portion of the skull and bears most of the triturating surface. It may be divided into the vertical plate forming the snout and the horizontal portion on the palate.

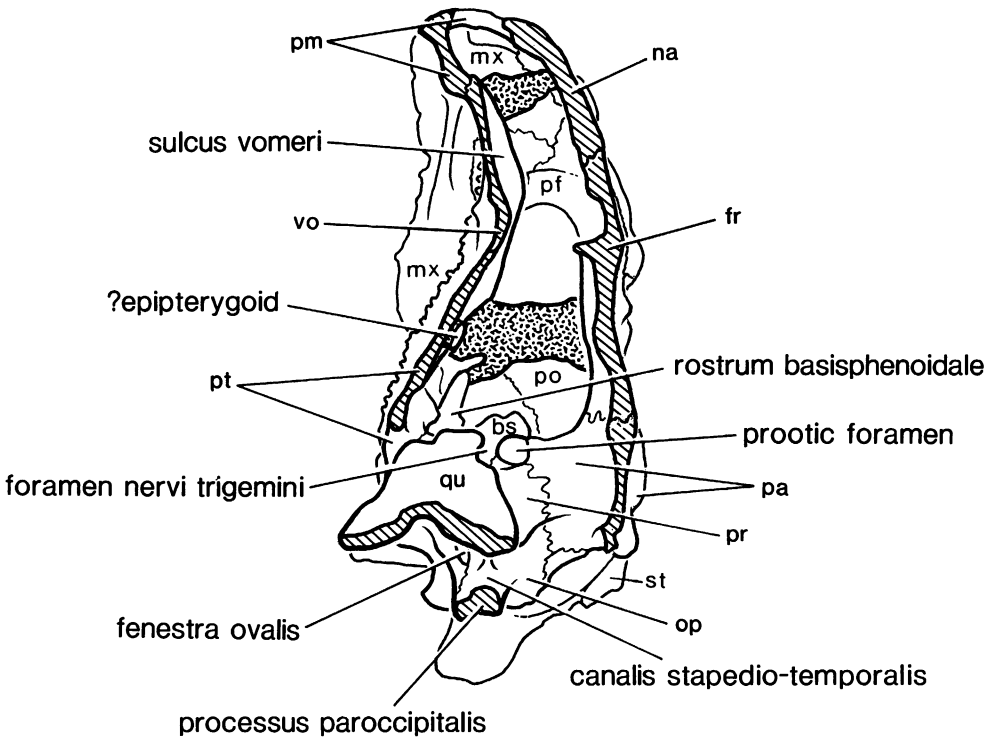


Fig. 49. Continued.

The vertical portion of the maxilla has a free ventral edge (the labial ridge) that contacts the premaxilla anteriorly, the jugal posteriorly, the lacrimal posterodorsally, the prefrontal dorsally, and the nasal anterodorsally. Anteriorly it forms the lateral margin of the apertura narium externa. The maxilla is distinctly higher anteriorly and rises between lacrimal and nasal. This part of the maxilla bears a prominent synapomorphy with other turtles. In *Captorhinus* the maxilla is low and the lacrimal is a wide element extending from the nares to the orbit. In *Proganochelys* and other turtles there is a large dorsal process of the maxilla that occupies much of the space formed by the lacrimal in *Captorhinus*. The maxilla of turtles, largely due to the presence of this dorsal process, is a dominant element in the formation of the preorbital region. Turtles, including *Proganochelys,* also have a posterior extension of the maxilla that reaches posteriorly to the posterior orbital margin. In *Captorhinus* it does not extend posteriorly to the orbit. This feature is not that clear cut and subject to variation within turtles. In *Captorhinus* the maxilla does not enter the orbital margin; a well-developed lacrimal-jugal contact prevents it. In *Proganochelys* the maxilla barely enters the orbital margin and the lacrimal-jugal contact is absent or very limited. Casichelydians have a maxilla that makes up a significant part of the orbital margin, many times half or more of its circumference. This is also correlated with the absence of the lacrimal which forms part of the orbital margin in *Proganochelys.*

The horizontal portion of the maxilla bears most of the triturating surface, the rhamphotheca or horny feeding surface synapomorphous for turtles. Despite some ambiguous figures and statements by Jaekel (1918a), none of the three *Proganochelys* skulls have any structures associated with marginal teeth. There are foramina in the triturating surfaces but these are irregular and I can detect no difference between these and ones in recent turtles. *Proganochelys* has a relatively high labial ridge separated from the lower lingual

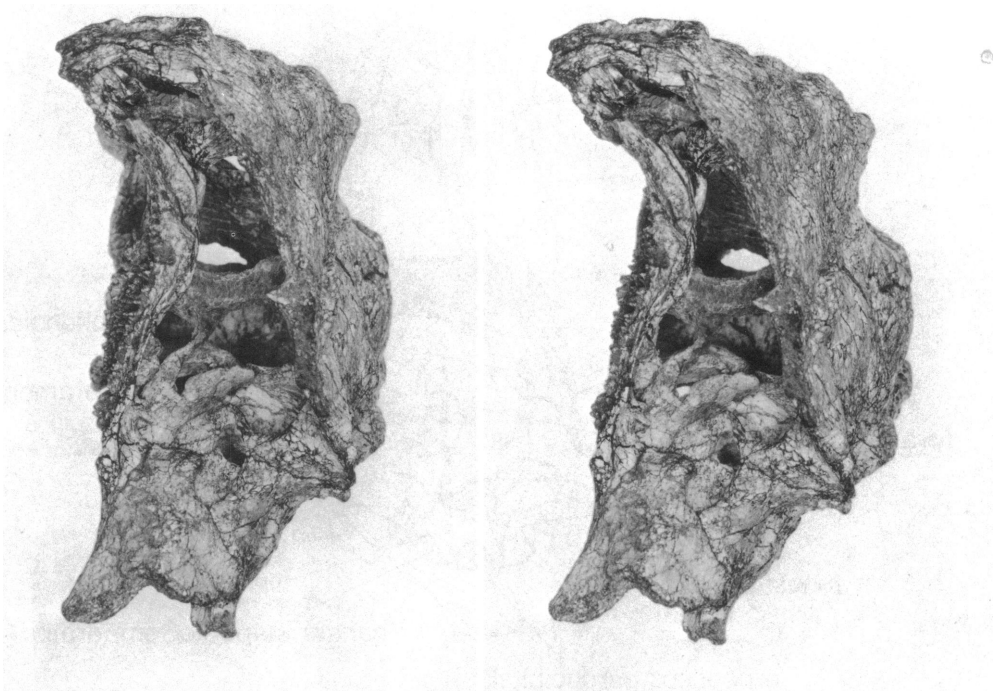


Fig. 50. *Proganochelys quenstedti,* SMNS 16980. Anterolateral oblique view of skull with left cheek removed. Compare with Figure 49.

ridge by a trough. The trough is curved, concave ventrally, and has no flat areas or other structures. The lingual ridge is distinct but less than one-third the height of the labial ridge. Both ridges are parallel except at the front of the skull where there is a slight expansion. The lingual ridge becomes very low or absent where it reaches the premaxilla.

There is some variation in the triturating surfaces among the *Proganochelys* skulls. The Berlin skull and SMNS 15759 have a more acuminate shape than SMNS 16980, but I interpret this as the result of crushing in the former. The labial ridge is higher in SMNS 15759 than in the other two skulls but I interpret this to result from breakage in the other specimens. The trough is wider and the ridges are slightly thicker in the Berlin skull than in the others, correlated with the slightly more massive bone thickness overall in the Berlin skull. The degree of distinctions is not great enough to warrant systematic recognition and it seems to me that these differences are best ascribed to a combination of preservation, individual variation, and growth.

The triturating surfaces of *Proganochelys* are not precisely the same in any other turtle. Almost all turtles have a greater expansion of the triturating surface and some development of a flat surface on the inter-ridge area. Some testudinoids (e.g., *Cuora, Kinixys*) have equally narrow triturating surfaces but these are most likely developments within the cryptodires. The triturating surface, however, is narrow in some pleurodires (e.g., *Pelomedusa, Chelodina*), although the rest of the triturating morphology is distinct from that of *Proganochelys* (the lingual ridge area is flat). More importantly, the triturating surface in *Glyptops* is very narrow, even narrower than in *Proganochelys.* Although we can argue that these are all instances of character acquisition within the various subgroups, it is still far from clear that an expanded triturating surface is synapomorphous at the level of Casichelydia. The best

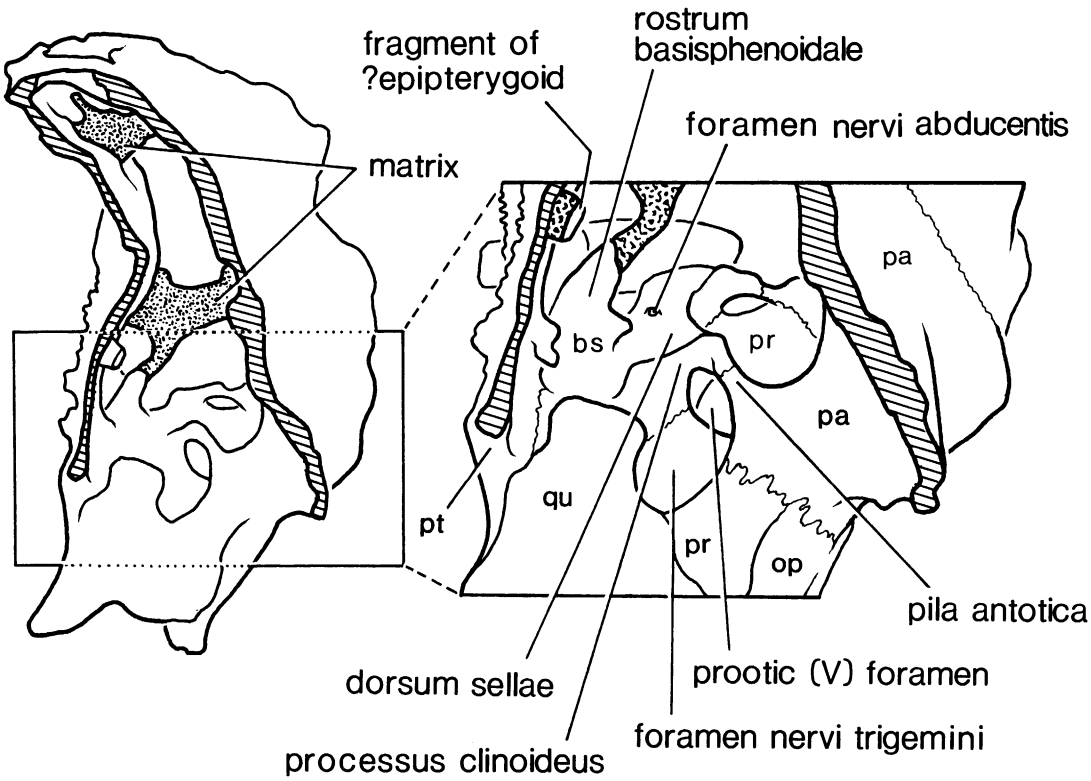


Fig. 50. Continued.

hypothesis at present is that narrow triturating surfaces are primitive for Casichelydia and that expansions have developed within subgroups of Casichelydia.

Medially the maxilla contacts the palatal elements thereby forming part of the internal nares. Anteriorly the maxilla meets the premaxilla but does not contact the vomer, as in most casichelydians. The maxilla forms the lateral margin of a relatively large apertura narium interna. The maxilla forms the narial margin in *Captorhinus* and most turtles, but in *Captorhinus* the apertura is long and narrow, paralleling the maxilla. In turtles, including *Proganochelys,* the apertura is less extensive. In comparison with most turtles, the apertura narium interna of *Proganochelys* is relatively large, although there is considerable variation within casichelydians.

Posterior to the narial margin, the maxilla has a short medial projection that contacts the palatine. This is best seen on the right side of SMNS 16980 where the palatine is slightly disarticulated and separated from the maxilla. Posteromedially the maxilla contacts the pterygoid, a contact that is absent in *Captorhinus* (because of the jugal-palatine contact), *Kayentachelys,* and *Pleurosternon.* Although present in most other turtles, this contact is probably an autapomorphy of *Proganochelys* because the primitive casichelydian condition appears to be that seen in *Kayentachelys* (i.e., maxilla, jugal, pterygoid, and palatine meeting at the foramen palatinum posterius).

Posteriorly the maxilla becomes thin and lies below and lateral to the anterior projection of the jugal.

VOMER
(figs. 16, 27, 40, 43)

The vomer is preserved, at least in part, in all three *Proganochelys* skulls. It is best seen in SMNS 16980, although its lateral limits are unclear. In the Berlin specimen the region

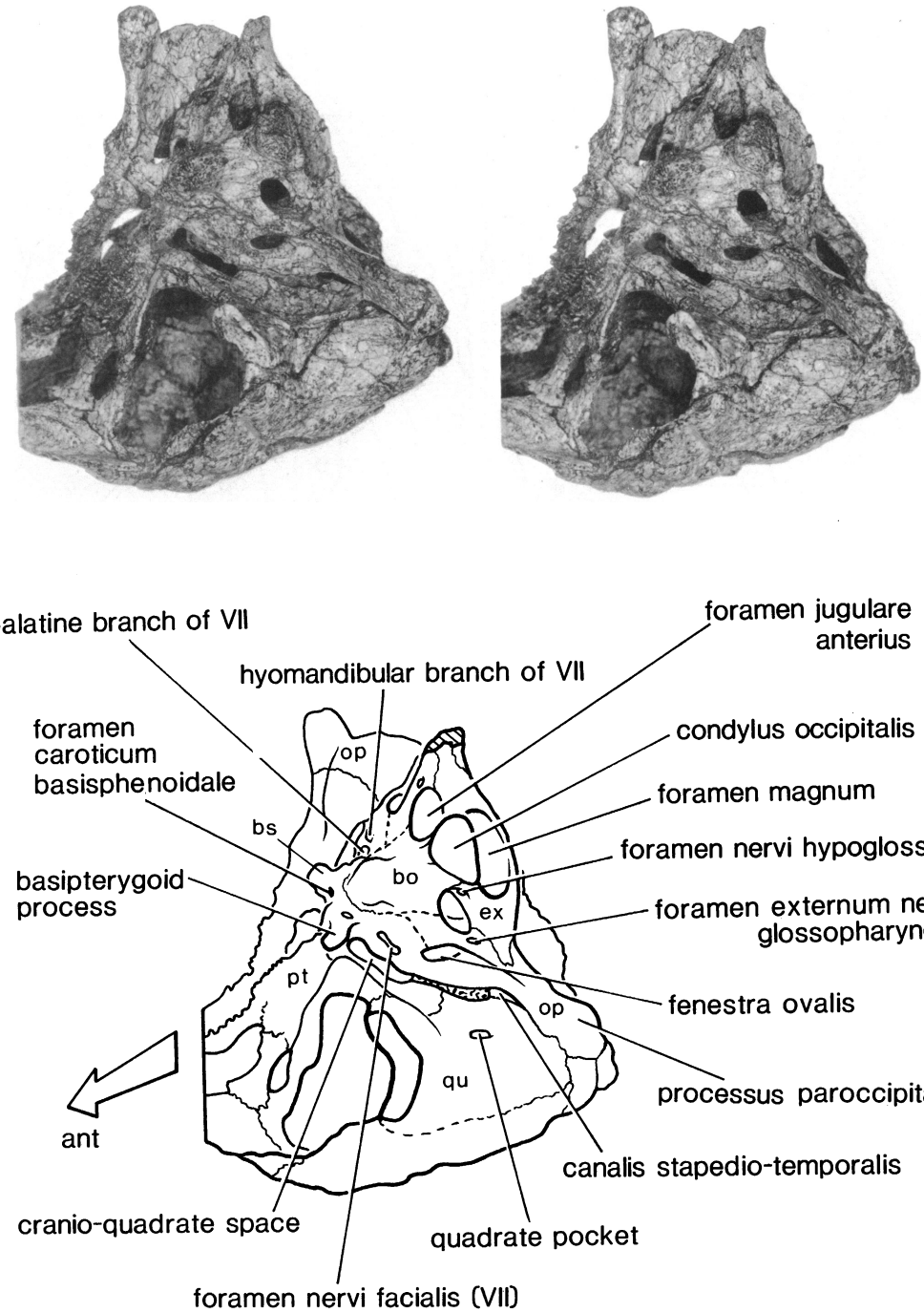


Fig. 51. *Proganochelys quenstedti,* SMNS 16980. Posteroventral oblique view of skull with left cheek removed. Arrow lies on midline. See also Figure 52.

is badly crushed but areas of the vomer can be discerned. SMNS 15759 is also crushed and even less of the vomer is visible.

From SMNS 16980 it can be seen that the vomer of *Proganochelys* is a paired element, as in the generalized amniote condition, but in contrast to all other turtles which have a single vomer. The sagittal suture separating the vomers extends for nearly their entire length.

The vomer in *Proganochelys* is an elongate, flat element, lying between the apertura narium interna at the anterior end of the palate. Anteriorly the vomer has a short, dorsally overlapping suture with the premaxilla. There is an unpaired opening on the midline in the vomer-premaxilla suture in SMNS 16980. The foramen appears to be natural but may be a consequence of postmortem damage in an area of thin bone. *Captorhinus* does not have such a foramen, and other turtles have a paired foramen, the foramen praepalatinum, in the vomer-premaxilla suture. The single foramen in *Proganochelys* may be the homolog of the foramen praepalatinum.

Laterally, the vomer forms the medial edge of the apertura narium interna in SMNS 16980. The other specimens barely have a recognizable apertura narium interna, as a consequence of lateral crushing. The posterior limits of the apertura can be estimated from the parts of the maxilla and palatine that are preserved. The apertura in *Proganochelys* as thus restored is relatively large and occupies a prominent portion of the palate.

Posteriorly the vomer contacts the pterygoid in a short suture. Posterolaterally the vomer reaches the palatine but this contact area is small as preserved but could have been more extensive. It is best seen on the right side of SMNS 16980 where the contact is preserved.

The ventral surface of the vomer shows a slight trough formed on the midline where the sagittal suture lies. The vomer is slightly convex dorsally when viewed from the side. The posterior half of the vomer has small teeth arranged roughly in two parasagittal rows. *Captorhinus* does not have teeth on the vomer but *Protorothyris* does have denticles, although they are arranged differently (Clark and Carroll, 1973: fig. 3) than in *Proganochelys*. Vomerine teeth would appear to be a generalized amniote feature.

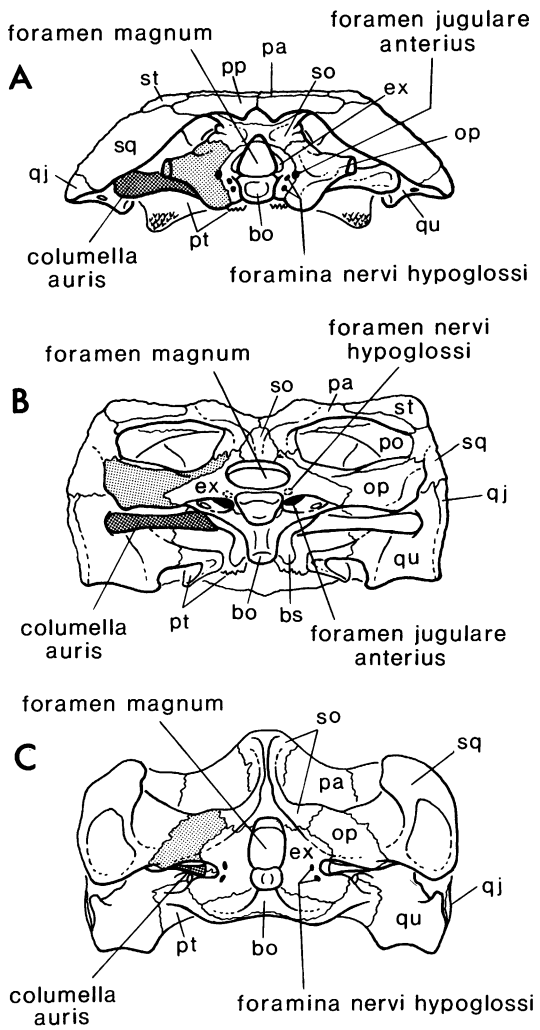


Fig. 52. Comparisons of occiputs. Opisthotic is in lighter stipple, columella auris (stapes) is in darker stipple. **A**, *Captorhinus* sp., from Heaton (1979) and specimens. **B**, *Proganochelys quenstedti*, SMNS 16980 with columella auris restored from MB 1910.45.2. **C**, *Eubaena cephalica*, from Gaffney (1979a).

The dorsal surface of the vomer in *Proganochelys* bears a parasagittal ridge that is close to the midline and forms the lateral margin of a trough, the sulcus vomeri, seen in other turtles. Because of the relatively large fossa nasalis and posterior position of the fis-

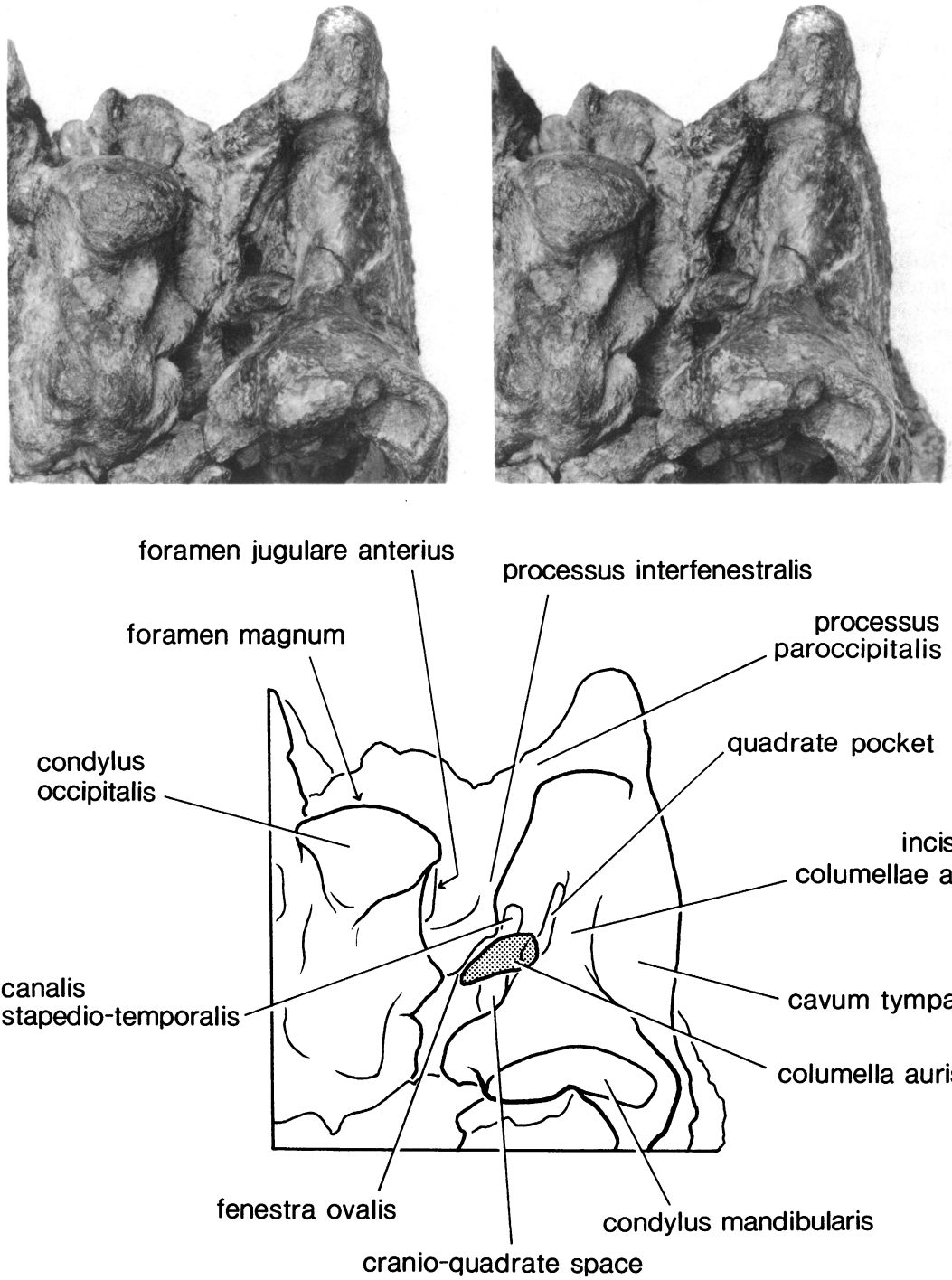


Fig. 53. *Proganochelys quenstedti,* MB 1910.45.2. Posteroventral view of right ear region with columella auris indicated by stipple. See also Figure 52.

TABLE 4
Comparisons of Palatal Elements

	Captorhinus	*Proganochelys*	Casichelydia
Dorsal process of premaxilla dividing nares	Yes	Yes	No
Teeth on premaxilla and maxilla	Present	Absent	Absent
Maxilla with dorsal process between nares and orbit	Absent	Present	Present
Maxilla extends to posterior margin of orbit	No	Yes	Yes
Maxillary contribution to orbital margin	Absent	Absent	Present
Vomer	Paired	Paired	Single
Location of palatal teeth	Palatine and pterygoid	Vomer, palatine and pterygoid	Pterygoid (or absent)
Teeth on ventral surface of palatine	Present	Present	Absent
Contribution of palatine to margin of apertura narium interna	Very small	Intermediate	Large
Orbitonasal ridge on palatine forming floor of nasal capsule	Present	Absent	Absent
Vomerine teeth	Absent	Present	Absent
Vomer expanded anteriorly and posteriorly	No	No	Yes
Apertura narium interna	Elongate, lateral slits	Less elongate and more medial than in *Captorhinus*	Oval and more medial than in *Proganochelys*

sura ethmoidalis, the sulcus vomeri of *Proganochelys* lies within the fossa nasalis rather than posterior to it as in casichelydians. The sulcus vomeri supports the cartilaginous septum interorbitale in recent turtles (see Gaffney, 1979a: fig. 81). This structure is not known to be ossified in any living or extinct turtle. Although *Captorhinus* does not have a distinct sulcus vomeri, the medial margin of the vomer bears a slight ridge that supports the interorbital septum, which is ossified in *Captorhinus* (Heaton, 1979). The vomer in *Captorhinus* differs from turtles in having a recurved alar projection (Heaton, ibid.: fig. 24) on its lateral margin. The chelonian vomer is relatively flat in this area. The lateral margin of the vomer in SMNS 16980 is a broken edge so the presence or absence of the alar projection in *Proganochelys* cannot be determined.

In most turtles the vomer is roughly dumbbell shaped with the anterior and posterior portions expanded and a narrow connecting bar separating the paired apertura narium interna. This condition of the vomer is found in pleurodires, *Kayentachelys,* as well as baenids, and seems to be a casichelydian synapomorphy. *Proganochelys* has a relatively flat vomer, that is curved concave ventrally but is not produced into the anterior and posterior enlargements. *Proganochelys* is advanced over *Captorhinus* in having the apertura narium interna closer together medially; in *Captorhinus* they are slits placed at the lateral margin of the palate.

The paired vomers of *Proganochelys* are homologous to the single vomer of casichelydians. Kunkel (1912) described the formation of the single vomer in *Emys* as the fusion of two lamellae during development.

PALATINE
(figs. 16, 27, 40)

The palatine is not preserved in its entirety in any *Proganochelys* skull, but it is best seen on the right side of SMNS 16980, where only some of the anterior portions are missing. The ventral surface of this bone is exposed on both sides of this skull and much of the dorsal surface is also, but some matrix has been retained on the dorsal surface for support of this thin element. SMNS 15759 has some of the posterior parts of both palatines visible in ventral view but they are both crushed and distorted, although the right side supplies some information.

The palatine in *Proganochelys* is a thin, roughly horizontal plate forming the anterior portion of the palate. Posteriorly the palatine has a long suture with the pterygoid, beginning laterally at the foramen palatinum posterius and extending medially where it curves anteriorly so that the contact is parasagittal and the pterygoid lies along the medial edge of the palatine for about half the length of the palatine.

Posterolaterally the palatine forms the medial and anterior margin of the foramen palatinum posterius while the posterior and lateral limits of the foramen are formed by the pterygoid. The pterygoid has a short contact with the palatine in the anterolateral edge of the foramen palatinum posterius. The foramen is complete on the right side of SMNS 16980, portions of it can be seen on the left side of SMNS 16980, and the entire foramen, crushed and distorted, can be made out on the left side of SMNS 15759. In the Berlin skull only fragments of the margin of the foramen are visible. In *Proganochelys* the foramen palatinum posterius is relatively large, about the same size as in *Chelydra.* Pleurodires and some cryptodires have foramina that are distinctly smaller.

In captorhinids there is a small foramen, the suborbital foramen of Heaton (1979) that lies between the palatine and jugal. It is likely that the suborbital foramen of captorhinids is homologous with the foramen palatinum posterius of turtles. Comparison of the palate in *Captorhinus, Proganochelys,* and other turtles shows that the foramen in turtles and the foramen in captorhinids agree in being formed anteromedially by the palatine and, if only the palatine is compared, at the same place on the palatine, i.e., its posterolateral edge. In casichelydians the primitive condition would appear to have the pterygoid, maxilla, jugal, and palatine making up the foramen, as in *Kayentachelys.* In most diapsids the foramen is also formed anteromedially by the palatine. In diapsids, however, the bones forming the rest of the margin of the foramen are more variable, with the ectopterygoid as well as the pterygoid, maxilla, and jugal commonly taking part. A comparison of structures in the foramen palatinum posterius of turtles and the infraorbital foramen of lizards is consistent with, but not strongly supporting, their homology. Bojanus (1819), Oelrich (1956), and Albrecht (1967) reported variable, small branches of the nasal artery and maxillary artery as well as branches of the maxillary nerve in the foramen. However, all authors (as well as dissections by this author) show that these foramina in turtles and lizards are mostly filled with connective tissue and the function of the opening is unclear.

Anterolaterally, the palatine has a long, straight contact with the maxilla in *Proganochelys.* This suture is best seen on the right side of SMNS 16980 where the palatine and maxilla are slightly disarticulated from each other. The palatine forms a horizontally elongate, concave pocket, opening laterally to receive a process from the maxilla, very much as in captorhinids and similar to that in lizards. This structure is best seen on the ventral surface.

As preserved on the right side of SMNS 16980, there is a large, irregular opening at the anterior edge of the palatine, its margins being formed by the maxilla laterally, the palatine posteriorly, the lacrimal anteriorly, and what is best interpreted as the prefrontal anteromedially. This opening is the position of the foramen orbito-nasale but many of the edges as preserved are broken. Only the anterior margin, formed by the lacrimal, seems to be original and also seems to indicate a much smaller foramen, quite comparable to that in *Captorhinus.* Unfortunately, the left side of SMNS 16980 and the other two *Proganochelys* skulls have no recognizable portion of the foramen preserved. As restored,

the palatine would extend anteriorly beyond its preserved margins to form the posterior limits of the foramen orbito-nasale and the prefrontal could also enter the margin medially.

On the dorsal surface the jugal overlies the maxilla so that there is a palatine-jugal contact in the floor of the orbit that is not present in ventral view. Simiarly, the palatine-lacrimal contact is covered ventrally. The palatine-prefrontal contact is preserved for only a short distance; medially both bones and the vomer have broken margins. There is an irregular opening in the middle of the palatine on both sides of SMNS 16980, the right side being larger than the left. I interpret both of these as postmortem damage.

In most turtles and other amniotes the palatine forms some part of the margin of the apertura narium interna. As a result of the breakage described above in the anterior part of the palatine and in the matching section of the vomer, the posterior margin of the apertura is not clearly preserved in SMNS 16980 and not at all in the other two *Proganochelys* skulls. It seems reasonable, however, to interpret this region as being not very much more extensive than it is at present, and to hypothesize the apertura as being formed posteriorly by these elements. In captorhinids the apertura narium interna is a long, thin opening principally formed by the maxilla laterally and the vomer medially with the palatine forming the small, posterior corner. In turtles, including *Proganochelys,* the palatine forms a larger portion of the edge of the apertura and the shape of the apertura is wider.

Another important difference between captorhinids and turtles is the participation of the palatine in the nasal capsule. As Heaton (1979) and Fox and Bowman (1966) illustrated, the palatine of captorhinids has a distinct ridge, the orbitonasal ridge of Heaton, on its dorsal surface that marks the posterior margin of the nasal capsule. In turtles the palatine bone does not form the floor of the nasal capsule and there is no orbitonasal ridge on the palatine.

On the ventral surface of the palatine in *Proganochelys* there are small teeth in a group near the palatine-pterygoid contact. These teeth are visible on the right side of SMNS 15759 (barely) and on both sides of SMNS 16980. The Berlin skull has teeth but the palatine ones cannot be diffentiated from the pterygoid teeth. They appear to be separated from the pterygoid teeth by a narrow gap but nonetheless continue the rows seen on the pterygoid. No other turtles have palatine teeth (*Kayentachelys* has teeth only on the pterygoid), but teeth are commonly seen on the palates of more generalized amniotes. The palatine teeth in captorhinids are clearly organized in parasagittal rows and these are very similar in number and position to those in *Proganochelys.*

PALATOQUADRATE ELEMENTS
(table 5, figs. 16, 40, 46)

QUADRATE
(figs. 16, 27, 46)

The quadrate is present and well preserved in SMNS 16980 and fairly well preserved in the Berlin skull, although sutures can be seen only in SMNS 16980. SMNS 15759 is lacking the left quadrate and only has the badly crushed anterior portion of the right one.

The chelonian quadrate is one of the most distinctively modified of the turtle head bones. Comparing the quadrate in *Captorhinus* with a casichelydian quadrate, it is hard to believe that they are homologous elements. *Captorhinus* (fig. 46), with the presumed generalized amniote condition, has a quadrate (Heaton, 1979: fig. 26) that is essentially the articular condyle, broadened transversely, with a flat parasagittal sheet of bone expanding dorsally for contact with the cheek elements. Casichelydians have a larger, C-shaped quadrate, exposed laterally and extending dorsally for much of the height of the skull, with the articular condyle comparatively inconspicuous. As Jaekel (1918a) showed, the quadrate of *Proganochelys* has many chelonian features, but it is nonetheless morphologically intermediate in many ways between turtles and more generalized amniotes.

The quadrate of *Proganochelys* is a relatively large, auricle-shaped element, concave posteriorly, convex anteriorly, bearing the condylus mandibularis ventrally, and reaching the skull roof dorsally and the cheek anterolaterally. The disarticulated quadrate of

TABLE 5
Comparison of Palatoquadrate Elements

	Captorhinus	*Proganochelys*	Casichelydia
Epipterygoid	Triangular	If present, probably columnar	Triangular
Ossified "pleurosphenoid"	Possibly present in part	Present	Absent
Palatine process of pterygoid	Extends anteriorly beyond level of palatine	Extends anteriorly about half length of palatine	As in *Proganochelys*
Medial contact of pterygoids	Moderate	Very limited	Moderate
Interpterygoid vacuity	Oval and wide	Elongate and narrow	Short and narrow
Anterolateral process of pterygoid	Does not reach foramen palatinum posterius	Extends beyond foramen palatinum posterius	Reaches foramen palatinum posterius
Transverse pterygoid flange	Present	Absent	Absent
Basicranial articulation	Open, between epipterygoid and basisphenoid	Open, between pterygoid and basisphenoid	Sutured closed betw. pterygoid and basisphenoid
Basipterygoid articulation surface	Faces posteriorly	Faces medially	Absent
Quadrate exposed laterally	No	Yes	Yes
Cavum tympani formed by quadrate	No	Yes, shallow	Yes
Opisthotic-quadrate contact	Absent	Present, small	Present, extensive
Pterygoid process of quadrate	Absent	Present	Present
Prootic-quadrate contact	Absent	Present	Present
Foramen stapediotemporale	Not formed in bone	Present, but no canal	Present, with bony canal

Proganochelys is more similar to the generalized lizard quadrate than to the *Captorhinus* condition in being dorsoventrally elongate. Ventrally, the quadrate in *Proganochelys* bears the condylus mandibularis, the articular surface with the lower jaws, preserved in both SMNS 16980 and the Berlin skull. Both agree in having the condylus similar to that in cryptodires, that is, relatively flat surface divided roughly into a medial and lateral area. In *Proganochelys* the medial half is flat to slightly convex, while the lateral half, situated at a slightly lower level, is concave, more so in the Berlin skull, which seems to be better preserved in this area than SMNS 16980. The condylus is rectangular with the medial half somewhat wider anteroposteriorly than the lateral portion. The condylus mandibularis of *Captorhinus* has a much deeper parasagittal groove, producing a surface that is nearly V-shaped in cross section. The condylus mandibularis in *Proganochelys* is at the end of the processus articularis, a column of bone very similar to those in other turtles.

Laterally the quadrate of *Proganochelys* forms a shallow but definite cavum tympani, similar in size and extent to lizards and very different from captorhinids, which have no structure of this sort. The cavum tympani of *Proganochelys,* however, is less extensive than in any other known turtle. Casichelydians have a cavum tympani extended posteriorly above the stapes and bent ventrally in varying degrees forming an incisura columella auris for the stapedial exit. Among casichelydians, *Kayentachelys* has the closest similarity to *Proganochelys* in having a very wide incisura columella auris. But it is distinctly advanced over *Proganochelys* in the development of the dorsal and posterodorsal portions of the quadrate, including an antrum postoti-

cum. *Proganochelys* has a barely distinguishable incisura columella auris, the cavum tympani is concave posteriorly, but it is broadly curved. The anterolateral extent of the cavum tympani in *Proganochelys* is somewhat shallower than in most turtles, but it is not that different; the greatest difference between the *Proganochelys* and casichelydian cavum tympani is in the dorsal portion. There is no antrum postoticum and no medial concavities in the cavum tympani of *Proganochelys.*

The quadrate in *Proganochelys* contacts the quadratojugal in an extensive, C-shaped, overlapping suture that is clear only in its dorsal portion; the ventral limits are poorly preserved in SMNS 16980 due to breakage of this apparently weak area. In *Captorhinus* the quadrate contacts the quadratojugal only in a relatively small sutural area just lateral to the condylus mandibularis. The dorsal portion of the quadrate is free of the cheek and the principal contact of the quadrate is the medial one with the pterygoid which extends for most of the height of the quadrate. In turtles, including *Proganochelys,* the quadrate is broadly sutured to the cheek via the quadratojugal, and the quadrate-quadratojugal contact area is greatly increased over *Captorhinus.*

Dorsally the quadrate of *Proganochelys* contacts the squamosal on the very top of the quadrate. Just posterior to this contact, the paroccipital process of the opisthotic lies against the posteromedial edge of the quadrate. The squamosal contact is a tight, interfingering suture as is the opisthotic-quadrate contact dorsally, but in ventral view the opisthotic and quadrate are separated by a thin layer of matrix. The opisthotic-quadrate contact is an important landmark in comparing *Proganochelys* and other turtles because it shows that although the ventral contacts between palatoquadrate and braincase do not exist in *Proganochelys,* the dorsal ones are advanced over generalized amniotes. Although the opisthotic does not reach the quadrate in *Captorhinus,* Heaton (1979) has argued that an "intercalary cartilage" similar to the kind seen in lizards, provided a functional contact between the bones, based on a rugosity on the quadrate. A contact does occur in lizards but it is possible that Heaton's contention is correct and an opisthotic-quadrate contact in *Proganochelys* is not as broad or as extensive as in casichelydians but it is more extensive and tighter than in lizards.

The quadrate of *Proganochelys* is distinctly advanced over that in *Captorhinus* and lizards and similar to that of other turtles in having a well-developed anteromedial pterygoid process. This is a thin sheet, overlapping the quadrate ramus of the pterygoid anterolaterally that extends anteromedially as the posterior wall of the fossa temporalis. This sheet terminates anteromedially in a blunt process that was probably continued in the remnant of the palatoquadrate cartilage. The dorsal margin of the pterygoid process slopes anteroventrally. It contacts the prootic along its posterodorsal edge and below this contact forms the lateral margin of the cranio-quadrate space, the opening between the middle ear and the orbito-temporal region. The dorsal margin is notched, just anterior to the termination of the prootic-quadrate contact, to form the ventral margin of the foramen nervi trigemini, which in *Proganochelys* is incomplete anterodorsally. Posterodorsally a ridge of the prootic forms the margin, although it is not as well defined as in casichelydians, while anterodorsally *Proganochelys* has a poorly developed processus inferior parietalis. Ventrally, the pterygoid process is tightly sutured to the pterygoid but its prootic contact appears to be much looser because the quadrate and prootic are separated by matrix, more so on the right side of SMNS 16980 than on the left side.

Dorsally, the quadrate forms the anterolateral margin of the canalis stapedio-temporalis, which in *Proganochelys* is so short as to be virtually the same as the foramen stapedio-temporale. As the prootic-opisthotic suture is not definitely determinable in this area, the degree of prootic-quadrate contact cannot be determined. The wall formed by the pterygoid and quadrate is aligned anteromedio-posterolaterally and broadly curved forming a concavity facing posteromedially. The cavity is the middle ear, the cavum acusticojugulare of casichelydians. In *Proganochelys* the quadrate forms the anterolateral wall of this chamber, much as in casichelydians, but the lateral, medial, and ventral limits are less developed in *Proganochelys.*

In casichelydians the stapes is a very thin

rod extending from the fenestra ovalis through the incisura columellae auris of the quadrate. The stapes may touch the quadrate as it passes near but it is generally suspended by soft structures so that there is no definitive articulation. In *Captorhinus* the massive stapes abuts against the quadrate in a definitive articulation that involves a depression on the quadrate facing posteromedially. In *Proganochelys* the stapes is preserved on the right side of the Berlin skull; it ends lying against the quadrate, just medial to the tympanic crest, about midway up the quadrate. The skull is badly crushed and the stapes may not be in its original position (see Columella Auris) but it seems to be in about the correct position. It terminates just adjacent to a pit on the quadrate that I interpret as an articulation scar for the stapes. In the Berlin skull this pit is a slit, much higher than wide but this is probably due to crushing. In SMNS 16980 the pit is nearly circular and can be seen to end blind; there is no foramen or canal leading from it. This pit is homologous to the columellar recess of Heaton (1979) and marks the position of articulation of the stapes on the quadrate. This condition in *Proganochelys* would be a retained primitive feature, as is the relatively thick stapes.

The incisura columella auris of *Proganochelys* seems to have been closely related to the stapedial articulation but does not have a distinct ridge or line for the attachment of a membrane. Rather, as in casichelydians, it would appear that *Proganochelys* had a tympanic membrane attached anteriorly and dorsally along the margin of the cavum tympani, which has a clearly marked line of attachment as in other turtles. Posteriorly and ventrally the tympanic membrane would not be attached to bone but this is only a difference of degree from the condition in casichelydians such as cheloniids, which have an incomplete tympanic ring and the membrane is attached to connective tissue posteroventrally. Thus the tympanic region of *Proganochelys* is advanced in the chelonian direction and does not offer new information concerning the possible presence or absence of a tympanum in *Captorhinus*. However, based on the morphology of *Captorhinus*, it seems very unlikely that a tympanum supported by bone or attached to the stapes was present in this taxon.

Epipterygoid
(figs. 47, 49, 50)

The presence of an epipterygoid must be considered questionable, although it is likely. The only specimen which may be interpreted as having an epipterygoid in place is SMNS 15759. Although this specimen is badly crushed and has generally poor preservation, for some reason ethmoidal ossifications are preserved. On the right side of this specimen, but best seen from the left side, is a rodlike structure that articulates ventrally on the dorsal surface of the pterygoid. Unfortunately, the margins of this bone are all broken edges and it may not be a rod at all, but perhaps a broader structure. The medial surface shows a low, vertical ridge, laterally it appears flat. It is possible that posteroventrally it is continuous with the pterygoid process of the quadrate, in which case it would definitely be an epipterygoid. Unfortunately, the poor preservation of this specimen and the presence in it of other unusual ossifications, definitely not epipterygoid, combine to make the identification questionable.

In SMNS 16980 there are flat, columnar bone fragments lying on top of each pterygoid but separated from them by a thick layer of matrix. The left side fragment is more anteriorly placed and longer than the right fragment. Both fragments are long and flat with no definite margins. It is possible that they were once vertical and that they are the same as the vertical rod seen in SMNS 15759. It is also possible that they fitted into the groove on the dorsal surface of the pterygoid, the usual position for the epipterygoid in both turtles and *Captorhinus*. However, these fragments could also be parts of the ethmoid ossification and not epipterygoid at all.

"Pleurosphenoid"
(figs. 47, 48)

The term pleurosphenoid is generally used for an ethmoidal ossification in crocodiles (Bellairs and Kamal, 1981) and the term should be restricted to that bone and its homologs. The ossification described here is very

unlikely to be homologous with the pleurosphenoid of archosaurs but it is very similar to that bone, and rather than devise a new term it seems best to refer to the structure in *Proganochelys* as a "pleurosphenoid," the quotes indicating nonhomology with the pleurosphenoid of archosaurs or any other amniote. The use of the two terms laterosphenoid and pleurosphenoid (as well as the other ethmoid ossifications) is considerably confused in the literature. I here follow Bellairs and Kamal (1981) in limiting the laterosphenoid to Squamata (particularly snakes) and pleurosphenoid to archosaurs, based on the hypothesis that the two bones are not homologs (see Bellair and Kamal, 1981, for literature regarding this discussion, particularly Rieppel, 1976). As will become clear below, the element in *Proganochelys* is unlikely to be homologous to either, but it is morphologically similar to the archosaur pleurosphenoid.

The "pleurosphenoid" of *Proganochelys* is found only in the Aixheim skull, SMNS 15759, and it can be seen primarily on the left side. It is a paired bone, the anteromedial margin of the right "pleurosphenoid" is visible from the left side, and part of the lateral surface is visible through the right orbit. It is the left "pleurosphenoid" however, that is best preserved, most accessible, and provides most of the information. The bone, as preserved, is an ovoid ossification with posteroventral processes delimiting parts of three foramina. The lateral surface is finished but rugose, as if for muscle attachment, and the bone appears to be the same texture and histology as the other endocranial ossifications; there is no indication that this is calcified cartilage. The anterior portion of the "pleurosphenoid" is an oval lobe as preserved, but only the anteroventral margins are natural; the anterior and dorsal edges are all broken but very thin, as if the original edges were close. There are low ridges on the ventral surface of the skull roof in *Proganochelys* but none strictly parallel the projected "pleurosphenoid" margins and there are no rugosities or any other indication of a sutural or even strong ligamentous attachment. The conclusion is, then, that in contrast to the pleurosphenoid of archosaurs (and laterosphenoid of snakes), the "pleurosphenoid" of *Proganochelys* was not strongly attached to the skull roof. An analogous situation can be seen in lizards where the orbitosphenoid ossification may be attached to the skull roof by membrane with no particular rugosities on the skull roof. Both SMNS 16980 and the Berlin skull have this region preserved and there is no indication of attachments in these specimens either. Anteriorly the lobe of the "pleurosphenoid" bows medially so that right and left "pleurosphenoids" constrict the intervening space. Anteroventrally the "pleurosphenoid" curves medially to form a partial floor for the spaces between the "pleurosphenoids." This morphology is very similar to portions of the planum supraseptale in the mature embryo (Kunkel, 1912; Bellairs and Kamal, 1981). The floor, however, is incomplete, the curved "pleurosphenoid" does not meet its mate in the midline, but the edges do appear broken and they may have met anteriorly.

In side view the "pleurosphenoid" of *Proganochelys* has a marked ventral excavation that is a formed margin and presumably is the dorsal and posterior margin of the foramen for the optic (II) nerve, the fenestra optica of Kunkel (1912). The relation of this foramen to the planum supraseptale of the mature chondrocranium is very close. Ventrally there is a short spur of bone acting as a partial ventral limit for the optic foramen; its anterior and ventral limits are broken but its thickness suggests that it was formerly more extensive, perhaps reaching the palate.

The "pleurosphenoid" of *Proganochelys* has a ventrally directed process, with the hypothesized optic foramen anterior to it and another foramen posterior. This latter foramen appears to be for the trochlear nerve (IV), possibly combined with the oculomotor nerve (III). The foramen is incomplete ventrally but whether or not this is a break cannot be determined. In any case, the process itself can be identified as the pila metoptica of the chondrocranium based on its general relations to the planum supraseptale and the posterior portions of the "pleurosphenoid." Posterior to the trochlear foramen, the "pleurosphenoid" has another descending process which may be identified as the pila

antotica (of Bellairs and Kamal, 1981; the pila prootica of Kunkel, 1912). This process in *Proganochelys* is attached to the processus clinoideus of the basisphenoid ventrally and has a short contact with the prootic posteriorly above a large foramen. In SMNS 15759 there is a break between the pila antotica and the processus clinoideus that may be a suture or a crack. In SMNS 16980, however, the processus clinoideus contacts the prootic with no indication of a suture and the interposition of another element. As the processus clinoideus is an ossification of the embryonic pila antotica, the difference between the two specimens may simply be in the degree of ossification of the pila antotica and the observed separation may be a crack. The foramen behind the pila antotica–processus clinoideus is the prootic foramen or trigeminal foramen. It is the point of exit from the cavum cranii of the trigeminal nerve (V) (all three branches), and is not to be confused with the more laterally placed foramen nervi trigemini formed at least in part by the parietal and palatoquadrate elements and containing only two branches of the trigeminal nerve (V_2 and V_3). In SMNS 15759 the dorsum sellae, medial to the processus clinoideus, is twisted anterolaterally so that the anterior surface of the dorsum faces partially laterally, below the trochlear foramen.

The above description of the "pleurosphenoid" in *Proganochelys* is consistent with the features of the mature chelonian chondrocranium and strongly implies that the "pleurosphenoid" is an ossification of the ethmoidal region of the chondrocranium in an adult. Unfortunately, there are only three chelonian taxa (*Chelonia, Dermochelys,* and *Chelydra* in Nick, 1912; see also Gaffney, 1979a) in which the adult persistent cartilage is described. The *Proganochelys* skull differs conspicuously from all recent turtles in this area in lacking a well-developed processus inferior parietalis and therefore the remaining cartilage described in *Chelydra* is much smaller than the "pleurosphenoid" of *Proganochelys.* The closest similarity is with *Dermochelys,* which has a small processus inferior parietalis and extensive chondrification in the adult. The similarity between *Dermochelys* and *Proganochelys* is the same as between *Proganochelys* and the mature chondrocranium of a hatchling and implies no relationship. In any case, no known turtle has any ossifications of any kind in the ethmoidal region of the planum supraseptale and pila metoptica. I have described (Gaffney, 1976: 522) an ossification in the pila antotica of *Plesiochelys,* which forms a connection between the prootic and the processus clinoideus thereby forming a prootic foramen. In the other direction, Heaton (1979) has described a well-developed ossified interorbital septum and planum supraseptale in *Captorhinus.* This is a vertical, median ossification with only a small part of the laterally expanded planum supraseptale ossified. No posterior ossifications were reported and no foramina or pilae were seen. My own examination of Heaton's material and other captorhinids supports this observation and it is apparent that the area of overlap in ossification between captorhinids and *Proganochelys* is small. The "pleurosphenoid" of *Proganochelys,* therefore, is best interpreted as an autapomorphy of that taxon.

Pterygoid
(figs. 16, 27, 40, 42, 43)

The pterygoid of *Proganochelys* is preserved virtually complete on the right side of SMNS 16980, the ventral surface is entirely visible, much of the dorsal surface is prepared (matrix remains on some of the pterygoid medially for support), and nearly all of the sutures are clear. The pterygoid on the left side of this specimen is less complete, the anterolateral areas are missing, but the rest of it is present with the medial area of the dorsal surface prepared free of matrix so that using both sides of this specimen results in almost complete understanding of the pterygoid morphology. The other two *Proganochelys* skulls have both pterygoids present, but the extensive palatal crushing prevents the addition of useful information to that seen in SMNS 16980. In fact, the condition of the palate in the Berlin skull, in which the pterygoids are overlapped and crushed together medially, led Jaekel (1918a) to erroneously describe the presence of a large median tooth plate and the absence of an interpterygoid vacuity.

The pterygoid of turtles is arguably the most important single bone in elucidating their re-

lationships (Gaffney, 1975, 1979a), and the pterygoid of *Proganochelys* is no exception. The pterygoid of *Proganochelys* can be described in general terms as being more similar to that bone in generalized amniotes, such as captorhinids, than to the pterygoid in other turtles. The pterygoid of generalized amniotes can be visualized as a triradiate structure (Oelrich, 1956): the palatine process is a flat plate extending anteriorly, the transverse process (processus pterygoideus externus of cryptodires) is also flat with a thickened margin extending laterally, and the quadrate ramus extends posterolaterally as a curved sheet oriented vertically. These areas are apparent in the pterygoid of *Proganochelys.*

The palatine process in *Proganochelys* is a distinct but narrow extension of bone lying medial to the palatine and reaching the vomer anteriorly. In other turtles there is no distinct process; the anterior margin of the pterygoid is usually roughly transverse, although it may undulate anteriorly as well as posteriorly. The contacts in casichelydians are usually the same, however, so that the pterygoid usually reaches the vomer. In captorhinids the palatine process is more extensive than in *Proganochelys*; the process goes anteriorly beyond the palatine and partially separates the vomer on the midline. The medial edge of the palatine process in *Proganochelys* meets the other pterygoid in a very short contact anteriorly, and posteriorly the pterygoids diverge to form the lateral edges of the interpterygoid vacuity. The pterygoids in captorhinids also meet on the midline but the length of the contact is longer than in *Proganochelys.* In captorhinids and generalized amniotes the interpterygoid vacuity is somewhat wider and more oval in shape than in *Proganochelys,* where the sides of the vacuity are more parallel. *Kayentachelys* is the only casichelydian to retain an interpterygoid vacuity, a feature now interpreted as primitive for casichelydians. The medial contact of the pterygoids anteriorly in *Kayentachelys* is more extensive than in *Proganochelys* and the interpterygoid vacuity is less extensive, being only about half the length of the vacuity in *Proganochelys.*

The transverse process and main body of the pterygoid in *Proganochelys* has an anterior contact with the palatine, forms the posterior and lateral margin of the foramen palatinum posterius (see Palatine for discussion), and extends anterolaterally to reach the palatine and maxilla anterior to the foramen palatinum posterius. This anterolateral process contacts the jugal in the floor of the orbit and on the anterior edge of the fossa temporalis inferior. This process is more extensive than in captorhinids, where it does not reach the suborbital foramen (= posterior palatine foramen), but it is similar in most casichelydians.

The lateral margin of the pterygoid in *Proganochelys,* homologous to the region of the transverse process in captorhinids, differs from that region in both captorhinids and casichelydians. In *Proganochelys* this margin is gently curved convex outward, without a distinct process. In captorhinids and other generalized amniotes there is a definitive transverse process, a thickened plate bearing denticles or teeth on the ventral surface. The transverse process is absent in all turtles. In cryptodires there is a much smaller processus pterygoideus externus, the presumed homolog of the captorhinid transverse process, which differs by having a vertical plate serving as a guide for the lower jaw. In pleurodires there is a processus trochlearis pterygoidei, also presumably homologous to the transverse process, that bears the bodenaponeurosis of the jaw musculature (Gaffney, 1975, 1979a). The condition in *Proganochelys* may be interpreted as intermediate between the captorhinids and the respective casichelydian conditions. In this view *Proganochelys* would be advanced over captorhinids in having lost the definitive transverse process but would be primitive with respect to other turtles lacking either the cryptodire or pleurodire condition. If this were accepted, both the vertical plate of the processus pterygoideus externus of cryptodires and the processus trochlearis pterygoidei of pleurodires could be hypothesized as synapomorphies of their respective groups. Conversely, an alternative that I favor less than the one just described, would interpret the *Proganochelys* condition as autapomorphic and consider the primitive chelonian condition as unknown.

The quadrate ramus or process of the pterygoid is a posterolateral curved sheet of bone,

oriented more vertically than the rest of the pterygoid, that extends to articulate with the quadrate. In *Proganochelys* this process is relatively short; in captorhinids and most turtles it extends almost to the condylus mandibularis of the quadrate while in *Proganochelys* it extends a little more than halfway to the condylus. This is presumably a *Proganochelys* autapomorphy. In captorhinids the quadrate ramus is relatively long and thin with a comparatively small surface for the quadrate articulation posterolaterally. In *Proganochelys* the quadrate ramus is stouter, thicker in section, and higher dorsoventrally so that there is less communication between the middle ear and the temporal fossa. Most of this increase results from the dorsal expansion of pterygoid and quadrate. In Casichelydia the quadrate ramus is even broader and thicker, acting as a major bracing element between the quadrate and braincase. Also in Casichelydia, in contrast to *Proganochelys* and captorhinids, the quadrate ramus has lost the shape of a curved vertical plate and is a more horizontal process with its articular surface tilted dorsolaterally. In captorhinids the quadrate-pterygoid articulation is an overlapping contact, the pterygoid lying posteromedially and the quadrate anterolaterally. As in lizards, this contact is not tight, is often disarticulated, and may have allowed movement during life. Although the overall morphology is similar in *Proganochelys,* the quadrate-pterygoid articulation appears to be very solid; there is no sign of displacement or separation in SMNS 16980 as is seen in other contacts in this skull. The posterodorsal portion of the quadrate ramus in *Proganochelys* contacts the prootic and possibly the opisthotic (see Prootic and Opisthotic for discussion). Anteroventral to this contact the cranioquadrate space lies between pterygoid and neurocranial elements.

The quadrate ramus of *Proganochelys* joins the rest of the pterygoid near the basicranial articulation where the pterygoid is very narrow. The posteromedial surface of the quadrate ramus is concave as it runs anteromedially where it meets the basicranial articulation. On the ventral surface of the pterygoid there is a low ridge continuous with the posterolateral margin of the pterygoid that runs posteromedially across the base of the quadrate ramus to bend posteriorly in the region of the basicranial articulation. Between this ridge and the elevated ventral surface bearing the pterygoid teeth, there is a trough, concave ventrally, that ends at the basicranial articulation. Ventral to the opening between the pterygoid and prootic-basisphenoid, that is, the cranioquadrate space, the quadrate ramus of the pterygoid curves posteriorly at its ventral margin to form a partial floor for the cranioquadrate space below the middle ear region. This, however, is not as extensive as in *Kayentachelys,* but it is advanced over *Captorhinus,* in which the curved quadrate ramus has no posterior development.

The open basicranial articulation is a fundamental feature of generalized amniotes and the akinetic condition of turtles is one of the most disinctive attributes of their skull. *Proganochelys* is of great interest because it is a turtle that has the generalized condition of the basicranial articulation. An extended discussion of the development and morphology of this region can be found in Gaffney (1979a). In captorhinids the basicranial articulation is between the epipterygoid and the basisphenoid. The epipterygoid has a well-developed ventral expansion that sends a curved process into a pocket of the pterygoid so that the actual articulation is borne by the epipterygoid (Warren, 1961; Heaton, 1979). Earlier (Gaffney, 1983), I suggested a similar epipterygoid contribution to the basicranial articulation in *Proganochelys,* but with further preparation of SMNS 16980 this now seems unlikely. Even now complete removal of matrix between the articulation surfaces has not been completed due to the very fragile nature of the bone. There are fragments of bone, presumed to be epipterygoid, lying on top of the pterygoid very close to the basicranial articulation and one of these, on the left side, appears to be continuous with a small crest of curved bone forming part of the articulation. Further preparation, however, has shown that the bone fragments are not continuous with the articulation surfaces (and the fragments may not be epipterygoid in any case, see Epipterygoid for discussion). As I now interpret the basicranial articulation, it is between pterygoid and basisphenoid only. The pterygoid part of the basicranial articu-

lation is in the shape of a trough oriented anterodorsomedially with the predominant direction dorsoventral. In SMNS 16980 the pterygoid very closely fits on the basisphenoid on the left side but on the right side the pterygoid is displaced laterally about 2 mm so that the pterygoid is only touching the basisphenoid on this side at the medial margin of the articulation trough on the pterygoid. This is the side that has been prepared so that most of the articulation surface is visible. Considering the tight articulation of the left side as stable, the right pterygoid has moved laterally and anteriorly with respect to the left side. As preserved, the joint surfaces closely fit each other and do not appear to allow much room for large cartilages as seen in recent lizards.

In *Proganochelys* the pterygoid articulating surface faces concave posteriorly primarily but also somewhat dorsally. In captorhinids the (epipterygoid) basicranial recess faces medially primarily and posteriorly to a lesser extent. In *Proganochelys* the articulation trough curves through about 150° while in captorhinids it is much less, so that the trough is shallower, effectively J-shaped as described by Heaton (1979). In *Proganochelys* the basicranial articulation surface is continued dorsally above the level of the horizontal plate of the pterygoid and is produced into a thin, curved process, concave posterolaterally. This curved process is what has caused the confusion about the epipterygoid. On the left and most accessible side of SMNS 16980, the process is broken and slightly displaced laterally and possibly posteriorly, giving it the appearance of a separate element. On the right side, however, the process, although not complete, can be seen to be part of the pterygoid. Neither lizards nor *Captorhinus* seem to have anything similar to this process (unless, of course, it does turn out to be the epipterygoid).

The dorsal surface of the pterygoid cannot be seen in its entirety on either side of SMNS 16980 but by combining information from both sides most of the area is known. Anterolateral to the basicranial articulation is a shallow groove that runs anteriorly and then curves anterolaterally. This appears to be similar to a groove seen on the dorsal surface of recent turtles which contains the unossified remnant of the palatoquadrate (pterygoquadrate) cartilage. Heaton (1979: fig. 24) has described and labeled a similar groove in *Captorhinus* as containing the inferior nasal artery and the hyoid ramus of the facial nerve. More lateral parts of the structure are called the orbitotemporal ridge. It seems more likely to me that this groove contained the palatoquadrate cartilage.

The anteromedial margin of the pterygoid in *Proganochelys* has a parasagittal ridge that is continuous with the ridge on the vomer but lower and disappears posteriorly. The remaining areas on the dorsal surface of the pterygoid in *Proganochelys* appear to be free of structures—very different from the condition in Casichelydia, in which the pterygoid has sulci and attachments for many structures.

On the ventral surface of the pterygoid in *Proganochelys* are slightly raised areas bearing small teeth, uniform in size and shape. The teeth are preserved on both pterygoids but are most complete on the right pterygoid. During preparation of the teeth it has been necessary to retain some matrix for support but many of them, on the right pterygoid, are free of matrix. About half of the teeth have the tips broken off. The tooth-bearing areas cover more than half of the ventral surface of the pterygoid in *Proganochelys,* a much greater area than is covered by teeth in *Captorhinus.* In *Captorhinus* the palatal teeth are organized in three distinct areas: a long, narrow row along the medial edge of vomer and pterygoid, an oval area on the transverse process, and an elongate grouping on the palatine and pterygoid placed roughly between the other two sets. In *Proganochelys* there are no teeth along the lateral and posterior margin of the pterygoid, the area of the processus pterygoideus externus, the presumed homologous area of the transverse process. The vomerine-pterygoid row is discernible in *Proganochelys,* although it is somewhat more extensive than in *Captorhinus,* and it merges posteriorly with the large grouping of teeth in *Proganochelys,* the set covering the central area of the pterygoid. As many as eight rows of teeth can be distinguished and these merge posteriorly to form only four or five rows. The preservation of the palatal teeth in the other two skulls of *Proganochelys* precludes

a detailed comparison with SMNS 16980 but there are no apparent differences not ascribable to postmortem changes. In the Berlin skull the teeth are encrusted with a tough coating, possibly iron oxide, that has prevented individual rows from being made out. The strong lateral crushing in this specimen has forced right and left pterygoid together, giving them the appearance of a single tooth plate. SMNS 15759 has been badly distorted but the central pterygoid and vomerine-pterygoid raised surfaces are visible, although individual teeth are not clear.

Kayentachelys is the only other turtle with palatal teeth and they are entirely on the pterygoid. They are arranged in loose rows but only in one central area in the middle of the pterygoid.

BRAINCASE ELEMENTS
(table 6, figs. 16, 43, 52)

SUPRAOCCIPITAL

The supraocciptal is present in all three skulls but it is complete and uncrushed only in SMNS 16980. Nonetheless, due to minute fracturing the sutures limiting this element are unclear in many areas. The supraoccipital of *Proganochelys* is an unpaired, medial element lying above the foramen magnum and extending anteriorly below the parietals to form the posterior portion of the braincase roof. As I interpret the sutures, only a relatively small portion of the supraoccipital is exposed on the outside of the skull. This exposed portion forms the dorsal margin of the foramen magnum and bears a low, sagittal ridge that I interpret as the homolog of the very prominent crista supraoccipitalis seen in other turtles. The development of such a crest in *Proganochelys* is barely advanced over *Captorhinus* and, when compared with all other turtles, can be considered as nearly absent. The supraoccipital in this area is nearly flat and lies roughly at a 45° angle to the horizontal. As I interpret a suture seen on the left side of SMNS 16980, the parietals meet in the midline, on the occipital surface, just below the skull roof. This condition is not found in Casichelydia nor *Captorhinus,* but it may represent the primitive chelonian condition. In *Captorhinus* the postparietals meet medially on the occiput below the parietals and above the supraoccipital. Postparietals are absent in *Proganochelys* and all other turtles.

The supraoccipital in *Proganochelys* has doubtful lateral contacts but there seems to be an opisthotic-supraoccipital suture laterally and one with the exoccipital posteroventrally. These contacts are interpreted from the right side of SMNS 16980 and are dubious.

Internally, the supraoccipital of *Proganochelys* broadly underlies the parietal and covers the posterior portion of the processus inferior parietalis. On the midline the supraoccipital ends abruptly, about midway along the length of the parietal, in an anteriorly facing facet that represents the change from bone to cartilage in the tectum synoticum (see Gaffney, 1979a: 107). This feature is common in turtles and indicates the persistence of a cartilaginous portion of the chondrocranium.

The supraoccipital of *Captorhinus* is characterized by a median ascending process (using terms of Price, 1935; Heaton, 1979) that extends anteriorly along the midline and paired lateral ascending processes that extend dorsally and laterally. All three processes provide the only contact between braincase and skull roof of *Captorhinus*; the median ascending process contacts the parietal sagitally and the lateral processus braces against the postparietals (Heaton, 1979: 53). These processes cannot be recognized in *Proganochelys*; the lateral ones are totally absent and the median one is incorporated into the broad, main body of the supraoccipital. These characters are closely correlated with the general fusion of braincase and skull roof in *Proganochelys,* differing only in extent from Casichelydia.

EXOCCIPITAL
(figs. 16, 40, 43, 52)

The exoccipital is preserved intact on both sides of SMNS 16980 where both internal and external surfaces are visible. Sutures delimiting the bone are not clear, although a few may be interpreted. In the Berlin skull, most of the area of the exoccipital is preserved but crushing and the absence of sutures preclude much useful information. SMNS 15759 has this region extensively damaged and little useful information is possible.

The dorsal limits of the exoccipital are in-

TABLE 6
Comparison of Braincase Elements

	Captorhinus	*Proganochelys*	Casichelydia
Crista supraoccipitalis	Slightly developed	Slightly developed	Well developed
Postparietal bone	Present	Absent	Absent
Lateral ascending process of supraoccipital	Present	Absent	Absent
Median ascending process of supraoccipital	Discrete, narrow contact with skull roof	Broadly expanded, widely sutured to skull roof	As in *Proganochelys*
Recessus scalae tympani enclosed by bone	Absent	Absent	Present
Foramen jugulare anterius	Small	Large	Small
Foramen jugulare posterius	Absent	Absent	Present
Basioccipital and basisphenoid	Relatively thin, no ventral tubercle	Relatively thick, ventral tubercle	Relatively thin, no ventral tubercle
Cranioquadrate space	Completely open	Partially enclosed dorsally	Completely enclosed dorsally & ventrally
Prootic-parietal contact	Absent	Present	Present
Prootic contacting pterygoid & quadrate	No	No	Yes
Foramen nervi trigemini completely formed by bone	No	No	Yes
Contact of processus clinoideus & parietal	Absent	Present	Absent
Relative size of fenestra ovalis	About 5 times casichelydians'	About 2 times casichelydians'	(basis of comparison)
Plane of fenestra ovalis parallel to midline	No	No	Yes
Processus interfenestralis of opisthotic with ventral extension	No	No	Yes
Fenestra perilymphatica defined by bone	No	No	Yes
Well developed cultriform process on basisphenoid	Present	Present	Absent
Paired basipterygoid processes	Present	Present	Absent
Dorsum sellae	Very high	Very high	Low
Sella turcica	Small	Small	Large
Foramina anterius canalis carotici interni	Close together	Close together	Separated
Retractor pits on basisphenoid	Present	Absent	Absent
Relative size of stapes compared to cavum labyrinthicum	Very large	Small	Small
Relative diameter of stapedial column	Thick medially, thinner distally	Moderate, but consistent for entire length	Thin, with wide footplate
Stapedial foramen and accessory processes of stapes	Present	Absent	Absent
Articulation of distal end of stapes with pit in quadrate	Present	Present	Absent

terpretable, particularly on the left side of SMNS 16980. The exoccipital forms the lateral margin of the foramen magnum, contacting the supraoccipital in the upper margin, so that the supraoccipital enters the margin of the foramen as in other turtles. Laterally the exoccipital extends as a flat plate lying posterior to the opisthotic. The exoccipital-opisthotic contact is not particularly clear but can be interpreted on the left side of SMNS 16980. Ventrally the exoccipital seems to form the dorsal and posterior margin of the foramen jugulare anterius. In *Proganochelys* the foramen jugulare anterius, the structure on the side wall of the braincase, is barely differentiated from what might be identified as the foramen jugulare posterius, which is the opening on the outside of the skull. Furthermore, the foramen jugulare posterius in casichelydians is formed in a wall posterior to and not continuous with the foramen jugulare anterius. This wall encloses the recessus scalae tympani. Therefore, the foramen jugulare posterious does not exist in *Proganochelys* or *Captorhinus.* Support for this can be seen in the structure forming the lateral margin of the foramen jugulare anterius. This is the processus interfenestralis of the opisthotic, bearing the foramen externum nervi glossopharyngei (see Opisthotic). The processus usually forms the anterior wall of the recessus scalae tympani in casichelydians and it does not form any of the foramen jugulare posterius. *Proganochelys,* then lacks an enclosed recessus scalae tympani of the typical chelonian type, and lacks the ventral processes of the opisthotic and exoccipital and lateral process of the basioccipital that form the enclosure.

The foramen jugulare anterius is extremely large in *Proganochelys,* larger than in most turtles, and much larger than in *Captorhinus.* The foramen contains the vena cerebralis posterius, the vagus (X), and accessory (XI) nerves in recent turtles, and it is hard to see why it is so gigantic in *Proganochelys.* The foramen is larger than the fenestra ovalis in *Proganochelys,* and its large size is related to many of the peculiarities of this part of the skull in this turtle. The otico-occipital region is comparatively open, with much of the bone reduced to struts separating the foramen magnum, fenestra ovalis, and large foramen jugulare anterius. The internal form of the foramen jugulare anterius in *Proganochelys* is an irregular oval, inclined posteriorly and laterally. Although the edges are formed, there is no precise rim defining the foramen, the edges are curved and continuous with the cavum cranii, much as in Casichelydia. The anterior margin of the foramen is produced posterolaterally, more than the posterior margin, so the posterior opening of the foramen jugulare anterius lies in a more horizontal plane, facing posteroventrally.

The foramen nervi hypoglossi (VII) in *Proganochelys* is single and lies in the strut of bone separating the foramen magnum and the foramen jugulare anterius. The foramen penetrates the strut anterior to its center so that there is more bone posterior to the foramen than anterior. The foramen is of a diameter comparable to other turtles but its length is relatively short due to the thinness of the bony strut. The foramen is aligned ventrolaterally and opens within the margin of the foramen jugulare anterius. Just dorsal to the foramen nervi hypoglossi is a small pit that does not have a canal or foramen in it; its function is unknown.

The anterior margin of the foramen jugulare anterius has a small, irregular opening into the cavum labyrinthicum, this opening appears to be the fenestra perilymphatica. Its position in *Proganochelys,* in the base of the processus interfenestralis and in the margin of the foramen jugulare anterius, is very similar to that in other turtles.

The contact of the exoccipital with the basioccipital is assumed to be extensive but no sutures are visible. Breaks in the Berlin skull led Jaekel (1918a) to place it low in the foramen magnum so that very little of the condylus occipitalis was formed by the exoccipital, but there is no evidence for this.

Basioccipital
(figs. 16, 27, 40, 43, 52)

The basioccipital is preserved at least in part in all three *Proganochelys* skulls, but it is best preserved in SMNS 16980, although most of its sutures are not clear. In the Berlin skull the basioccipital is also preserved in relatively good condition—none of it seems to be missing, but its contacts are also appar-

ently fused and surrounding elements have been crushed medially into the bone.

The basioccipital of *Proganochelys* is a relatively large element, making up an indeterminant amount of the condylus occipitalis, forming the basioccipital tubercle, and flooring the posterior part of the cavum cranii. In *Proganochelys* the basioccipital (along with the basisphenoid) is a very thick element, much thicker than in *Captorhinus,* lizards, or other turtles. Its anterior contact with the basisphenoid is visible only on the ventral surface (see Basisphenoid); the contact cannot be made out on the floor of the cavum cranii. The ventral surface of the basioccipital in *Proganochelys* has a large ventral tubercle, quite different from anything seen in captorhinids or casichelydians. This tubercle is preserved in both the Berlin skull and SMNS 16980. It is relatively larger in the Berlin skull and has a low groove tending to separate the tubercle into two paired convexities. The tubercle in SMNS 16980 has no sign of this separation but the original bone surface seems to have been eroded slightly. The ventral surface of the tubercle is a continuation of the ventral surface of the basisphenoid. Posterior to the basispterygoid process the median ridge on the basisphenoid disappears at about the position of the basisphenoid-basioccipital suture. In the vicinity of this contact there are low, lateral bulges, probably formed by both bones. The basioccipital tubercle is an obtuse, ventral projection, somewhat narrower than long, that is separated from the condylus occipitalis by a right angle bend in the ventral bone surface. The presence of the large basioccipital tubercle in *Proganochelys* is morphologically related to the great thickness of the braincase floor and the position of the condylus occipitalis at the level of the dorsal surface of the floor. There could be a smooth transition from the condyle to the ventral surface of the skull but the change is abrupt and the tubercle results.

The condylus occipitalis in *Proganochelys* is borne on a short neck, shorter than in most turtles, but more developed than in *Captorhinus.* In *Captorhinus* the articulation surface is barely differentiated from the occipital base. In *Proganochelys* the condylus is concave ventrally and ventrolaterally but dorsolaterally there are strong processes forming the ventrolateral limits of the foramen magnum and separating it from the foramen jugulare anterius that comes almost to the articular surface.

The condylus occipitalis has an articular surface with the atlas that is wider than high and is roughly triangular in posterior view, with the broad base dorsal and all the angles rounded. The Berlin skull is slightly narrower in the articular surface than SMNS 16980, but this may be a result of crushing. The Berlin skull has a small concavity in the middle of the condylus, often seen in casichelydians, but this is absent in SMNS 16980, possibly due to erosion or immaturity.

None of the specimens show exoccipital-basioccipital sutures, so the makeup of the condylus occipitalis in *Proganochelys* is not known.

The degree of participation of the basioccipital in the foramina nervi hypoglossi and the foramen magnum is not known and these structures are discussed under Exoccipital.

The posterior floor of the cavum cranii is presumably formed at least in part by the basioccipital but in the absence of sutures this region will be described here even though the actual bones involved are not known. The foramen magnum begins virtually at the condylus occipitalis, much as in *Captorhinus,* while in casichelydians there is more of a separation due to the development of a neck on the condyle. The floor of the foramen magnum is flat, curving dorsolaterally at its margins. Anteriorly on the midline there is a small pit, that may possibly be a nutrient canal. This pit lies at about the level of the foramen nervi hypoglossi. This foramen is a single foramen in *Proganochelys,* in contrast to *Captorhinus* and turtles where there are two or more. The foramen is in the large strut forming the ventrolateral margin of the foramen magnum. Anterior to the pit the floor of the cavum cranii drops slightly, particularly to either side of the midline, leaving a low, broad ridge in the center. This depression leads posterolaterally into the foramen jugulare anterius. Anterior to the foramen is the area of the hiatus acusticus. The basisphenoid-basioccipital suture is not visible in the floor of the cavum cranii, but a small knob, possibly the basis tuberculi basalis, may mark the position of this suture. It is not definitely determinable

but it seems likely that the basioccipital enters the rim of the hiatus acusticus in *Proganochelys* as in other turtles.

Prootic
(figs. 16, 40, 43, 45)

All three *Proganochelys* skulls have both prootics present but the degree of preservation varies. Sutures delimiting the prootic are not entirely clear on any specimen. The prootic is best preserved in SMNS 16980 where it is nearly complete and uncrushed on both sides. In SMNS 15759 the right prootic is crushed and obscured while the left prootic, although conspicuously distorted, shows sutural contacts with the "pleurosphenoid." The prootics are barely identifiable in the Berlin skull, the ear region is badly crushed, but a stapes is present on the right side allowing unambiguous identification of the fenestra ovalis.

The prootic of *Proganochelys* is a roughly cuboid element forming part of the lateral wall of the braincase and the anterior portion of the cavum labyrinthicum, and it is intimately involved in the other structures of the ear region. Comparison of the prootic in *Proganochelys* with generalized amniotes and casichelydians shows a broader agreement between *Proganochelys* and generalized amniotes because the fusion of the palatoquadrate and neurocranium in casichelydians strongly affects the attachments and structures of the prootic.

The prootic in casichelydians is roughly cubical or block-shaped (see Gaffney, 1979a, Prootic), while the generalized condition for amniotes, as seen in most lizards and captorhinids, is a flatter, roughly triangular element (for example compare Oelrich, 1956: fig. 11, of the prootic in *Ctenosaura* with Gaffney, 1979a: fig. 52, of the prootic in various turtles). The reasons for this difference lie in the additional contacts of the prootic associated with the fusion of the basipterygoid articulation and enclosure of the cranioquadrate space in casichelydians. *Proganochelys* retains the generalized amniote condition in having an open basipterygoid articulation and an unenclosed cranioquadrate space.

The following description relies primarily on SMNS 16980 in which both prootics are relatively well preserved. As in Gaffney (1979a) the description of the prootic contacts is followed by description of the structures. The lateral surface of the prootic clearly shows an anterodorsal suture with the parietal on both sides of the skull. This suture begins at the posterior margin of the foramen nervi trigemini and extends posterodorsally. The same suture may be followed on the internal surface where it lies in a slightly more dorsal position. This prootic-parietal contact is a distinctive chelonian feature absent in generalized amniotes. In this feature *Proganochelys* is characteristically chelonian, casichelydians being advanced only in the slightly greater development of the contact area. This parietal-prootic contact is also visible in SMNS 15759, but is not as clear as in SMNS 16980. A comparison of this region in *Proganochelys* with that in generalized amniotes shows greater similarity with lizards than with *Captorhinus*. In *Captorhinus* the parietal is a totally flat plate with no descending process and no contact between parietal and prootic. In many lizards, however, there is a ventral flange of the parietal, apparently not homologous with the chelonian processus inferior parietalis, that comes very close to the alar process (crista alaris) of the prootic from which it is separated by varying amounts of connective tissue. This approximation of parietal and prootic in lizards takes place at about the same place with respect to the prootic and foramen nervi trigemini in turtles.

Posteriorly, the prootic of *Proganochelys* contacts the opisthotic as in all amniotes. However, the prootic-opisthotic suture is not visible in any of the three specimens of *Proganochelys* and was apparently fused. This is somewhat unusual because the sutures separating the three cavum labyrinthicum ossifications, namely prootic, opisthotic, and supraoccipital, are usually the most persistent in recent turtles. The general position of the prootic-opisthotic suture can be estimated in *Proganochelys* by using the position of the paroccipital process, fenestra ovalis, and stapedial groove as landmarks for comparison.

On the internal surface of SMNS 16980, the prootic contacts the supraoccipital posterodorsally as in other turtles and amniotes

generally. On the external surface the parietal covers most of the supraoccipital and prevents a prootic-supraoccipital contact. Ventromedially the prootic presumably has a broad contact with the basisphenoid, but the suture is not clearly visible and the two bones appear to be fused. There are places on the internal surface of SMNS 16980 where a prootic-basisphenoid suture can be interpreted and these agree with the position in other turtles. On the left lateral surface of SMNS 16980 there is a crack in the "correct" place for prootic-basisphenoid suture, in the ventral margin of the foramen nervi trigemini, but this can be seen to extend ventrally, cutting across several bones.

Laterally the prootic of casichelydians has a broad suture with the quadrate and usually contacts the pterygoid; both contacts are in the area of the enclosed cranioquadrate space. Generalized amniotes have an open cranioquadrate space with either no contact or a loose, sliding contact between pterygoid, quadrate, and prootic. *Proganochelys,* in contrast to all other turtles, has an open cranioquadrate space and no sutural contact with quadrate or pterygoid. The pterygoid-quadrate contact is a squamous one in which a thin, vertical sheet of the pterygoid lies anteromedial to a thin, vertical sheet of the quadrate. Together they form the lateral wall of the cranioquadrate space in generalized amniotes (see Goodrich, 1930: figs. 263 and 493).

In *Proganochelys* the dorsal portion of the pterygoid plate curves dorsomedially and comes very close to the prootic. On the left side of SMNS 16980 there seem to be small areas of contact but these may be displaced fragments of bone. There is a clear separation here with the gap filled with matrix.

The structures formed by the prootic in turtles are described in Gaffney (1979a, beginning on p. 115) and the order will be followed here. The processus trochlearis oticum is a synapomorphy of cryptodires and is formed by the prootic and quadrate. The anterolateral margin of the prootic that would bear the processus has no indication of thickening in *Proganochelys.* There is an anterior overhang formed by the prootic and parietal that looks superficially similar to a processus trochlearis oticum, but is related to the position of the trigeminal ganglion and forms its upper margin.

The passage of the stapedial artery through the skull is distinctly marked on the prootic of casichelydians but generalized amniotes, such as captorhinids and lizards, have no such indication. The stapedial artery of generalized amniotes rises dorsally along the anterior edge of the paraoccipital process. In lizards, if the pterygoid flange of the quadrate is sufficiently well developed, there may be a poorly defined stapedial opening formed between the quadrate and paroccipital of the opisthotic. There are no structures in captorhinids interpretable as showing the pathway of the stapedial artery (except the stapedial foramen in the columella). In casichelydians there is a well-defined canal, the canalis stapedio-temporalis, that is formed by the prootic and quadrate. In *Proganochelys* a well-defined canal is absent but the path of the stapedial artery is visible. An irregularly shaped stapedial opening is formed by the prootic, quadrate, and opisthotic, although the prootic-opisthotic sutures are absent, the actual degree of participation of these elements is speculative. This opening appears homologous with the foramen stapedio-temporale of casichelydians while the canalis stapedio-temporalis, formed by broad contact of prootic and quadrate, is absent in *Proganochelys.* On the dorsal surface of the prootic, possibly formed in part by the opisthotic, is a well-defined transverse groove extending medially from the foramen stapedio-temporale. Very similar grooves occur in recent turtles and they contain the stapedial artery. *Proganochelys* might therefore be advanced to a slight degree over the generalized amniote condition in the possession of a groove for the stapedial artery and a foramen stapedio-temporale, but the absence of a canalis stapedio-temporalis and the open cranioquadrate space are entirely consistent with the generalized amniote condition.

At this point it might be well to describe the entire cranioquadrate space in *Proganochelys* because the prootic is so closely related to the structures in it. The cranioquadrate space is defined anterolaterally by a curved wall made up by thin sheets of the pterygoid and quadrate. The wall is curved concave posteromedially. Posteroventrally

the space is open but dorsomedially it is limited by the prootic and opisthotic. Dorsolaterally the stapedial artery exists via an opening between the quadrate and the paroccipital process of the opisthotic. Dorsally the pterygoid-quadrate wall nearly contacts the prootic. The cranioquadrate space is greatly constricted anteriorly and becomes an irregular opening formed by the pterygoid ventrolaterally, the prootic dorsomedially, and the basisphenoid ventromedially. This opening appears to be homologous to the anterior portion of the canalis cavernosus of casichelydians and would contain the vena capitis lateralis and the hyomandibular branch of the facial nerve (VII). The columella (stapes) would traverse the space from the fenestra ovalis to the stapedial recess on the quadrate. The general size of the cranioquadrate space in *Proganochelys* is remarkably large when compared with lizards and *Sphenodon,* the only living amniotes retaining the generalized condition. In captorhinids the cranioquadrate space appears to be roughly intermediate in size between *Proganochelys* and living amniotes. It is possible that the large cranioquadrate space of *Proganochelys* is related to the hypertrophy of middle ear soft parts seen in other turtles.

The path of the facial (VII) nerve and its branches is of considerable interest in chelonian systematics even though the determination of its branches is often difficult for living turtles—to say nothing of extinct taxa. Nonetheless, the major features of the facial nerve pathway are determinable in *Proganochelys* and this supplies an interesting perspective for comparison with other taxa. In SMNS 16980, the fossa acustico-facialis is present and relatively well preserved on both sides of the skull. Although the prootic-opisthotic suture is not visible, the fossa is presumably formed entirely within the prootic as in other turtles and amniotes in general. Although the canalis leading to the three foramina in the fossa acustico-facialis have not been freed of matrix, it is very likely that the anteroventral foramen is the exit of the facial nerve, the foramen nervi facialis, and that the other two are for the acustic nerve. These identifications are indicated by the positions and observed directions of the foramina and are consistent with those of other turtles. The ventral opening of the foramen nervi facialis is on the ventral surface of the prootic, adjacent to the anterolateral margin of that bone. It is a prominent foramen, anterior and slightly medial to the fenestra ovalis, and lateral to the ventrally protruding basisphenoid. The foramen nervi facialis seems to be best preserved on the left side of the SMNS 16980. Here is an oblong opening with a ventral strap of bone extending along its narrowest part to divide the foramen into an anteromedial opening and a posterolateral opening (figs. 27, 51). In amniotes the facial nerve divides immediately upon leaving the primary neurocranium into two branches, an anterior palatine branch and a posterior hyomandibular (or stapedial) branch (Goodrich, 1930: figs. 263 and 449). The strap dividing the ventral limits of the foramen nervi facialis in *Proganochelys* can be readily interpreted as this division with the palatine branch exiting via the anteromedial foramen and the hyomandibular branch exiting via the posterolateral foramen. On the right side of SMNS 16980 the strap is not preserved in its entirety, although a constriction is present. The foramen nervi facialis has been cleaned dorsally and shows that it is a single canal above the strap and that the canal trends dorsally through the prootic as in the foramen nervi facialis of other amniotes.

This division of the foramen nervi facialis by a strap of bone is apparently unique to *Proganochelys*; casichelydians have the region ossified by other elements while generalized amniotes, like captorhinids and lizards, do not have this condition. Whether or not this is an autapomorphy of *Proganochelys* or the primitive chelonian condition cannot be entirely settled at present, but it is more likely to be the primitive chelonian condition.

If the identification of the two main branches of the facial nerve suggested above is correct, then the further extensions of these branches through the cranioquadrate space will not be reflected in bone. In *Proganochelys,* in contrast to other turtles, the palatine nerve would go anteriorly through the oblong opening marking the anterior restriction of the cranioquadrate space while the hyomandibular would travel posteriorly to the stapes where it would branch into the chorda tym-

pani and hyomandibular nerve proper. The geniculate ganglion of the facial nerve (see Gaffney, 1979a, Prootic, for reference) usually occurs where the palatine nerve branches off the main trunk of the facial nerve, and, in *Proganochelys,* this would presumably be just above the strap of bone dividing the distal end of the foramen nervi facialis into two foramina.

In *Proganochelys* there is no completely ossified foramen nervi trigemini homologous to that structure in casichelydians. The prootic and quadrate form, respectively, the posterior and ventral margin of a notch lateral to the cranioquadrate space that apparently marks the exit of V_2 and V_3 from the braincase into the temporal fossa and would therefore be the homolog of the foramen nervi trigemini in other turtles. In casichelydians the processus inferior parietalis and the crista pterygoidea combine witih the prootic (and in many cryptodires, the epipterygoid) to form a completely ossified foramen nervi trigemini (condition not known in *Kayentachelys*). In the generalized amniote condition the trigeminal notch is formed solely by the prootic and the apparent participation of the quadrate in the trigeminal notch of *Proganochelys* is distinct from the condition in other turtles as well as generalized amniotes. I think, however, that this is the primitive chelonian condition which is obscured by the contact of the prootic and pterygoid anterior to the quadrate in casichelydians.

The prootic of *Proganochelys* also has another structure related to the trigeminal nerve. Medial to the incomplete foramen nervi trigemini is a foramen formed by the parietal dorsally, the prootic posteriorly, and the basisphenoid anteriorly. Unfortunately, the prootic-basisphenoid suture is not clear although it is best interpreted as lying in about the middle of the ventral margin of the foramen. The parietal has a triangular spur that protrudes anteroventrally to contact the processus clinoideus of the basisphenoid. The foramen thus produced is the fenestra prootica, as identified in the chondrocranium (Kunkel, 1912). Usually this structure is not present as a distinct feature formed by bone in the adult; the pila prootica usually ossifies only at its base as the processus clinoideus. *Plesiochelys* is reported (Gaffney, 1976) also to have an ossified pila prootica but in that case it is made up almost entirely of the prootic bone. The contact of the processus clinoideus and the parietal in *Proganochelys* is thus unique and best interpreted as an autapomorphy.

The fenestra ovalis in *Proganochelys* is well preserved and prepared internally as well as externally in SMNS 16980, while in the Berlin skull the fenestra is badly crushed but it has the stapes preserved in situ. The fenestra ovalis of *Proganochelys* is a relatively large opening with a fully ossified and formed rim. In most casichelydians the fenestra is incomplete ventrally, remaining cartilaginous throughout life. There are no sutures allowing for the differentiation of bones around the fenestra ovalis in *Proganochelys* but it is probably formed by the prootic anteriorly and the opisthotic posteriorly, as in other turtles. The shape of the fenestra ovalis in *Proganochelys* is ovoid and sightly tear-shaped with the anterior portion being larger than the posterior margin which tapers visibly. The rim of the fenestra is thick compared to that of other turtles and lizards. The fenestra ovalis is large in *Proganochelys,* filling most of the space between the anterior edge of the prootic and the processus interfenestralis of the opisthotic. The basis columellae in *Proganochelys* is not entirely visible in the Berlin specimen but it does not seem to be any different in size from the rest of the stapedial shaft. Using rough estimates of the size differences between the Berlin skull and SMNS 16980, it would appear that the stapes of *Proganochelys* did not fit tightly into the fenestra ovalis, but this must be considered speculative.

Comparison of the fenestra ovalis in *Proganochelys* with that in casichelydians shows the opening in *Proganochelys* to differ primarily in two features: its greater relative size and its skewed position with respect to the stapes. It is difficult to produce quantitative evidence; but, subjectively estimated, the diameter of the fenestra ovalis in relation to the size of the skull seems larger in *Proganochelys,* by perhaps a factor of two, when compared with that in other turtles. Captorhinids are characterized by a relatively gigantic stapes and a fenestra ovalis that seems to be larger than in *Proganochelys* by a factor

of five or more. Lizards, even in comparison with casichelydians, have a fenestra ovalis that is miniscule. *Proganochelys* thus resembles captorhinids in having a relatively large fenestra ovalis.

In casichelydians the fenestra ovalis is circular (usually incompletely ossified ventrally but cartilaginous) and is oriented in a single dorsoventral plane parallel to the midline of the skull. In captorhinids the footplate of the stapes is very large and it does not lie in a simple, flat plane parallel to the midline; rather, it is skewed so that the anteroventral margin is closer to the midline than the posterolateral margin. In *Proganochelys* the margin of the fenestra ovalis is also skewed so that its anteroventral margin is closer to the midline but the degree of skewing is less than in captorhinids. Comparing all turtles with captorhinids, the smaller fenestra ovalis and more parallel orientation of the fenestra may be interpreted as chelonian synapomorphies, while an even smaller fenestra ovalis and fully parallel orientation with the midline are interpreted as casichelydian synapomorphies.

Opisthotic
(figs. 16, 40, 43, 51, 52)

The opisthotic is preserved in all three *Proganochelys* skulls, but it is complete and uncrushed only in SMNS 16980. Even in this specimen, however, many of the sutures limiting the bone are unclear.

As described under Prootic, the opisthotic-prootic suture appears fused but it is presumed to be roughly transverse, the prootic being anterior to it and the opisthotic posterior; this is the condition in most amniotes. The absence of information about this suture in *Proganochelys* precludes detailed comparisons with other turtles and captorhinids, but the suture's position is comparable in captorhinids and turtles and *Proganochelys* is at least consistent with this. Ventromedially the opisthotic contacts the basioccipital but the exact position of this suture is not visible. Posteriorly the opisthotic contacts the exoccipital and at least some of this suture can be determined, particularly on the right side of SMNS 16980. Here the suture runs in occipital view from the ventral margin of the paroccipital process dorsomedially, much as in other turtles. Ventrally the suture turns medially and runs into the roof of the foramen jugulare anterius, again similar to other turtles (Gaffney, 1979a: fig. 49). The lateral overlap of the exoccipital onto the paroccipital process of the opisthotic is not developed in captorhinids to the same degree seen in *Proganochelys* and other turtles. This may be interpreted as a chelonian synapomorphy. Dorsally the exoccipital-opisthotic suture is lost.

Because the parietal largely covers the supraoccipital dorsally, the medial margin of the opisthotic meets the parietal in dorsal view, but beneath the parietal the opisthotic contacts the supraoccipital. There may be some opisthotic-supraoccipital contact exposed on the dorsal surface, depending on whether or not the exoccipital contacts the parietal. The opisthotic rarely contacts the parietal in casichelydians but the two bones do approach one another, and sometimes meet. In captorhinids and other generalized amniotes, however, these bones are widely separated due to the absence of a descending process of the parietal.

Posterolaterally, the opisthotic in *Proganochelys* contacts the squamosal, a contact that is absent in captorhinids but characteristic of turtles. Heaton (1979: 56) stated that in *Captorhinus* the paroccipital process of the opisthotic bore an "intercalary cartilage" that joined the opisthotic to the occipital flange of the squamosal. In lizards the paroccipital process reaches the squamosal, much as in *Proganochelys,* and that is presumably the generalized amniote condition, its absence in *Captorhinus* not withstanding. Casichelydians are advanced over *Proganochelys* in having a distinctive, broad contact between the anterolateral surface of the paroccipital process of the opisthotic and the quadrate.

Just beneath the opisthotic-squamosal contact in *Proganochelys* the opisthotic and quadrate lie very close to each other but are separated by matrix and do not appear to be suturally connected. This condition appears to be similar to that in lizards where the bones are loosely attached by connective tissue. The opisthotic and quadrate separate from each other anteromedially where the stapedial artery runs between them to exit from the cranioquadrate space.

The opisthotic in *Proganochelys* may be

divided into two regions (as in other turtles): an anteromedial region containing the posterior part of the cavum labyrinthicum and a posterolateral region consisting of the processus paroccipitalis and associated structures. The cavum labyrinthicum portion is only visible to a limited extent and the disposition of the semicircular canals is not determinable. The posterior margin of the fenestra ovalis is presumably formed by the opisthotic (see Prootic for further description).

The opisthotic forms the processus interfenestralis, a sheet forming the posterior wall of the fenestra ovalis and penetrated by a small canal here identified as containing the glossopharyngeal (IX) nerve. In *Proganochelys* the opisthotic continues medial to the processus interfenestralis to form a wall separating the cavum labyrinthicum from the foramen jugulare anterius. The processus interfenestralis of casichelydians is defined by Gaffney (1979a: 363) as follows:

> A ventral process of the opisthotic extending into the cavum acustico-jugulare and separating the cavum into two parts, lateral and posterior, the latter being the recessus scalae tympani. The foramen internum nervi glossopharyngei and foramen externum nervi glossopharyngei generally penetrate the dorsal portion of the process. The anterior surface of the processus walls the cavum labyrinthicum.

Comparison of *Proganochelys* with other turtles reveals an absence of some diagnostic features of the processus interfenestralis in *Proganochelys.* First of all, *Proganochelys* does not have a typical cavum acustico-jugulare as found in other turtles; the middle ear region is entirely open ventrally and posteriorly. Although I have identified a portion of the opisthotic as the processus interfenestralis, there is no ventral process reaching the level of the floor of the basicranium. The anterior surface of the structure in *Proganochelys* does form the posterior wall of the cavum labyrinthicum, but the absence of a complete ventral process and of further ossifications defining a cavum acustico-jugulare prevent the recognition of a recessus scalae tympani.

In casichelydians the medial margin of the processus interfenestralis forms the lateral margin of the fenestra perilymphatica, an opening formed primarily by the opisthotic that communicates between the cavum labyrinthicum and the recessus scalae tympani. I have been unable to find this structure or even a homologous area in *Proganochelys* (see below under Foramen jugulare anterius). Comparison of this area in *Captorhinus* shows even greater divergence from the casichelydian condition and for once *Proganochelys* is not clearly an intermediate. In fact, comparison of the region around the foramen jugulare anterius among captorhinids, *Proganochelys,* and casichelydians is difficult due to the morphologic divergence. Captorhinids apparently have the glossopharyngeal (IX) nerve exiting with the vagus (X) nerve via the vagus foramen of Heaton (1979). Presumably this foramen also contained the "jugular" or vena cerebralis posterior and the accessory (XI) nerve. Thus it would be homologous with the foramen jugulare anterius of turtles, even though the latter does not contain the glossopharyngeal (IX) nerve. Thus the path of the glossopharyngeal nerve cannot be used in captorhinids as a landmark for the processus interfenestralis, and the region between the vagus foramen and fenestra ovalis is a broad, curved surface consisting of most of the opisthotic. As the paroccipital process, however rudimentary, is identifiable in captorhinids, the best we can do is to surmise that the processus interfenestralis of turtles is roughly homologous with the region of the base of the processus paroccipitalis in captorhinids. The separation of the glossopharyngeal (IX) nerve in its own canal is interpreted as a chelonian synapomorphy, and the appearance of this canal in other amniotes is interpreted as a parallel derivation (there is evidence for developmental as well as morphologic differences in any case, see Rieppel, 1980). The ventral extension of the processus interfenestralis and the presence of a fenestra perilymphatica defined by bone is interpreted as a casichelydian synapomorphy.

Basisphenoid
(figs. 16, 27, 40, 43, 50)

The basisphenoid is present in all three *Proganochelys* skulls although it is nearly complete only in SMNS 16980. The Berlin skull has the ventral area of the bone apparently undistorted and visible, while in SMNS 15759 the lateral areas are visible but distorted as a result of postmortem deformation.

The basisphenoid of *Proganochelys* is much more similar to that in generalized amniotes, such as *Captorhinus,* than to other turtles. There is a well-developed cultriform process, paired basipterygoid processes, very high dorsum sellae, very small sella turcica with the foramen anterius canalis carotici interni small and very close together; these are all generalized features of amniotes based on captorhinids and lizards. None of the sutures of the basisphenoid in SMNS 16980 are clear although some can be made out. The Berlin skull has a distinct basisphenoid-basioccipital suture.

Anteriorly the basisphenoid of *Proganochelys* has a cultriform process, an anterior extension from the base of the basisphenoid. The process forms about half the entire length of the basisphenoid and extends between the pterygoids in the center of the interpterygoid vacuity. The process is not perfectly preserved, showing fine surface breaks, but the anterior termination is in matrix and shows no indication of having been broken off, and I conclude that its preserved length is an accurate indication of its original length. In cross section the cultriform process is V-shaped but the ventral keel is somewhat rounded as preserved. The ventral keel continues posteriorly as a ridge on the main body of the basisphenoid between the basipterygoid process to the level of the foramen posterius canalis carotici interni. The dorsal surface of the cultriform process seems to have a low trough developed on it, although it has not been possible to prepare much of the area. Posteriorly, the trough is continuous with the sella turcica. Near the base of the cultriform process, where it joins the main body of the basisphenoid, the lateral margin of the cultriform process has paired flanges or spurs that rise above the main stem of the process. These spurs are similar to ones often, but not always, seen in recent cheloniids, lying on either side of the fused rostrum basisphenoidale.

The sella turcica in *Proganochelys* is very small, simply the depression where the plate of the dorsum sellae and the rostrum basisphenoidale join. There is a slight depression, a continuation of the trough running down the rostrum, but no indication of the distinctive retractor pits seen in *Captorhinus* and lizards. The foramina anterius canalis carotici interni are not entirely prepared out due to their difficult position, but the openings face anteriorly and are separated only by a relatively thin bar of bone, much as in lizards. The foramina are in the posterior wall of the sella turcica, at the base of the dorsum sellae, somewhat lower than in lizards; the condition is very different in *Captorhinus,* which has the foramina anterius canalis carotici interni placed all anterior to a large rectractor pit out on the rostrum basisphenoidale. In contrast to *Captorhinus* and lizards, *Proganochelys* has no canal for the palatine nerve and artery, which presumably ran just lateral to the basisphenoid dorsal to the basipterygoid process.

The dorsum sellae of *Proganochelys* is a high, flat plate, facing anteroventrally with the foramen nervi abducentis prominently placed on each side, laterally about halfway up the plate. Just lateral to the foramen, the basisphenoid curves posterolaterally and bears a low ridge that is continuous dorsally with the processus clinoideus. The anterior surface of the dorsum sellae bears no midline or other ridge as seen in *Captorhinus* and some turtles, nor is there any depression or indication of a retractor pit as seen in *Captorhinus* and lizards. The dorsal margin of the dorsum sellae in *Proganochelys* is slightly curved, concave dorsally in anterior view. In cross section the dorsum sellae forms a relatively thin overhang where the anteroventrally facing anterior surface meets the dorsally facing dorsal surface. The overhang is greater than in lizards or *Captorhinus,* or nearly all turtles. Lateral to the dorsum sellae in *Proganochelys* is the well-developed, paired, processus clinoideus. This process extends dorsally and then curves posterodorsally to meet a process from the parietal and enclose a large foramen. The processus is also curved laterally to form an anteriorly aligned trough, concave laterally. The processus clinoideus of *Proganochelys* is more extensive than in nearly all Casichelydia and only slightly more extensive than in most lizards. An accurate determination of its homolog in *Captorhinus* is difficult. In any case, the area of bone dorsal to the canalis nervi abducentis is similar in *Captorhinus* and *Proganochelys.*

The foramen nervi abducentis of *Progan-*

ochelys runs from the anterior surface of the dorsum sellae, through the bone to emerge on the floor of the cavum cranii, as in most turtles. The posterior opening is well posterior to the processus clinoideus, farther back than in most turtles, but closer to the midline than in most turtles. There is variation in this within casichelydians and this position is probably not systematically significant.

The basisphenoid of *Proganochelys* is very thick in cross section, much thicker than in *Captorhinus,* lizards, or casichelydians. The basisphenoid-basioccipital contact can be made out on the ventral surface of SMNS 16980 and it is anterior to the large median tubercle and posterior to the foramen posterius canalis carotici interni. The contact of the two bones within the skull must be extensive because both elements are very thick but it is not visible in SMNS 16980. Jaekel (1918a: fig. 46) reported it in the Berlin skull as being a roughly vertical, transverse contact, much as what would be expected. The position of the suture ventrally does seem to be more posterior in the Berlin skull than in SMNS 16980, so that the basisphenoid encroaches onto the anterior limits of the basioccipital tubercle. The ridge marking this suture cannot be seen microscopically in the Berlin skull.

The prootic-basisphenoid suture (see Prootic) is not clear in SMNS 16980 but one can be interpreted in the margin of the prootic foramen. The rest of the prootic contact is presumably along the dorsolateral part of the basisphenoid but cannot be made out.

Columella Auris
(figs. 52, 53)

Among the three *Proganochelys* skulls the columella auris, or stapes, is preserved only on the right side of the Berlin skull. It appears to be preserved in its normal position, but its present curvature is probably the result of the strong lateral deformation seen in this skull. The stapes is a stout, columnar element, much thicker than in any other known turtle. Its diameter is about the same as that of the fenestra ovalis. The medial edge of the stapes is not visible because the fenestra ovalis of the Berlin skull is collapsed around the stapes, obscuring its articulation with the skull. The medialmost portion of the stapes shows no change in shape to form an expanded footplate, and it is unlikely that a definitive footplate existed, due to the relatively large diameter of the stapes. The stapes is oval in cross section, the long dimension being dorsoventral; although this is possibly the result of crushing, it is most likely the original shape. As preserved, the stapes is curved almost into an S-shape, but this seems to be the result of crushing. The quadrate of the Berlin skull is rotated posteriorly and medially in comparison to SMNS 16980, and if the stapes were restored in SMNS 16980 with the same relations to the surrounding structures as in the Berlin skull, it would be nearly straight. In the Berlin skull the stapes is oriented posterolaterally and strongly ventrally, but in the restored condition the ventral component is very slight and would be nearly horizontal.

The distal end of the stapes in *Proganochelys* terminates abruptly in a slight concavity. This concavity appears to be natural; it is not a broken surface, but some of the margins are damaged. The stapes articulates anteromedially with the medial surface of the quadrate, just anterior to the margin of the incisura columellae auris. It is possible that this contact is postmortem and that in life the distal end of the stapes was suspended free of the quadrate by ligaments or cartilage. Just dorsal to the stapedial-quadrate contact is an elongate pit or pocket formed by the quadrate. This pit seems to be homologous with the columellar recess in *Captorhinus* (Heaton, 1979), which is the articulation site for the stapes. Although the stapes does not, at present, actually lie in this pit in the Berlin skull, it is likely that this is the result of postmortem replacement, and that in life the stapes of *Proganochelys* terminated on the medial surface of the quadrate at the quadrate pit.

The stapes of *Proganochelys* is conspicuously different from that in *Captorhinus* in being much less massive in comparison to the rest of the skull and in lacking the stapedial foramen, processes, and expanded footplate. Thus it is similar to turtle stapes in being columnar, rodlike, and solid. However, the stapes in *Proganochelys* is plesiomorphic in comparison to that of casichely-

dians in its relatively large diameter and apparent articulation with the quadrate. Other turtles have a very thin stapes and a proximally expanded footplate, either flat or conical. The column of the stapes extends lateral to the incisura columellae auris and articulates with the tympanic membrane by means of a cartilaginous extrastapes. One may speculate that in *Proganochelys* the stapes, although still retaining a quadrate articulation, may have had a cartilaginous extrastapes articulating with the tympanic membrane.

LOWER JAW ELEMENTS
(table 7, figs. 54–61)

All three *Proganochelys* skulls have the lower jaws preserved; only the right ramus of SMNS 15759 lacks a large portion, namely the portion posterior to the processus coronoideus. All of the three jaws are damaged to some extent, SMNS 16980 being the best preserved and having the best sutures. The Berlin skull has lower jaws that are badly fractured but the bone preservation is fairly good and some sutures can be seen. In SMNS 15759 lateral compression has caused plastic flow in contrast to the obvious breaks in the Berlin specimen. The following description and restorations rely primarily on SMNS 16980 but they are supplemented by the other specimens. None of the jaws reveals very much in the way of internal information but breaks developed during preparation provide some internal details in SMNS 16980.

Dentary

The dentary is present on both sides of the lower jaw in all three *Proganochelys* skulls. The bone is nearly complete in SMNS 19680 and the Berlin skull but in SMNS 15759 the posterior portion of the left dentary is missing. None of the dentaries are entirely complete with clearly defined sutural limits. The dentaries in SMNS 15759 and the Berlin skull show some sutures but the best information comes from SMNS 16980.

The contacts of the dentary in *Proganochelys* are with the large splenial medially, the angular posteroventrally, the surangular posterolaterally, and, presumably with the coronoid posterodorsally, although the sutures with this latter element are not clear. There is a short posterodorsomedial contact with the prearticular. The dentary of *Proganochelys* is basically similar to other turtle dentaries; there are no indications of teeth or structures associated with teeth. The "rudimentären Zahnanlagen" or "Zahngruben" of Jaekel (1918a: fig. 61) are the openings of nutrient canals found in the areas covered by the horny rhamphotheca of all turtles. Consistent with the proportions of the skull, the lower jaw of *Proganochelys* has a somewhat longer distance posterior to the processus coronoideus than in casichelydians and a relatively large fossa meckelii.

The triturating surfaces of *Proganochelys* seem to be borne entirely on the dentary, although the absence of clear coronoid sutures makes this prone to later emendation. The jaws are relatively narrow in contrast to those of most other turtles but of about the same width as in captorhinids. The triturating surface is clearly demarcated by well-defined lingual and labial ridges that parallel each other and are separated by a trough. The trough is shallow posteriorly near the processus coronoideus and becomes deeper more anteriorly where the ridges are higher.

Near the symphysis the lingual ridge disappears and the trough becomes a ventromedially sloping surface. The labial ridge is straight and horizontal in lateral view and forms a moderately sharp cutting edge, similar to that of *Plesiochelys*. The labial ridge extends from the base of the processus coronoideus to the symphysis where it is continuous with the labial ridge of the other ramus with no change at the symphysis. The lingual ridge begins at the base of the processus coronoideus and rises as it extends anteriorly to become higher than the labial ridge. The lingual ridge ends anteriorly before reaching the symphysis so that the triturating surface is curved and sloping at the symphysis. The lingual ridge is sharp, thinner than the labial ridge, and broken for most of its length in SMNS 15759 and the Berlin specimen. The lingual ridge is better preserved in SMNS 16980, particularly on the right side.

The triturating surface is much narrower in SMNS 15759 than in the other two specimens but this seems to be the result of lateral crushing. This specimen and the lower jaws of the Berlin skull have greater breakage of

TABLE 7
Comparison of Lower Jaw Elements

	Captorhinus	*Proganochelys*	Casichelydia
Dentary tooth bearing	Yes	No, covered with horny beak	No, covered with horny beak
Lateral exposure of angular	Extensive	Intermediate	Small
Fossa meckelii	Larger	Smaller	Smaller
Area articularis mandibularis	Entirely on articular bone	Shared by prearticular, articular & surangular	As in *Proganochelys*
Retroarticular process well developed	Yes	Yes	Yes and no
Prearticular extends well anterior to foramen intermandibularis caudalis	No	No	Yes
Dorsal opening of fossa meckelii	Very large, faces medially	Intermediate in size, faces dorsally	Small, faces dorsally
Splenial bones	Large, meet in midline and cover all of dentary	Large, do not meet in midline, some of dentary exposed	Smaller, do not meet midline, much of dentary exposed

both triturating ridges than in SMNS 16980, but this is also interpreted as postmortem damage. However, SMNS 16980 has a lower jaw that is not as deep as the other two and, although this condition does seem to have been exaggerated by lateral deformation, this is not a sufficient explanation. If the relatively small size of SMNS 16980 is the result of growth differences, then the shallower lower jaw may also be related to this condition. As far as can be determined, the jaw depth is the only difference among the three jaws, aside from size (see table 8), that does not appear to be the result of postmortem factors.

The triturating surface morphology of *Proganochelys* is similar to that seen in many other turtles, but the combination of well-developed ridges separated by a narrow trough, with the lingual ridge rising higher than the straight labial ridge and disappearing short of the symphysis, is unusual and not precisely the same as in any other turtle. Is the entire morphology primitive for turtles or are some elements autapomorphic? This is a difficult question to answer because the outgroup, generalized amniotes—particularly captorhinids—have teeth and no triturating surface. Comparison can be made between *Proganochelys* and the presumed primitive morphotype of casichelydians based on presumed plesiomorphic conditions. The narrow width of the triturating surface does seem to be plesiomorphic for all turtles; captorhinids have a narrow jaw and this appears to be a good comparison. Also the straight labial ridge, lacking a symphyseal hook or notch, is similar to that of captorhinids and may be hypothesized as primitive for turtles. The high lingual ridge does occur in cryptodires and pleurodires but its distribution is too sporadic systematically to conclude that it would necessarily be primitive for either group. This condition does occur, although modified, in baenids, meiolaniids, and pelomedusids so the possibility does remain viable. The symphyseal morphology of the lingual ridge varies greatly in turtles and it is very difficult to see a pattern for this area. A low lingual ridge meets at the symphysis in baenids and pelomedusids and a high one meets in meiolaniids but the *Proganochelys* condition is common in testudinoids and chelids. There are no strong arguments against the entire triturating morphology of *Proganochelys* being primitive for Testudines, but only the narrow surface with parallel ridges is clearly plesiomorphic.

The triturating surface morphology that is most similar to *Proganochelys* can be found in *Plesiochelys etalloni* (Gaffney, 1976: fig.

Fig. 54. *Proganochelys quenstedti,* SMSN 15759. Stereophotographs of lower jaws.

Fig. 55. *Proganochelys quenstedti,* MB 1910.45.2. Stereophotographs of lower jaws.

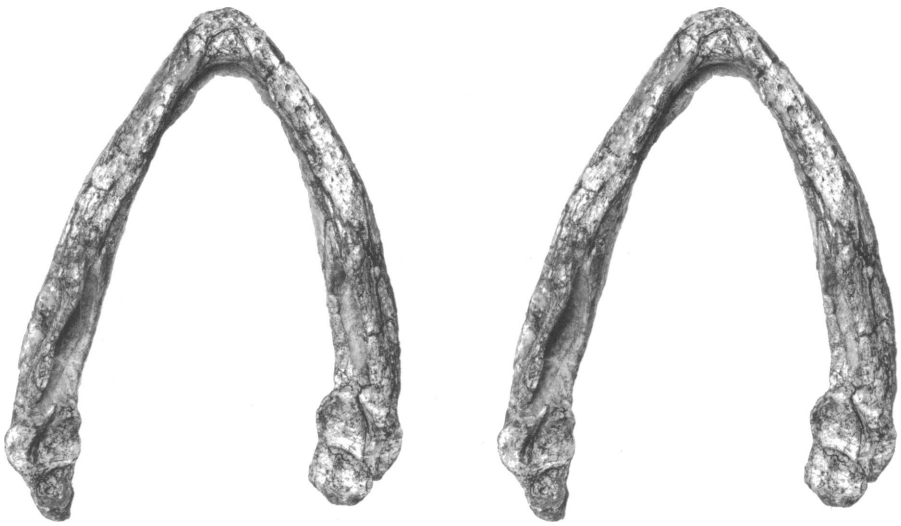


Fig. 56. *Proganochelys quenstedti,* SMNS 16980. Stereophotographs of lower jaws.

45). The rami in this species are relatively narrow, the ridges are separated by a shallow trough, and the lingual ridge does not meet at the symphysis. The ridges in *Plesiochelys etalloni* differ in being more curved in lateral view, having more of a dorsal projection at the symphysis, having a wider trough, and lingual labial ridges about the same height.

The symphysis of the lower jaw in *Proganochelys* shows no indication of a suture; both rami are solidly fused. A section at the symphysis shows the distinct labial ridge, ventrally sloping triturating surface with no lingual ridge, and a posterior-facing convexity above the sulcus cartilaginis meckelii. Ventrally the symphysis is thin, in contrast to most turtles. The sulcus cartilaginis meckelii is a distinct groove at the symphysis, as in many turtles, and extends laterally with no change in size. The sulcus is exposed for only a short distance beyond the symphysis because of the great anterior extent of the splenial which covers the sulcus medially.

The external surface of the lower jaw in *Proganochelys* is rugose with a texture similar to that of the skull, but there is no clear marking to determine the extent of the rhamphotheca in any of the three jaws. The rugosity and size of nutrient foramina increase dorsally and anteriorly as the triturating surface is approached and there is every reason to conclude that a horny rhamphotheca was present but its extent is indeterminant.

A foramen dentofaciale majus does not appear to be present, although the bone surface is too poorly preserved in all three jaws to be sure of the absence of a small foramen.

Angular

Some portion of the angular is preserved in all three specimens but a complete angular can be seen only on the right and left side of SMNS 16980. The angular forms the ventral margin of the posterior part of the jaw. The dentary-angular contact is clear in SMNS 16980 and is an interdigitating suture at the level of the foramen intermandibularis caudalis with one long process extending anterior to the foramen along the ventral margin of the lower jaw. On the internal surface the dorsal margin of the angular is a nearly straight, horizontal suture extending directly posteriorly from the foramen intermandibularis caudalis. This suture can be seen in all three specimens anteriorly but it disappears

near the posterior end of the jaw. On the external surface the dorsal margin of the angular has a straight, horizontal suture with the surangular but this suture is also visible only anteriorly in SMNS 16980 and SMNS 15759. The posterior limits of the angular are not determinable but the posterior fusion of lower jaw bones is common in turtles.

In all casichelydians the angular has very little exposure on the lateral side of the lower jaw. The bone usually curves around onto the external surface only at the posterior end of the jaw. In *Captorhinus* the angular covers about half of the external surface of the posterior portion of the lower jaw. *Proganochelys* is advanced over *Captorhinus* in having much less angular exposure but it is still distinctly more than in casichelydians. On the internal surface the angular extends well anterior to the foramen intermandibularis caudalis in most cryptodires, but less so in *Meiolania,* while in *Proganochelys* the angular extends only to the foramen intermandibularis caudalis (except for a thin process on the ventral surface). In *Captorhinus* the angular just reaches the foramen but the foramen itself appears to be farther anterior relative to other structures in comparison to *Proganochelys.* The extension of the angular anterior to the foramen intermandibularis caudalis appears to be a casichelydian synapomorphy. Jaekel (1918a: fig. 57) identified the anterior portion of the angular as the dentary. This region is ambiguous in the Berlin specimen but it is clear in SMNS 16980. On the external surface Jaekel's limits for the angular are accurate as I interpret them.

Surangular

The surangular is a large, flat bone forming most of the posterior external surface of the lower jaw and is preserved to some degree in all three *Proganochelys* specimens. As usual, it is best preserved in SMNS 16980. Jaekel's (1918a: fig. 57) limits for the surangular agree with my own interpretations, except for my recognition of the coronoid bone in lateral view (see below). The surangular of *Captorhinus* (Heaton, 1979: figs. 2, 30) is closer in size to that in advanced cryptodires than to *Proganochelys.* The surangular is a long element in *Captorhinus,* limited to forming less than half of the posterior part of the jaw. The large angular occupies the rest. In many advanced cryptodires the posterior extent of the dentary limits the size of the surangular which is restricted to the posterodorsal margin of the jaw. In *Proganochelys,* however, the surangular covers most of the posterior half of the jaw, much as in *Meiolania* and baenids, although the surangular is larger in the latter due to a smaller angular. The surangular of *Proganochelys* does have a primitive feature in that it extends anteriorly beneath the processus coronoideus while in casichelydians the surangular usually (but not always, pelomedusids and some testudinids are exceptions) is restricted to the area posterior to the processus coronoideus.

The surangular forms the lateral wall of the fossa meckelii. In *Proganochelys* the fossa is a large space with a large dorsal opening between the processus coronoideus and the area articularis mandibularis. The size of the fossa is roughly comparable with that in other turtles. *Captorhinus* has a fossa meckelii and a dorsal opening that are larger than in *Proganochelys.*

Posteriorly, the surangular in most casichelydians forms the lateral third or more of the area articularis mandibularis and contacts the articular medially. In *Captorhinus* the articulation is borne entirely by the articular bone. Fortunately, the articular-surangular suture is visible in both the Berlin skull and in SMNS 16980 and it has the typical chelonian condition.

The foramen nervi auriculotemporalis does not appear to be preserved, although the bone surface in all three jaws is too poorly preserved to be sure of the absence of a small foramen.

Coronoid

The region of the coronoid is preserved in the Berlin skull and SMNS 16980 and to some extent in the right ramus of SMNS 15759. The anterior limits of the bone seem clear in SMNS 16980, the small processus coronoideus is separated anteriorly from the dentary by a space filled with matrix on both sides. Posteriorly, however, there are no clear separations, although the most likely ones would produce a very small coronoid (this is the

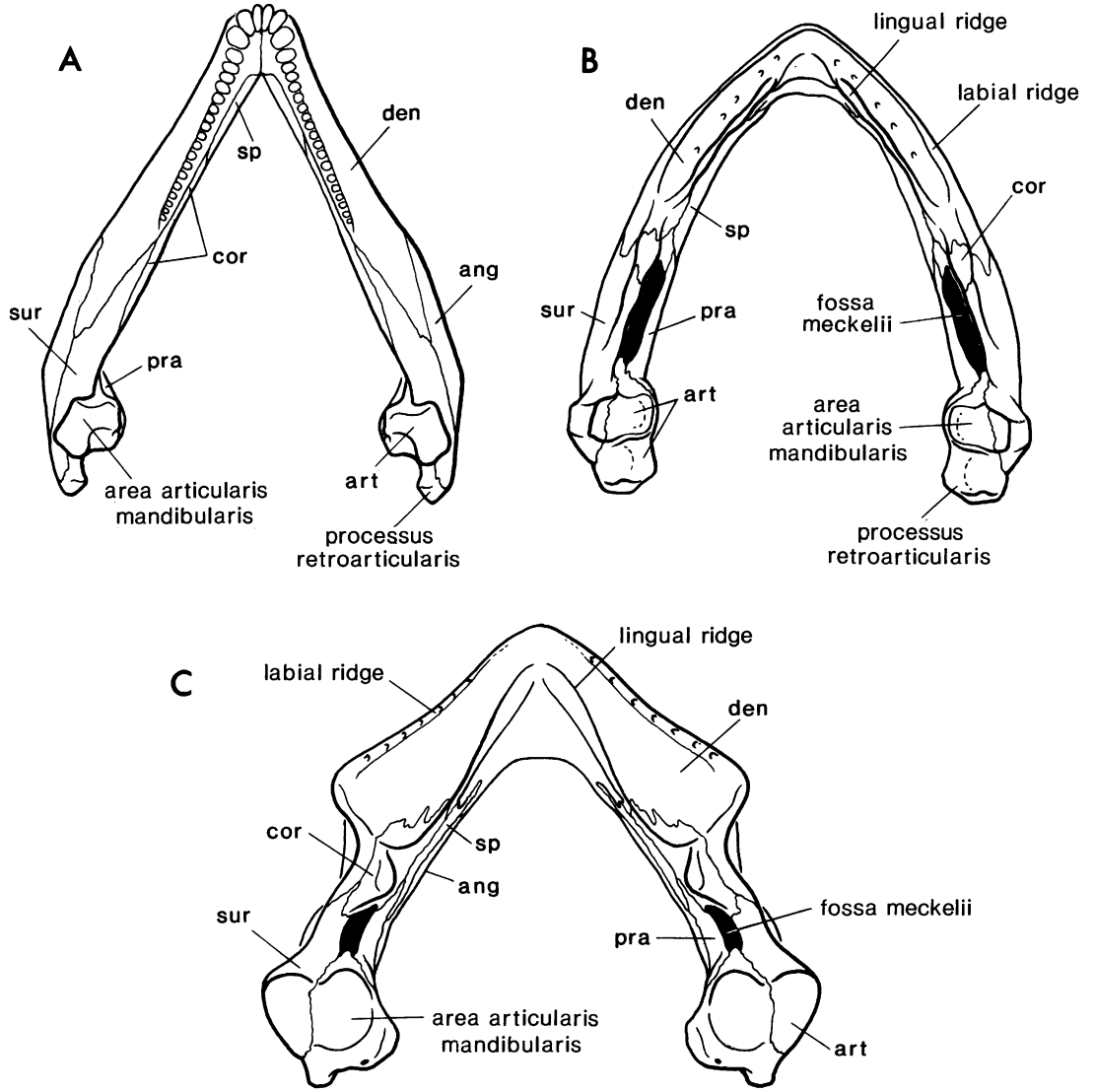


Fig. 57. Comparisons of lower jaws in dorsal view. **A,** *Captorhinus* sp., from Heaton (1979) and specimens. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Palatobaena bairdi,* AMNH 8277, partially restored from Gaffney (1982).

interpretation presented in the figures by dotted lines). Jaekel (1918a: fig. 57) identified the coronoid as a large, flat element on the internal surface, based particularly on the right ramus. Comparisons of the left ramus and SMNS 16980, however, indicate that this is a broken, dorsally displaced, piece of the prearticular rather than the coronoid. Instead, the best interpretation, based primarily on SMNS 16980 and the Berlin skull, is that of a relatively small coronoid forming the processus coronoideus and restricted to that structure, not extending onto the triturating surface nor forming a significant part of the fossa meckelii.

In most casichelydians and *Captorhinus* the coronoid is a large element, although it is clearly distinct in both groups. In *Captorhi-*

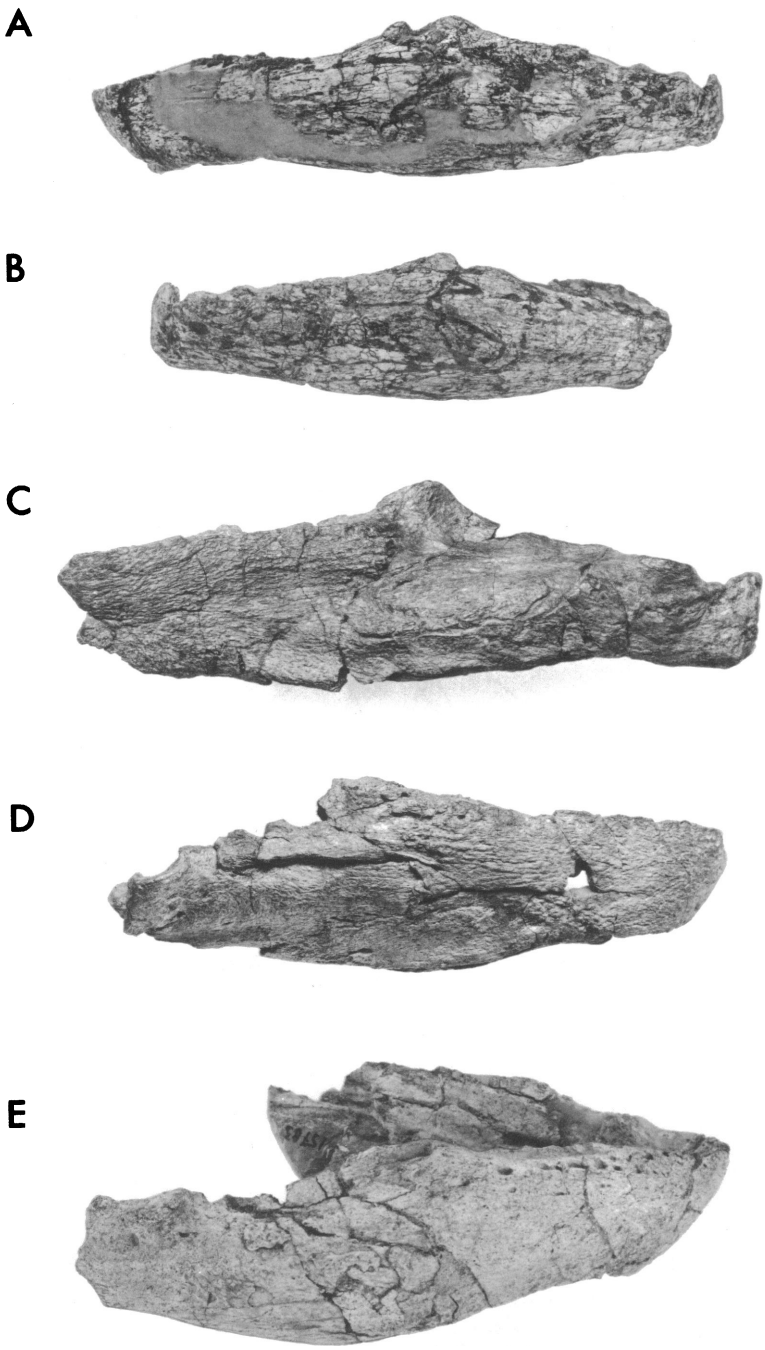


Fig. 58. *Proganochelys quenstedti.* Lateral views of lower jaws. **A,** SMNS 16980, left ramus. **B,** SMNS 16980, right ramus. **C,** MB 1910.45.2, left ramus. **D,** MB 1910.45.2, right ramus. **E,** SMNS 15759, entire lower jaw from right side.

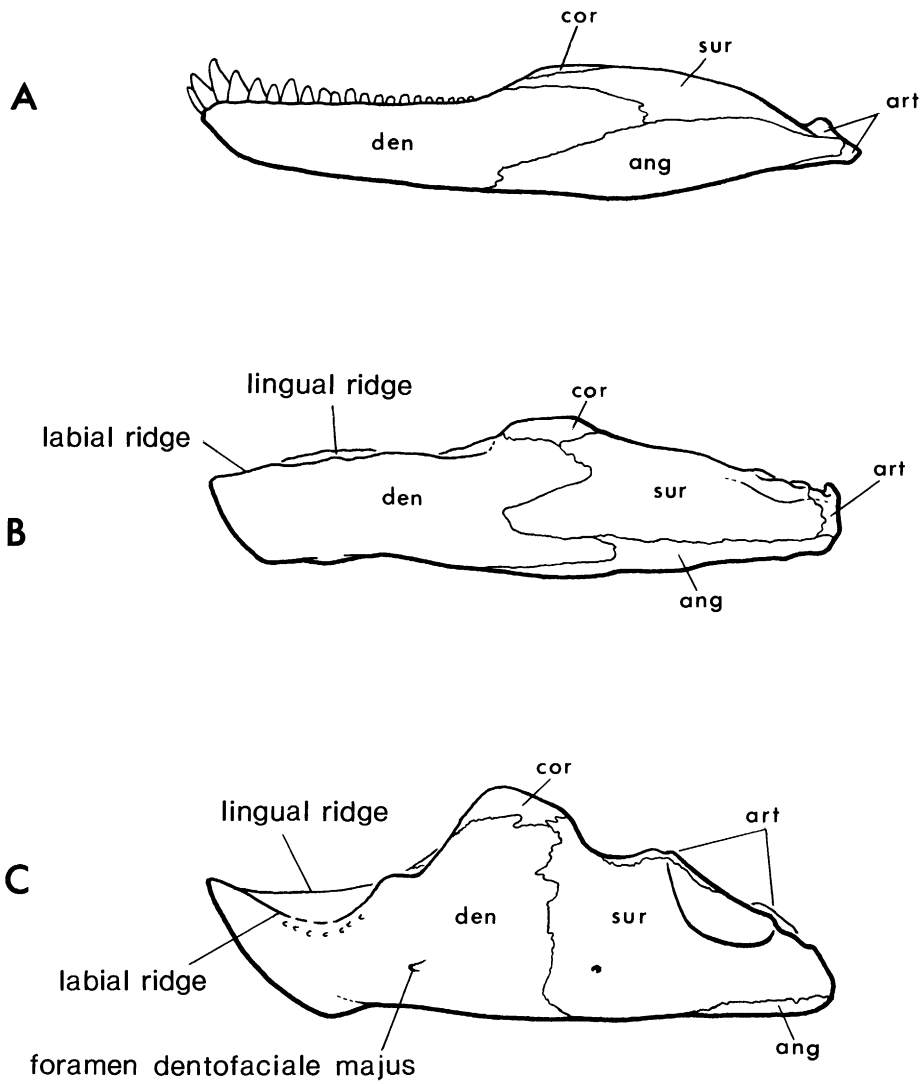


Fig. 59. Comparisons of lower jaws in lateral view. **A,** *Captorhinus* sp., from Heaton (1979). **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Palatobaena bairdi,* AMNH 8277, from Gaffney (1982).

nus there is only a barely recognizable processus coronoideus. *Proganochelys* and *Meiolania,* however, differ only slightly. *Captorhinus* has a coronoid that extends anteriorly to lie medial to nearly half of the tooth row and curves ventromedially to form the anterior margin of the fossa meckelii. It seems clear that the coronoid of *Proganochelys* does not extend anteriorly even though it does in most casichelydians. *Meiolania* also has a restricted coronoid, but I interpret the condition as independent autapomorphies for both taxa.

The coronoid of *Proganochelys* contacts the dentary anteriorly, the surangular laterally, and the prearticular medially. The right side of SMNS 16980 has some bone floating in an open suture that may be coronoid; if so, then a contact with the splenial was also present.

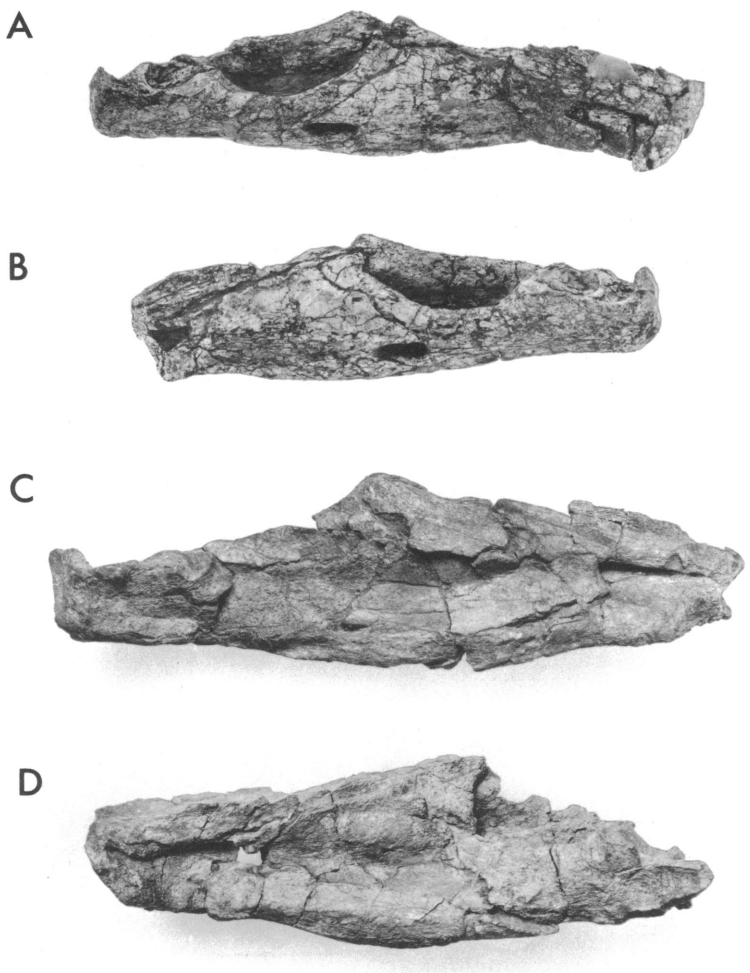


Fig. 60. *Proganochelys quenstedti,* medial views of lower jaws. **A, B,** SMNS 16980. **C, D,** MB 1910.45.2.

Articular

Portions of the articular are preserved in all three specimens; both the Berlin skull and SMNS 16980 have the area preserved satisfactorily. The articular of *Proganochelys* is very similar to that bone in other turtles, it is an irregular blocklike element lying at the posterior end of the jaw and bears the central part of the area articularis mandibularis. It has a clear parasagittal suture with the surangular laterally, as can be seen in the Berlin skull and SMNS 16980, and it has a parasagittal suture with the prearticular medially, which can be seen in the Berlin skull. The area articularis mandibularis is thus formed by three bones in *Proganochelys*: prearticular, articular, and surangular. Although there is variation in this condition among the various casichelydian groups, the same pattern is common in cryptodires and appears to be primitive for that group and probably for all turtles. In *Captorhinus* and other generalized amniotes, the area articularis mandibularis is formed almost entirely by the articular bone

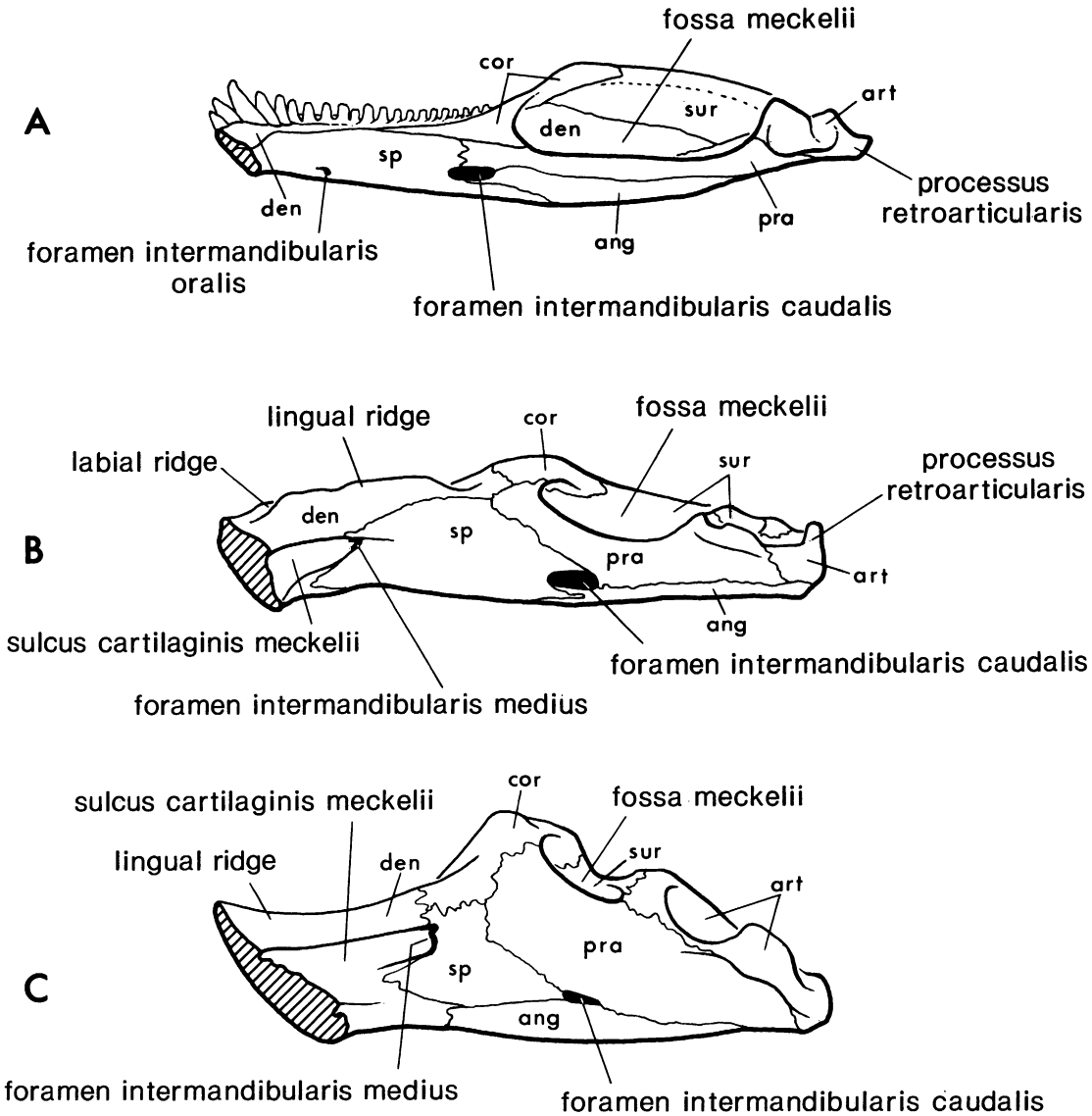


Fig. 61. Comparisons of lower jaws in medial view. **A,** *Captorhinus* sp., from Heaton (1979). **B,** *Proganochelys quenstedti,* SMNS 16980, see Figure 60. **C,** *Palatobaena bairdi,* AMNH 8277, from Gaffney (1982).

so that the three-element condition may be interpreted as a chelonian synapomorphy.

Although the area articularis mandibularis in *Proganochelys* is formed by three bones, it is convenient to describe the entire structure here. The area is a well-defined concavity, wider than long, lying just posterior to the fossa meckelii. The concavity has a shallow, parasagittal groove for the surangular-articular suture in SMNS 16980, and in the Berlin skull an additional groove marking the prearticular-articular contact, but there is no medial longitudinal ridge as commonly found in cryptodires dividing the concavity into two regions. The typical pleurodiran hemispherical area articularis mandibularis is therefore best interpreted as a pleurodiran synapomorphy. The limits of the area in *Progan-*

ochelys are formed by an irregular ridge that is particularly distinct posteriorly. The condylus mandibularis of the quadrate can be articulated with the lower jaw in both the Berlin specimen and SMNS 16980. The quadrate articulation is not a convexity but a curved concavity, formed such that the medial half is lower than the lateral half. This medial half fits into most of the area articularis mandibularis while the lateral half fits into the lateral margin of the area articularis mandibularis formed by the surangular. The resultant contact is not particularly close and some cartilage presumably covered both articular surfaces. However, there does not appear to have been much opportunity for fore-and-aft or side-to-side movement of the lower jaw in relation to the skull, although this is very difficult to determine in an extinct animal.

In the Berlin skull, where contacts between the articular, prearticular, and surangular can be seen, the surangular forms about one-third to one-half of the lateral portion of the area articularis mandibularis, the articular forms the central quarter or more, and the prearticular forms the medial quarter. This condition is similar to that found in many cryptodires and is interpreted as primitive for them and a synapomorphy for turtles.

Proganochelys has a particularly large and well-developed retroarticular process with a morphology that is unique among turtles. Posterior to the area articularis mandibularis, the retroarticular process forms a concavity on its dorsal surface that is nearly two-thirds the size of the area articularis mandibularis. The posterior end of the retroarticular process is developed into a distinctive dorsal flange that forms the posterior margin of the concavity. Other turtles, as well as *Captorhinus,* have large retroarticular processes, but a dorsal process is unique to *Proganochelys.* Pleurodires and some primitive cryptodires, such as baenids and *Meiolania,* lack a retroarticular process, but *Kayentachelys* has a moderately well-developed one. The articular of *Proganochelys* forms part of the posterior limits of the fossa meckelii as in other turtles, and it bears a short flange that extends into the fossa meckelii.

The path of the chorda tympani usually is in or near the articular bone in turtles, but none is apparent in any of the *Proganochelys* jaws. However, the bone preservation is not good enough to be sure that a small foramen is not present.

Prearticular

The prearticular is preserved in all three *Proganochelys* skulls but is best seen in the Berlin skull and SMNS 16980. It is a long, fairly slender element lying medial to the fossa meckelii and extending posteriorly past the area articularis mandibularis. Anteroventrally, the prearticular has a long, straight suture with the splenial; this contact runs anterodorsally from the posterior margin of the foramen intermandibularis caudalis to the region of the processus coronoideus. Anterodorsally, the prearticular appears to contact the dentary, but it is possible that the coronoid prevents a dentary contact. It is likely that at least the dorsalmost portion of the prearticular contacts the coronoid. Posteriorly the prearticular lies medial to the articular and possibly forms part of the retroarticular process. Unfortunately the posterior end of the jaw lacks sutures in all specimens. Ventrally, posterior to the splenial contact, the prearticular has a straight, horizontal suture with the angular.

The prearticular in *Captorhinus* is a long, thin element forming the medial margin of the fossa meckelii. In Casichelydia the prearticular is a much broader element with an extensive anterodorsal expansion. The *Proganochelys* prearticular is advanced over the *Captorhinus* condition in having an anterodorsal component and greater size, but it does not reach the extent seen in casichelydians. The prearticular of casichelydians extends well anterior to the foramen intermandibularis caudalis but in *Captorhinus* and *Proganochelys* it just reaches or barely extends beyond the foramen.

The dorsal opening of the fossa meckelii in *Captorhinus* is very large and opens more medially than dorsally while in casichelydians the opening is relatively small and opens dorsally. *Proganochelys* is intermediate in this condition; the size of the opening is definitely smaller than in *Captorhinus,* but larger than in most other turtles. The prearticular forms the medial margin of the opening and it is

the dorsal expansion of this bone that is involved in the change from a lateral-facing to a dorsal-facing opening. *Proganochelys* clearly has a dorsally oriented opening; the prearticular expansion is only slightly developed so that much of the fossa meckelii is open medially because the medial margin is lower than the lateral margin as in *Captorhinus* but in contrast to casichelydians.

Posteriorly the prearticular has a medial flange that bears part of the area articularis mandibularis on its dorsal surface (see Articular). The posterior limits of the prearticular and the degree of its participation in the formation of the retroarticular process are not determinable because the sutures appear to be fused.

Splenial

The splenial is preserved to a useful extent in all three specimens but it is most complete in SMNS 16980. In *Proganochelys* it is a large, flat element lying medial to the dentary and covering the sulcus cartilaginis meckelii and fossa meckelii which lie lateral to it. The dorsal margin of the splenial contacts the dentary just below the lingual ridge, while the ventral area contacts the dentary and curves ventrolaterally to form the ventral margin of the jaw. Posteriorly the spenial contacts the prearticular and posteroventrally the angular. The splenial forms all but the posteroventral margin of the foramen intermandibularis caudalis. Anteriorly the margin of the splenial is free, exposing the sulcus cartilaginis meckelii on the dentary. A notch in the dorsal part of the anterior margin of the splenial marks the foramen intermandibularis medialis.

In *Captorhinus* the splenial is a very extensive element that entirely covers the medial surface of the dentary and the splenials meet at the symphysis. Most turtles lack splenials but they occur in chelids among extant taxa, and in plesiochelyids, baenids, meiolaniids, and other extinct taxa. Although the splenial of plesiochelyids and meiolaniids is larger than in other casichelydians, it is not as large as the *Proganochelys* splenial. *Proganochelys* is therefore advanced over *Captorhinus* in having a splenial that does not meet in the midline and exposes some of the dentary, and casichelydians have a splenial smaller than the one in *Proganochelys* as a synapomorphy.

THE SKULLS OF SMNS 15759 AND MB 1910.45.2

Although both of these skulls are described to a certain extent in the main comparative section, most of that description is based on the better preserved SMNS 16980. In order to more fully document these two specimens, a separate description of each is provided here.

SMNS 15759
(figs. 23, 26, 30, 33, 36, 39, 47)

This skull is light in color, nearly white, as are many Stubensandstein vertebrate fossils, and is preserved in a light green matrix, a mixture of sand and clay. Strong pressures have compressed this skull laterally and obliquely, so that the right half is shifted ventrally relative to the left half. Apparently the skull was broken by parasagittal fractures and repaired with plaster that now lies between and within these surfaces. This specimen seems to have been subjected to more plastic flow of the bone and less gross crushing than the Berlin skull. Very few sutures are visible and this seems to be due to original fusion because in some areas the bone appears to be well enough preserved to show them clearly.

Dermal Roofing Elements: The skull roof of SMNS 15759 is narrower than in SMNS 16980 and the cheek is higher, the angle where the roof and cheek join being much more medially placed. It is very likely that this condition is the result of lateral compression and deformation rather than true biologic difference. Some evidence supporting lateral deformation can be seen in table 8, where the interorbital width of SMNS 15759 is about 6 cm while in SMNS 16980, a smaller skull, the interorbital width is actually greater, 7 cm. The dorsal part of the skull roof in SMNS 15759 is almost complete; only portions of the posterolateral margin and a section in the region of the presumed prefrontal are missing. The surface of the bone is best preserved among the three *Proganochelys* skulls in SMNS 15759 and consists of a coarse network of grooves. The scale areas, particularly on the skull roof, are clearly delimited by

TABLE 8
Size Comparison (in centimeters) of Three *Proganochelys* Skulls

	SMNS 16980	SMNS 15759	MB 1910.45.2
Premaxilla-condyle length	9.7	12.0[a]	13.3
Premaxilla-posterior edge of parietal	8.1	11.6	12.0[a]
Width of skull over orbits	7.0	6.0[b]	7.4[b]
Width of skull at mandibular articulation	8.1	6.0 (est.)[b]	7.6[b]
Width of maxillary triturating surface	0.6 (R & L)	0.7 (R & L)	1.2 (R & L)
Length of triturating surface (measured parallel to skull margin)	4.4 (R) 4.7 (L)	5.3 (R) 6.8 (L)	– (R) 7.2 (L)
Width of condylus mandibularis	1.6	–	2.1
Width of orbit	3.2 (R & L)	3.3 (R)[b] – (L)	3.5 (R) 3.8 (L)
Distance between posterior margin of orbit and incisura columella auris	3.9 (R) 3.5 (L)	4.6 (R) – (L)	5.8 (R) 3.8 (L)
Distance between anterior margin of orbit and posterior margin of apertura narium externa	2.0 (R & L)	2.7 (R) 3.2 (L)	2.9 (R & L)
Comparison of premaxilla-condyle length[d]	72.9%	91.0%	100%[c]
Comparison of premaxilla-parietal skull length[d]	67%	96%	100%
Comparison of triturating surface width[d]	54%	59%[c]	100%
Comparison of triturating surface length[d]	63%[c]	84%[c]	100%
Comparison of distance betw. posterior margin of orbit and incisura columella auris[d]	60%	86%	100%[c]
Comparison of distance betw. anterior margin of orbit and posterior margin of apertura narium externa[d]	69%	100%[c]	100%
Average of six cranial comparisons listed above	64.3%	86%	100%
Comparison of maximum carapace length[d] (see Table 11)	83%	92% (est.)	100%
Maximum length of lower jaw ramus	9.4 (R) 9.8 (L)	11.2[a] (R) 8.2[a] (L)	11.5 (R) 13.0 (L)
Depth of lower jaw at processus coronoideus	2.2 (R) 2.4 (L)	3.1 (R) indet.	3.7 (R) 3.6 (L)
Depth of lower jaw midway along triturating surface	1.6 (R) 1.5 (L)	2.3 (R) 2.4 (L)	2.5 (R) 2.6 (L)
Width of lower jaw at widest point below processus coronoideus	1.2 (R) 1.1 (L)	0.7 (R) indet.	1.2 (R) 1.1 (L)
Comparison of lengths[d]	75%[c]	86%	100%
Comparison of lower jaw depth at processus coronoideus[d]	63%[c]	83%	100%
Comparison of lower jaw depth midway along triturating surface[d]	61%[c]	92%[c]	100%[c]
Average of three above comparisons	66%	87%	100%

[a] One margin measured is a broken edge.
[b] Measurement obviously influenced by postmortem deformation.
[c] Average of right and left measurements.
[d] Berlin skull = 100%.

distinct grooves and raised areas within the scute (see Scale Area for description). The apertura narium externa is preserved on both sides of the internarial process and is narrowly oval. The internarial bar is smooth and lacks the surface texture. The dorsal margin of the apertura has a protuberant rugosity in SMNS 15759 which is absent in the other two skulls.

The snout region in SMNS 15759 is mostly complete and bears a similar surface texture to the skull roof, although not expressed as distinctly. The orbits are relatively larger and higher than in SMNS 16980. Although the margins of the right orbit are nearly complete, this is best interpreted as a result of plastic deformation similar to that which has taken place in the palate. The right cheek posterior to the orbit is a mixture of bone and plaster, the entire internal surface is covered with

TABLE 9
Comparison of the Three *Proganochelys* Skulls

	SMNS 16980	SMNS 15759	MB 1910.45.2
Postmortem damage	Microscopic fracturing of bone with little apparent displacement	Severe lateral compression with plastic deformation	Severe lateral compression with fracturing
Sutures	Open, except in braincase where most elements are fused	Nearly all fused	Nearly all fused
Relative size (Berlin skull as 100%)	60–70%	80–90%	100%
Pitted, rugose surface on anterior margin of nasal	No	Yes	Yes
Scale expression	Poor	Good	Poor
Skull shape as preserved	Low and broad	High and narrow	High and narrow
Labial ridge	Low	High	Intermediate
Lower jaw	Shallow	Deep	Deep

plaster, and the differentiation of the two is difficult to determine externally. On the right side the dermal skull stops at a broken edge just posterior to the anterior margin of the cavum tympani, a small portion of the cavum is preserved. Dorsally the posterior margin of the parietals is a natural edge above the supraoccipital area but the remaining margins are broken. On the left side almost all of the cheek behind the orbit is missing; the few preserved bone sections along the orbital rim are supported in plaster.

The ventral surface of the skull is visible in SMNS 15759 between the orbits. As usual in this specimen, sutures are not clear here but some low ridges, apparently defining the position of the olfactory roots, are on the area of the frontals.

PALATAL ELEMENTS: The palate of SMNS 15759 is badly deformed by lateral compression. The triturating surface has most of the labial ridge broken on both sides, and the ridge as preserved is restored based on the few remaining fragments of the original on the left side. Similarly much of the lingual ridge is broken but its restoration is based on more original bone, again on the left side. The anterior part of the palate has a long area of bone in the region of the vomer that extends posteriorly to the interpterygoid vacuity. It is, however, separated laterally by matrix from the rest of the skull due to large areas of missing bone. Some of the palatine is present, at least on the left side, where the foramen palatinum posterius is present and a contact between the palatine and maxilla can be seen.

PALATOQUADRATE ELEMENTS: The pterygoid is preserved on both sides but they are both badly distorted. The interpterygoid vacuity can be made out, although in the absence of SMNS 16980 it would have been difficult to interpret as such. The basipterygoid articulation is badly crushed and the braincase has been shifted so that its midline and palatal midline no longer line up. It is not possible to see any articular surfaces and interpretation of an open basipterygoid articulation would be unlikely in the absence of SMNS 16980. The tooth rows on the pterygoid can be made out; although few actual teeth are preserved, it is primarily the raised areas supporting the teeth that are visible. As noted under Epipterygoid, it is possible that this element is present in SMNS 15759, although its poor preservation makes description difficult. The right quadrate is partially preserved; the condyle, pterygoid process, and part of the cavum tympani remain. The left quadrate is all gone.

BRAINCASE ELEMENTS: The braincase of SMNS 15759 is generally poorly preserved but it is the only specimen to retain the "pleurosphenoid" ossification (see "Pleurosphenoid" for description). In occipital view it can be seen that the braincase lacks the occipital

condyle and the posterior and right lateral areas of the basioccipital. Although badly deformed, the fenestra ovalis can be made out on both sides and just above it the groove for the stapedial artery. The foramen stapedio-temporalis and other posterior structures are gone. The anterior part of the foramen jugulare anterius can barely be recognized; its posterior area is broken away. The supraoccipital area is fairly well preserved and closely resembles SMNS 16980. The paroccipital processes are missing.

MB 1910.45.2
(figs. 21, 24, 28, 31, 34, 37, 53)

The skull described by Jaekel (1918a) has had considerable influence on chelonian paleontology and, in retrospect, it is unfortunate that the specimen is so poorly preserved. Strong lateral compression has crushed the sides of the skull toward the midline in a direction similar to SMNS 15759, but while much of the deformation in SMNS 15759 is plastic flow, in the Berlin skull the deformation is more straightforward breakage and visible cracking. For example, the palatal deformation that resulted in the incorrect reconstruction by Jaekel (1918a: fig. 47) is caused by the telescoping of the two halves of the palate over each other, while in SMNS 15759 the palate is even narrower but the bones are not slid over each other. The result is that in the Berlin skull some areas, such as the palate and basicranium, are almost completely useless morphologically, while others, such as the triturating surfaces and cavum tympani are well preserved. The direction of deformation is such that the left side of the skull is posterior and somewhat ventral to the right side.

The Berlin skull is dark in color, the bone is nearly black while the matrix is dark reddish-brown with frequent incrustations of what appear to be iron oxides. The bone is minutely fractured and under the microscope it is difficult to discern sutures or fine structures. As in SMNS 15759 most of the sutures appear to be fused. The surface of the skull is covered with small bumps and coarse trabeculae, different from the surface texture of SMNS 15759; in fact, all three skulls have different surface textures. Most of the skull surface is scarred and scratched from preparation, but matrix still remains in most of the indented areas. Some parts of the skull have been restored in plaster and the plaster was painted, resulting in considerable difficulty in determining the limits of missing bone (see Jaekel, 1914, plate 5, for figure of the skull at an early stage of preparation). Jaekel's (1918a) figures, especially the photographs in plate 4, which are of good quality, give no indication of plastered areas. Supposed sutures have been painted on the skull but in nearly all cases there is no evidence for sutures in these positions. Although most of the plaster has been identified and the paint removed, at least at the edges, the entire skull needs a complete preparation effort.

Dermal Roofing Elements: The nasal area of the Berlin skull has no indication of sutures but the presumed descending process of the nasal is incomplete with the ventral portion broken off and not reaching the premaxilla. As in SMNS 15759, the process is smooth while the more dorsal portion of the nasal is very rugose. The upper part of the skull seems to have been pushed back here so that in life the nasal would have been nearly on a vertical line with the premaxilla as in SMNS 16980. The margin of the apertura narium externa is damaged but it does not appear to have been significantly different from that of SMNS 16980. The interior of the fossa nasalis cannot be seen. The "postnasalia" of Jaekel (1918a: fig. 32 in particular) do not exist. The area indicated in figure 32 on the left side of the skull is mostly plaster with no discernible sutures.

No sutures are visible on the underside of the skull roof; much of the interior is still filled with matrix. In the anterior wall of the orbit on both sides the descending processes of what appear to be the prefrontals can be seen, and these agree with the other two skulls. As preserved, the processes nearly meet in the midline but this is the result of crushing. The area marked "Lacrymalia" by Jaekel (1918a: fig. 32) seems to be lacrimal and maxilla without discernible sutures. The median skull elements are not distinct; most of Jaekel's sutures seem to be poorly preserved sulci (see Scale Areas).

On the right side of the skull the cheek is crushed medially beneath the skull roof which forms a slight overhang and considerably dis-

torts the shape of the orbit. The right side is restored behind the orbit in the area of the postorbital and where the squamosal forms the posterior margin of the skull.

PALATAL ELEMENTS: One of the few sutures visible in the Berlin skull is the premaxilla-maxilla contact on the outside of the skull. More posteriorly the maxilla-jugal contact appears to be in a low trough, much as in SMNS 16980, and in the position drawn by Jaekel (1918a). In palatal view the premaxillary-maxillary triturating surfaces are relatively well preserved with distinct labial and lingual ridges separated by a curved trough. Medial to the triturating surfaces most of the bone is badly deformed but the apertura narium interna and portions of the palatine can be seen. The vomer is visible in the midline and a midline suture separating paired vomers can be made out.

PALATOQUADRATE ELEMENTS: The pterygoids and associated elements have been telescoped on the midline, completely obliterating the interpterygoid vacuity and seriously distorting the shape of these elements. The teeth are imbedded in an incrustation of matrix (and perhaps iron oxide) that obscures the position of the midline and the symmetry of the palate. Using SMNS 16980, a midline can be hypothesized and this suggests that the palate is crushed farther to the right in relation to the basisphenoid and basioccipital, thick elements that have survived postmortem damage better than the palate.

The position of the basicranial articulation can be made out and, using SMNS 16980, it is possible to identify some of the articulation surfaces as being consistent with those of SMNS 16980. Unfortunately, some of the area of the basicranium was apparently opened but glued back together during preparation. The quadrate process of the pterygoid can be seen and some of the quadrate-pterygoid contact is visible; its position is as in SMNS 16980. Although the quadrates of the Berlin skull are somewhat damaged, in general their preservation is good and allows useful information to be obtained (see Quadrate). The right stapes is preserved and is described elsewhere (see Columella Auris).

BRAINCASE ELEMENTS: A sagittal view of the posterior part of the braincase is provided by Jaekel (1918a: fig. 46), but there are problems with this figure. Apparently the figure was made during preparation when the skull had been broken along parasagittal fractures, because at present the cavum cranii is filled with matrix and glue. Therefore, the features described by Jaekel cannot be validated or falsified. There is a hole drilled into the matrix for a mounting rod.

The occipital condyle is well preserved but the basioccipital-exoccipital contacts figured by Jaekel are cracks. Ventrally, the basioccipital tubercle is well preserved and relatively larger and better developed than in SMNS 16980. The foramen jugulare anterius and processus interfenestralis can be made out on both sides of the Berlin skull. These features and the foramen stapedio-temporalis are described elsewhere (see Quadrate, Opisthotic).

SIZE COMPARISONS AMONG *PROGANOCHELYS* SKULLS

The three available skulls of *Proganochelys* differ in shape and size as preserved and in order to identify morphologic features that may be related to growth it would be important to determine what the size relations are among the three skulls. SMNS 16980 is nearly undistorted, but the other two skulls suffer from serious lateral compression and other deformations not easily identified. Even the determination of the relative degree of size difference among the three skulls is difficult because so many of the measurements are apparently affected by postmortem deformation. Table 8 lists a series of measurements that were made on all three skulls and lower jaws. The length measurements, taken parallel to the midline, would presumably be less affected by the lateral crushing, and this is reflected in comparing the premaxilla-condyle length to the skull width over the orbits. In order to reduce the effect of lateral deformation, five measurements taken parallel to the midline and one measurement of the triturating surface width were compared among the skulls by choosing the Berlin skull as 100 percent. These measurements do vary but they suggest that SMNS 16980 is about 60 to 70 percent smaller than the Berlin skull. The lower jaw measurements also tend to agree with these figures.

POSTCRANIAL MORPHOLOGY

DORSAL SURFACE OF CARAPACE (table 10, figs. 69–74)

Marginal Scutes

Marginal scute markings are most completely seen on SMNS 16980 and the Berlin specimen but some can also be seen on SMNS 17203, SMNS 17204, SMNS 10012, and SMNS 15759. A complete marginal series can be seen only on the left side of SMNS 16980 which has 16 marginals. However, the Berlin specimen appears to have an additional marginal at the beginning of the series so that there would be 17 in this specimen. The discrepancy between the Berlin carapace and SMNS 16980 is of some interest because it must be considered in light of a possible taxonomic distinction between the two. A close comparison of the anterior marginals shows that the Berlin specimen has an additional marginal formed anterior to the first marginal in SMNS 16980 and that the marginals posterior to this one in the Berlin specimen agree closely in the two shells. The first marginal in SMNS 16980 has the same shape and is in the same relative position as the second marginal in the Berlin specimen; that is, this marginal lies anteromedial to the first supramarginal and contacts it in a short, diagonally trending sulcus. Furthermore, the marginals lateral to this one are also similar in position and shape. In order to facilitate the description of the marginals among the *Proganochelys* shells, I will refer to the first marginal of SMNS 16980 as marginal 2 and the first marginal of the Berlin specimen as marginal 1. Unfortunately, none of the other specimens has this region sufficiently well preserved to determine the presence or absence of marginal 1.

Marginal 1 of the Berlin specimen lies between the cervical scute and marginal 2. Jaekel (1918a) numbered this scute "1" in his figure 7 but presumably considers it as "2" in figure 23 because the scute lateral to it is numbered "3". In figure 23, Jaekel counts the cervical as the first marginal due to a supposed sulcus down the midline (I do not see one). Figure 7 is a ventral view and he numbered the serrations, thereby missing his subdivided cervical. (Both figures, nonetheless, end up with the same number of marginals, a situation discussed below.) I also disagree with Jaekel's drawing of this scute (ibid.: fig. 23). In his figure of the marginal in question (marginal 1 of my numbering), he shows a medial contact with the first vertebral scute but as I see it (fig. 69) the cervical scute forms the posterior border of marginal 1 with only a narrow contact with the first vertebral. Marginal 1, as seen in the Berlin specimen, fits between marginal 2 and the cervical scute and lies on a projection of bone that is similar to the serrations forming marginals 2 and 3 but is smaller in size. As presently restored, SMNS 16980 has what appears to be a small projection on the right side of the nuchal in the position of marginal 1. However, this projection is an anomaly of preparation, a block of material has been added between two pieces of the cervical scute, causing a separation within the cervical scute area.

Is the presence of an extra scute in the marginal series of the Berlin specimen of taxonomic significance or should it be interpreted as individual or growth variation? The Berlin carapace is larger and has generally better definition of sulci and surface texture consistent with the interpretation of an individual older than SMNS 16980. However, in view of the very small sample, it is impossible to come up with a definitive answer to this question.

Marginal scute 2 (again, the first marginal on SMNS 16980) is preserved only on SMNS 16980 and the Berlin specimen (it is probably also present in SMNS 17204, but poor preservation precludes accurate identification, see below). It lies on an anteriorly projecting serration smaller in size than marginal 3 but larger than marginal 1 (in the Berlin specimen). Marginals 2 and 3 differ from the other anterior marginals in having more pointed tips. In SMNS 16980 marginal 2 forms the lateral margin of the nuchal embayment and has a posteromedial sulcus with the cervical scute, while in the Berlin specimen marginal 2 has a medial contact with marginal 1. In both specimens marginal 2 has a posterolateral contact with supramarginal 1 and a

lateral contact with marginal 3. In the Berlin specimen marginal 2 has a narrow posterior contact with vertebral 1, while in SMNS 16980 the cervical scute and supramarginal 1 meet to prevent contact of marginal 2 and vertebral 1.

At this point it should be noted that SMNS 17204 (fig. 86) has a portion of the anterior carapace margin preserved on the left side. Unfortunately, it is not really possible to precisely identify the marginal scute impression or to determine the midline due to poor preservation. At least three marginal scute impressions can be seen and they are probably 1–3 or 2–4. If they are identified as marginals 1, 2, and 3, it would strengthen the hypothesis that the degree of expression of marginal 1 is a growth phenomenon, not a taxonomic distinction, because SMNS 17204 is a larger individual than SMNS 16980. However, the poor preservation and ambiguous nature of sulci and scute definition precludes positive identification of these marginals.

Marginal 3 (seen distinctly only in SMNS 16980 and the Berlin specimen) is bounded medially by marginal 2 and laterally by marginal 4 and its posterior margin is a transverse sulcus with supramarginal 1. In SMNS 16980 marginals 3 and 4 are the anteriormost edge of the shell while in the Berlin specimen marginal 3 is anteriormost but this could be due to damage of marginal 4 in the latter shell.

Marginal 4, as preserved in SMNS 16980 and the Berlin specimen, is bound medially by marginal 3, laterally by marginal 5, and posteriorly by supramarginals 1 and 2. Marginal 3 lies directly anterior to the center of supramarginal 1 while the center of marginal 4 is anterior to the sulcus between supramarginals 1 and 2 so that the posterior margin of marginal 4 extends between and partially separates supramarginals 1 and 2.

Marginal 5 is quite similar to 4; it is roughly the same shape and partially separates supramarginals 2 and 3. It is best seen in SMNS 16980 but is also visible in the Berlin specimen. SMNS 15759 has a portion of the shell with marginals preserved in the right anterior quadrant. There is a prominent sulcus between two marginals that I interpret as marginals 4 and 5. In contrast to the other specimens, which do not seem to have the surface texture particularly well preserved, these two marginals in SMNS 15759 show about four or five low, parasagittal ridges that become more pronounced near the sulcus with the supramarginals. The Berlin specimen shows similar ridges on the more posterior marginals and, presumably, this pattern was found in most of them originally.

Marginal 6 is more elongate than 5, and while 5 still has a fair degree of serration, marginals 6 through 11 have only a shallow notch at the intermarginal sulcus and a slight bulge in the middle of the scute area. Marginal 5 is mostly on the anterior edge of the carapace but it begins the curve posterolaterally and marginal 6 is more lateral than anterior.

Marginals 6 through 9 cannot be differentiated on the Berlin specimen due to loss and crushing, but they can be made out on the left side of SMNS 16980 and to a certain extent on the right side as well. Marginals 7 through 10 are similar in shape and relation to the supramarginals. These marginals are relatively thin and long and have an alternating relationship with the adjoining supramarginals, very much as in the more anterior marginals.

Marginal 11 is larger in size than marginals 7 through 10 and begins the curve around the posterior margin of the carapace but it does not have a pronounced projection forming a serrated margin as in the more posterior marginals. Marginal 12 is the most anterior of the distinctly serrated marginals. Although marginals 11 and 12 still have a roughly alternating pattern with respect to the supramarginals, the degree of overlap is changed so that, for example, marginal 11 contacts a greater portion of supramarginal 8 than supramarginal 9. In the more posterior marginals, the intermarginal sulci tend to line up with the intersupramarginal sulci, as in marginals 14 and 15 and supramarginals 11 and 12, and the alternating arrangement of the more anterior scutes is modified.

Most of the above description is based on the Berlin specimen and SMNS 16980 but at this point additions can be made from SMNS 17204. This specimen, which has a generally poorly preserved carapace, does have the left posterior marginals 9 through 16 well preserved and the following description takes

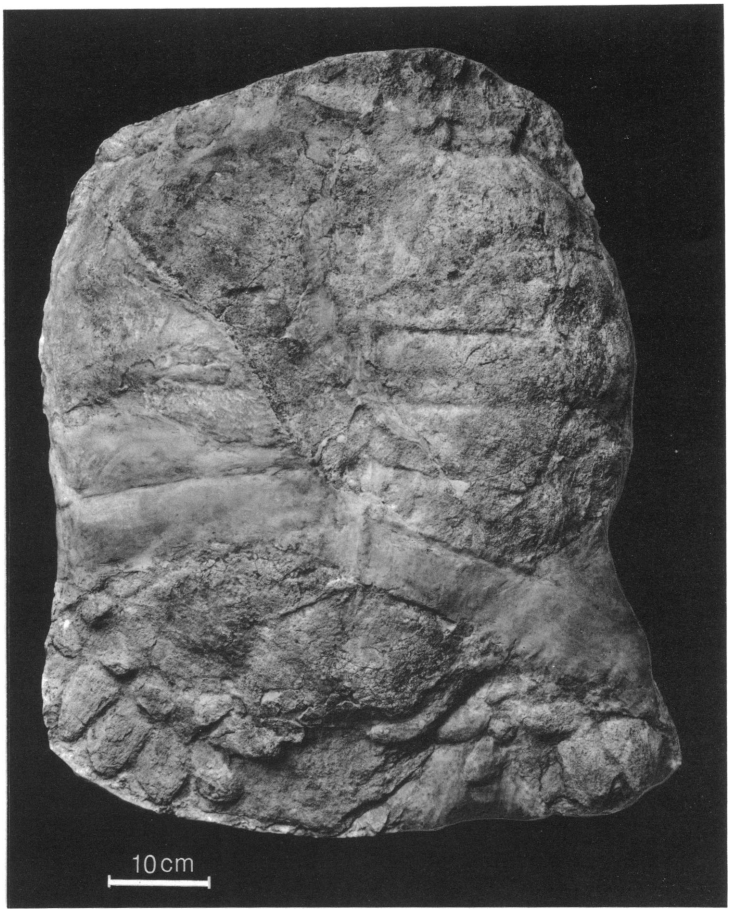


Fig. 62. *Proganochelys quenstedti,* SMNS 10012. Dorsal view of carapace.

this specimen into account as well as the other two.

The posterior marginals 13 through 16 are strongly serrated with tips more acuminate and pronounced than in the anterior serrated marginals. Marginals 13 through 15 extend in a posteromedial curve but at marginal 16 the curve changes so that marginal 16 is directly medial to marginal 15, rather than posteromedial, and this begins the pygal embayment. Marginal 16 is relatively smaller than marginals 13 through 15, particularly in SMNS 17204, where marginal 16 is about half the size of the same marginal in the other two shells. Marginal 14 contacts supramarginal 11 for its entire length, both scutes being about the same width, but supramarginal 12 is relatively large and forms the posterior contact for marginals 15 and 16. The proximal portions of marginals 12 through 14 are preserved in SMNS 15759 and they agree with those of the other shells.

The last marginal, 17, is about the same size as 16 but has a less pronounced serrated tip. In SMNS 17204, marginal 17 differs from those of SMNS 16980 and the Berlin specimen because the degree of serration is reduced to a low bulge in SMNS 17204. Although marginals 16 and 17 of this specimen are unusually small in comparison to those of the other two shells, the more anterior peripherals of SMNS 17204 are developed as in the other shells. Marginal 17 contacts marginal 16 laterally but the extent of contact apparently varies, even within one specimen; however, this area is not entirely clear on all the specimens. There is usually a broad contact between marginal 17 and supramarginal

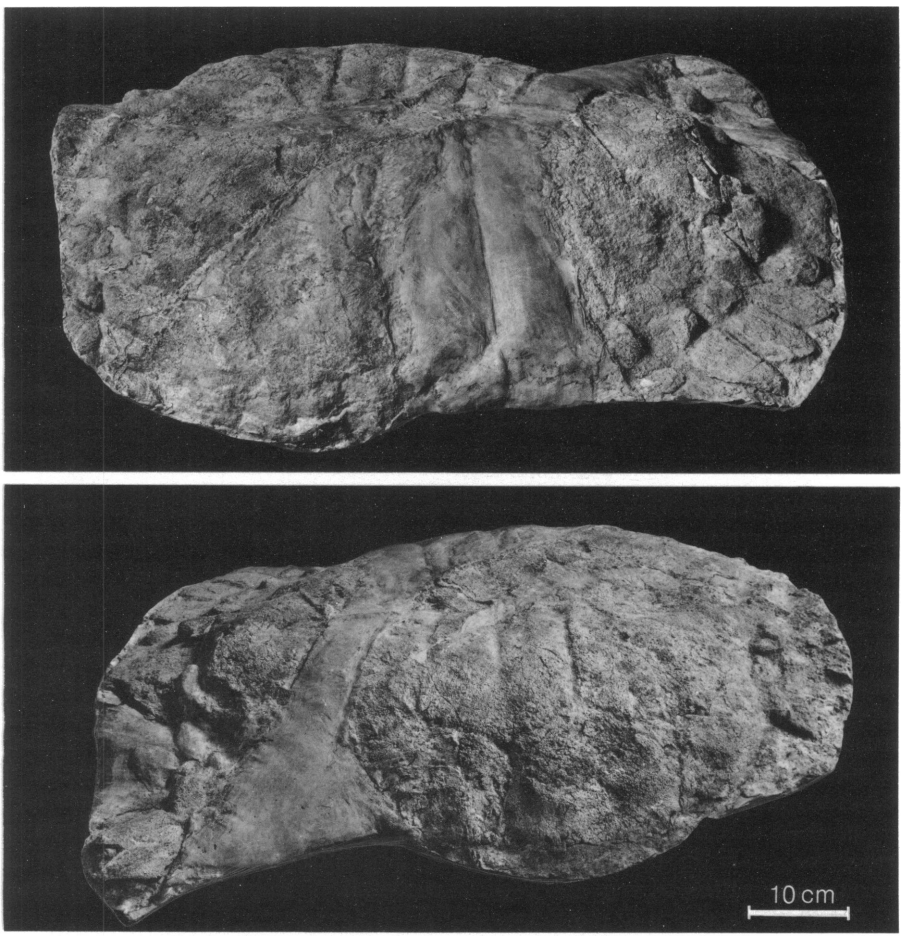


Fig. 63. *Proganochelys quenstedti,* SMNS 10012. Upper, left lateral view of carapace; lower, right lateral view of carapace.

2 anterolaterally and an anterior contact between this marginal and vertebral 4. Medially, marginal 17 is bordered by the supracaudal scute.

Supramarginal Scutes

Proganochelys has 12 pairs of supramarginal scutes in contrast to casichelydians, which are not known to have more than three pairs of supramarginals; there are three pairs in *Platychelys* and three pairs in *Proterochersis.* This latter genus, however, has a peculiar arrangement of posterior scutes so that it appears that the posterior marginals are actually supramarginals extending to the edge of the carapace. If so, *Proterochersis* might be interpreted as having seven or eight pairs of supramarginals. The form and position of the supramarginals in *Proganochelys* are the least well preserved of the carapacial scutes, numbers 6 through 8 being the most dubious. The supramarginals can be seen primarily in SMNS 16980 and the Berlin specimen, with portions identifiable in SMNS 15759 and SMNS 17204. Jaekel (1918a) restored the Berlin shell with 11 pairs of supramarginals, but even though the lateral portions of that specimen are poorly preserved, it seems to me that 12 is the correct number.

The supramarginals of *Proganochelys* form an uninterrupted row of scutes extending from

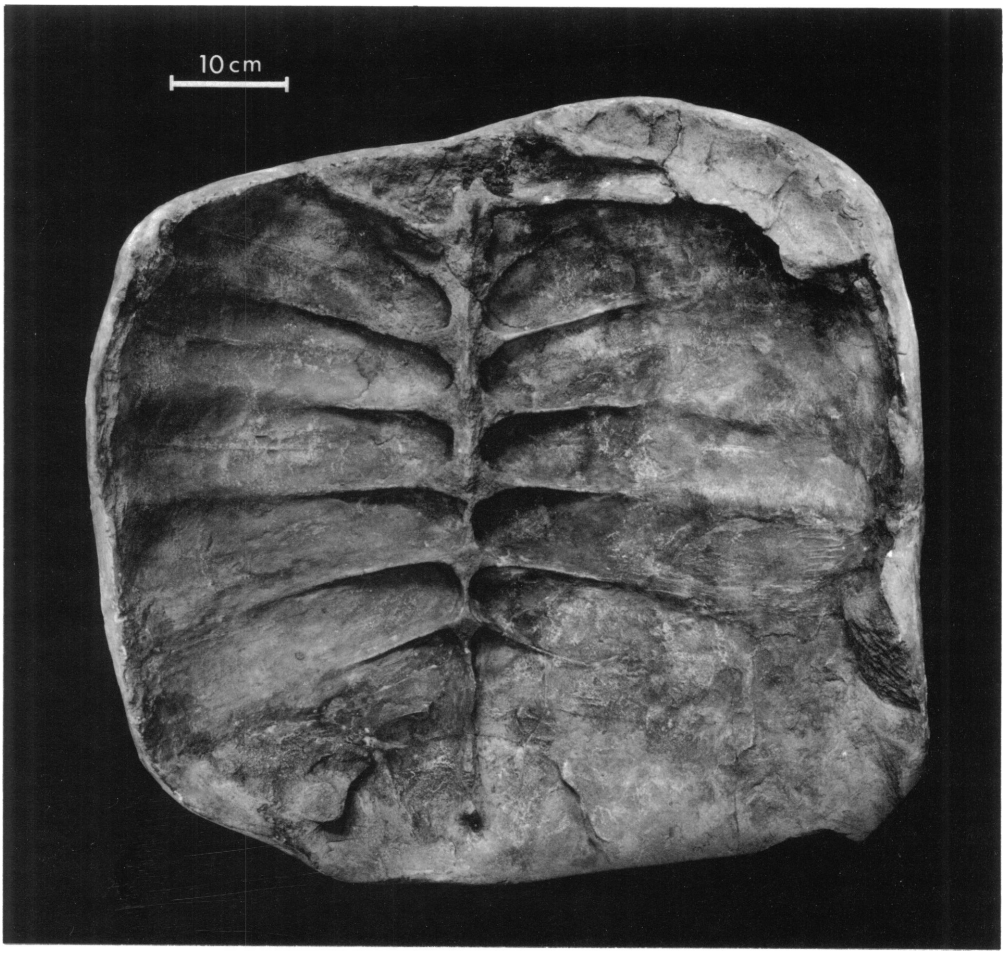


Fig. 64. *Proganochelys quenstedti,* SMNS 10012. Ventral view of carapace. See text for discussion.

the 2nd to the 17th marginal and lying between the marginals and pleurals. The first supramarginal is wider transversely than long and contacts pleural 1 posterolaterally, supramarginal 2 laterally, marginal 4 anterolaterally, marginal 3 anteriorly, and marginal 2 anteromedially. In the Berlin specimen marginal 2 contacts vertebral 1 to prevent supramarginal 1 from reaching marginal 1 and the cervical scute, but in SMNS 16980 supramarginal 1 contacts the cervical scute at about the position that marginal 1 is formed in the Berlin specimen. (The Berlin specimen has marginal 1 but SMNS 16980 does not.) As far as I can determine, this is the most striking difference between the supramarginals of SMNS 16980 and those of the Berlin specimen. Supramarginal 1 of SMNS 15759 is preserved with clear sulci but the more medial sulci are ambiguous and the margin of the shell is broken, preventing identification of marginal scutes. Nonetheless, SMNS 15759 appears to have a scute pattern as in the Berlin specimen, with the first vertebral separating supramarginal 1 from the nuchal. Supramarginal 1 in SMNS 15759 is relatively larger than in the other shells and supramarginal 2 is quite small so that the sulcus between these two supramarginals nearly lines up with the sulcus between marginals 4 and 5, rather than alternating as in the other shells.

Supramarginals 2, 3, and 4 are similar in shape to 1, but slightly smaller. They alternate with the marginals and lie along the an-

terior edge of pleural 1. There is some evidence that the left supramarginal 3 on the Berlin specimen may be constricted in the middle or even subdivided but this is only speculative. Right supramarginals 2 through 7 are uninterpretable on this specimen. The intersupramarginal sulci from 1 to 8 (roughly) are relatively short and the marginals approach the pleurals in an alternating pattern. The supramarginal-pleural sulci, however, tend to be straighter, with a less undulating line. Pleural 2 is bordered by supramarginals 5 and 6 (and possibly a portion of 7) and pleural 3 is bordered by supramarginals 7, 8, and the anterior half of 9.

The posterior supramarginals, 9 through 12, tend to be slightly larger and more equidimensional than the anterior ones. Supramarginal 9 (the posterior half), 10, 11, and 12 form the posterolateral and posterior border of pleural 4. Supramarginal 12 is the largest supramarginal and is roughly pentagonal. Its anterior border is pleural 4, the anteromedial border is vertebral 4, the posteromedial border is marginal 17, and the posterior border is marginals 15 and 16.

The anterior supramarginals are broadly convex while the more posterior supramarginals, particularly 9 through 12, have a low but acuminate tip near the posterolateral edge of the scute.

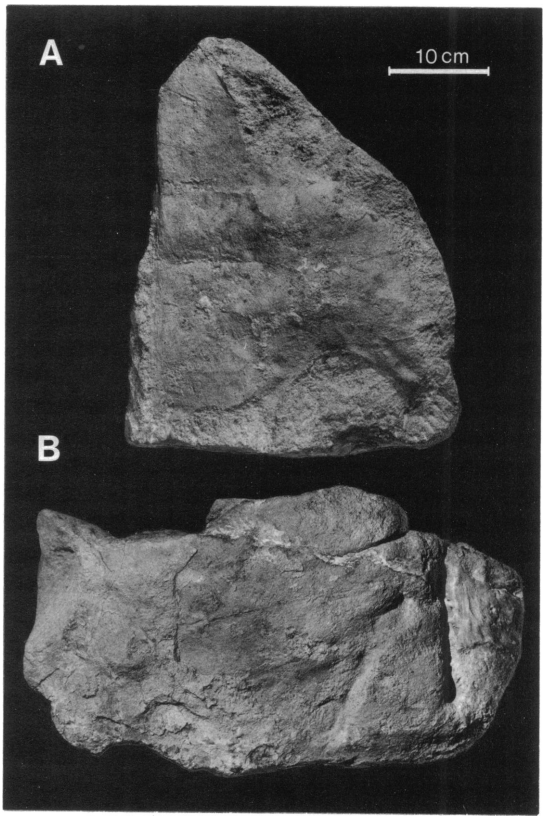


Fig. 65. *Proganochelys quenstedti,* SMNS 10012. Portions of internal molds with only small fragments remaining, anterior toward top of page. **A,** left half of plastron, posterior lobe missing; **B,** posterior section of left side of carapace.

Pleural Scutes

Proganochelys has four pairs of pleural scutes, the only series of carapacial scutes that agree in number with those of Casichelydia. Useful portions of the pleurals are preserved primarily in the Berlin specimen, SMNS 16980, and SMNS 15759, with some portions identifiable in SMNS 17203. The distal contacts of the pleural scutes with the supramarginals have been dealt with above.

The first pleural scute in *Proganochelys* is the smallest, it contacts vertebral 1 posteromedially, pleural 2 posteriorly, and supramarginals 1 through 4 in a curved line from the anterior margin to the lateral margin. Pleurals 2 and 3 are about the same size and shape; they alternate with the vertebrals to produce a zig-zag sulcus pattern. Pleural 2 contacts vertebral 1 anteromedially and vertebral 2 posteromedially, while pleural 3 contacts vertebral 2 anteromedially and vertebral 3 posteromedially.

Pleural 4 is smaller than 2 and 3 but larger than pleural 1. It contacts vertebral 3 anteromedially, vertebral 4 posteromedially, and supramarginals 9 through 12 posterolaterally.

The pleurals are generally flat with a very weak series of radial ridges, best seen on pleurals 3 and 4 (except in SMNS 16980, which has poor preservation of surface texture). Pleural 4 has a low convexity near its medial border. The pleurals and vertebrals have sulci that undulate in a fairly regular pattern to produce a distinctive margin to these scutes that I have not seen in other turtles. Unfortunately, interpleural sulci are not apparent in SMNS 17203, the only carapace with cos-

Fig. 66. *Proganochelys quenstedti,* SMNS 15759. Right portion of carapace set into plaster reconstruction. Upper, dorsal view; lower, right lateral view.

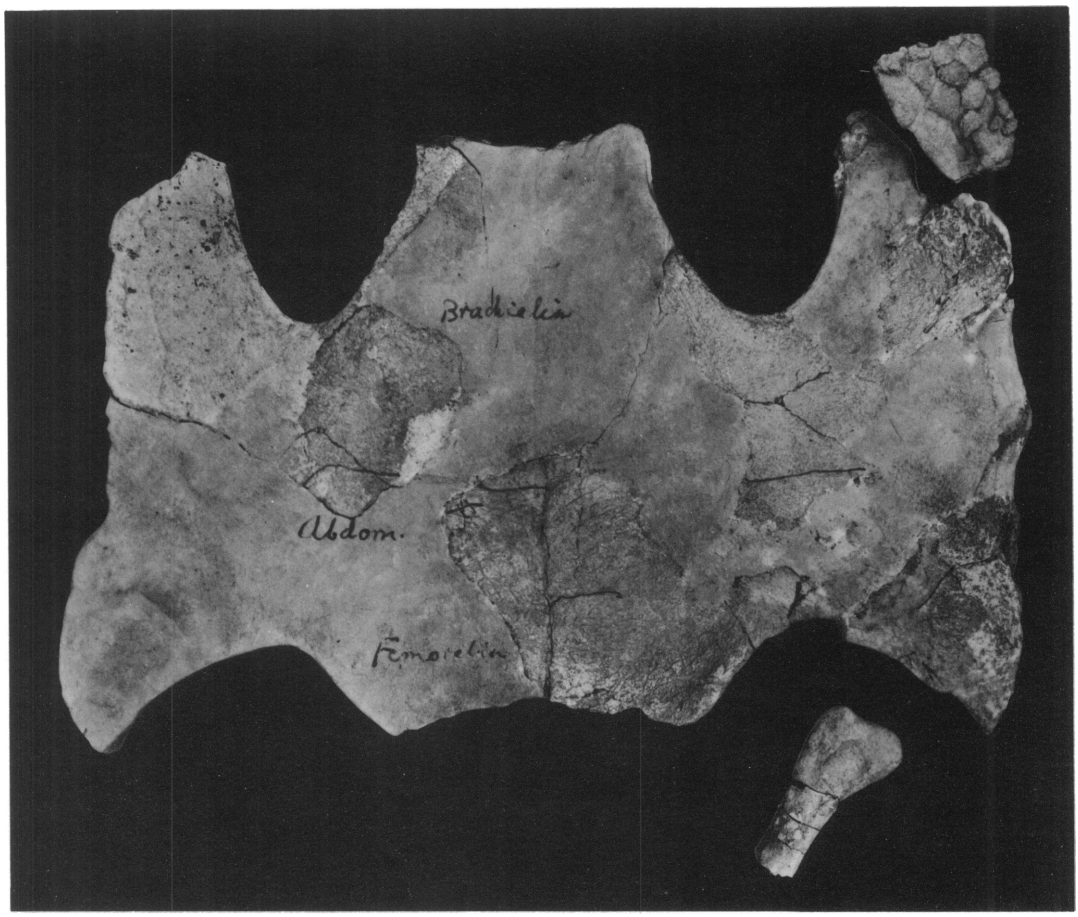


Fig. 67. *Proganochelys quenstedti,* SMNS 15759. Ventral view of plastron (now missing, see text), with fragments of left forearm osteoderms and left femur. Photograph courtesy of SMNS.

tal sutures, and it is not possible to determine where the interpleural sulci fell on the costals.

Vertebral Scutes

Proganochelys is unique among turtles in having only four, rather than five, vertebral scutes. Fortunately, the intervertebral sulci can be identified in SMNS 17203, the *Proganochelys* specimen showing neural and costal sutures. The vertebrals are best seen in SMNS 16980 and the Berlin specimen with some visible in SMNS 15759.

Vertebral 1 is the largest and occupies a considerable area at the front of the carapace. The anterior margin is embayed medially to receive the cervical scute and associated scutes. In the Berlin specimen vertebral 1 contacts marginals 1 and 2 but in SMNS 16980 the contact of the cervical scute and supramarginal 1 prevents this contact. Vertebrals and pleurals alternate so that the widest part of each vertebral contacts an interpleural sulcus. The intervertebral sulcus between vertebrals 1 and 2 is transverse and straight but the sulci forming the posterior two intervertebral contacts are bent with the center pointing anteriorly. Vertebral 4 is the smallest, contacts pleural 4 anterolaterally, supramarginal 12 posterolaterally, and the pygal and marginal 17 posteriorly.

The vertebral scute areas have a distinctive surface pattern, best seen in the Berlin specimen. There is a series of low ridges radiating

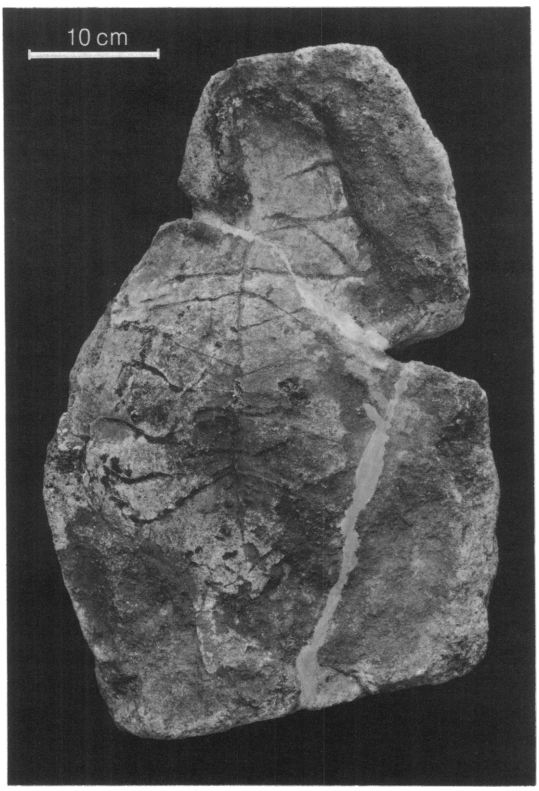


Fig. 68. *Proterochersis robusta,* SMNS 15479. External mold of plastron.

from a convexity near the posterior margin of each scute. Anteriorly, a low midline ridge can be made out. The posterior convexity on vertebral 4 is more prominent than in the other vertebrals.

SMNS 17203 shows that the intervertebral sulcus of the first and second vertebrals falls on the third neural, the second and third intervertebral sulcus on the fifth neural, and the third and fourth intervertebral sulcus on the seventh neural. A comparison with other turtles shows that these correspond with vertebrals 2 through 5 rather than 1 through 4 as in *Proganochelys. Proganochelys,* then, lacks the sulcus separating vertebrals 1 and 2 of the casichelydians. Vertebral 1 is a very large scute in *Proganochelys,* but the sulcus between vertebrals 1 and 2 in other turtles usually falls on neural 1, and neural 1 cannot be identified in *Proganochelys* at present. Nonetheless, it is apparent that vertebral 1 of *Proganochelys* is comparable with vertebrals 1 and 2 in other turtles; similarly vertebral 2 of *Proganochelys* is comparable to vertebral 3 of other turtles, vertebral 3 is comparable with vertebral 4, and vertebral 4 is comparable with vertebral 5. In evolutionary process terms, whether vertebral 1 of *Proganochelys* was subdivided or whether a new scute was added anterior or posterior to vertebral 1 cannot be determined.

Is the condition of the vertebrals in *Proganochelys* primitive for turtles or an autapomorphy for *Proganochelys*? The absence of a shelled outgroup again makes such a question impossible to answer definitively.

Nuchal Region

Sutures differentiating a nuchal bone are not discernible on any of the specimens although the region is preserved in the Berlin specimen, in SMNS 16980, SMNS 17204, and SMNS 15759. *Proganochelys* has a pronounced nuchal embayment bordered posteriorly by a C-shaped, shallow cervical scute. In SMNS 16980 this scute is broad, contacting supramarginal 1 laterally but in the Berlin specimen marginal 1 (absent in SMNS 16980) occupies some of the cervical scute area of SMNS 16980 resulting in a narrower cervical. The cervical scute area is convex with the anterior surface flattened vertically.

Pygal Region

The posterior margin of the carapace in *Proganochelys* has a pygal embayment bordered anteriorly by a broad, shallow supracaudal scute. The supracaudal scute has paired knobs that rise above the surface and extend posteriorly to a slight extent. Jaekel (1918a) interpreted this as two scutes but I have found no median sulcus in any specimen.

The ventral surface of the Berlin specimen has what may be tentatively identified as sutures surrounding a suprapygal but there are none for a pygal, although one was presumably present.

INTERNAL MORPHOLOGY OF CARAPACE (figs. 75–88)

Nuchal Region

The nuchal embayment appears deeper in the Berlin specimen than in SMNS 16980 but

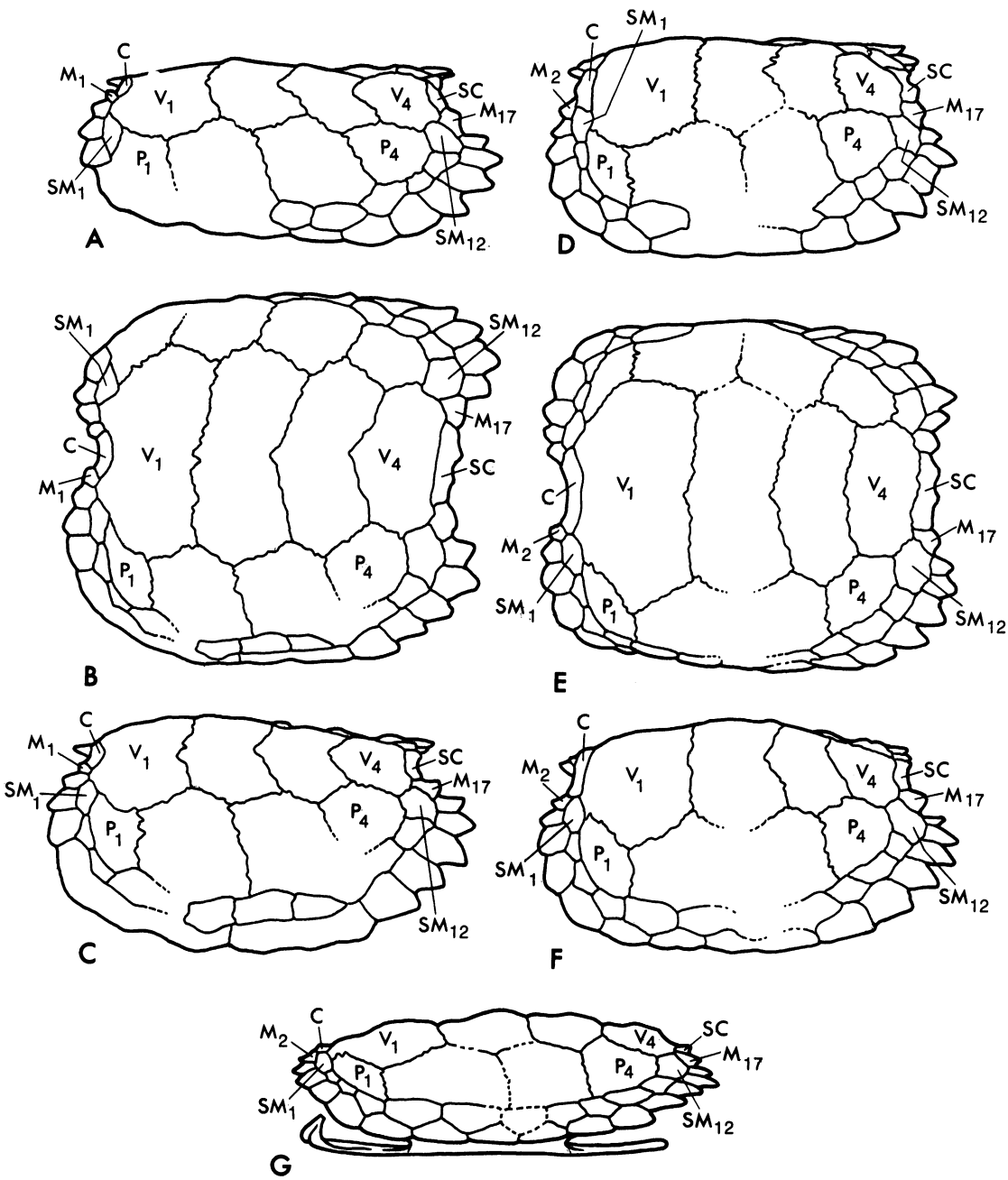


Fig. 69. Comparison of the carapacial scales in two specimens of *Proganochelys quenstedti.* **A–C,** MB 1910.45.2; **D–G,** SMNS 16980. Figures A and D are the right sides reversed to ease comparison with the other views. Broken lines indicate dubious sulci. Figure G is a reconstructed left side view of SMNS 16980. Figures A, C, D, and F are dorsolateral oblique views; while figures B and E are dorsal views. Abbreviations: **C,** cervical scute; **M,** marginal scute; **P,** pleural scute; **SC,** supracaudal scute; **SM,** supramarginal scute; **V,** vertebral scute. From Gaffney (1985a).

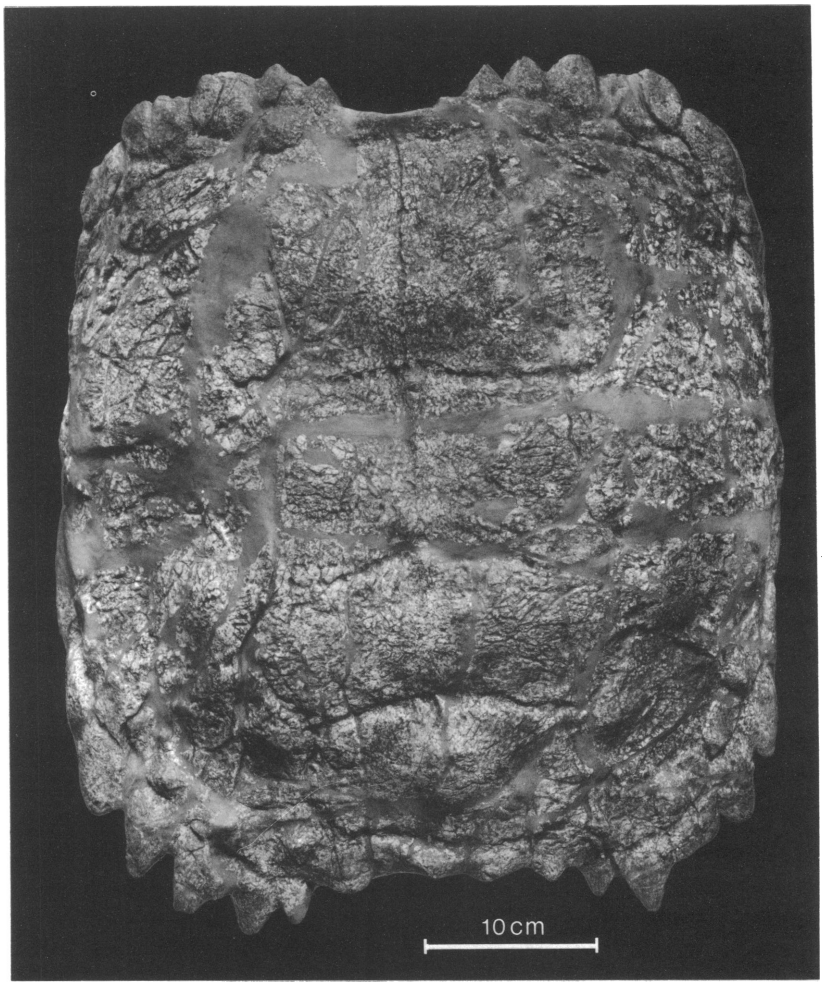


Fig. 70. *Proganochelys quenstedti,* SMNS 16980. Dorsal view of carapace.

this is due to the presence in the Berlin specimen of the first marginals, anteriorly projecting processes that tend to make the embayment more acute. The anterior edge of the nuchal embayment is thicker than the other shell margins and is truncated in the form of a vertical plane, curved to meet the tapering edge of the marginals on either side. The limits of the nuchal bone (assuming that one was present) are not visible on any specimen. The ventral surface of the nuchal region indicates that the body wall was attached along the bone margin, rather than more posteriorly, so that there was no overhanging area of bone as seen in some other turtles. Lateral to the nuchal embayment, *Proganochelys* does have such an overhang.

On the midline of the ventral surface posterior to the margin is an attachment area for the dorsally expanded neural spine of the eighth cervical vertebra. In the Berlin specimen the neural spine is firmly fused to the shell and the lower portion of the spine with the centrum is broken off, but in SMNS 16980 the entire eighth cervical is free. In SMNS 16980 there is a concavity for the reception of the eighth cervical spine and it is likely that this represents a sutural attachment. Again, the presumed juvenile nature of SMNS 16980 can be invoked to explain this difference between the two specimens. There is no indication of an articular facet for the seventh cervical. *Meiolania platyceps* has well-developed articular facets for both seventh and

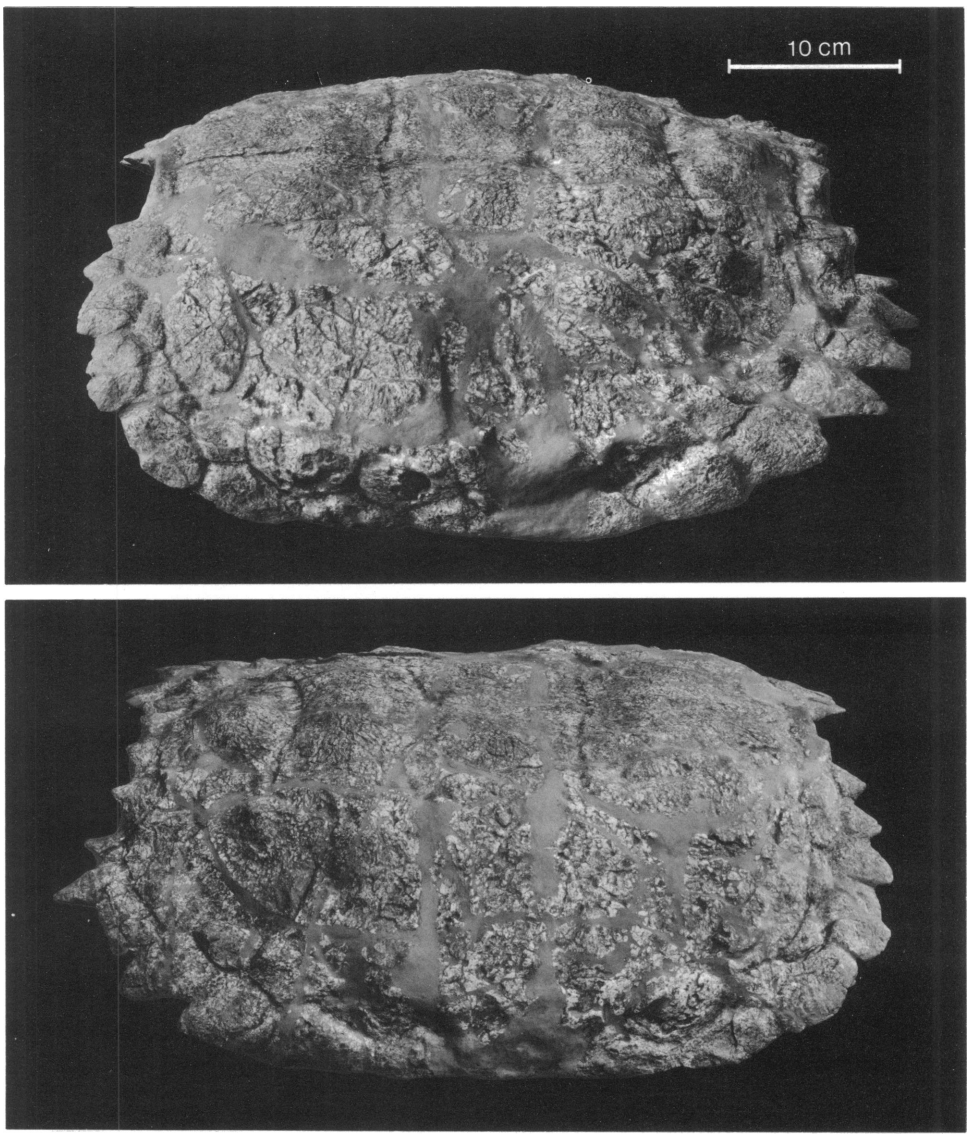


Fig. 71. *Proganochelys quenstedti,* SMNS 16980; carapace. Upper, dorsolateral oblique view of left side, anterior toward left; lower, dorsolateral oblique view of right side, anterior toward right.

eighth cervical spines, while chelonioids have an articulation facet for the eighth cervical spine. Both of these are movable and not sutural articulations; they are interpreted as nonhomologous with the condition in *Proganochelys.*

The area lateral to the midline and anterior to the rib of the first thoracic vertebra is unusually complex in *Proganochelys.* Into this space projects the rib of the eighth cervical, the dorsal process of the scapula, and the dorsal process of the epiplastron. In the Berlin specimen these elements (except for the scapula, which is placed too low) can be seen articulated in approximately natural position (fig. 81), while in SMNS 16980 the ventral surface of the carapace is preserved disarticulated from the epiplastral process (fig. 98). The dorsally expanded epiplastral process has a broad sutural attachment to the carapace just posterior to marginals 2 and 3. Behind the epiplastral process is a pit, concave ven-

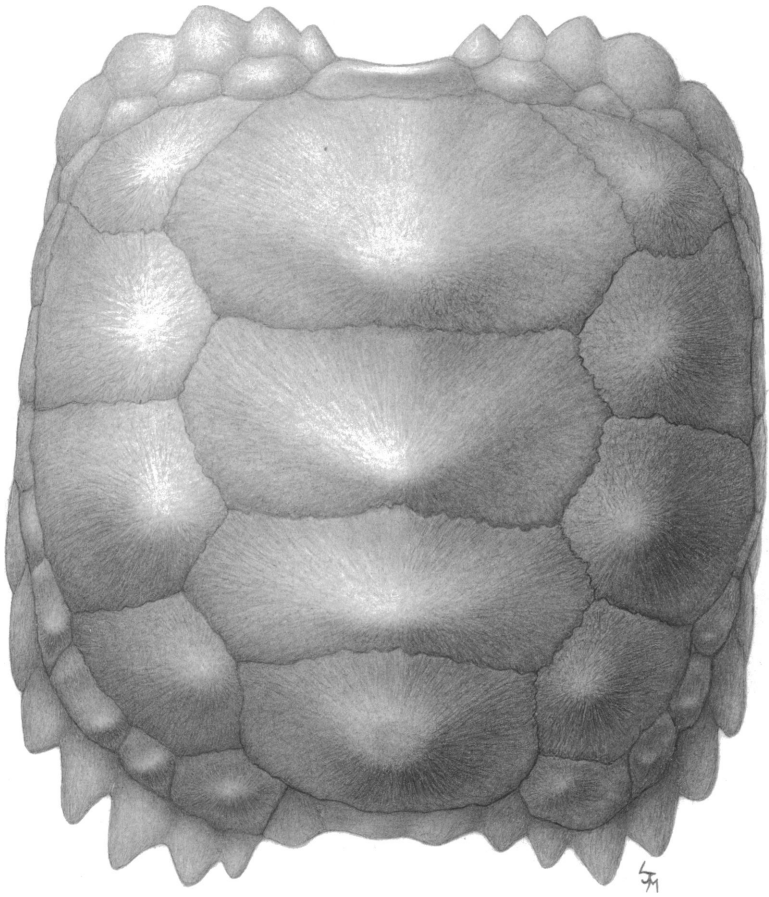


Fig. 72. *Proganochelys quenstedti,* SMNS 16980. Dorsal view of carapace corrected for crushing to show scale arrangement and shape. Surface texture poorly preserved and not indicated. See Figure 70.

trally, that appears to contain the articulation for the dorsal process of the scapula (fig. 82). The rib of cervical 8 (fig. 83) is curved laterally and seems to fit behind the scapular process. This entire morphology is known so far only in *Proganochelys* but it may still be the primitive condition for turtles. The articulation of the scapula behind the clavicle (epiplastra) is normal in amniotes and that is still the situation in *Proganochelys.*

Thoracic Vertebrae

The thoracic vertebrae of *Proganochelys* agree in number and general morphology with those of other turtles. There are ten thoracic centra in *Proganochelys* and these can be seen in SMNS 16980, the Berlin specimen, and, to a lesser extent, in SMNS 10012 and SMNS 17203. The Berlin specimen has sutures preserved between the centra and I agree with Jaekel's (1914: fig. 7) figure of them. This, it might be noted, is inconsistent with the presumed adult nature of the Berlin specimen in comparison to SMNS 16980 which has these sutures fused. Also, SMNS 17203 has portions of three thoracic centra visible in articulation in ventral view and they agree with the Berlin centra.

The first thoracic centrum is slightly short-

er than the rest and has a platycoelous articulation with the eighth cervical. There are no prezygapophyses preserved on the Berlin specimen but poorly preserved processes of bone can be seen in SMNS 16980 and SMNS 10012 that seem to be prezygapophyses. Unfortunately, articular facets are not visible in these specimens. Both eighth cervicals preserved (SMNS 16980 and the Berlin specimen) have a flat, posterior central articulation and, combined with the attachment of the eighth cervical neural spine to the carapace, demonstrate the the joint between the first thoracic and the eighth cervical had very limited mobility at best, in contrast to those of most other turtles. Furthermore, there is evidence that the centrum of the eighth cervical articulated by means of a small posterolateral facet with the ribhead of the first thoracic. Both of the preserved eighth cervicals have small facets and the first thoracic rib of SMNS 16980 on the left side appears to articulate with the eighth cervical when the latter is placed in articulation with the thoracic vertebra. The rib of the eighth cervical in the Berlin specimen has an articular facet that appears to contact the scapula, another suggestion of limited movement.

Thoracic centra 2–8 generally agree in morphology. They are roughly hourglass-shaped with anterior and posterior expansions. The central articulations are, to the extent seen, flat ankyloses as in other turtles. The rib heads in *Proganochelys* are unusually broad and have extensive contact areas on the thoracic centra. The anterior and posterior expansion of the thoracic centra are the articulation areas with the rib heads. All of the thoracic ribs in *Proganochelys* (and the eighth cervical as well) articulate with two thoracic centra, the centrum articulating with its own rib anteriorly and with the rib of the posterior centrum posteriorly. In other words, thoracic centrum 3 articulates with thoracic rib 3 anteriorly and thoracic rib 4 posteriorly. (To make things even clearer, thoracic rib 3 is fused to the second costal and is the second costal rib.) This overlap occurs in all turtles to some extent but usually the posterior thoracics tend to lose the articulation with the posterior rib and maintain a complete articulation with their own rib anteriorly. It is interesting to note that by comparison with other amniotes this latter condition would be considered primitive for turtles; yet it does not occur in *Proganochelys,* which agrees with other turtles.

The thoracic centra of *Proganochelys* are not particularly deep or shallow in cross section, they have a low keel that widens between central articulations. The neural spine attachment to the overlying neurals appears to be a solid plate from first thoracic to tenth thoracic but the region is not well preserved in any of the specimens and small fontanelles cannot be ruled out. Sutures that would allow differentiation of the neural spines are not preserved.

The ribs of the thoracic vertebrae do show some differences from those of other turtles. The first thoracic rib in *Proganochelys* is relatively large, larger, in fact, than the other thoracic ribs. In most other turtles the first thoracic rib is very small and usually extends only for a short distance along the first costal. Turtles such as *Meiolania* and *Glyptops* have a large first thoracic rib that may extend to the plastral buttress. The first thoracic rib of *Proganochelys,* however, is deeper, more robust, and has a free distal end, in contrast to that of nearly all other turtles. Medially, the rib has a synarthritic articulation with the anterior half of the first thoracic centrum and (as discussed above) a probable articulation with the posterior margin of the eighth cervical. The rib head narrows gradually to a shaft that remains free of the carapace to produce an oval shaped opening that is broader medially than laterally. The rib head is large but not as wide or deep as the rib head of the second thoracic in SMNS 16980. In the Berlin specimen the first thoracic rib head appears to be about the same size as the second. The first thoracic rib is attached to the costal at the position of the scapular articulation. The attachment is not entirely clear; it appears to be fused in SMNS 16980 and sutured into a groove in the costal in the Berlin specimen, but poor preservation may have obscured the contact in SMNS 16980.

The shaft of the first thoracic rib is a thin plate slightly curved, concave anteriorly, becoming thinner laterally and ventrally. The plane of the shaft is inclined posteroventrally and, on the right side of the Berlin specimen, the shaft itself curves posteroventrally to ex-

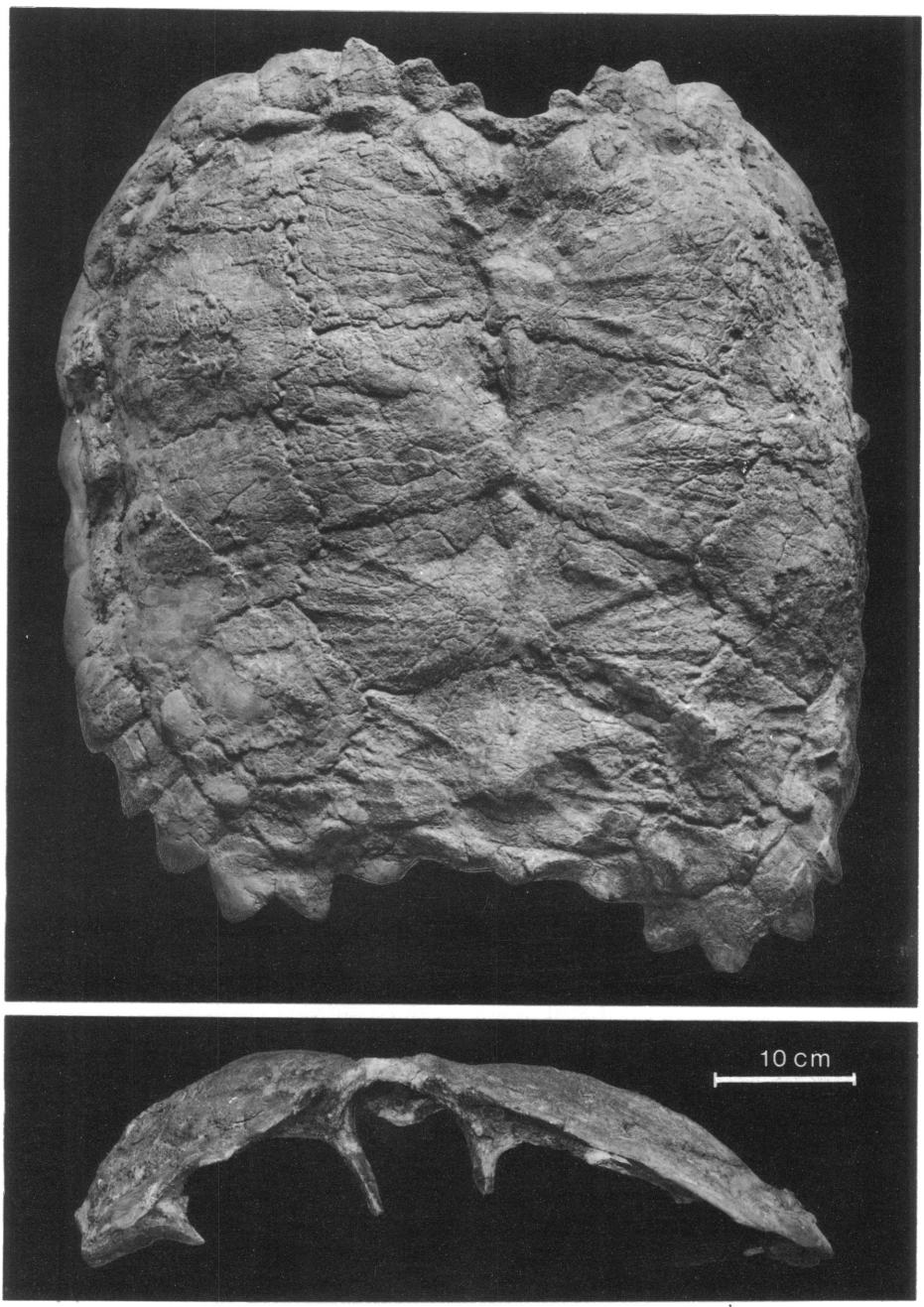


Fig. 73. *Proganochelys quenstedti,* MB 1910.45.2; carapace. Upper, dorsal view (from Gaffney, 1985a); lower, anterior view with dorsal processes of epiplastra ("cleithra") attached to carapace. Type specimen of "*Triassochelys dux*" Jaekel.

tend free of the costal at the distal end of the rib. Jaekel (1914: fig. 7) figured the distal end as being free of the carapace as in the Berlin specimen although at present this portion is broken off. In SMNS 16980 the right rib end was free up to 1979 but was obscured during

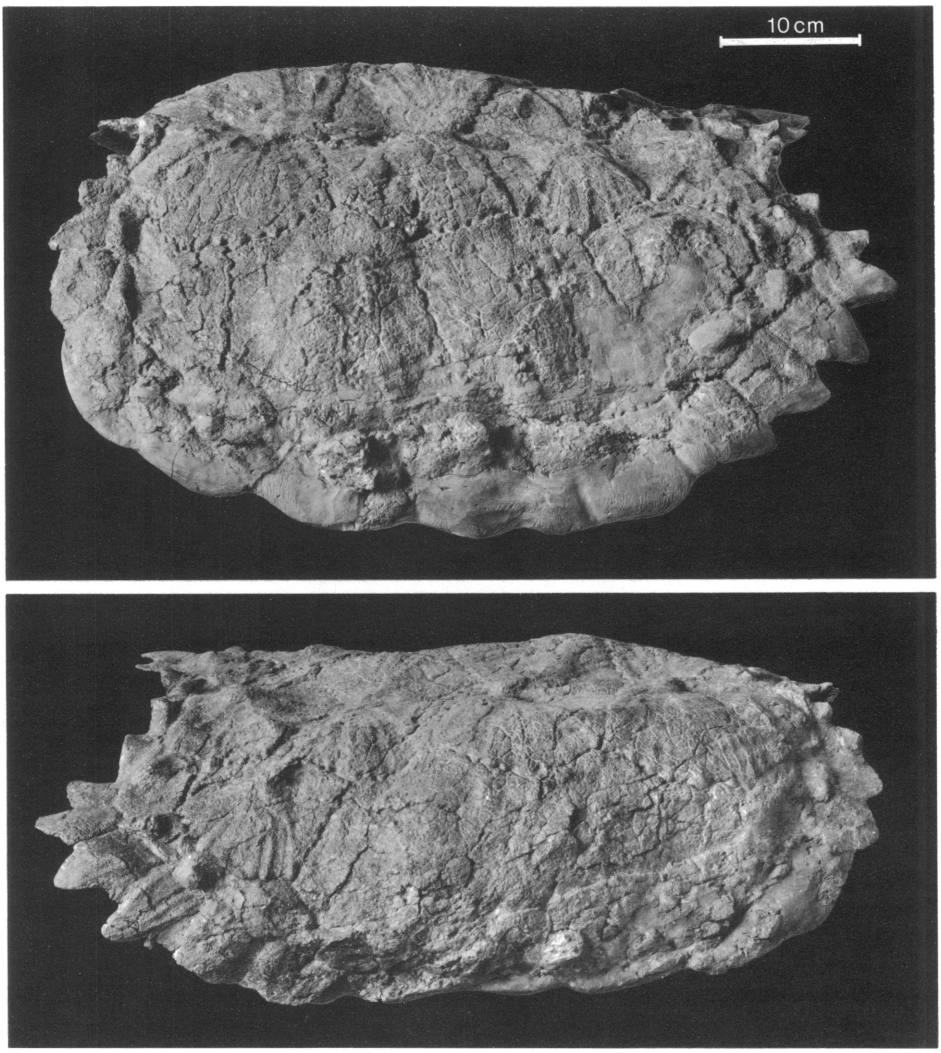


Fig. 74. *Proganochelys quenstedti,* MB 1910.45.2; carapace. Upper, dorsolateral oblique view of left side, anterior toward left; lower, dorsolateral oblique view of right side, anterior toward right.

later repair work. In none of the available specimens can the extent of the free end be determined, but on the left side of the Berlin specimen the rib touches or nearly touches the plastral buttress. At the point where the rib shaft rises from the vertebral centrum to join the carapace, the rib is relatively thick and is confluent with a low, anteriorly directed ridge on the carapace. Lateral to this ridge and anterior to the rib is a pit in the carapace where the scapula articulates (figs. 77, 82). This pit is obscured somewhat in SMNS 16980 and on the left side of the Berlin specimen, but the right side of the Berlin shell has the pit and the surrounding structures relatively well preserved (fig. 82). The scapular pit is oblong in shape, wider transversely than sagittally, and does not penetrate deeply into the carapace. The anterior margin of the pit is a shallow, raised surface that becomes a ridge for the articulation of the dorsal process of the epiplastron. In the Berlin specimen the epiplastral processes are articulated and seem to have been pushed posteriorly to

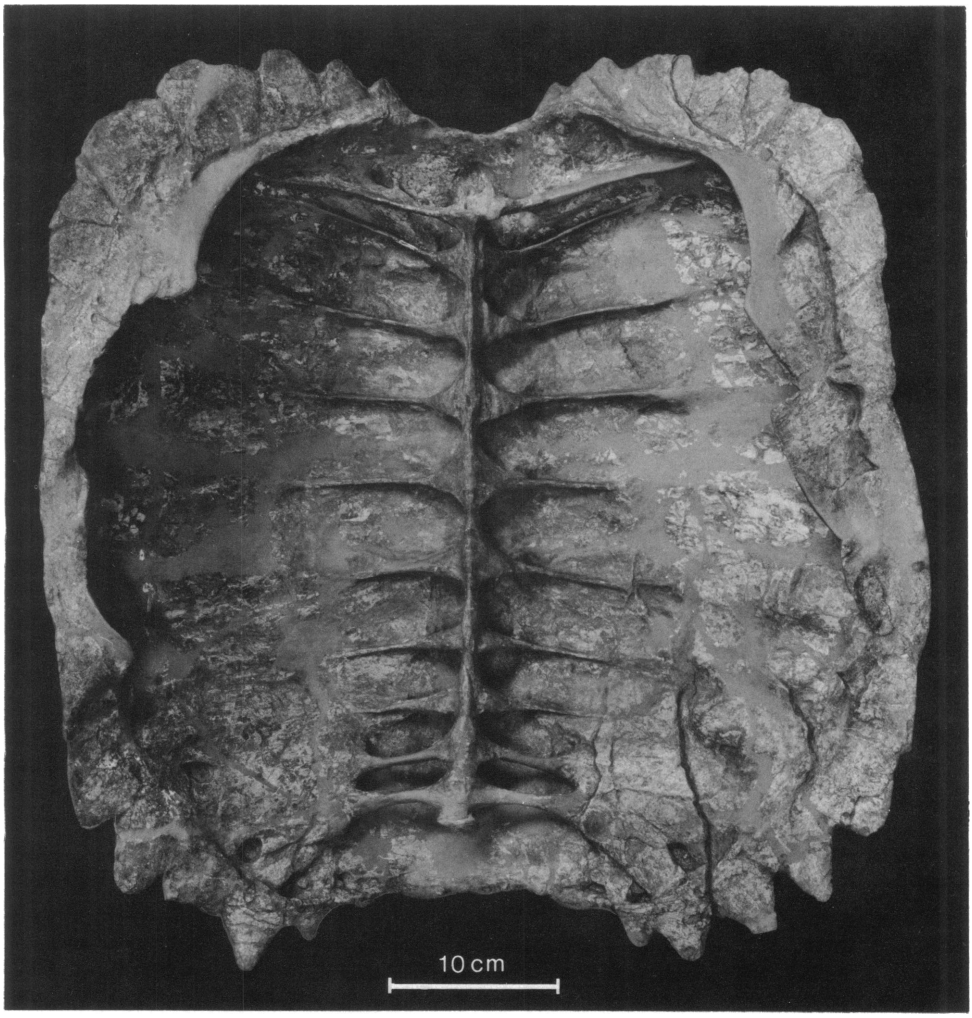


Fig. 75. *Proganochelys quenstedti,* SMNS 16980. Ventral view of carapace. From Gaffney (1985a).

overhang more of the scapular pit than they probably did in life. In SMNS 16980 the rearticulation of the epiplastral processes onto the carapace (fig. 96) substantiates the conclusion, based on the Berlin specimen, that the anterior margin of the scapular pit was the posterior surface of the epiplastral process. The lateral margin of the scapular pit is indistinct and is formed by the intersection of the first thoracic rib and the lateral extension of the epiplastral process.

The second thoracic rib ridge in *Proganochelys* angles anterolaterally at a slightly greater angle than the first thoracic rib shaft and so they appear to intersect, particularly in the Berlin specimen, which has a more complete first thoracic rib. Actually, however, in the Berlin specimen the second rib ridge underlies the comparatively deep shaft of the first thoracic rib laterally. In SMNS 16980 it can be seen that the two rib ridges do not intersect. The second thoracic rib is the first costal rib in all turtles, including *Proganochelys.*

The succeeding thoracic ribs are variably preserved in the available specimens. They are least distorted in SMNS 16980 but in some areas the bone preservation in this specimen is not as good as in the Berlin shell. The rib heads in the latter shell, however, have

been crushed dorsoventrally although the sections of the ribs attached to the carapace appear to be relatively undistorted. The whole carapace of the Berlin specimen (fig. 73) has been distorted so that the rib ridges on the right side are angled posterolaterally to a greater degree than those on the left. The left side agrees closely in this feature with SMNS 16980 and SMNS 10012. The rib heads of thoracic 2–8 in *Proganochelys* are somewhat unusual among turtles in being swollen; rib heads 1, 9, and 10 are less so. The crushing of the rib heads in the Berlin specimen reveals that they are not solid bone but somewhat cancelous. The rib heads are broader than deep (that is, the anteroposterior dimension is greater than the dorsoventral) and they are not flat, as in the expanded rib heads of some other turtles. The anterior rib heads develop into a plate of bone laterally that tends to be concave anteriorly as it extends dorsally onto the flat part of the costal as a rib ridge. The more posterior ribs extend laterally as a bar of bone as the shaft reaches the costal.

Each thoracic rib head is separated to a varying degree from the overlying carapace (fig. 78). Dorsally, the heads of thoracic ribs 3 to 8 have thin, transverse walls that meet the carapace to a varying extent producing openings, the costovertebral tunnel, of different sizes (best seen in SMNS 16980). The opening formed between the first thoracic rib and the carapace is larger than any of the others except thoracic ribs 9 and 10. The opening formed by the second thoracic rib is less than half that size, being greatly decreased in width due to more of the rib shaft being attached to the carapace. The third thoracic rib has a well-developed transverse dorsal plate that leaves only a small opening, less than one-fourth the size of the one immediately preceding it. The openings above thoracic ribs 4 and 5 are even smaller, merely slits of a few millimeters in depth and about one centimeter in width. Thoracic rib 6 either has no opening or a small one, similar in size to the two preceding it; matrix and poor preservation prevent its determination. The seventh thoracic rib has an opening about midway in size between those seen in ribs 2 and 3, while the opening above thoracic rib 8 approaches the size of the opening formed by the first thoracic rib. Thoracic ribs 9 and 10 are distinctive in having the largest openings between rib shaft and carapace of all the thoracic ribs, number 10 being larger than 9. The position of the attachment of the rib shaft to the carapace moves laterally from thoracic 7 to 10 (equaling costal ribs 6 to 9), resulting in the increased size of the opening between rib shaft and carapace. In many primitive turtles, such as *Proterochersis, Pleurosternon, Kayentachelys,* and *Glyptops* the costo-vertebral tunnel expands posteriorly; that is, the posterior thoracic rib attachments are farther from the midline than the anterior ones. The free rib portions of thoracic ribs 9 and 10 are connected at their base by a web of bone. The base of the tenth thoracic rib, on the ninth costal, bears a raised tubercle for the articulation of the ilium (fig. 77).

The tenth thoracic centrum has a more or less platycoelous articular surface but with a slight median concavity for the articulation of the first sacral vertebra. The neural spine of the first sacral articulates in a depression on the carapace while the second sacral overlaps the posterior edge of the carapace and half of the vertebra projects posteriorly beyond the shell.

Costal Bones

The shape of the costal plates themselves is not well known in *Proganochelys.* With a few exceptions the only definite costal sutures are those seen in SMNS 17203 (see below for description) but even in the absence of good sutural information there are features on the ventral surface of the costals that can be described. The thoracic ribs, discussed above, are continuous with laterally directed ridges that decrease in height distally. These ridges, however, are much better developed in *Proganochelys* than in most other turtles because they are distinct for nearly half the distance to the lateral margin of the shell. These ridges are more extensive in the Berlin specimen and in SMNS 10012 than in SMNS 16980. The ridges in all the shells are higher and longer distally on the anterior costals and decrease in size posteriorly. Between these ridges the costals form concave troughs with the midline of the trough containing a narrow groove that extends laterally toward the edge of the shell. Jaekel (1918a: figs. 7, 30) iden-

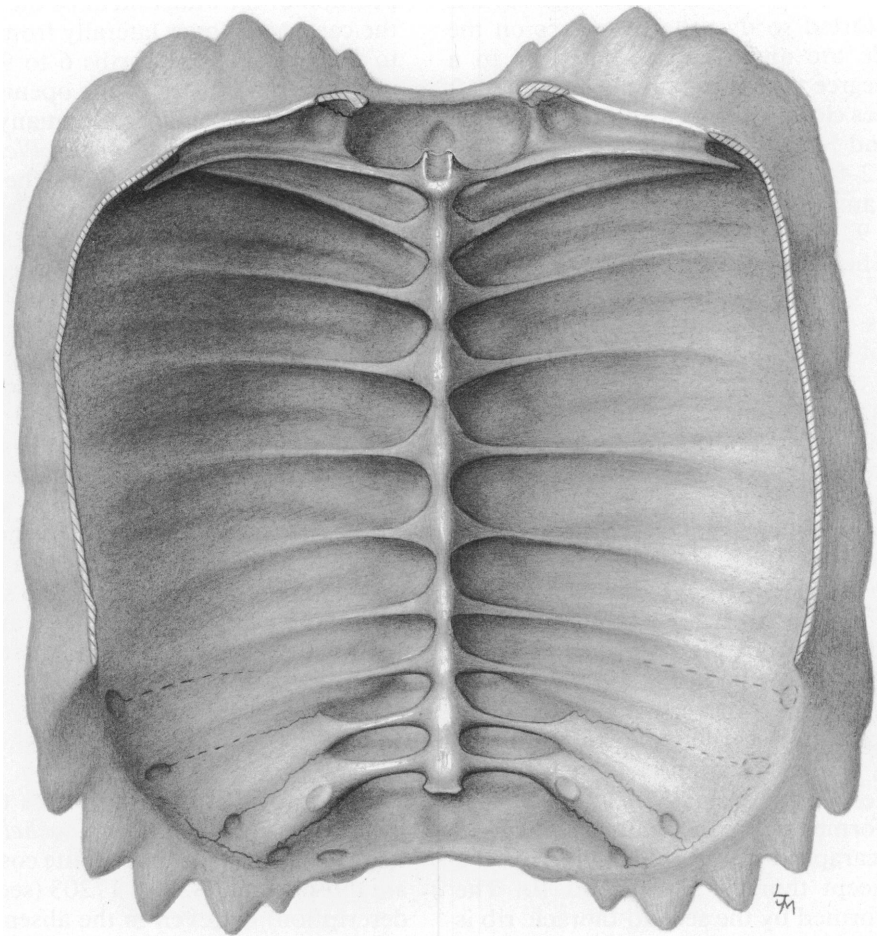


Fig. 76. *Proganochelys quenstedti,* SMNS 16980. Partially restored ventral view of carapace.

tified these as intercostal sutures and they may be in the position of the intercostal sutures. However, I think it more likely that they represent the position of a nerve or vessel, rather than a suture. These troughs run straight without any indication of interdigitating and seem to extend laterally onto what should be peripheral bones with no sign of a costal-peripheral suture. Nonetheless, the intercostal sutures of SMNS 17203 do lie in approximately these positions.

Some costal sutures are visible in SMNS 16980 and, combined with costals from SMNS 17203, provide interesting information. The ninth and part of the eighth costals in SMNS 16980 have sutures. The ninth costal curves posteriorly from the rib shaft (of the tenth thoracic rib), widens slightly as it reaches the distal margin of the carapace, and seems to have a tapered end fitting into the adjacent peripheral (marginal 15). A disarticulated left ninth costal from SMNS 17203

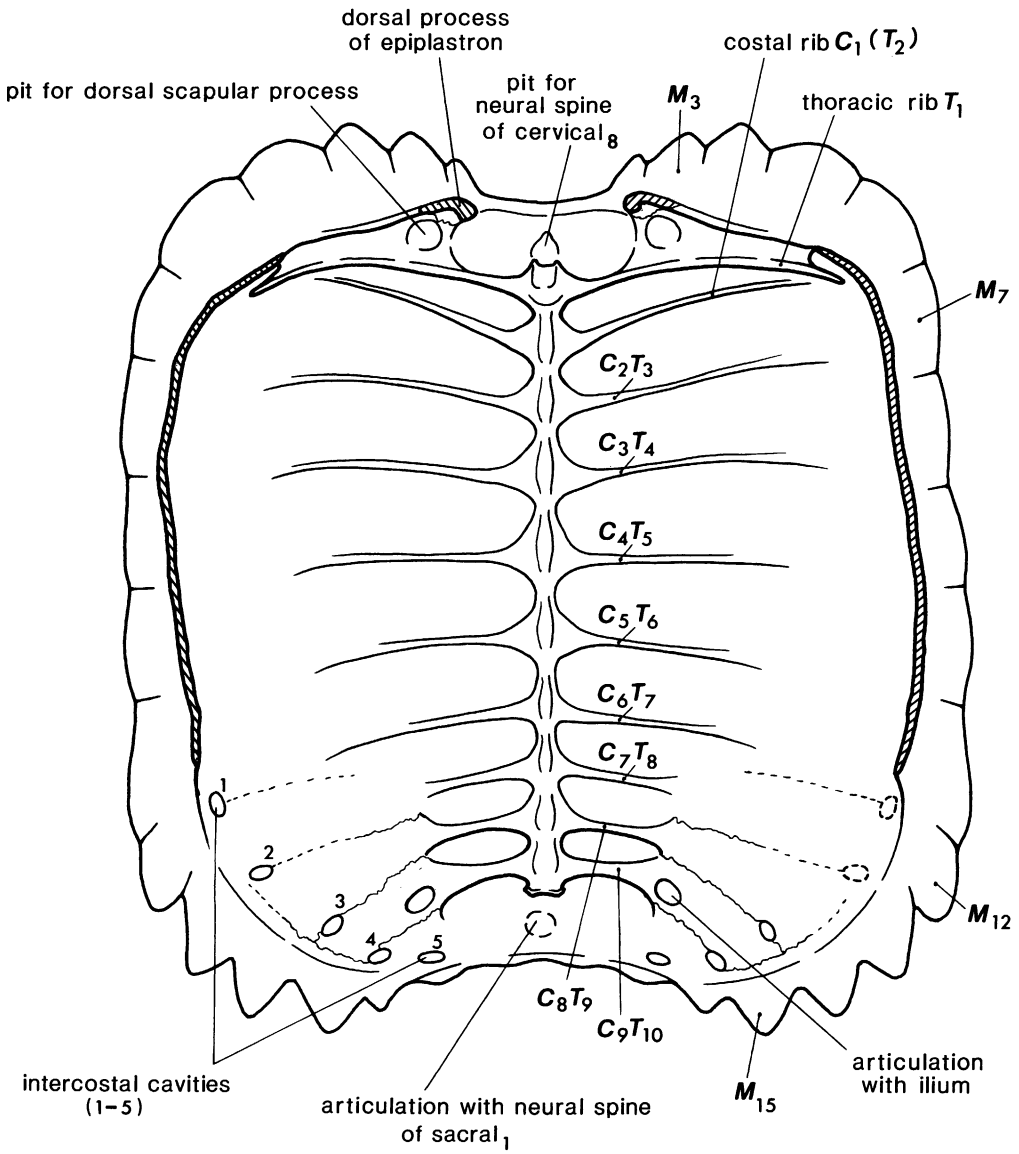


Fig. 77. *Proganochelys quenstedti,* SMNS 16980. Ventral view of carapace. Abbreviations: **C,** costal rib; **M,** marginal scale; **T,** thoracic rib.

shows what seems to be a tapering distal margin but breakage makes this equivocal. The ninth costal bears a pronounced raised tubercle about halfway along its length for the articulation with the ilium. Although the surface of the tubercle is rugose, comparison and articulation of the pelvis indicates that the pelvis was not sutured to the carapace and that the articulation was movable as in many cryptodires. The anterior margin of the ninth costal is a roughly curved suture with the eighth costal, both meeting on the same level. The posterior margin of the ninth costal is slightly raised with respect to the more posterior bone (as seen in ventral view), presumably the pygal or suprapygal.

The eighth costal has its more proximal intercostal sutures visible in SMNS 16980

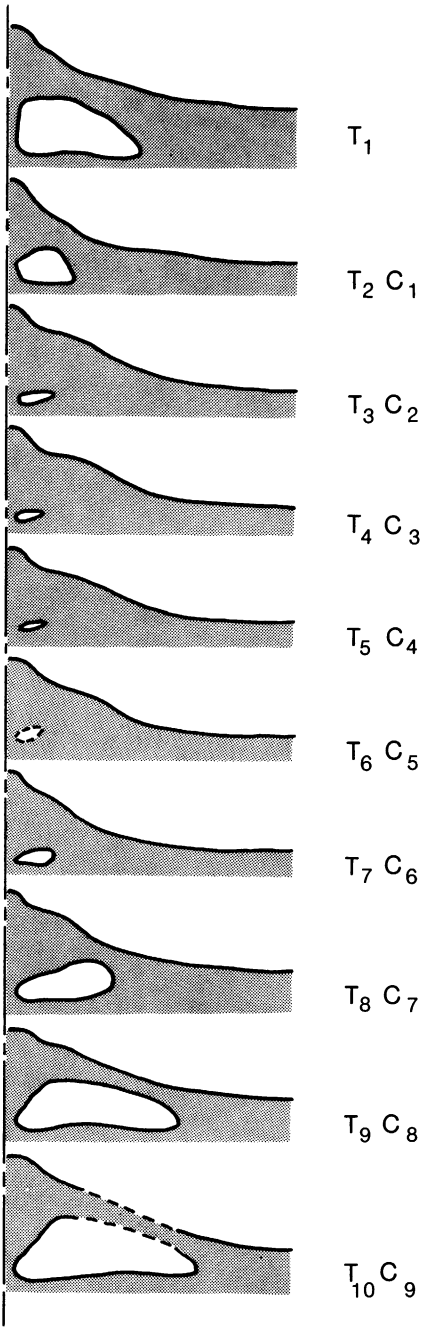


Fig. 78. *Proganochelys quenstedti,* cross section through ribs and thoracic vertebrae of carapace showing size of costo-vertebral tunnel; ventral toward top of page, line at left is midline. Abbreviations: **C,** costal rib; **T,** thoracic rib.

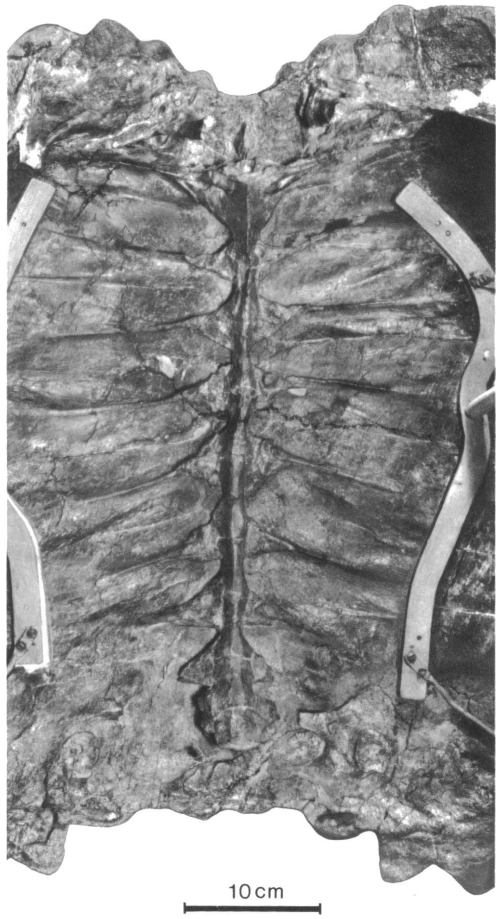


Fig. 79. *Proganochelys quenstedti,* MB 1910.45.2. Ventral view of carapace.

and they seem to indicate that this bone becomes wider distally than costal nine. This does not agree with Jaekel's (1918a: fig. 7) sutures which are shown as parallel to each other, but both specimens are questionable in the clarity of these sutures.

Another feature of the posterior region of the carapace on its ventral surface is a series of small concavities (fig. 77), usually placed at or near the peripheral bones. These concavities do not penetrate through the shell and, where relatively well preserved (such as on the left side of SMNS 16980), have a flat dorsal surface rather than a conical termination. As preserved in the Berlin specimen and in SMNS 16980 these concavities tend

to be oval or circular but this may be a result of preparation and the original shape may have been triangular. Five pairs of concavities can be identified on these two shells. Starting with the most posterior pair as number one, the description will proceed anteriorly. The most posterior pair of concavities is best seen in the Berlin shell where they form conical indentations (in contrast to the remaining concavities) in the last pair of peripherals (marginal number 17). In the Berlin shell it is quite clear that these peripherals are hollow but in SMNS 16980 they are offset in relation to the thickest portion of the peripherals, but as the sutures in this area are nonexistent, it is still possible that the concavities lie in the center of the bone itself. Nonetheless, it is interesting to note that the concavities in this position are more extensive and clearer in the Berlin specimen, a presumed adult, than in SMNS 16980, a presumed juvenile.

The second pair of concavities is best seen in SMNS 16980. Each lies at the junction of the posterior margin of the ninth costal and the contact of marginals 15 and 16. The anterior margin of the concavity is the ninth costal and is clearly delimited but the posterior margin is not well defined. Contrary to the most posterior pair of concavities, this pair does not seem to be a result of a hollow peripheral; rather, it appears to be the result of incomplete ossification at a triple suture junction. The second pair of concavities is not readily seen in the Berlin specimen, probably due to coincident damage and poor preservation on both sides.

The third pair of concavities are clearly seen on both the Berlin specimen and SMNS 16980. In the latter specimen it can be seen that they lie at a triple junction of costals eight and nine and a peripheral (or peripherals), in the area between marginals 14 and 15. The concavities are irregularly oval, generally well defined, and slightly larger than the other pairs.

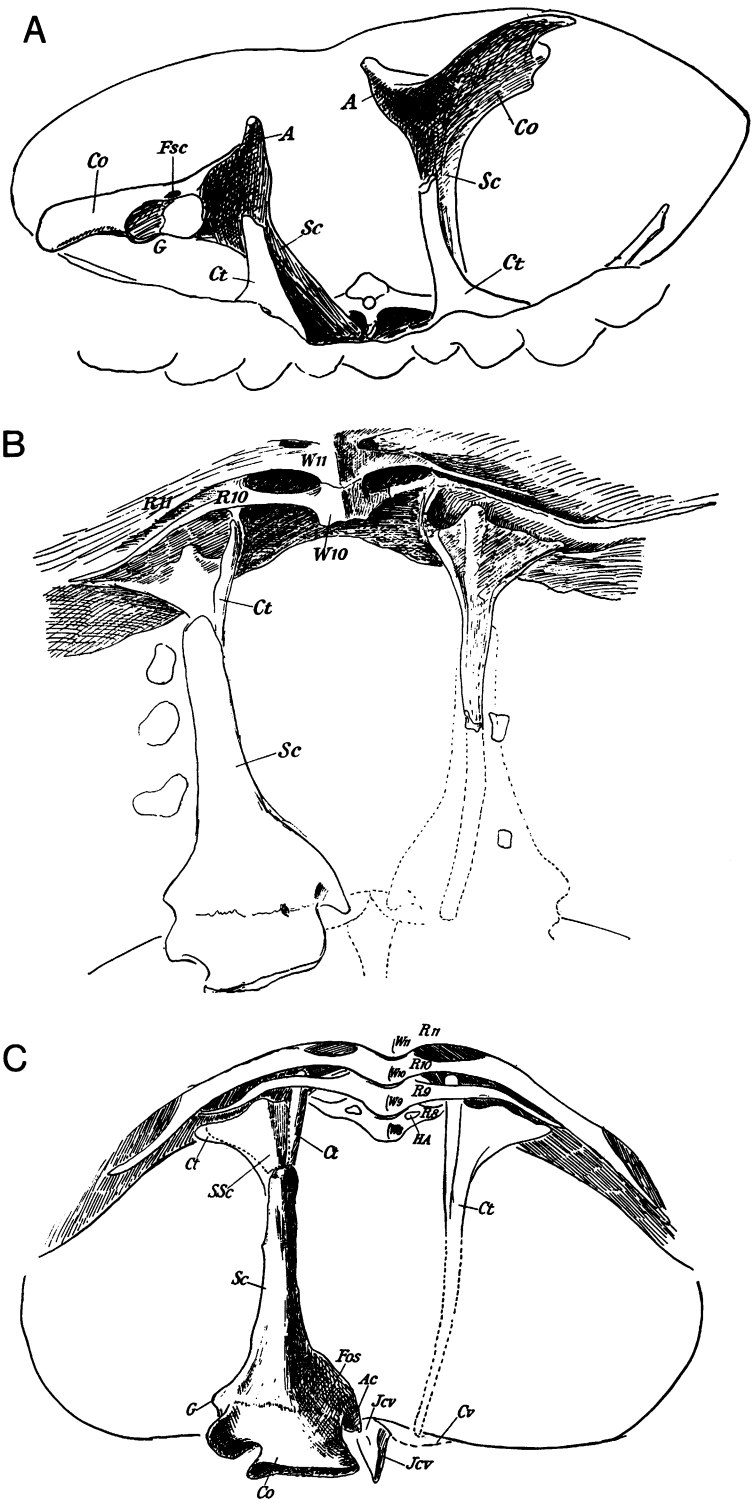
The fourth and fifth pairs of concavities are only clear on SMNS 16980. The relevant areas in the Berlin specimen have features that could be interpreted as these concavities (Jaekel, 1918a, fig. 7, figures the fourth pair), but they are obscured by breakage and plaster. Although the limits of peripheral bones are unclear, it does seem that these concavities lie in the distal portion of the intercostal sutures between costals 7 and 8, and 6 and 7. These concavities are best seen on the right side of SMNS 16980, number 4 being roughly tear-drop shape and 5 being oval.

The most posterior of these concavities is best interpreted as a hollow peripheral that is more clearly expressed than the other peripherals, and has nothing to do with the costals. The four more anterior concavities are clearly related to incomplete ossification of the distal intercostal sutures, a condition common to many other adult turtles as well as juveniles.

Proganochelys differs from other turtles in that the openings do not penetrate through the shell and apparently have discrete, curved margins. The shape of these concavities in *Proganochelys* has obviously been affected by preparation but it is clear that none of them penetrated the shell. It is possible that a medial flange of an associated peripheral or costal covers the opening dorsally. These concavities do provide some information about costal/peripheral relations. Costal 9 quite conveniently fits into the base of the peripheral covered by marginal 15 and costal 8 could curve so that its tapered end (providing it has one) would fit into the peripheral of marginal 14, but costal 7 is opposite the base of marginal 12, leaving marginal 13, or rather its associated peripheral, unattached to a costal. In the absence of sufficient sutural data for the peripheral bones, this must be considered speculative.

Bridge Region

Unfortunately the bridge areas of the available specimens are the most damaged and least informative of the preserved areas of the shell. Crushing was concentrated here during fossilization and the addition of plaster and other substances during preparation combine to obscure genuine features from ones added during reconstruction. Of the two specimens with the bridge apparently intact, the Berlin specimen is the worst: the left side is almost entirely restored and the bone that is present on the right side badly crushed and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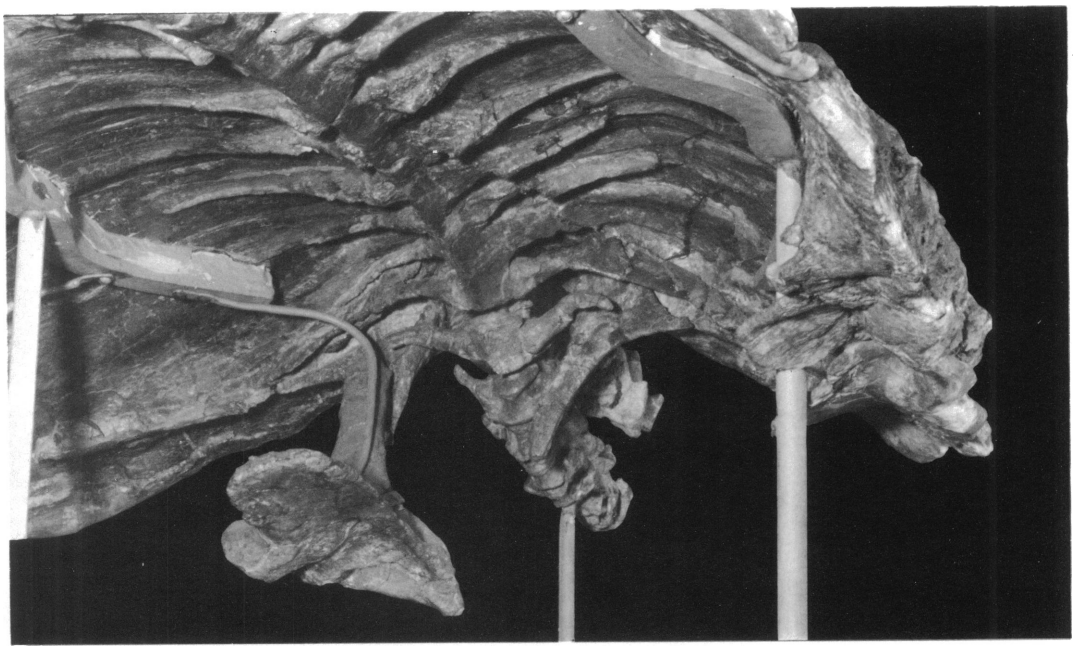

Fig. 81. *Proganochelys quenstedti,* MB 1910.45.2. Posterior view of anterior portion of mounted skeleton with left scapula-coracoid and cervicals in articulation. Compare with Figures 82, 83.

distorted. In SMNS 16980 the bridge areas retain most of the bone and are only partially obscured by crushing and restoration. SMNS 17203 supplies some information on bridge peripherals and SMNS 17204 shows some external features (described under Marginals).

To the extent that it is known, the bridge region of *Proganochelys* does not differ markedly from that of other turtles. The plastral buttresses are relatively extensive, but they do not extend onto the costals as in most other turtles. Both SMNS 16980 and SMNS 17203 show clear sutures between plastron and peripherals and indicate that the hyoplastral buttress extends anteriorly to the level of the first costal, much as in other turtles. The anterior and anteromedial limits of the hyoplastral buttress can be seen at the present time only in drawings and photographs made of SMNS 16980 in 1979, while it was still in many pieces and before it was extensively

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Fig. 80. *Proganochelys quenstedti,* MB 1910.45.2. Figures from Jaekel (1918a) showing relations of scapula-coracoid and "cleithra" (dorsal processes of epiplastra) to shell as hypothesized by Jaekel. **A,** the apparent original position of both scapula-coracoids and "cleithra" in the upside-down shell in anterior view. **B, C,** anterior end of shell in posterior view with scapula-coracoid and "cleithrum" (dorsal process of epiplastron) in hypothesized life position. See text for discussion. Abbreviations: **A, Ac,** acromion process; **Co,** coracoid; **Ct,** "cleithrum" (here interpreted as the dorsal process of the epiplastron); **Cv,** epiplastron (restored, completely absent in this specimen); **Fos, Fsc,** supracoracoid foramen; **G,** glenoid; **HA,** opening between capitulum and tuberculum of rib heads of cervical 7; **JCV,** entoplastron; **R8,** rib of cervical 7; **R9,** rib of cervical 8; **R10,** rib of first thoracic vertebra; **R11,** rib of second thoracic vertebra (=first costal rib); **Sc,** scapula; **SSc,** "suprascapularia" a cartilaginous extension of the scapula hypothesized by Jaekel to lie above the scapula and behind the "cleithrum" (there is no evidence that it existed); **W8,** cervical 7; **W9,** cervical 8; **W10,** first thoracic vertebra; **W11,** second thoracic vertebra.

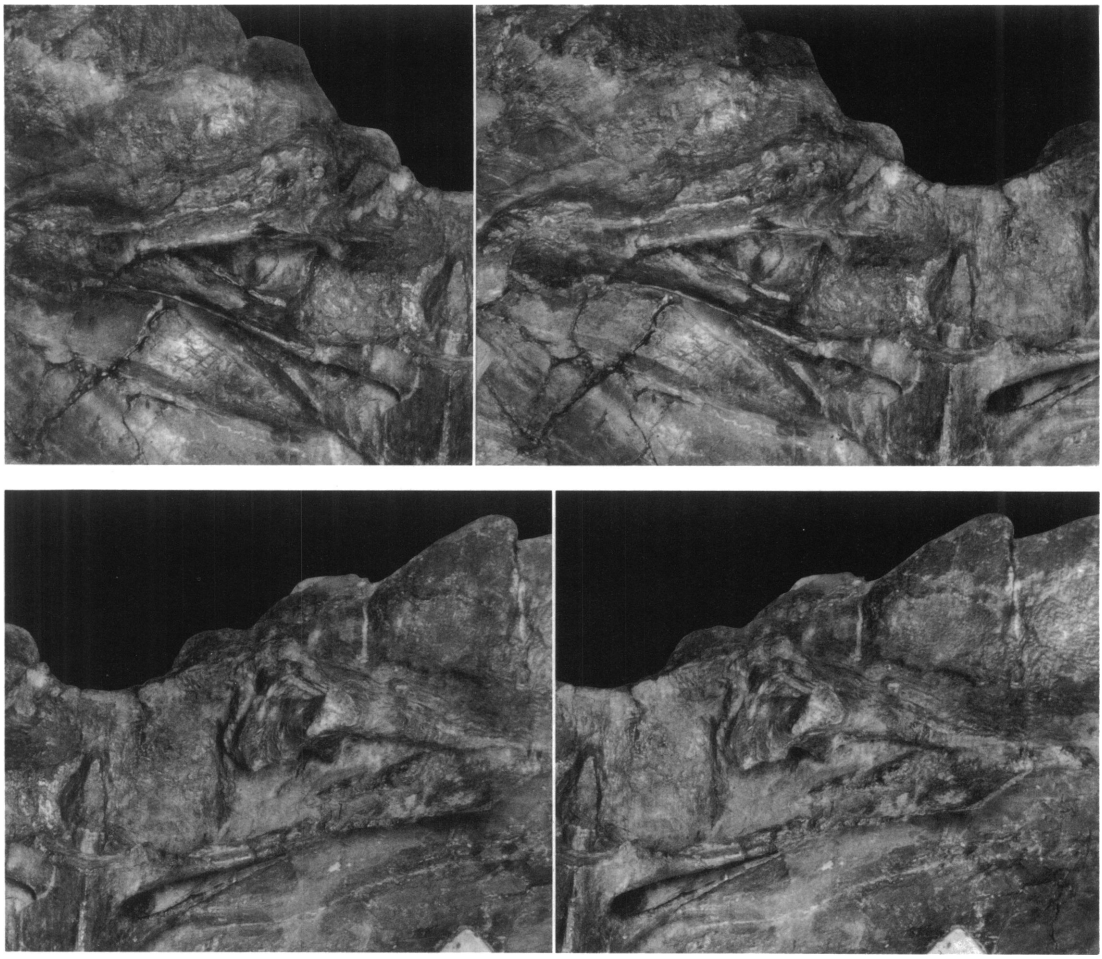

Fig. 82. *Proganochelys quenstedti,* MB 1910.45.2. Ventral view of anterior portion of carapace. See also Figures 81, 83.

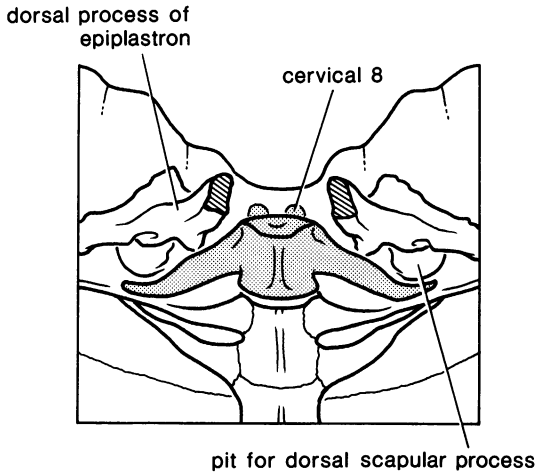

Fig. 83. *Proganochelys quenstedti,* MB 1910.45.2. Ventral view of anterior portion of carapace, partially restored and showing position of cervical eight (stippled). See also Figures 81, 82.

repaired. The buttress extends to the base of the fifth marginal where it meets a ridge that runs anteromedially to reach the nuchal embayment and the epiplastral process. This ridge apparently was the attachment area for the body wall. The peripheral bone sutures to this buttress are partially preserved in SMNS 17203 but unfortunately there are not enough present to determine their number or relative position with respect to the posterior peripherals.

The hypoplastral buttress extends posteriorly to the base of the eleventh marginal so that the hypoplastral or inguinal buttress is much less extensive than the hyoplastral or axillary buttress.

The plastral/peripheral suture as seen in SMNS 17203 forms an even margin to the carapace, continuing the margin formed by the more anterior and posterior peripherals. The bridge peripherals are roughly C-shaped in cross section with the internal surfaces continuing the curve of the carapace down onto the plastron. The bridge peripherals in *Proganochelys* are distinct from the other peripherals in having two separate plates, as in most other turtles. The bridge peripherals are also relatively shallow in *Proganochelys,* compared with the more anterior and posterior peripherals. Based on SMNS 17203, it seems likely that the mesoplastron contacted the bridge peripherals but that cannot be definitely determined.

In SMNS 16980 the bridge peripherals have a lateral ridge on the external surface that is continuous with the margin of the more anterior and posterior peripherals. From the fragments of bridge peripherals in SMNS 17203 it would appear that the marginal scutes overlapped the bridge peripheral bones as in most other turtles, rather than being coincident as in the posterior marginals and peripherals of *Proganochelys.* In the Berlin specimen the bridge peripherals have a flange that accentuates the lateral ridge seen in SMNS 16980, but I think that this is due to crushing and inaccurate reconstruction in the Berlin specimen and that the connection in SMNS 16980 is more accurate.

PLASTRON
(table 10, figs. 89–97)

EPIPLASTRON

The epiplastron is preserved completely only in SMNS 16980 (figs. 89, 90), in which the dorsal processes are broken at their base but still present. The ventral plate and much of the shaft is preserved in SMNS 17203, SMNS 17204, and a disarticulated ventral portion is preserved in SMNS 15759. The expanded dorsal process of the epiplastron is preserved attached to the carapace in the Berlin specimen, MB 1910.45.2.

Jaekel (1918a) identified a pair of bones at the front of the ventral surface of the carapace as cleithra, based on their position relative to the scapula-coracoid. In his specimen, MB 1910.45.2, the anterior part of the plastron was missing so he was unable to see that his "cleithra" were dorsal processes of the epiplastra. Even during the greater part of this study I did not realize that the epiplastral processes and the cleithra were the same until this was pointed out to me by J. Kelly and F. Ippolito during the mounting of the cast of the articulated skeleton. The earlier statements reaffirming the presence of cleithra by Gaffney and Meeker (1983) and Gaffney (1985a) are incorrect.

The epiplastron of *Proganochelys* consists of a roughly flat, horizontal plate, seen in all other turtles, and a dorsal process rising at right angles to the plate, present only in *Proterochersis* and *Kayentachelys.* Sutures of the

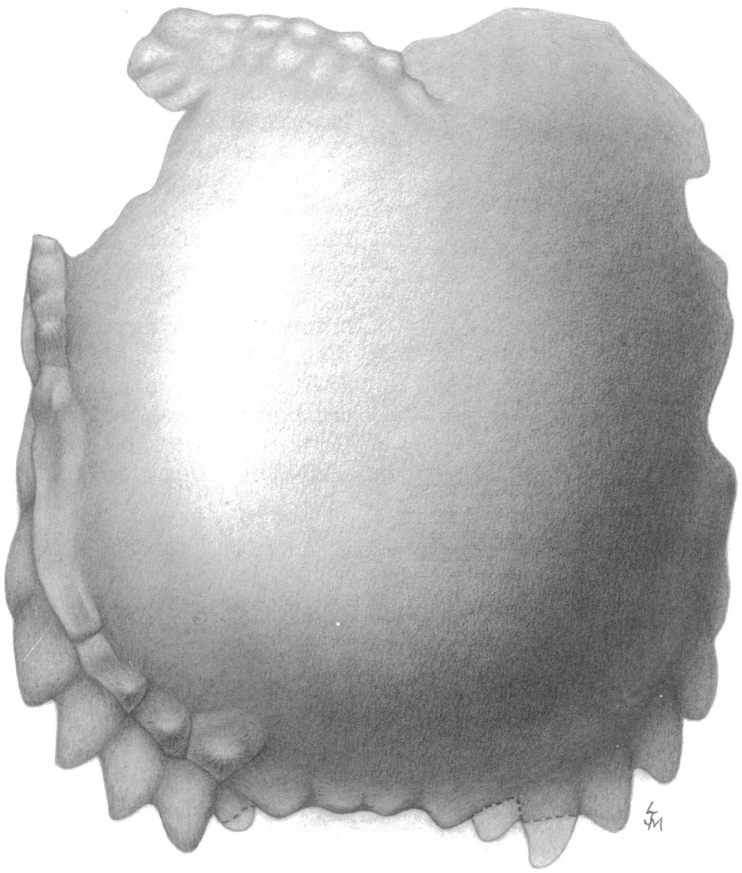

Fig. 84. *Proganochelys quenstedti,* SMNS 17204. Partially restored carapace in dorsal view showing scute areas around periphery, central area stylized. See Figure 86.

ventral plate can be seen in SMNS 17203, SMNS 17204, SMNS 16980, and the disarticulated SMNS 15759. The epiplastral-hyoplastral suture is the most apparent and it is visible in SMNS 17204 (right side), SMNS 17203 (left side), and SMNS 16980 (both sides). This suture runs anteromedially from the lateral margin of the plastron for a few centimeters; then the entoplastron is exposed separating hyoplastron and epiplastron. Although the entoplastral-hyoplastral suture remains clear in SMNS 17204 and SMNS 16980, the epiplastral-entoplastral suture becomes ambiguous in SMNS 17204 and can be seen only on the left side of SMNS 16980. The epiplastra do not meet in the midline on the ventral surface.

On the dorsal surface of the plastron some epiplastral sutures can be seen in SMNS 16980 but not in any other specimen. The left side of this plastron shows the epiplastral-hyoplastral suture at the lateral margin of the anterior plastral lobe, and it trends anteromedially in about the same position and direction as the suture on the ventral surface. Anteromedially the entoplastron borders the epiplastron and this suture can be seen in part on both sides of SMNS 16980. The entoplastron appears to extend anteriorly almost to the front of the plastron, separating the

TABLE 10
Comparison of the Shell in *Proganochelys* and the Earliest Pleurodire and Cryptodire

	Proganochelys	*Proterochersis*	*Kayentachelys*
Vertebral scutes	4	5	5
Pleural scutes	4	4	4
Supramarginal scutes	12	3	None
Marginal scutes	16 and 17	14	12
Vertebral scutes very wide	Yes	Yes	Yes
Cervical scute	Broad	Narrow	Narrow
Inframarginal scutes	Not known	Four	Four
Plastral scutes	7 pairs	9 pairs plus one on midline	7 pairs
Costals	9	?	8 (9 as a variant)
Posterior peripherals and marginals	Congruent	Probably alternating	Alternating
Costo-vertebral tunnel greatly reduced along mid-thoracic ribs	Yes	No	No
Attachments of posterior thoracic ribs separated from midline to greater extent than anterior ones	Yes	Yes	Yes
Carapacial caudal notch	Present, separating marginals	Present, separating marginals	Absent, marginals meet on midline
Eighth cervical neural spine sutured to nuchal	Yes	No	No
Thoracic rib heads	Wide, swollen	Wide	Narrow
Pelvis sutured to carapace and plastron	No	Yes	No
First costal rib larger than second costal rib	Yes	No, first costal rib smaller	No, first costal rib smaller
Musk ducts	?	Absent	Present
Peripherals scalloped	Yes	No	No
Dorsal process of epiplastron	Very large, wide attachment to carapace	Very large, probable attachment to carapace	Small, no attachment to carapace
Epiplastra meet on midline	No	No	No
Gular/intergular scute projections	Large	Small	Absent
Well-developed plastral buttresses	Absent	Present, extend beyond marginal bones	Absent
Mesoplastra	One pair meeting in midline	Two pairs meeting in midline	One pair meeting in midline
Intergular scutes separating gular scutes	Yes	Yes	Yes

epiplastra for nearly their entire length on the dorsal surface. The epiplastral-entoplastral suture, however, becomes less clear anteriorly and the medial area of contact between the epiplastra cannot be made out with a high degree of confidence. As interpreted here, the entoplastral-epiplastral suture comes very close to the base of the dorsal process of the epiplastron.

The conventional terminology of plastral scales is based on the arrangement seen in most Recent testudinoids. Hutchinson and Bramble (1981) questioned the homology of some of these scales, particularly between

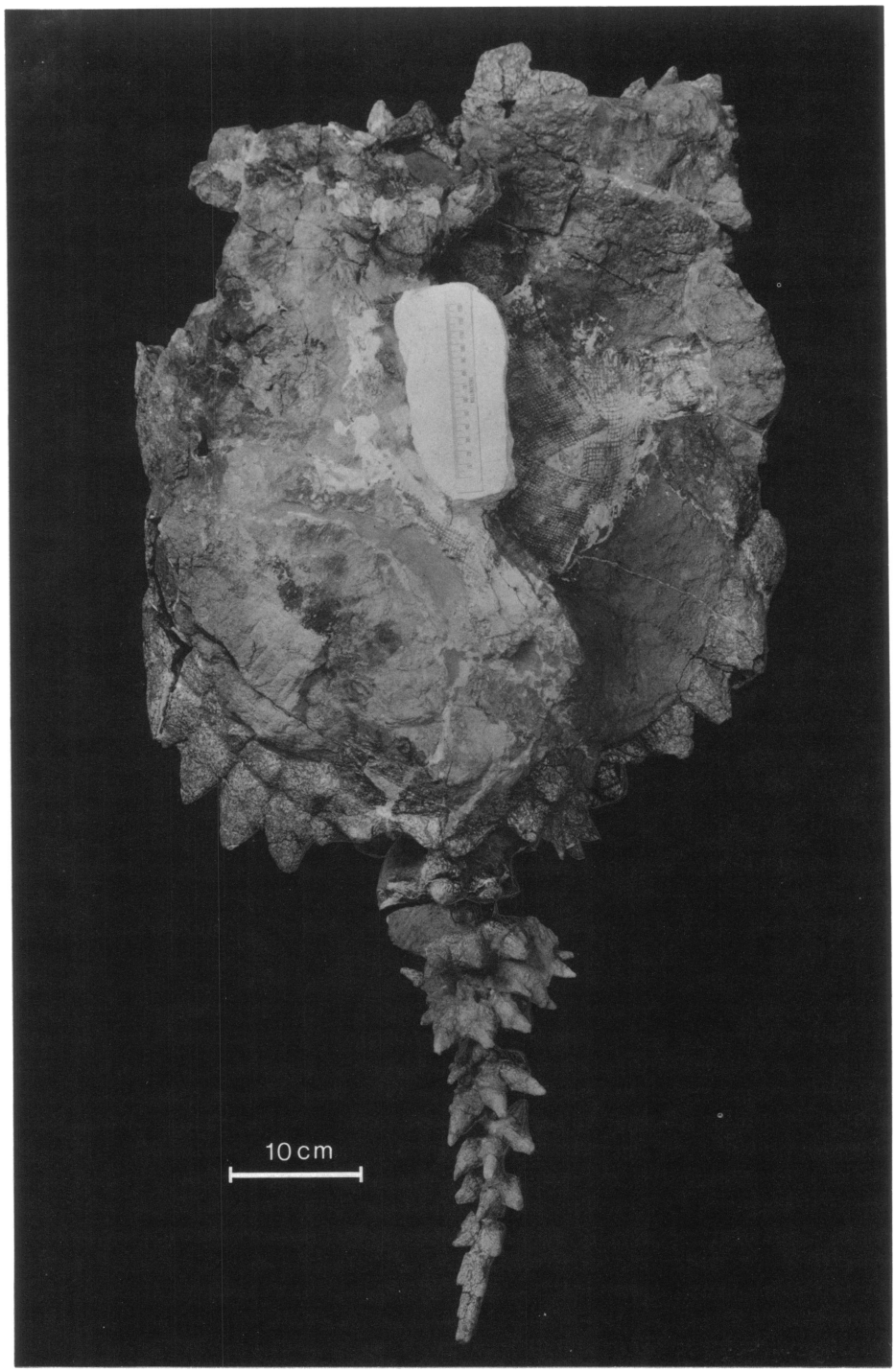

Fig. 85. *Proganochelys quenstedti,* SMNS 17204. Dorsal view of shell and associated elements.

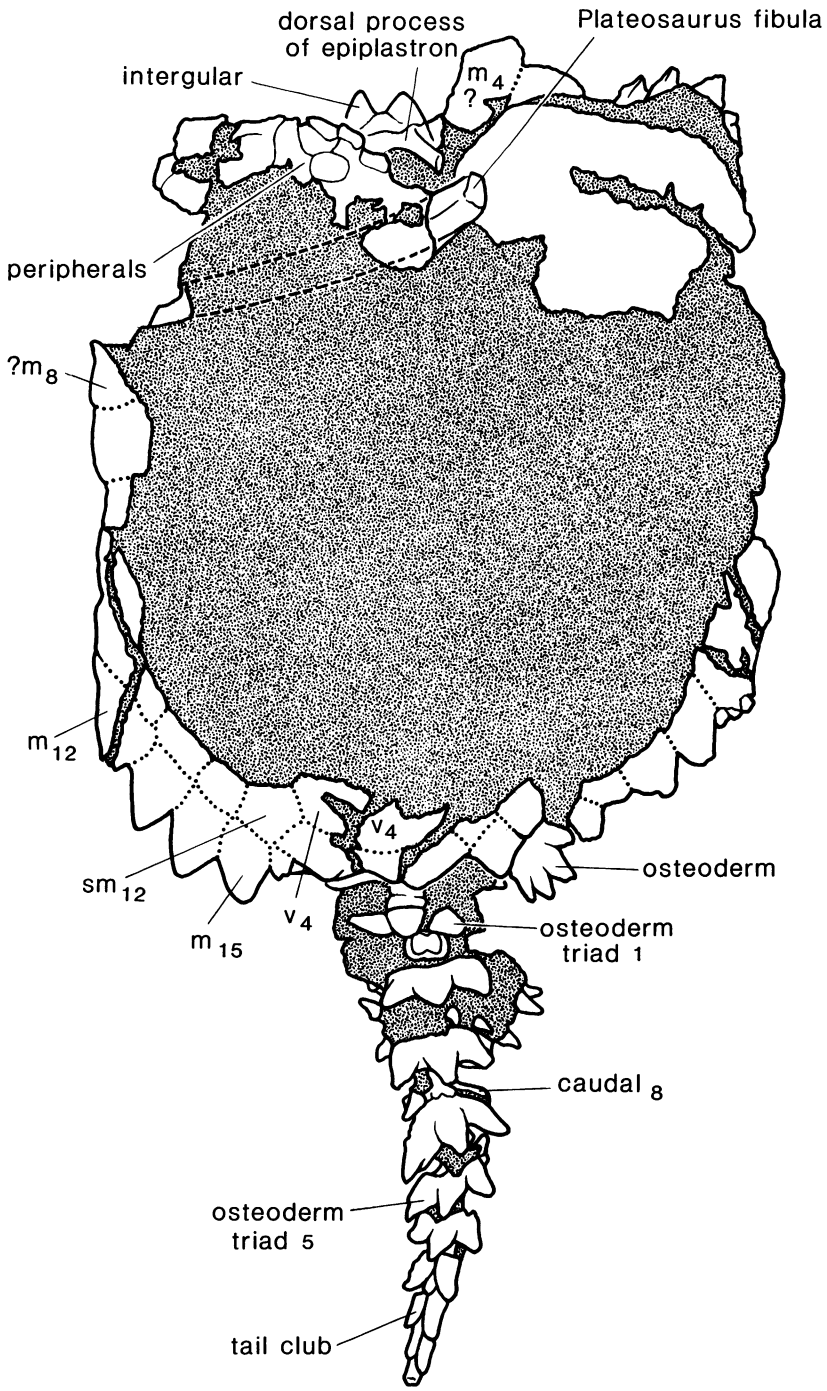

Fig. 86. *Proganochelys quenstedti,* SMNS 17204. Dorsal view of shell and associated elements. Abbreviations: **m,** marginal scute, **sm,** supramarginal scute; **v,** vertebral scute. See also Figure 97.

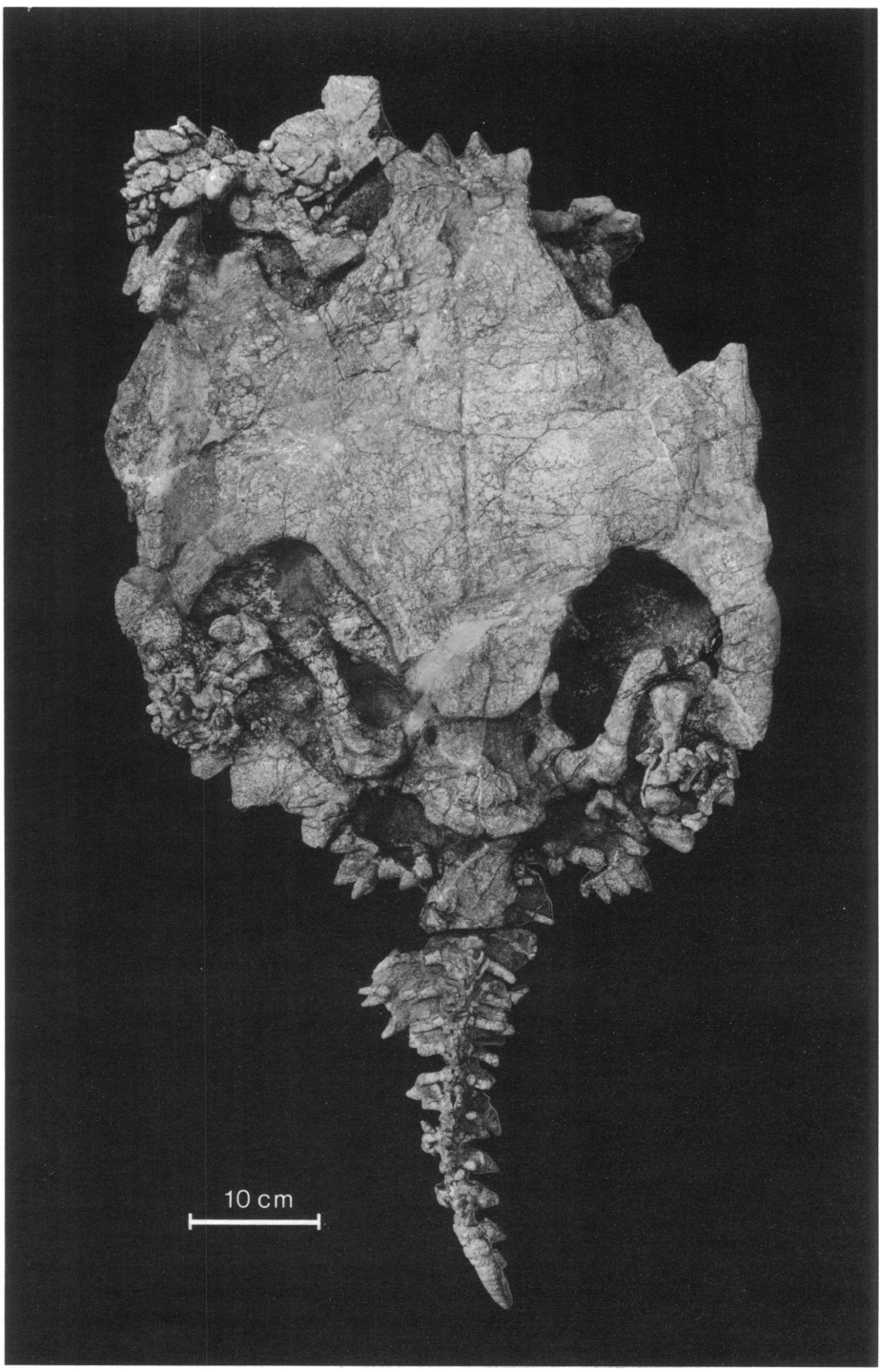

Fig. 87. *Proganochelys quenstedti,* SMNS 17204. Ventral view of shell and associated elements. From Gaffney (1985a).

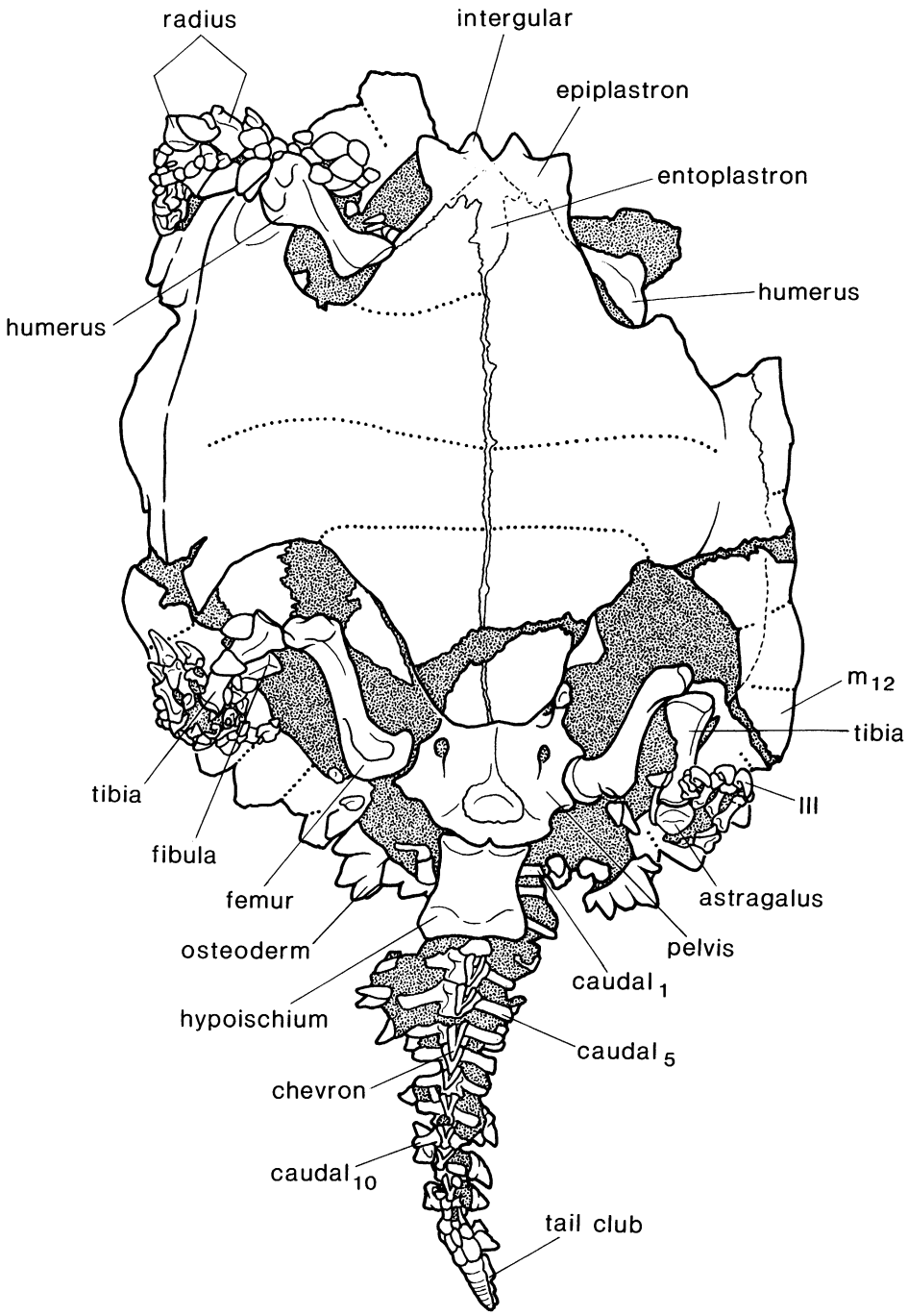

Fig. 88. *Proganochelys quenstedti,* SMNS 17204. Ventral view of shell and associated elements. Abbreviations: **m,** marginal scute; III, third digit of pes.

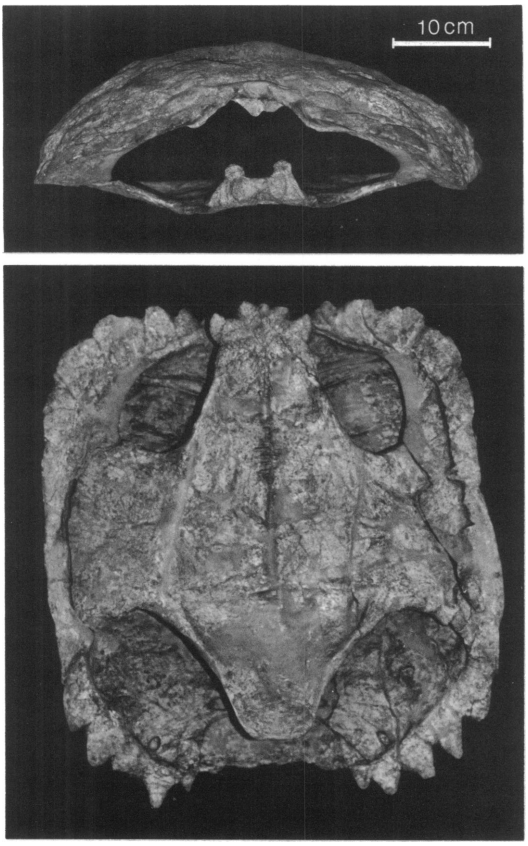

Fig. 89. *Proganochelys quenstedti,* SMNS 16980. Upper, anterior view of shell; lower, ventral view of shell.

certain trionychoids and other cryptodires. Some of their conclusions also affect the scale terminology of primitive turtles like *Proganochelys.* The scales in question are the two most anterior pairs, usually called intergulars and gulars, which Hutchinson and Bramble (ibid.) proposed to call gulars and extragulars, respectively. However, they use as their primary criteria "postulates" that rely on the recognition of general evolutionary trends and functional scenarios. These postulates seem to me too speculative to be the basis for homology arguments. I do agree with one of their conclusions: the conventional scheme of plastral terminology ". . . cannot be uncritically applied to all turtles" (Hutchinson and Bramble, 1981: 84). The homologies of the anterior scales in particular are unresolved and I agree that the identification of gular scales in primitive turtles does not mean that these are homologous with the gular scales of the testudinoids. On the other hand, I do not see the balance of evidence showing that the intergulars (in the conventional sense) of primitive turtles are the homologs of the gulars of testudinoids, which is also a conclusion of Hutchinson and Bramble (1981). Therefore, I use the conventional terms but restrict the homology to casichelydians which have seven pairs of plastral scales. I do not see convincing criteria for establishing the homology in cases where anterior plastral scales have been reduced in number.

Proganochelys has a pair of gular and intergular scutes that are formed into distinctive tuberosities. The scute areas are best seen in SMNS 16980 and SMNS 17204 but are also visible in SMNS 17203 and SMNS 15759. The intergular scutes are about the same size as the gulars but have smaller tuberosities. The intergulars completely separate the gular scutes and contact the humeral scutes on the midline. The intergular scutes meet for most of their length along the midline and extend from the epiplastra onto the entoplastron. They taper posteriorly and slightly separate the anterior portions of the humeral scutes. Between the intergular scutes at the very anterior margin of the plastron is a small, median tubercle that appears to represent a median scute. The position of the scute is somewhat dorsal to the axis of the other tubercles so that in SMNS 17204 (figs. 88, 97) it is not visible in ventral view because the end of it is broken off. The gular scutes cover tubercles or projections that are larger than those in the intergular area. These gular projections curve anteriorly in SMNS 16980 but are aligned on a straighter axis in SMNS 17204. The gular scute areas may extend to the margin of or onto the entoplastron but no specimen is sufficiently well preserved to determine the precise position of this scute with respect to the entoplastron. The intergular and gular projections are more acuminate in SMNS 17204 than in SMNS 16980. On the dorsal surface of the plastron these scute areas are marked by a low ridge and change in bone rugosity that seem to mark the body wall margin. The intergular and gular projections lie outside this ridge.

In SMNS 17203 (fig. 102) the epiplastron

preserved has no natural edges but agrees in general with the other specimens, and it is unlikely that much bone is missing. The axis of the gular projection is more lateral than in the other specimens and it is relatively much larger than the intergular projection, but it is difficult to determine whether or not that is original or a result of postmortem damage.

Gular and intergular projections developed to the extent seen in *Proganochelys* are not found in any other turtle that I am aware of. Some testudinids have even larger projections but these are formed by what may be nonhomologous scales. In the absence of a shelled outgroup, it is hard to determine whether or not the gular/intergular projections of *Proganochelys* are an autapomorphy of that genus or are plesiomorphic for turtles.

The dorsal processes of the epiplastra in *Proganochelys* are of considerable interest because they provide the first paleontological evidence testing the idea that the epiplastra are clavicles (fig. 137), a hypothesis that has been based primarily on developmental evidence and adult morphology of Recent turtles. The dorsal process is columnar, circular in cross section at its base, and arises abruptly from the horizontal part of the epiplastron. The base, particularly well preserved in SMNS 15759, is a rugose area tapering dorsally to the main part of the shaft. As preserved in SMNS 17204 (fig. 97), the two dorsal processes extend dorsally at a posterolateral angle, diverging from each other. This specimen is badly crushed in places and there are large fragments of what seems to be a *Plateosaurus* fibula in the anterior end of the shell, but the dorsal epiplastral processes are symmetrical as preserved and do agree with what is available from the other specimens. The dorsal limits of the processes are broken off and do not contact the carapace.

The dorsal process of the epiplastron in *Proganochelys* has a wide, dorsally expanded articulation to the carapace. The dorsal expansion is in the mediolateral plane and is curved slightly in cross section, concave posteriorly. The dorsal expansion is thicker on the medial edge at the base of the main stem of the process, and is thinner laterally where the expansion tapers off into an elongate process. In SMNS 16980 the dorsal expansion is much smaller than in the Berlin specimen and the lateral process barely exists. The Berlin dorsal process has a dorsally flattened surface for articulation with the carapace, which in SMNS 16980 is more vertical. The carapace articulation in the Berlin specimen appears to be a tight sutural contact along its anterior margin, but posteriorly the epiplastral process is separated off the carapace. This may be an artifact because in the Berlin specimen there does not seem to have been any potential movement between carapace and dorsal process. In SMNS 16980, however, the epiplastral process does not tightly articulate with the carapace. To some extent this appears to be the result of preservation and the removal of bone during preparation, but cartilage or connective tissue may have been prominent in the articulation.

The epiplastral process of *Proganochelys* is continuous laterally with the body wall ridge of the carapace and it would appear that the anterior surface of at least the dorsal portion of the process was only covered by skin. Posteriorly the dorsal process is slightly concave and forms the anterior wall of a pit, particularly well developed in the Berlin specimen, for the articulation of the dorsal process of the scapula. The concavity for the scapula continues ventrally along the posterior surface of the epiplastral process for about half its length. The stem of the dorsal process of the epiplastron is triangular to irregularly circular in the Berlin specimen and flattened mediolaterally in SMNS 16980.

A comparison of the epiplastron of *Proganochelys* with the clavicle (fig. 137) in generalized amniotes is in order here. Useful figures and descriptions of amniote clavicles can be found in Romer (1956) but the best figures and descriptions of a generalized form are in Holmes (1977). Holmes described *Captorhinus aguti,* which is singularly appropriate for comparison with *Proganochelys* because I have argued that it is a close relative of turtles (Gaffney and McKenna, 1979; Gaffney and Meylan, 1988); yet it has a clavicle that is of generalized amniote morphology. The generalized amniote clavicle is a roughly C-shaped element with a horizontal ventral plate comparable to, but not as distinct as, the chelonian epiplastron. There is a strong, posteromedial contact with the interclavicle, as is the case with the entoplastron in turtles.

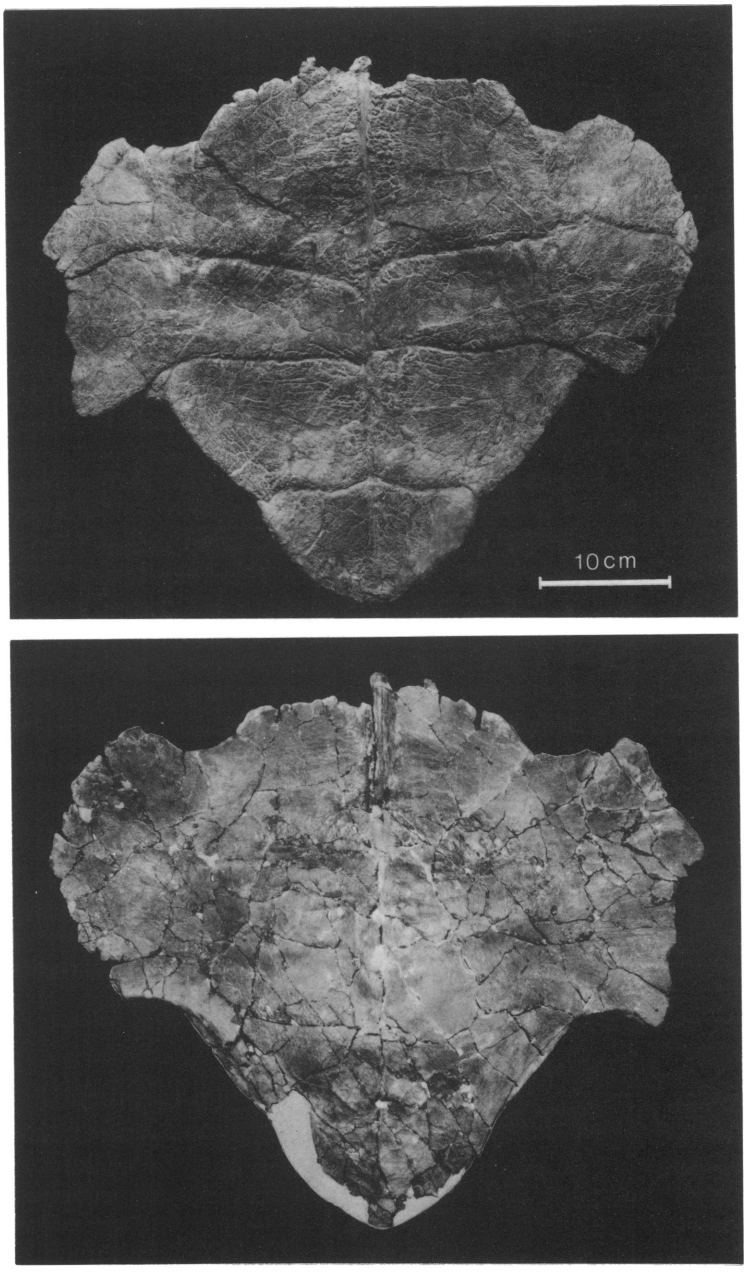

Fig. 90. *Proganochelys quenstedti,* MB 1910.45.2. Plastron. Upper, ventral view; lower, dorsal view.

The clavicles meet medially, anterior to the interclavicle, as do the epiplastra of most turtles. The dorsal process of the clavicle in *Captorhinus* is a flattened element curving dorsally in a broad arc rather than a columnar element extending abruptly from the horizontal epiplastron, as is the dorsal process in *Proganochelys.* A significant difference between turtles and generalized amniotes is the fact that the scapula-coracoid has a broad attachment to the posterior margin of the clavicle in other amniotes while in turtles the de novo hyoplastron attaches to the clavicle (= epiplastron) and the scapulacoracoid has

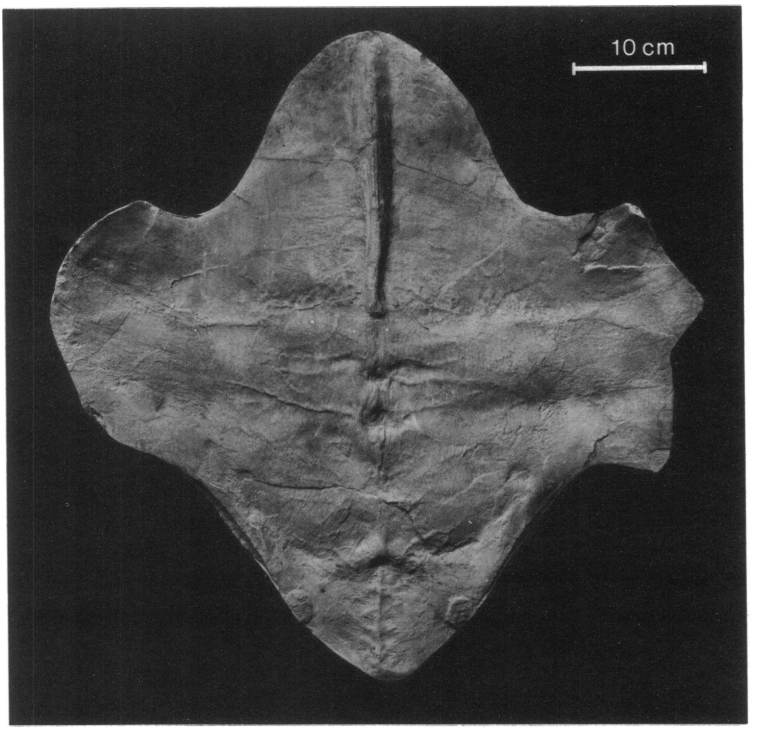

Fig. 91. *Proganochelys quenstedti,* MB 1910.45.2. Cast of dorsal surface of plastron showing surface morphology; anterior lobe largely fictitious.

a very reduced, but (usually) still persistent, contact with the clavicle (epiplastron). In generalized amniotes the dorsal process of the clavicle has an overlapping contact with the splintlike cleithrum, an element absent in captorhinids, *Proganochelys,* and all other turtles. It should be noted that Jaekel's (1918a) various reconstructions involving the epiplastra and entoplastra (repeated in Romer, 1956: fig. 144) are erroneous, as the Berlin specimen lacks epiplastra and has only a portion of the stem of the entoplastron preserved.

Entoplastron

The entoplastron of *Proganochelys* is preserved in SMNS 16980, SMNS 17204, and a portion of the stem in the Berlin specimen. While the bone is absent in SMNS 17203, the epiplastron and hyoplastron that are present provide some information on the shape of the missing entoplastron.

The entoplastron of *Proganochelys* as seen in dorsal view is a large, arrow-shaped element, with relatively long posterolateral extensions that nearly reach the margin of the plastron and a long median process that extends posteriorly along the midline to reach or nearly reach the mesoplastra. Anteriorly the entoplastral limits are difficult to make out but the epiplastral-entoplastral suture can be seen on the left side on both the dorsal and ventral surfaces of SMNS 16980. The entoplastron extends anteriorly to separate the epiplastra for nearly their entire length, and a median scale tubercle (lying between the intergulars) is probably formed by the entoplastron (contrary to the statement in Gaffney, 1985a: 20). The anterior margin of the entoplastron is straight on each side of the midline. The posterior margin contacts the hyoplastra and the lateral processes separate them from the epiplastra nearly to the edge of the plastron dorsally but for a shorter distance on the ventral surface. The entoplastron is raised above the internal surface of the hyoplastron but it is at about the same

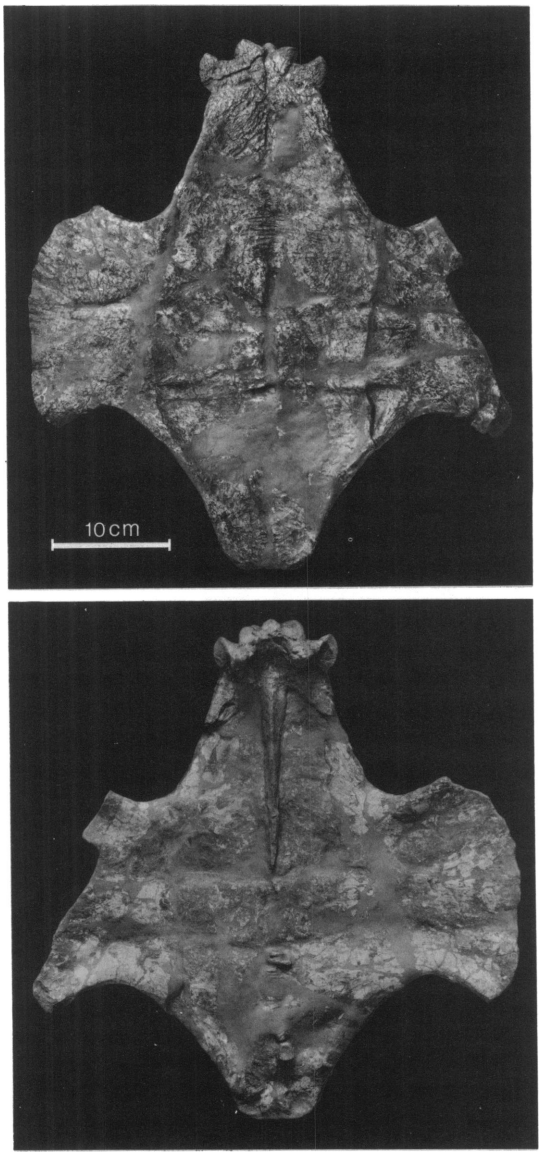

Fig. 92. *Proganochelys quenstedti,* SMNS 16980. Upper, ventral view; lower, dorsal view. Abbreviations: **AB,** abdominal scute; **AN,** anal scute; **ent,** entoplastron; **epi,** epiplastron; **FE,** femoral scute; **GU,** gular scute; **hyo,** hyoplastron; **hypo,** hypoplastron; **HU,** humeral scute; **IN,** intergular scute; **meso,** mesoplastron; **PE,** pectoral scute; **Pub. art.,** articulation of lateral pubic process.

level as the epiplastra. The ventral surface is comparatively flat with no differentiation of elements, other than the poorly discernible sutures.

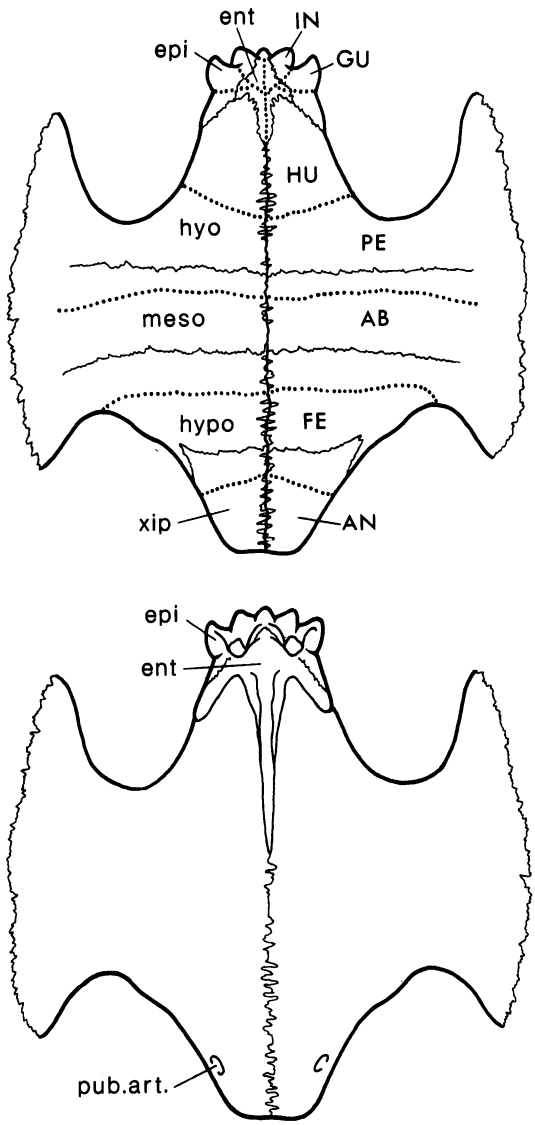

Fig. 92. Continued.

The posterior median process or stem of the entoplastron is triangular in cross section with a low ridge on its dorsal surface. It overlaps most of the median hyoplastral suture and only a short portion of the stem is exposed ventrally. Entoplastral-hyoplastral sutures are not entirely clear but SMNS 16980 and SMNS 17204 show that there is an interfingering contact between the two bones on the ventral surface. This contact results in a roughly arrow-shaped exposure of the en-

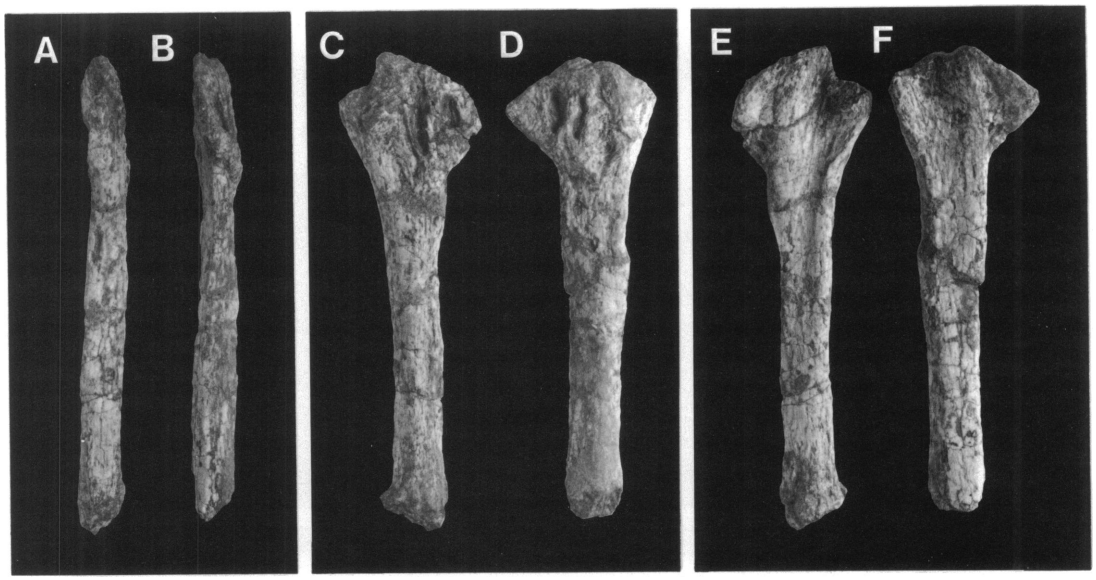

Fig. 93. *Proganochelys quenstedti,* SMNS 16980. Dorsal processes of epiplastra ("cleithra"). **A,** left process in medial view; **B,** right process in lateral view; **C,** left process in anterior view; **D,** right process in anterior view; **E,** left process in posterior view; **F,** right process in posterior view. Rugose surfaces visible in C and D attach to carapace.

toplastron on the ventral surface, similar in shape but smaller in size to the exposure of that bone on the dorsal surface.

The entoplastron of *Proganochelys* is quite similar to that bone in other turtles (e.g., *Chelydra*) except in size; it is relatively larger than any other turtle entoplastron. This would appear to be primitive for turtles because generalized amniotes have relatively larger interclavicles. The arrow-shaped interclavicle seems to be a derived condition for turtles; primitive amniotes have interclavicles that are expanded anteriorly but generally lack the posterolateral processes seen in *Proganochelys* and other turtles. The posterior process or stem of generalized amniotes is relatively shorter than in *Proganochelys* and *Proterochersis* and this may be a synapomorphy of turtles.

Hyoplastron

The hyoplastron is preserved in SMNS 16980, SMNS 17203, SMNS 17204, and the Berlin specimen. The anterior contact is with the entoplastron and epiplastron (described above) and can be seen in SMNS 16980 and SMNS 17204, but the posterior contact with the mesoplastron can be seen clearly only in the juvenile SMNS 17203 (fig. 102).

The hyoplastron of *Proganochelys* is similar to that in other turtles, a large element forming the axillary notch and buttress, and most of the anterior plastral lobe. The hyoplastron forms the axillary notch and buttress by curving dorsally and anteriorly from the flat ventral plate toward the bridge peripherals of the carapace. In contrast to some turtles, such as baenids, *Proganochelys* lacks well-developed plastral buttresses, the hyoplastron curving anteriorly to the level of the anterior edge of the plastron but not above the plane of the peripherals. The buttresses do not curve medially to overlap the vertical plane of the plastron as in many turtles. The posterior contact of the hyoplastron is with the mesoplastron, described below.

Mesoplastron

Proganochelys has one pair of mesoplastra readily seen in SMNS 17203 (fig. 102). In this specimen the left mesoplastron contacts the posterior margin of the hyoplastron in a su-

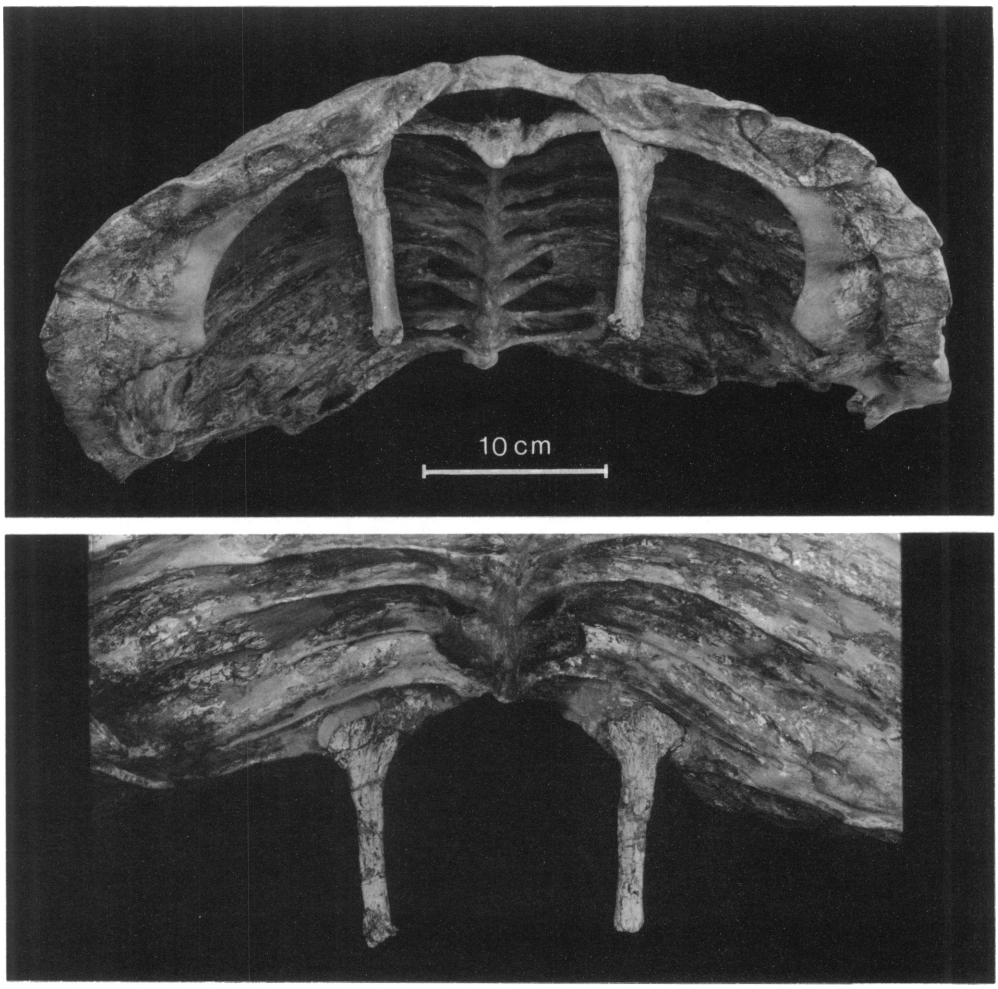

Fig. 94. *Proganochelys quenstedti,* SMNS 16980. Upper, anterior view; lower, posterior view. Dorsal processes of epiplastra articulated with carapace. Processes should angle ventromedially rather than hang straight. See Figure 96.

ture that is transverse medially and curves anterolaterally. The only other hyoplastral-mesoplastral sutures preserved are short segments in SMNS 16980. The sutures in SMNS 16980 agree with SMNS 17203. Apparently the mesoplastron expands laterally to contact the bridge peripherals. The mesoplastron of SMNS 17203 has finely feathered bone processes extending out from its margins forming a small medial fontanelle between hyoplastra and mesoplastra and a larger one between mesoplastra and hypoplastra. All these fontanelles are presumably due to the immaturity of SMNS 17203; the other specimens of *Proganochelys* lack them. However, the dorsal surface of the Berlin plastron has two foramina now filled with plaster that lie in the midline in about the presumed position of the hyoplastra-mesoplastra and mesoplastra-hypoplastra junctions and it is possible that these foramina are remnants of the fontanelles. SMNS 16980 shows strong interdigitating sutures all along the midline without foramina or fontanelles.

All three bridge elements of the plastron, hyoplastron, mesoplastron, and hypoplas-

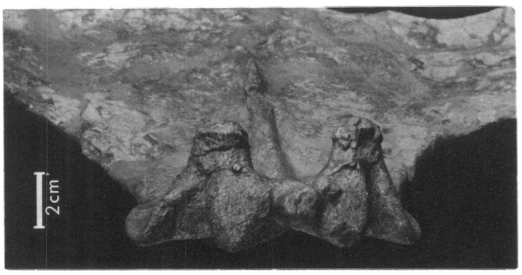

Fig. 95. *Proganochelys quenstedti,* SMNS 16980. Anterior view of plastron showing broken bases of dorsal processes.

tron combine to form a low, lateral ridge that marks the change from the flat, horizontal main plate of the plastron to the dorsolaterally curving bridge.

Hypoplastron

The hypoplastron is preserved in SMNS 16980, SMNS 17203, SMNS 17204, and the Berlin specimen, but sutures are only visible in SMNS 17203, and for short segments in SMNS 16980.

The hypoplastron of *Proganochelys* agrees with that of other turtles; it forms the inguinal notch, the inguinal buttress, and a major part of the posterior plastral lobe. The inguinal notch is larger than the axillary notch but the inguinal buttress is smaller than the axillary buttress; there is less bone curving around the inguinal notch to contact the bridge peripherals there than in the axillary notch. In SMNS 17203 there is a median fontanelle between mesoplastron and hypoplastron that presumably is due to the juvenile nature of this specimen (see above). In contrast to the finely feathered median margin of the hyoplastron in SMNS 17203, the hypoplastron of this specimen has at least five median processes (on the left hypoplastron) that extend across the midline and presumably interfinger in the adult. SMNS 16980 has segments of this sutural area preserved and they are strongly interfingered on the midline with no vacuities remaining. The hypoplastron tapers posteriorly at a strong angle, more so than the anterior lobe of the plastron, to the region where it meets the xiphiplastron. The sutures with the xiphiplastron are best seen in SMNS

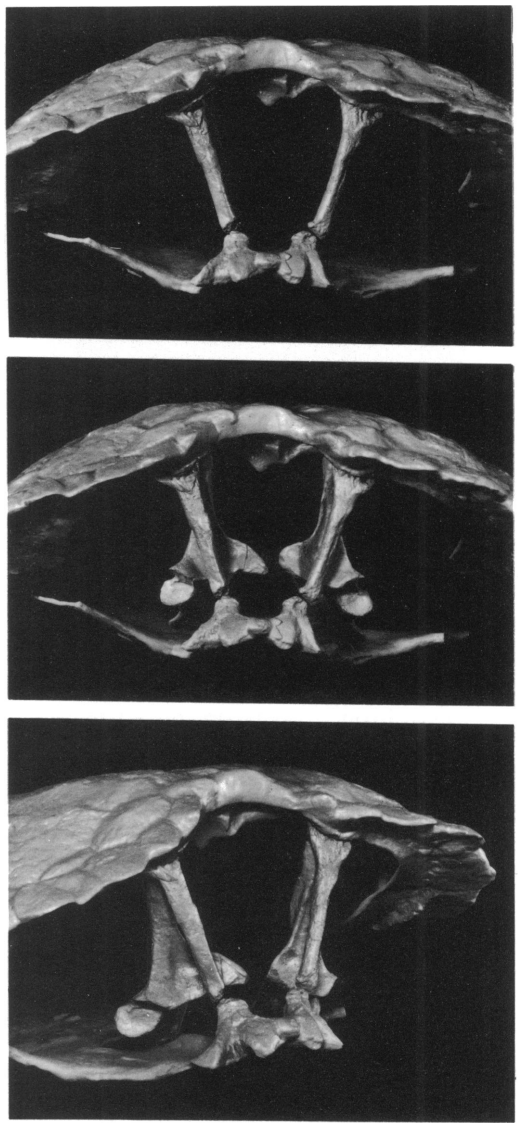

Fig. 96. *Proganochelys quenstedti,* SMNS 16980. Cast of shell showing relative positions of dorsal processes of epiplastra and scapulae. Upper, anterior view of shell with dorsal processes of epiplastra in life position (broken at base). Middle, anterior view of shell with scapulae added behind epiplastra. Lower, anterolateral view of shell with dorsal processes of epiplastra and scapulae. See also Figures 93, 94, 97.

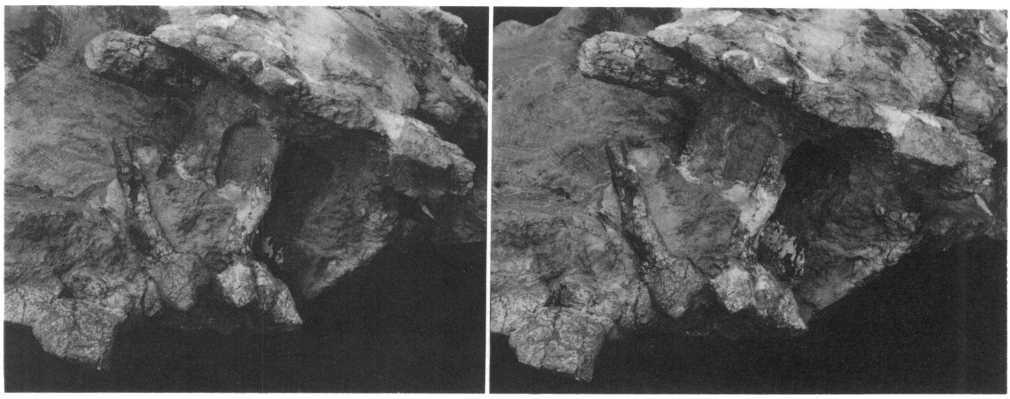

Fig. 97. *Proganochelys quenstedti,* SMNS 17204. Anterior end of shell in anterior view. See Figures 86, 96.

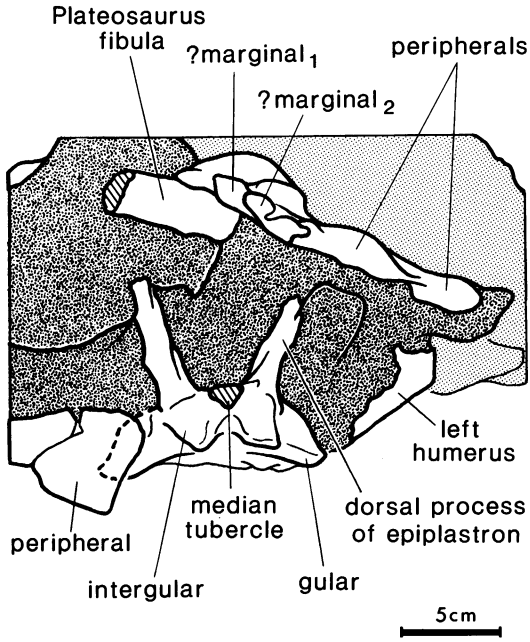

Fig. 97. Continued.

17203 but can also be interpreted in the Berlin specimen and are described below.

Xiphiplastron

The xiphiplastron is preserved in the following specimens: SMNS 17204, ventral surface only is visible and sutures are not apparent; SMNS 17203, ventral surface only is visible and sutures are clearly seen; SMNS 16980, both surfaces visible and sutures are not apparent; and the Berlin specimen, both surfaces visible with a probable suture visible on the dorsal surface. The suture seen in SMNS 17203 is finely interfingering with the hypoplastron, begins medially and extends transversely to a point near the margin of the plastron where it produces a sharp, anterior process fitting into a notch in the hypoplastron, before terminating at the edge of the plastron. This process of the xiphiplastron and notch in the hypoplastron is found in most other turtles and can be considered primitive for turtles. On the dorsal surface of the Berlin specimen a similar sutural pattern is expressed as a groove and shows the xiphiplastral process fitting into the hypoplastron.

The xiphiplastron of *Proganochelys* is relatively small and has sides that are more parallel than the hypoplastron, resulting in a posterior plastral lobe with two regions. As restored, the Berlin specimen appears to have a posterior lobe in which the xiphiplastra continue at the same tapering angle as the hypoplastra to produce a xiphiplastral termination that is more acuminate than in the other specimens. However, a close examination of this plastron reveals that only the midline margin and a segment along the right edge of the xiphiplastron containing the pubic articulation are actually bone; the remaining xiphiplastral margin is restored and the evidence for an acuminate margin is lacking.

The dorsal surface of the xiphiplastron has a facet for the nonsutural articulation of the lateral pubic process. This facet is visible on

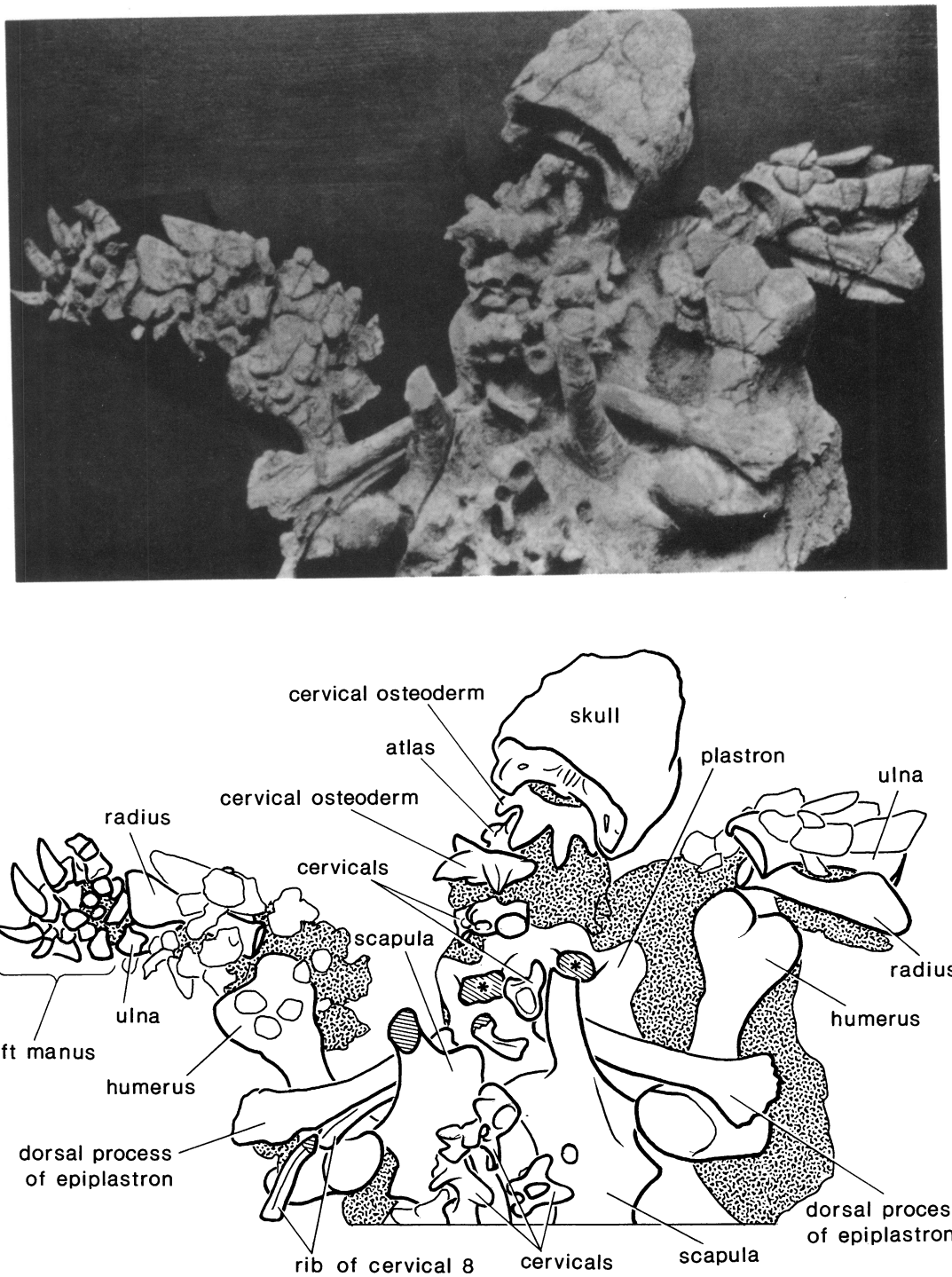

Fig. 98. *Proganochelys quenstedti,* SMNS 16980. Upper, photograph from Berckhemer (1938) showing anterior portion of specimen without carapace during preparation; lower, identification of elements in Berckhemer figure based on comparison of specimen with photograph. Asterisks (*) show the broken bases of the dorsal processes of the epiplastra. The specimen was subsequently disarticulated.

the right side of the Berlin specimen, where it is a slightly raised oval, and on both xiphiplastra of SMNS 16980, where it is a shallow concavity in a thickened portion of the xiphiplastron. Although Recent turtles generally lack definitive pubic facets, they also occur in *Kayentachelys,* baenids, *Glyptops, Meiolania,* and other extinct taxa.

Plastral Scutes

Unfortunately, the entire plastral scute system is not preserved in any one *Proganochelys* specimen, and the restored pattern (fig. 92) is based on combining information from nearly all the plastra. The Berlin specimen has the best preserved sulci and external surface texture but most of the anterior lobe is missing in this specimen. None of the specimens show scute marking in the plastral bridge area where inframarginals, axillary and inguinal scutes would be expected. This appears to be due to poor preservation in these areas rather than the absence of such scutes.

The large paired intergular scutes separate the gulars and contact the humerals on the entoplastron. The prominent tubercles formed by the intergulars and gulars are described under the Epiplastron, the element bearing most of these scutes. A small, median tubercle is formed by its own scute.

The humeral scutes are slightly separated along the midline at their anterior margin by the intergulars. The humeral scute extends from about the posterior third of the epiplastron to about the middle of the hyoplastron where it meets the pectoral. The resulting sulcus is visible in SMNS 16980 where it angles anterolaterally to a slight extent. SMNS 17204 has a series of grooves in this area, unfortunately not symmetrical, that may be dubiously interpreted as the humeral-pectoral sulcus. The Berlin specimen lacks much of the anterior plastral lobe and, in comparison with SMNS 16980, the break would seem to be just anterior to the humeral-pectoral sulcus, but the Berlin specimen has no sign of that sulcus. Because the Berlin specimen has such well preserved sulci, I conclude the humeral-pectoral sulcus was anterior to the break which would put it distinctly anterior to its position in SMNS 16980. This could be of systematic significance but, in view of the incomplete nature of the Berlin specimen, the presence of this feature must remain dubious. In overall position, extent, and relation to underlying bones, the humeral scute of *Proganochelys* does not significantly differ from that in most other turtles. The position of the humeral-pectoral sulcus is somewhat more anterior in *Proganochelys* than in many other turtles but not uniquely so.

The pectoral scute of *Proganochelys* covers the posterior portion of the hypoplastron and extends onto the mesoplastron. The hyoplastral-mesoplastral sulcus can be seen best in the Berlin specimen but it is also preserved in SMNS 16980 and SMNS 17204. In these specimens the sulcus runs transversely across the mesoplastron to the area where the plastral bridge begins to curve dorsally where the sulcus has a shallow bend to curve slightly posterolaterally. The abdominal scute is narrower than the pectoral scute and covers the posterior part of the mesoplastron extending posteriorly onto the hypoplastron. In contrast to the humeral-pectoral sulcus, the abdominal-femoral sulcus in *Proganochelys* stretches across the base of the posterior lobe as in most turtles rather than being placed farther out on the lobe.

The femoral scute covers the hypoplastron posteriorly and extends onto the xiphiplastron. The femoral-anal sulcus is clearly defined only in the Berlin specimen; the area is not well preserved in the other specimens. The sulcus is transverse with a slight posterolateral trend. The anal scute covers the remaining portion of the xiphiplastron.

The plastral scutes are all paired (again, with the possible exception of the median tubercle discussed above), and meet at a median sulcus best seen in the Berlin specimen but with segments preserved in SMNS 16980 and SMNS 17204. This sulcus is relatively straight and does not have the sinuous pattern seen in some turtles.

The plastral scute pattern in *Proganochelys* does not present a significant departure from that seen in such presumably generalized turtles as *Kayentachelys, Glyptops,* and *Pleurosternon.* The small, median tubercle on the anterior lobe may represent a scute and, if so, would be a departure from this pattern. *Proterochersis* does differ from the "normal" pattern of seven scute pairs, as seen in *Proganochelys* and *Kayentachelys.*

Proterochersis has extra scute pairs be-

TABLE 11
Measurements (in centimeters) of *Proganochelys* Shells

	MB 1910.45.2	SMNS 16980	SMNS 17203	SMNS 17204	SMNS 10012	SMNS 15759
Midline carapace length	53.5	48.5	40.0*	51.0 +?	60.0	59.0*
Maximum carapace length	67.0	56.0	45.0*	—	—	62.0*
Maximum carapace width	—	51.0	51.0–53.0	53.0	54.0*	—
Midline plastron length	—	48.0	41.5	46.5	—	—

* Estimated.

tween the pectorals and abdominals (possibly related to the second pair of mesoplastra) at the end of the anal, and a single scute separating the latter pair. Whether these are synapomorphic for pleurodires, for all turtles, or a *Proterochersis* autapomorphy cannot be determined at present. The presence in *Proganochelys* of paired intergulars completely separating the gulars and partially separating the humerals is further evidence that this homology is primitive for turtles.

The surface texture of the plastron in *Proganochelys* is well preserved only in the Berlin specimen. In this shell, the plastral texture can be seen to differ from the carapacial texture in lacking the circular and radial ridging seen in many of the carapace scutes. There is a system of fine grooves, randomly branching, that produce a pattern of low relief on the plastron. These grooves tend to spread out from a few centers and in some areas parallel the plastral margins and/or the scute margins.

DESCRIPTION OF SMNS 17203 (figs. 99–103)

This specimen of *Proganochelys* is so different in morphology and preservation from the other specimens of this taxon that it merits independent description. I interpret the morphologic differences as due to growth; SMNS 17203 seems to be a younger individual than the other *Proganochelys* specimens based on:

1. Smaller size—it is the smallest known *Proganochelys* specimen (table 11);
2. nearly all preserved sutures are open;
3. morphology of elements is what would be expected in a juvenile *Proganochelys* if extrapolated from Recent turtle development.

Nonetheless, it is possible, but very unlikely, that SMNS 17203 is a different taxon, considering the very small sample of specimens available on which to test a growth-stage hypothesis.

The preservation of SMNS 17203 is similar to the other two Trossingen *Proganochelys*; there is more crushing and the bone is often broken into minute fragments, making interpretation difficult. SMNS 17203 consists of about ¾ of the carapace and plastron with some articulated limb elements and a number of disarticulated bones, presumably removed during preparation. Due to the absence of specimen numbers and the mixing together of elements belonging to SMNS 16980 and SMNS 17203, the identification of these loose bones as to individual is based on size and fit with adjacent elements. As shall be seen, this problem affects description of the shell of SMNS 17203 because there are some loose bone nodules and plates that probably represent peripherals or other elements that can no longer be identified with certainty. The carapace and plastron of SMNS 17203 are crushed dorsoventrally so that the original curvature is lost. Some elements, like the left shoulder girdle, penetrate through the carapace surface while others, like the pelvis, have been displaced in a horizontal plane. The right anterior quadrant of the shell, consisting of right costals 1–4, right hyoplastron and mesoplastron, and associated peripherals, is missing. As would be expected in a juvenile turtle, the peripherals were only loosely connected to the rest of the shell although some were apparently disarticulated during preparation (see below).

Beginning with the anterior of the carapace, there is no sign of a nuchal bone, although the curvature of the preserved peripherals and the position of the plastral

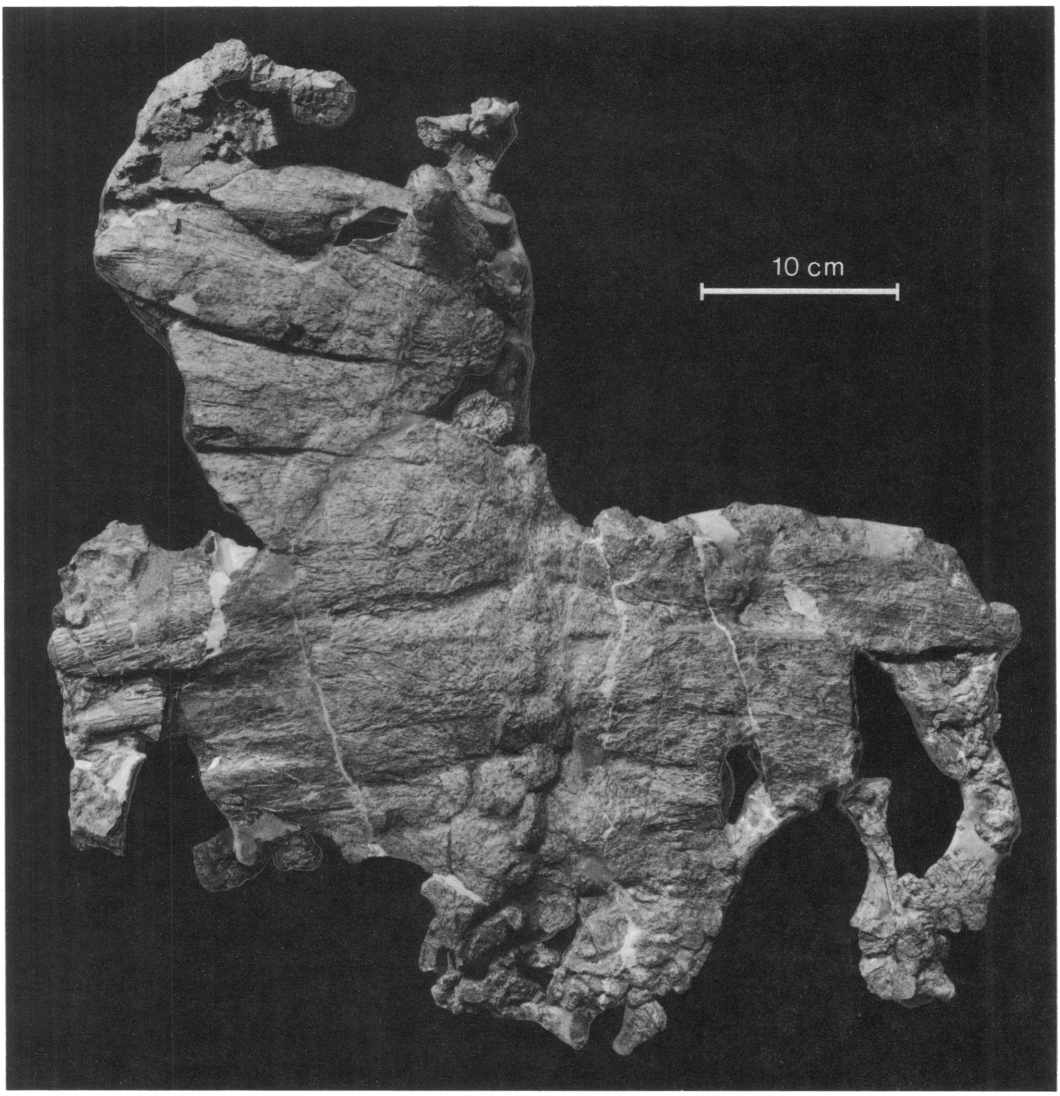

Fig. 99. *Proganochelys quenstedti,* SMNS 17203. Dorsal view of shell and associated elements.

elements indicate that there was room for one. Presumably it is missing rather than absent, or unossified in SMNS 17203. The left first costal, although incomplete, is identifiable. The medial edge of this costal is gone but the lateral edge shows a tapering margin that ends in what appears to be the distal shaft of the first costal rib. The ventral side of this costal is mostly covered with matrix but enough has been prepared to show the rib of the first thoracic vertebra, a rib that extends the length of the first costal in *Proganochelys* and precedes the first costal rib (which is the second thoracic rib). The posterior edge of the first costal overlaps part of the anterior edge of the second costal, due to postmortem displacement.

The second costal is distinctly larger than the first costal even though its medial and lateral limits do not seem to be natural edges. As preserved, it would appear to be about one-third larger than the first costal. The second costal shows some tapering laterally but the posterolateral edge is broken and the ta-

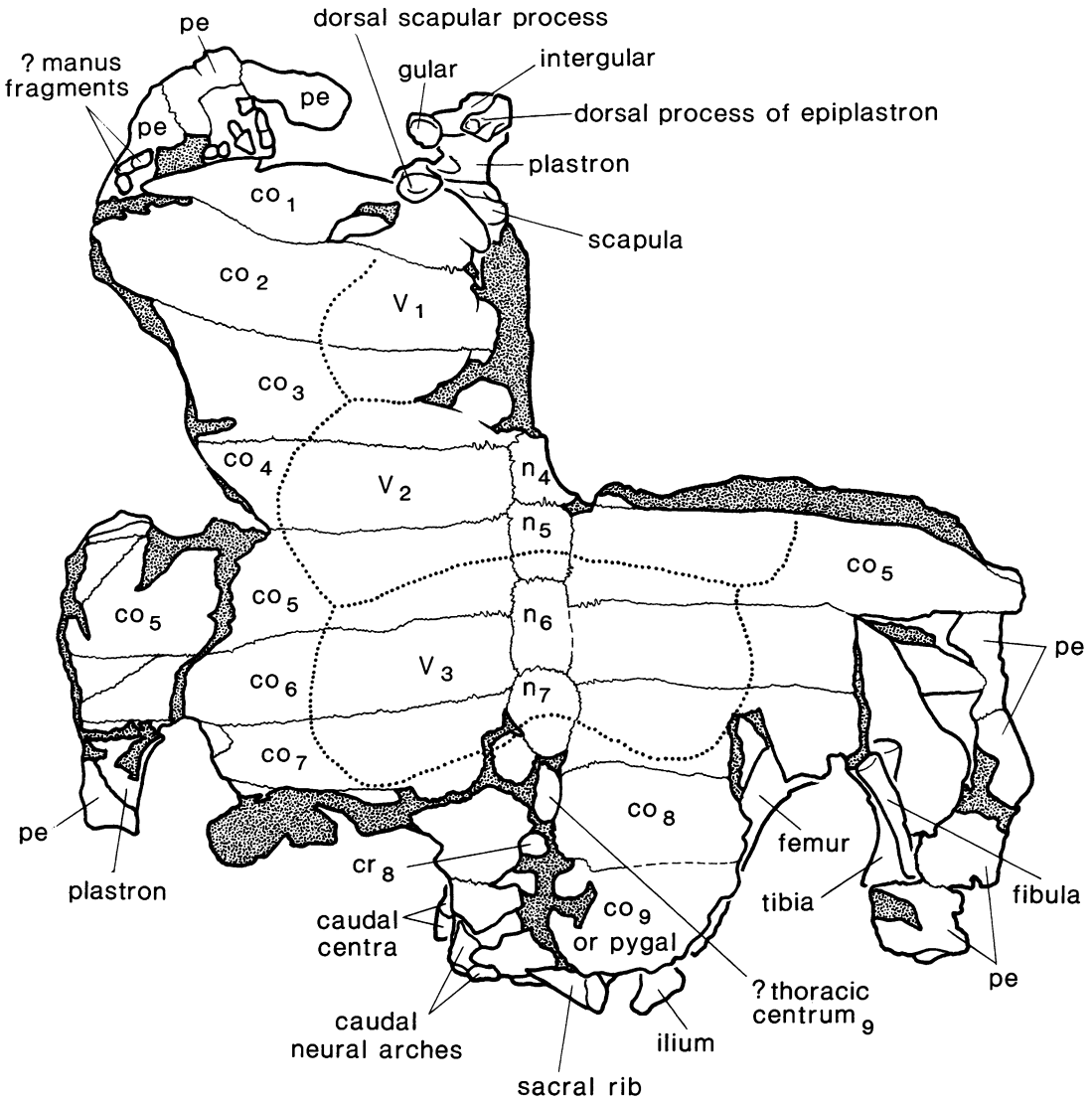

Fig. 100. *Proganochelys quenstedti,* SMNS 17203. Dorsal view of shell and associated elements. Abbreviations: **co,** costal bone; **cr,** costal rib; **n,** neural bone; **pe,** peripheral bone; **V,** vertebral scute.

pering may only be preservational. Both third and fourth costals are missing one-third or more of their lateral regions. When compared with presumed adult shells and with the preserved edges of SMNS 17203, costals 3 and 4 look as if they should be the largest of the costals. These two costals have a medial contact with the neurals which suggests that the more anterior costals are not missing much bone medially, even though their natural limits are not preserved.

Costals 5–8 are present on both sides and have their medial margins preserved. Costal 5 has anterior and posterior margins that are transverse to the midline and nearly parallel. The more anterior costals have margins that tend to trend more anterolaterally while more posterior costals tend to trend more posterolaterally. Right costal 5 has a tapering margin laterally where in other turtles it would be expected to insert into a peripheral. Portions of peripherals are preserved on both sides of

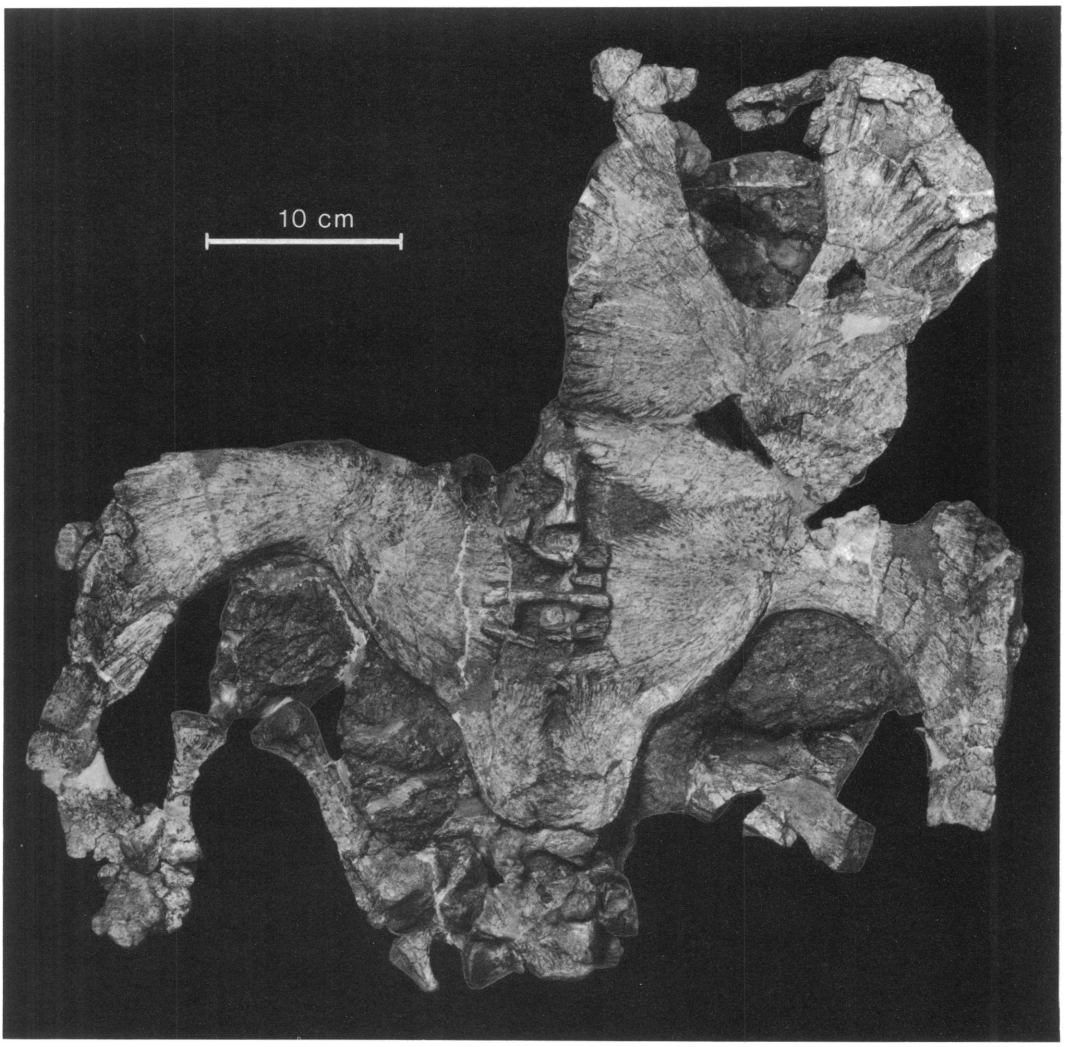

Fig. 101. *Proganochelys quenstedti,* SMNS 17203. Ventral view of shell and associated elements.

SMNS 17203 but they underlie the costals which actually protrude lateral to the peripherals. I think that this condition has been caused by the flattening of an arched carapace which has pushed the costal ends beyond the original margin of the shell and turned the peripherals ventrally. Both lateral ends of costal 6 are preserved although the one on the right is separated from the main body of costal 6 by a missing section of shell. Costal 7 is incomplete on both sides but part of the tapering lateral margin is visible on the left one, and the absence of costal bone on the peripherals lying lateral to both costals indicates that costal 7 was relatively short. The posterior margin of left costal 7 is broken and part of its medial margin has been broken and displaced slightly. The right seventh costal is broken in a number of places and its posterior margin is not well preserved.

The medial portions of costal 8 are present on both sides with what appears to be a small eighth neural or portion of a thoracic neural spine or centrum lying between. As preserved, the eighth costals are very short but both have broken lateral limits, and their original size is unknown. However, the absence of costal bone in matrix on the left side

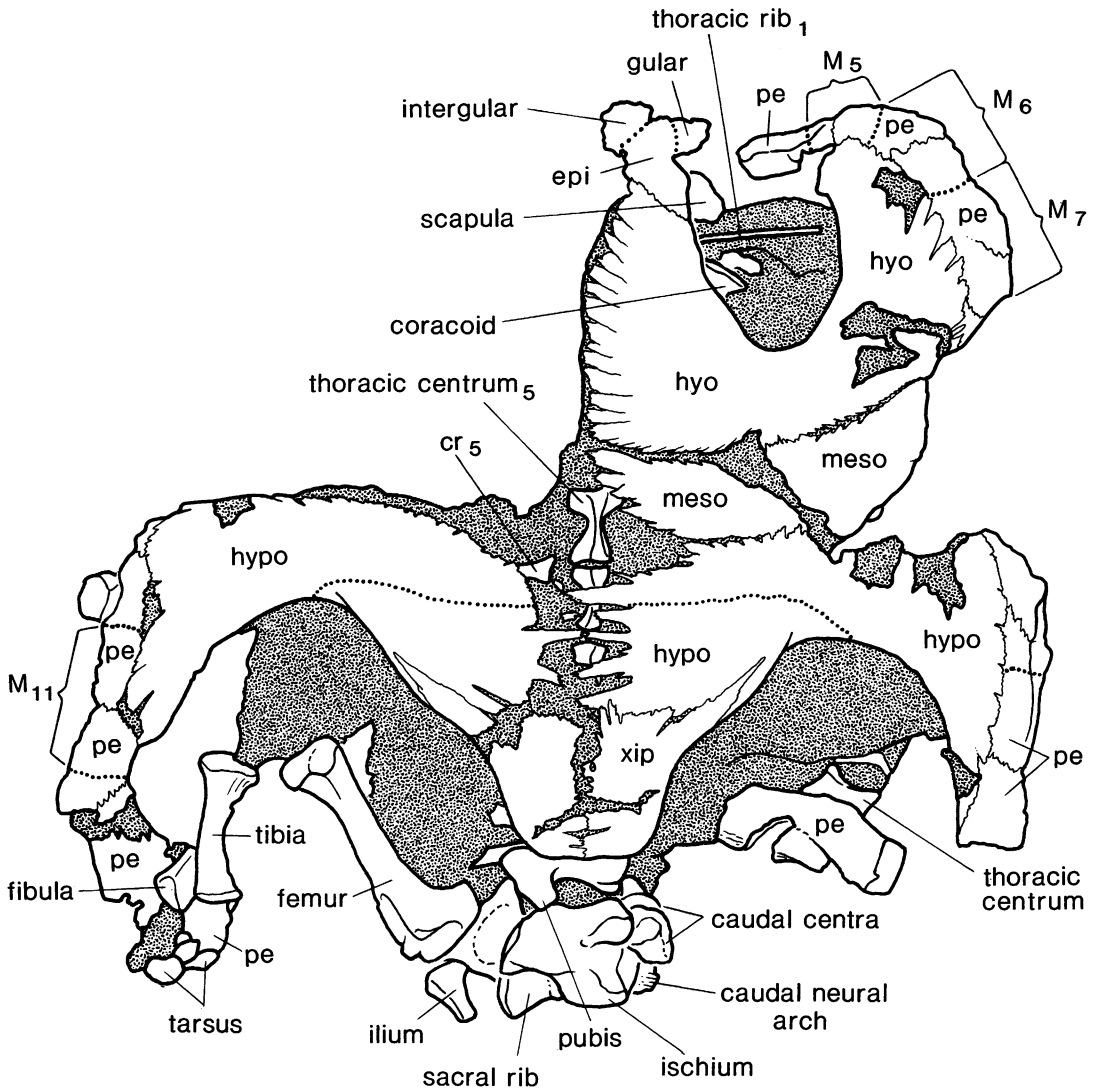

Fig. 102. *Proganochelys quenstedti,* SMNS 17203. Ventral view of shell and associated elements. Abbreviations: **cr,** costal rib; **epi,** epiplastron, **hyo,** hyoplastron; **hypo,** hypoplastron; **M,** marginal scute; **meso,** mesoplastron; **pe,** peripheral bone; **xip,** xiphiplastron.

and the sharp decrease in size of other posterior costals suggest that only small portions of the eighth costals are missing.

Proganochelys is unique among turtles in having a ninth costal element. All other turtles have a ninth "costal" vertebra (or, more properly, the 10th thoracic) that has a rib usually articulating with the eighth costal but not forming a costal of its own (except as an individual variation; I have seen *Chelydra* specimens with a separate ninth costal lying ventral to the eighth costal but not expressed dorsally). In SMNS 17203 there is what appears to be a poorly preserved ninth costal on the right side and a disarticulated left ninth costal. The disarticulated costal is about half rib shaft with the costal plate making up the distal half. The distal limits are not entirely clear but it would seem that not much of the bone is missing. Due to the crushed nature of the posterior part of the shell in SMNS 17203 and the absence of clear sutures in

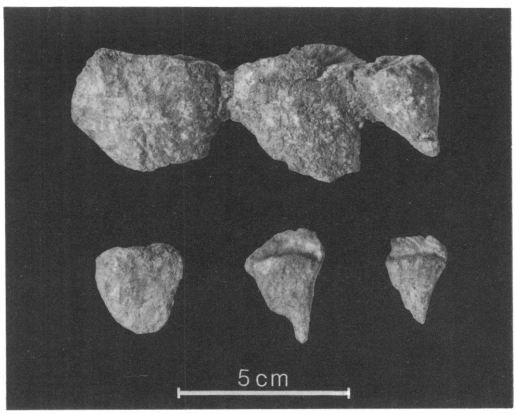

Fig. 103. *Proganochelys quenstedti.* Upper row, three posterior peripherals, probably bearing left marginals 14–16 of SMNS 17203. Lower row, possible peripherals or osteoderms, could belong to SMNS 16980, 17203, or 17204.

other *Proganochelys* specimens, there is a possibility that costal 9 is not expressed on the dorsal surface of the carapace, being covered by the eighth costal. I do not think that is likely because I detect a suture between the proximal portions of costals 8 and 9 on the right side of SMNS 17203 and there is a clear suture on the ventral surface of SMNS 16980.

The posterior carapace bone (i.e., pygal and suprapygal) of *Proganochelys* remains a mystery. The area posterior to the eighth costal in SMNS 17203 is a mush of bone and matrix with no sign of the carapacial margin. The presence or absence of pygal and/or suprapygal cannot be determined. The recognizable elements in this area in SMNS 17203 are portions of the right pelvis, a sacral rib, and a caudal neural arch and centra. It is possible that some of the bone posterior to costal 8 is the pygal. This would be suspected from SMNS 16980.

SMNS 17203 is the only *Proganochelys* specimen with clearly defined neurals. Four neurals are preserved which I identify as numbers 4–7 based on their relation to the costals and assuming the relationship is the same as in most other turtles. The neurals are clearly separated from the surrounding elements and may even be displaced slightly, but their preservation is such that their margins are irregular due to postmortem crushing and distortion. The first preserved neural, here identified as neural 4, has a short anterolateral contact with the third costal and a long lateral contact with the fourth costal. The anterior margin of this neural is barely visible and there is no trace of any neurals anterior to this one. Only the left lateral margin of neural 4 is preserved and it would appear to have six sides. Neural 5, however, is better preserved and does have six sides, with a very short anterolateral contact with the fourth costal. Neural 6 looks rectangular but the sides are slightly curved so that given some postmortem damage a six-sided outline is quite possible. Neural 6 has a longer anterolateral contact with the fifth costal than the other neurals have with their anterior costals. The seventh neural is slightly displaced above the general level of the carapace and its margins are damaged. As preserved, it is pentagonal with a transverse anterior margin and a tapering posterior margin suggesting that it might be the last neural with a pair of costals meeting behind it. However, all the margins of this neural are irregular when examined in detail and few of them appear to be original. A poorly defined lump of bone behind the seventh neural is tentatively identified as the eighth neural. It is much smaller than the others.

The ventral surface of SMNS 17203 shows three thoracic vertebrae which are attached to the ventral surface of the neurals. By matching features on both surfaces it can be seen that these centra are thoracics 5–7. On the ventral side costal ribs 5 and 6 are exposed showing their relation to those thoracic centra. The general relations and shape of the centra are similar to those found in the other *Proganochelys.* The fifth thoracic is best preserved of the three and, as far as I can determine, the others agree with it. This centrum is expanded at both ends with the anterior end larger than the posterior because it receives about two-thirds of the costal rib head articulation while the posterior end articulates with about one-third of the rib head, much as in other turtles. There is a blunt ridge running on the ventral surface of the centrum. The synarthritic articulation with adjacent thoracic centra is transverse. The centra are slightly displaced and separated from one another. The articulation with the neurals is not exposed but comparison of dorsal and

ventral surfaces shows that these thoracic centra overlap the neural bones as in most other turtles. The sutures between the centra and between the centra and rib heads agree with sutures seen in the Berlin specimen in this region of the carapace and support the interpretation of similar traces in that specimen as sutures.

The peripherals of SMNS 17203 are poorly preserved, presumably because they were relatively loosely attached to the rest of the shell, but they still provide the only clear evidence of sutures between the peripheral bones. On the left anterior margin of SMNS 17203 is a section of peripherals attached to the axillary buttress of the left hyoplastron. Although the sutures are not clear within this group, I think that two can be made out with some confidence and a third is likely, giving a probable count of four peripherals in this series. The posterior three are articulated with the hyoplastron and allow comparison with other specimens. The most anterior peripheral is beyond the hyoplastral contact and is attached to the shell only by its lateral margin. This bone is poorly preserved, preventing identification of sulci or sutures but a possible suture is largely obscured by glue and broken bone. This bone seems to be roughly in the position of marginal scutes 4 and 5 in other specimens. The anterior margin of the bone is inclined posteromedially, which would agree with the margin of the other shells in this area. The one sulcus that is relatively well defined is somewhat lateral to the medial margin of the hyoplastral buttress and can be identified as separating marginals 6 and 7 by comparison with SMNS 16980. The position of this sulcus shows that for this series of peripherals the scales overlap the bones and the sulci do not coincide with sutures. Unfortunately, these peripherals are visible primarily in ventral view; their dorsal surface is obscured by bone fragments (some of which may belong to the forelimb), matrix, and glue.

The bridge peripherals attaching to the inguinal or hypoplastral buttress are preserved on both sides. Due to the dorsoventral crushing of the shell, the costals seem to have rotated the dorsal part of the bridge peripherals ventrally and laterally. There are portions of three peripherals on the left side; the most anterior one has only its posterior portion preserved, the next one is complete, and the most posterior one has only its forward part preserved. The anterior two contact the hypoplastron for their entire length as preserved but the hypoplastron barely reaches the last one. All three have a moderate carina developed along their lateral margin, but it is less developed than the bridge carina of other *Proganochelys* shells. The bridge peripherals of SMNS 17203 can be seen to consist of two laminae meeting at about right angles but the bones are relatively long and narrow.

Three peripherals are preserved on the right side of SMNS 17203 and the first one corresponds with the second one preserved on the left side. This peripheral is sutured to the hypoplastron for its entire length while the one posterior to it has only a short hypoplastron contact. There are ill-defined sulci visible in approximately the same positions on both sides and, based on the position of the medial margin of the inguinal buttress in SMNS 16980, these can be identified as marginals 10–12. In this area the scales overlap the peripheral bones. On the right side there is one peripheral more preserved than on the left. This peripheral is not well preserved and the suture is obscured due to epoxy and glue. As preserved, this peripheral makes a sharp medial bend and lies over the right tarsus and hind feet elements to which it is attached. This peripheral should lie in the vicinity of the 12th marginal where a medial bend of the carapace margin takes place. A disarticulated and poorly preserved bridge peripheral lies in matrix in the left inguinal notch adjacent to what appears to be a centrum of a thoracic vertebra. I cannot identify the position of this peripheral.

In the SMNS Trossingen turtle collection are some loose elements which are probably associated with SMNS 17203. One particular series of three triangular bones (fig. 103) I interpret as three posterior peripherals of SMNS 17203. These elements are hollow; the larger two are fused at their base but the smallest is separated from the others by a small amount of matrix. The base margins have what appear to be original edges. When examined in cross section, the bones are symmetrical; I cannot detect a basis for discriminating a dorsal from a ventral surface and, therefore, cannot determine whether these are

right or left peripherals. Two of these are much larger than the third; this, taken with the degree and direction of tapering, leads me to identify them as marginals 14–16. From these elements it is clear that the sulci and sutures coincide, at least to the extent that these are determinable. There are a few other triangular, hollow ossicles, even smaller than those just described, that may be peripherals. The problem is that they are also identical to many of the dermal ossicles found in the limbs and tails. The hollow, flattened-out cone shape appears to be typical for dermal ossicles and posterior peripherals alike. The other peripherals of SMNS 17203 are also hollow with a dorsal and ventral lamina but in the presumed older shells most of these fill with bone.

DESCRIPTION OF TYPE SPECIMEN OF *PROGANOCHELYS QUENSTEDTI* (fig. 104)

Although this specimen was named as a new genus and species by Baur in 1887, it was not described or figured until 1889 by Quenstedt. The specimen is a large steinkern formed in a very hard quartz sandstone and does not retain any of the original bone. The surface is well preserved in some places but fine detail is lacking. Quenstedt's figures (1889: pls. 1 and 2) are reversed left to right (not unusual in lithographs), and are somewhat stylized so that "irregularities" have been straightened out. This is especially apparent in the plastron which has been given a very clean, regular appearance, in contrast to the rough surface actually present. This specimen has also been figured and discussed by Fraas (1899: fig. 2; pl. 8, figs. 1 and 2, lateral and ventral views), and Hennig (1923: fig. 56, dorsal view).

The steinkern does not accurately preserve the anterior margin of the carapace; instead the most obvious anterior margin is the imprint of the first thoracic rib. Anterior to this rib some low grooves can be seen and the one traversing the midline is the margin of the nuchal embayment. On either side of the embayment and anterior to the first thoracic ribs are two long holes extending from the dorsal surface anteroventrally to emerge on the anterior face of the steinkern. Quenstedt (1889: 122) identified these as molds of the scapulae, but they can be more accurately identified as molds of the dorsal epiplastral processes based particularly on the tear-drop shape of the dorsal attachment to the carapace.

The first thoracic rib mold is deeper and more extensive than the other rib mold, as would be expected from examination of a carapace. This rib mold extends ventrolaterally and is confluent with the plastral portion of the bridge. Unfortunately it is not clear enough to determine where the carapace intersected on the bridge. The mold for the eighth cervical centrum can be seen on the midline slightly separated from the first thoracic centrum. The succeeding thoracic centra show the typical swollen rib attachments seen in the other specimens of *Proganochelys*. Thoracic rib ridges 1–7 can be seen as grooves on both sides while thoracic rib 8 is preserved on the right side only. The ribs vary in their angle of intersection with the midline as in the other *Proganochelys* specimens.

The plastron in the Tübingen steinkern lacks the anterior and posterior margins but more than half of each lobe is present. The structures restored by Fraas (1899: pl. 8) were purely speculative and are now seen to be incorrect in view of later specimens. The posteriormost section of the epiplastron-hyoplastron suture can be seen on both right and left sides but the other ridges and nonsymmetrical irregularities are not sutures. The lines added by Fraas to indicate the mesoplastral sutures are broad convexities that do not correspond to what I would interpret as sutures. A strong midline groove indicates the posterior process of the entoplastron.

The bridge area of the Tübingen steinkern is better preserved than the internal bridge surfaces of the other *Proganochelys* specimens and does provide information not available elsewhere. A series of five low grooves appear to be continuations of the rib grooves and are interpreted as the terminal portions of costals 2–6. Sutures are not apparent and the limits of peripheral bones are obscure. The steinkern shows a relatively flat plastron meeting the carapace at roughly right angles with a series of bulges (pockets in the bone) alternating with the presumed rib grooves.

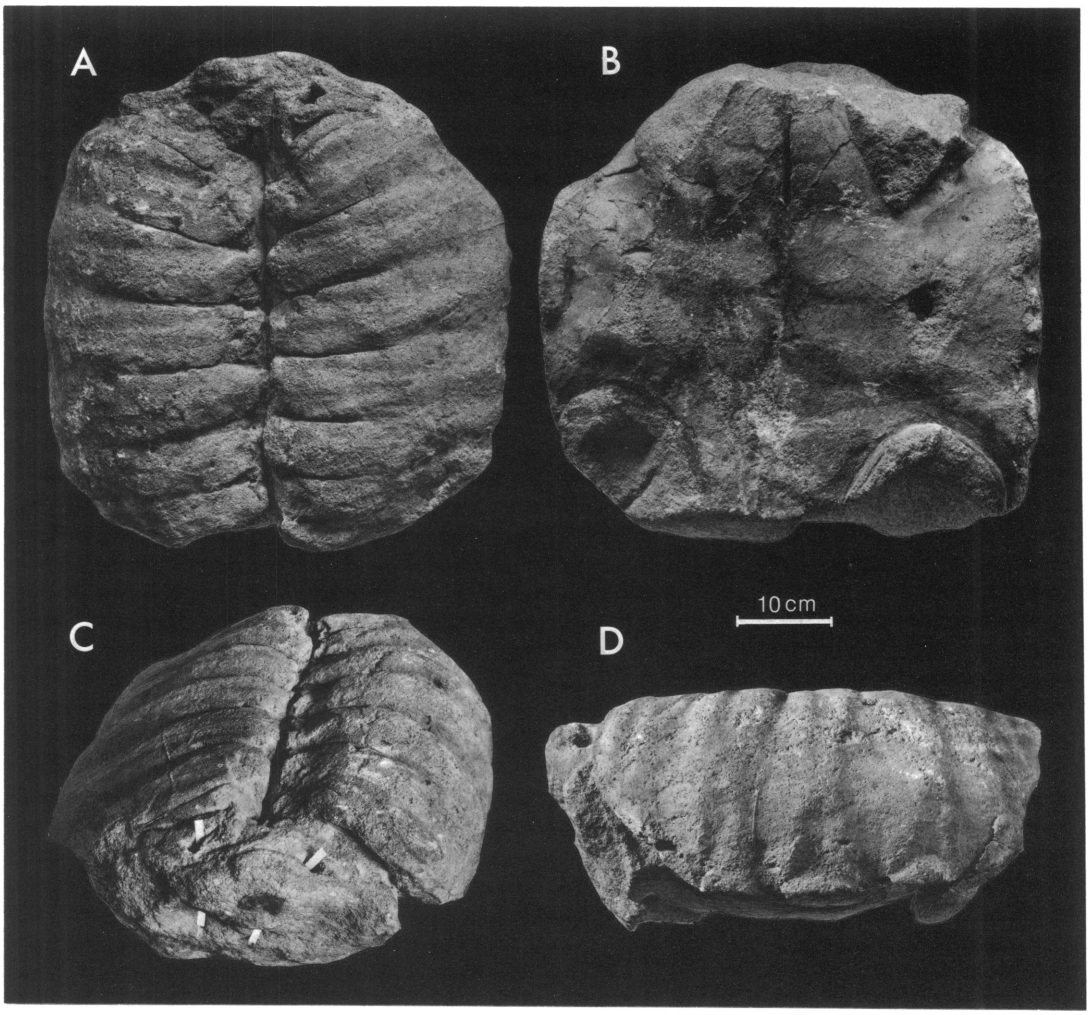

Fig. 104. *Proganochelys quenstedti,* University of Tübingen (uncataloged). Steinkern of shell, type specimen of *Proganochelys quenstedti* Baur (*Psammochelys keuperina* Quenstedt). **A,** dorsal (anterior toward top of page); **B,** ventral (anterior toward top of page); **C,** anterodorsal oblique with white strips of paper placed in holes representing dorsal processes of epiplastra; **D,** left lateral.

The cross-sectional outline of the Tübingen steinkern is of some interest because all of the *Proganochelys* shells suffer from some degree of crushing and additional information on the curvature of the carapace is welcome. The steinkern, however, is also distorted, as can be seen from the fact that it is not symmetrical in anterior view (see Quenstedt, 1889: pl. 1). The distortion seems to have resulted in the right side being forced in the direction of the left so that the midline of the carapace lies to the left of the midline of the plastron. The degree of curvature of the right half of the carapace is less pronounced than the left half. Dorsoventral crushing does not seem to be prominent in the steinkern. If the lateral distortion is subjectively corrected, the Tübingen steinkern fits the reconstruction based on SMNS 16980 (fig. 69). *Proganochelys* does not have a high-domed shell as in *Proterochersis* and baenids but it is higher than the flattened shell in the Berlin specimen.

The Tübingen steinkern has the following

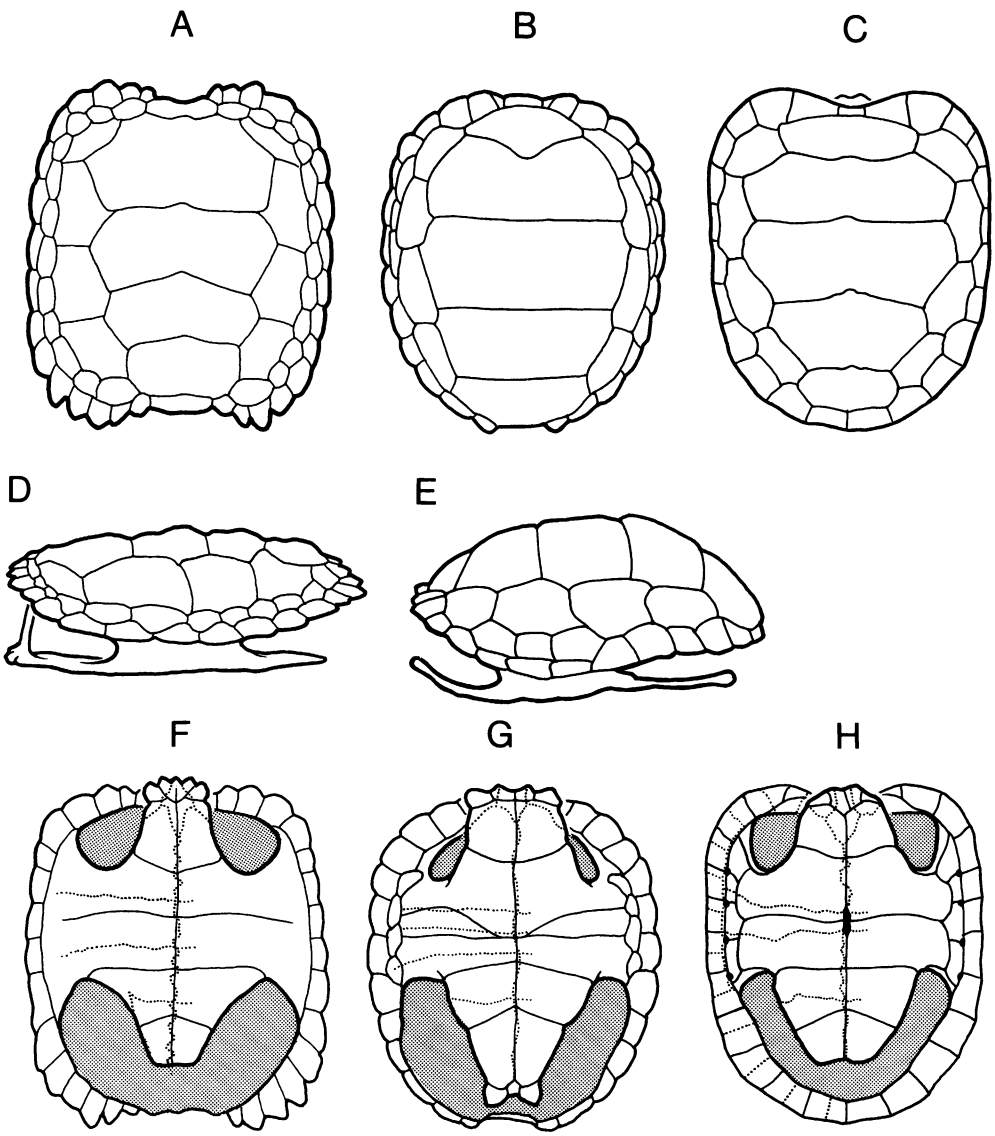

Fig. 105. Comparisons of shells of pre-Late Jurassic turtles. **A–C,** dorsal views; **D, E,** lateral views (anterior to left); **F–H,** ventral views. A, D, F, *Proganochelys quenstedti,* SMNS 16980, Late Triassic. B, E, G, *Proterochersis robusta,* composite based on SMNS 17561, 17755, 18440, and 16442, Late Triassic. C, H, *Kayentachelys aprix,* Early Jurassic, from Gaffney et al. (1987). Detailed sutural patterns are known only for the plastra of *Proganochelys* and *Proterochersis* so that carapacial sutures of *Kayentachelys* are left out.

features characteristic of, but not unique to, *Proganochelys*:

1. Large dorsal processes of epiplastra;
2. swollen thoracic rib heads;
3. nuchal embayment;
4. detailed similarities of internal surface of carapace and plastron;
5. relatively large size.

There are no characters that would allow separation of the Tübingen specimen and SMNS 16980.

TABLE 12
Preserved Material of Cervicals and Caudals

	SMNS 16980	SMNS 17203	SMNS 17204	SMNS 15759	MB 1910.45.2
Atlas	+ (part)	–	–	–	+
Axis	+	–	–	–	+
Cervical 3	+	–	–	+	+
Cervical 4	+	–	–	+	+
Cervical 5	+	–	–	+	+
Cervical 6	+	–	+	–	+
Cervical 7	+	–	+	–	+
Cervical 8	+	–	–	–	+
Number of caudals	14	18	13	–	–
Tail club	+	+	+	–	–

VERTEBRAL COLUMN
(table 13, figs. 106–121)

CERVICALS

Cervical vertebrae are present in four of the five *Proganochelys* specimens (table 12). The best set is the complete series preserved in the Berlin specimen, MB 1910.45.2. These vertebrae (figs. 112–120) are missing only a few of the neural spines and appear to be only slightly distorted. SMNS 16980 (fig. 111) also has a complete set (cervicals 5 and 7 are now missing, however) but these cervicals are more distorted and damaged than in the Berlin specimen. These two specimens form the basis of the cervical descriptions. Cervicals 6 and 7 are present in SMNS 17204 and they agree closely with those elements in SMNS 16980 except that they are slightly larger. Three articulated cervicals are present in SMNS 15759 but these are badly distorted by dorsoventral crushing. They appear to consist of the posterior half of cervical 3, all of cervical 4, and the anterior half of cervical

TABLE 13
Comparison of Cervical Vertebrae

	Captorhinus	*Proganochelys*	Casichelydia
Axis intercentrum/atlas centrum fused	Yes	Yes	Yes
Atlas rib ossified	Yes	No	No
Atlas neural arch articulates with skull via proatlas	Yes	No	No
Central articulations	Amphicoelous (deep) notochordal	Amphicoelous (shallow) not notochordal	Amphicoelous (shallow) not notochordal
Alternation of neural spine height	Yes	Probably	No
Ossified intercentra	Present	Absent	Usually present
Cervical ribs	Free on all cervicals	Free on cervicals 2 to 5, fused on cervicals 6 to 8	Present, but primitive condition not known; in *Meiolania* cervicals 2 to 6 are free and fused on 7 and 8
Number of cervical vertebrae	5 to 7	8	8
Neural spine of eighth cervical attached to carapace	–	Yes	No

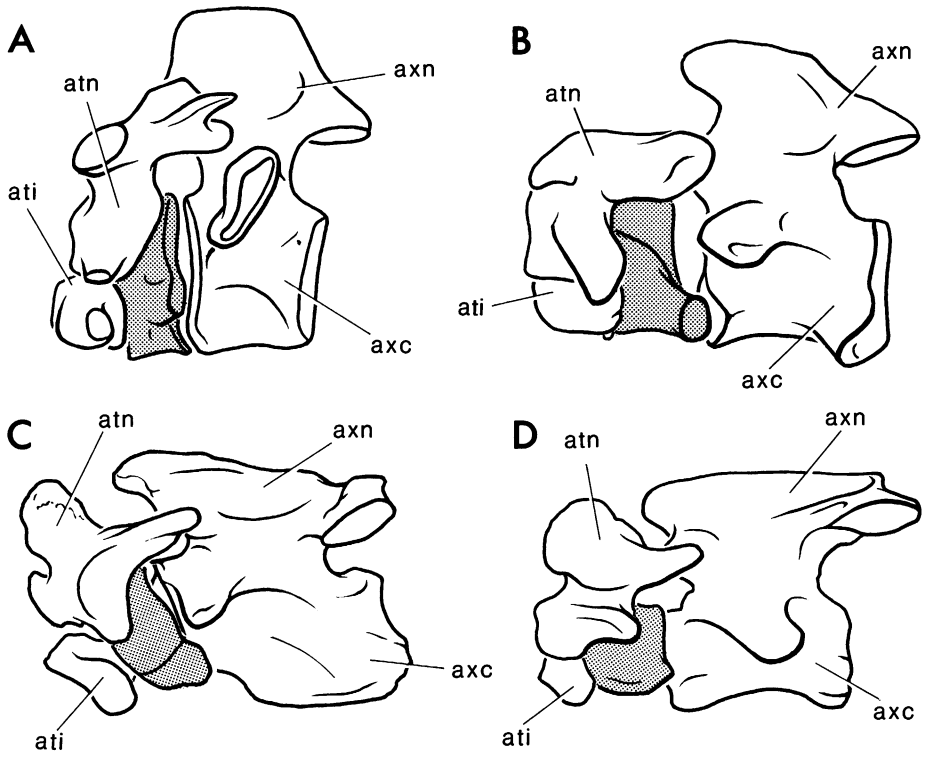

Fig. 106. Comparative views of atlas-axis complex in left lateral view, anterior to the left. **A,** *Captorhinus* sp. (after Dilkes and Reisz, 1986 and AMNH 19385, 19386; **B,** *Proganochelys quenstedti,* MB 1910.45.2; **C,** *Macroclemys temmincki,* AMNH 36602; **D,** *Podocnemis expansa,* AMNH 62947. Atlas centrum is stippled for landmark. Abbreviations: **ati,** atlas intercentrum; **atn,** atlas neural arch; **axc,** axis centrum; **axn,** axis neural arch.

5. Although some disarticulated centra, dubiously identified as caudals, are present in SMNS 17203, no definite cervicals are present.

Because the cervicals of MB 1910.45.2 are the best preserved, they are completely documented here in both stereophotographs (figs. 113–120) and line drawings (fig. 112). The cervicals of SMNS 16980, however, do present some important differences and are figured as line drawings (fig. 111).

The atlas is completely preserved only in MB 1910.45.2. In SMNS 16980 only the centrum and the atlantal intercentrum are present. Jaekel (1918a) misidentified elements of the atlas and thought that the atlantal intercentrum was the entire atlas and that the atlantal centrum was the axis. This gave him an incorrect count for the entire vertebral column, resulting in nine rather than eight cervicals. In his figure 23 (Jaekel, 1918a), "W" and "W_2" should be the first cervical and all the remaining cervicals are actually one less than the number he has given them (also in his fig. 27). Later authors corrected Jaekel's misidentification of the atlas-axis but accepted his identification of the last cervical as being incorporated into the carapace. Most of the literature (Romer, 1956; Williams, 1950; Hoffstetter and Gasc, 1969) has therefore stated that *Proganochelys* (=*Triassochelys*) had seven cervicals. The neural spine of cervical 8 in *Proganochelys* is sutured to the carapace but the rest of the vertebra is not and there are eight cervicals as in all other turtles.

As in other turtles and *Captorhinus,* the atlas of *Proganochelys* (fig. 106) consists of four elements: paired neural arches anterodorsally, an intercentrum anteroventrally, and

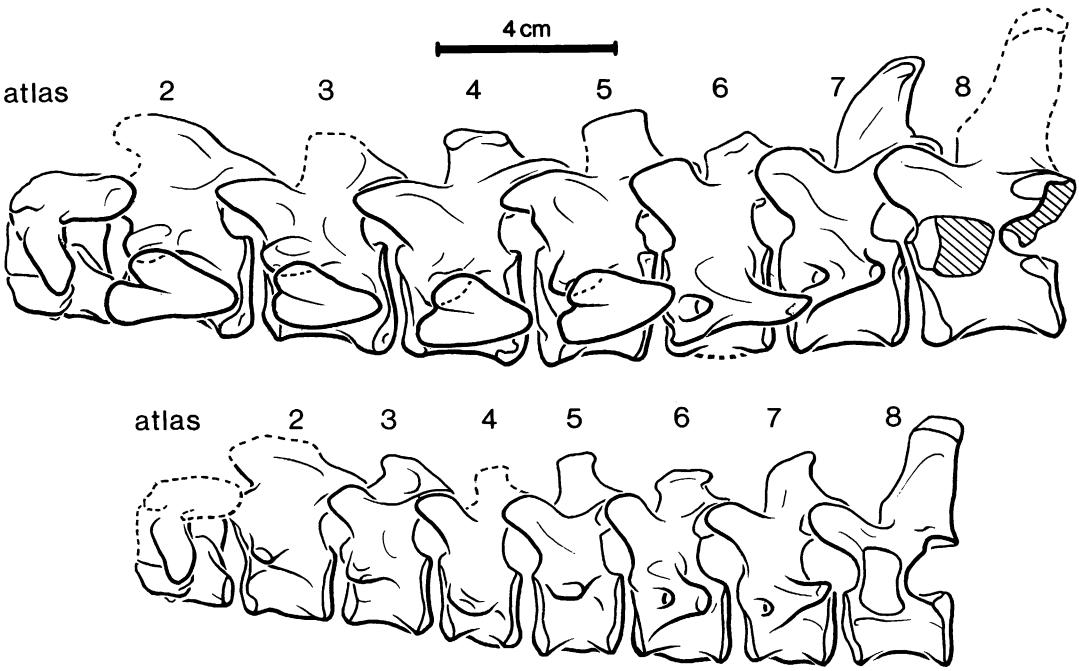

Fig. 107. *Proganochelys quenstedti.* Cervical vertebrae in left lateral view; missing areas restored by dashed lines; drawings are to scale with each other. Upper, MB 1910.45.2 with ribs in articulation as mounted. Rib of cervical 8 cut through at base because of length. Lower, SMNS 16980. Free ribs not articulated; rib of cervical 8 removed at suture.

a centrum posteriorly. *Proganochelys* has no sign of a suture differentiating the axis intercentrum; it is presumably fused to the atlas centrum as in *Captorhinus* and Casichelydia but in contrast to synapsids and the presumed primitive amniote condition (Heaton and Reisz, 1986). The chelonian neural arch (Kasper, 1903) can be roughly divided into a dorsal portion covering the neural cord and having a posteriorly directed postzygapophyseal flange articulating with the axis, and a ventral portion bearing articular facets for the occipital condyle, the atlantal centrum, and the atlantal intercentrum. The atlas of *Proganochelys* agrees well with that of casichelydians.

On the lateral surface of the neural arch in the Berlin specimen is a posteroventrally trending ridge that Jaekel (1918a: fig. 23) identified as a rib but there is no free rib here, no rib facets, and no sign of a fused rib. In contrast to *Captorhinus, Proganochelys* apparently does not have an atlantal rib. *Meiolania* (Gaffney, 1985b) is the only turtle known to have (as a variation on some specimens) a presumed cartilaginous rudiment of an atlantal rib.

In *Captorhinus* (Peabody, 1952; Fox and Bowman, 1966; Dilkes and Reisz, 1986) the neural arch of the atlas articulates with the occiput of the skull via the proatlas, a feature primitive for amniotes. There is no sign of a proatlas or proatlantal articulation in *Proganochelys* or any other turtles. The posterodorsal spine seen on the atlantal neural arch of *Captorhinus* and other generalized amniotes is absent in *Proganochelys* and other turtles.

The posteroventrolateral corner of the atlantal centrum (presumably the fused axis intercentrum) bears the capitulum articulation of the axis cervical rib. This rib has its tuberculum articulation with the diapophysis on the axis. In *Captorhinus* the atlantal articulation is very large and extends the height of the atlas centrum while in *Proganochelys* the articulation is smaller and restricted to the posteroventrolateral corner. This is also

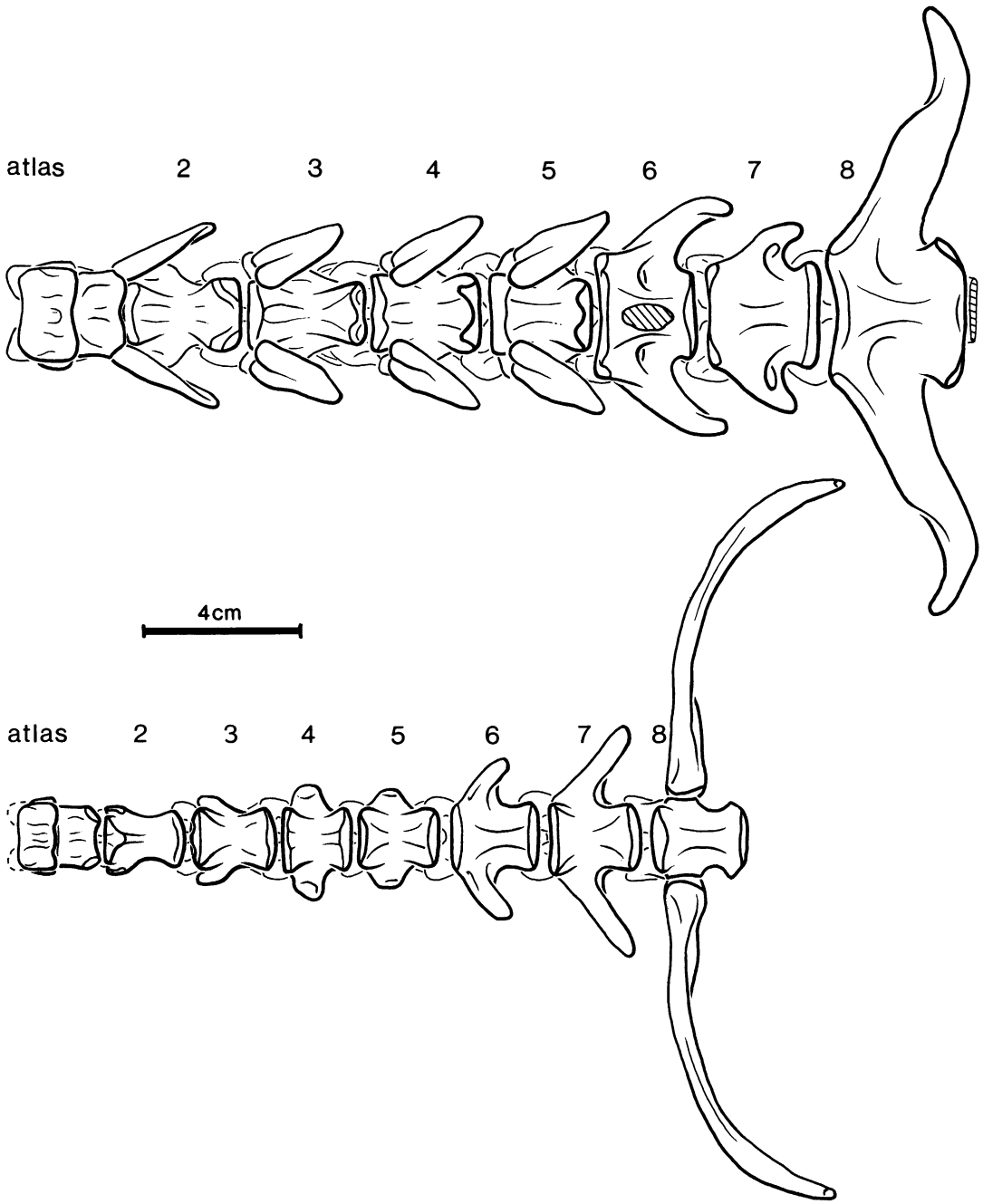

Fig. 108. *Proganochelys quenstedti.* Cervical vertebrae in ventral view, to scale with each other. Upper, MB 1910.45.2, free ribs in articulation as mounted. Lower, SMNS 16980, free ribs not articulated except for cervical rib 8.

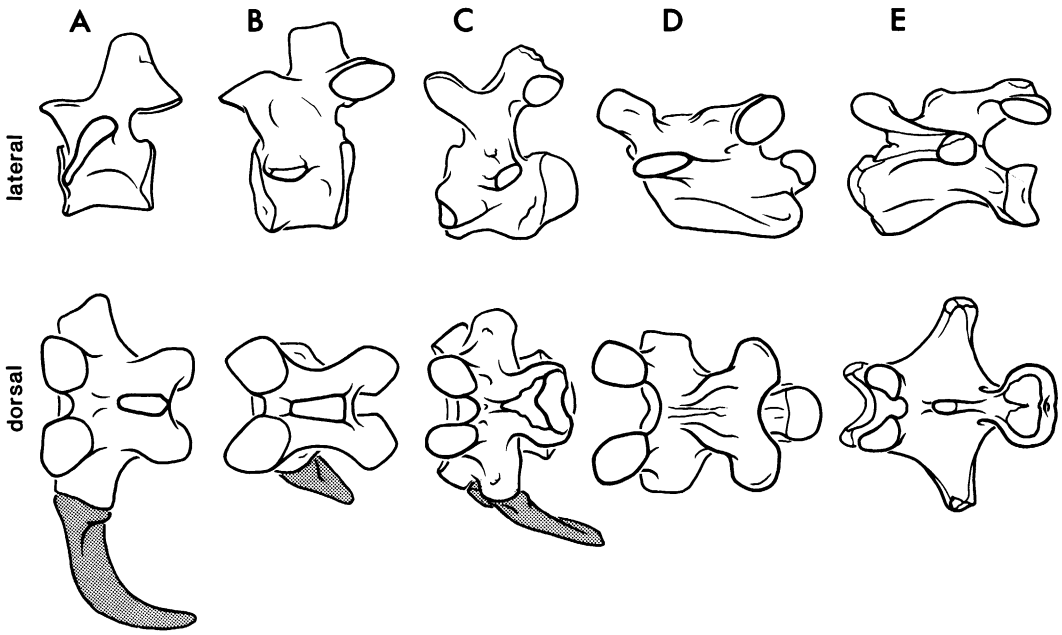

Fig. 109. Comparisons of the fifth cervical vertebra. Upper row, lateral view; lower row, dorsal view; anterior to left; cervical ribs in stipple. **A,** *Captorhinus* sp., from Heaton and Reisz (1986) and AMNH 19390–19392. **B,** *Proganochelys quenstedti,* MB 1910.45.2. **C,** *Meiolania platyceps,* from Gaffney (1985b). **D,** *Macroclemys temmincki,* AMNH 36602. **E,** *Podocnemis expansa,* AMNH 62947.

very similar to the condition in *Meiolania,* the only other turtle known to have a rib on the axis. It is likely, however, that better preserved primitive cryptodires, such as *Kayentachelys* and *Pleurosternon,* will also have cervical ribs.

The centrum of the atlas is solid in *Proganochelys,* rather than perforated by the notochord as in *Captorhinus* (Peabody, 1952). The centrum in *Proganochelys* is narrower than in most other turtles, as are all the cervicals of *Proganochelys.*

The axis is preserved in both MB 1910.45.2 and SMNS 16980, but the neural spine is broken in both. Jaekel's (1918a: fig. 23) figure shows the neural spine intact and the figures here have been restored on that basis. The axis in *Proganochelys* is similar to the axis in other turtles, differing from *Captorhinus* in not being notochordal and slightly longer and narrower. The neural spine has (in Jaekel's figure) an anterior midline projection as in other turtles. The transverse process of the axis bears the tuberculum of the axis rib articulation. The ventral part of the centrum is laterally embayed to form a low ridge or keel, as in the other cervicals of *Proganochelys.*

Cervicals 3–7 in *Proganochelys* are similar to one another and differ primarily in neural spine height and rib fusion. Although not entirely clear, it appears that neural spines of *Proganochelys* show alternation in height similar to that in *Captorhinus* (Vaughn, 1970; Heaton and Reisz, 1980; Dilkes and Reisz, 1986). The neural spines of cervicals 4 and 6 are lower than the adjacent cervicals and are the basis of this interpretation. This supposed alternation, however, may have nothing to do with this generalized amniote feature. Rather, it may be related to the position of the neck osteoderms, although these are supposed to articulate over the first and third cervicals (Jaekel, 1918a: fig. 23). The spines of cervicals 3–6 are relatively simple blades with a dorsal expansion or cap, differing only in height. Cervical 7 has a distinctive posteriorly curved spine that is higher than the more anterior cervicals. Cervical 8 has the

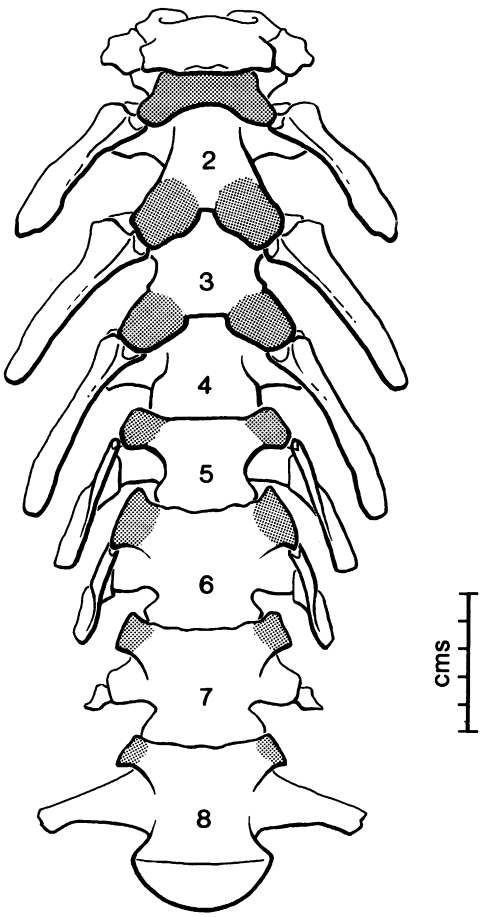

Fig. 110. *Meiolania platyceps,* Pleistocene, Australia. Ventral view of cervicals with intercentra shown in stipple. Compare with Figure 108. From Gaffney (1985b).

highest spine and is suturally attached to the carapace.

The prezygapophyses are also quite similar from cervical 3 to 8. The prezygapophyses of the second cervical are facing dorsolaterally as in other turtles, but the other prezygapophyses are facing dorsomedially. The degree to which the prezygapophysis faces medially changes. In cervical 3 the prezygapophysis articular facet is relatively flat and faces more dorsally than medially. Cervical 4 is nearly the same, but 5 has a definite change so that there is a greater medial orientation. Cervicals 6 and 7 continue this but the degree of change is not as marked as that between 4 and 5, possibly as a result of distortion. The plane of the articulation also changes so that at cervical 5 there is a slight curvature (concave dorsally) which is very marked by cervical 7. The eighth cervical has the most medially facing prezygapophysis articulation; it is about 45° (both sides are different in SMNS 16980). The articular surface of the eighth is nearly flat rather than curved, however.

The postzygapophyses of the third cervical are more divergent than the second and are more rounded and thinner. The V between them is shallower. The postzygapophysis of the fourth cervical is missing in SMNS 16980 but preserved in the Berlin specimen. The postzygapophyses of cervicals 3–5 are very similar but starting with about six and becoming more pronounced with seven, the separation of the postzygapophysis and arch is reduced. The preservation of the postzygapophyses of cervical 8 in both specimens is poor.

The centra of the cervicals in *Proganochelys* are all amphicoelous with a relatively shallow concavity compared with notochordal centra seen in *Captorhinus* and generalized amniotes. The centra are oval in anterior and posterior view. They are longer than high but are not as elongate as in most other turtles, but they are more elongate than in *Captorhinus.* The length of the centra seems to be about the same throughout the column; differences appear to be due to breakage of the central rims. Ventrally each centrum is seen to have a low ridge formed by the lateral concavities. Each centrum is constricted or hollowed ventrally below the rib articulations. The ventral ridge is simply a straight area that is not hollowed out.

The ribs of *Proganochelys* are one of the more interesting features of this fascinating relict from the past. Ribs are preserved on the Berlin neck from the second to the eighth cervical. The second through fifth cervicals have free ribs, while cervicals 6 to 8 have the ribs fused. SMNS 16980 has the same pattern; the fused ribs are present, but only a few fragmentary free ribs are present and they are disarticulated. In *Meiolania* only the rib of the eighth cervical is fused; the rest are free (Gaffney, 1985b). The orientation of the ribs on the Berlin specimen is, at present, dependent on how they are glued on. No infor-

mation exists on the original articulation. However, the free ribs of *Proganochelys* do not differ greatly among themselves.

In comparison with *Meiolania,* the cervical ribs of *Proganochelys* are seen to lack, at least in the material as preserved, the small, nodular intercentra. These are variably fused in *Meiolania,* but there is no ossification in *Proganochelys,* although there are spaces for intercentra. As in *Meiolania* they would lie between centra and articulate with the capitulum of the rib.

The transverse process of the axis in the Berlin specimen is at the anterior edge of the centrum and the diapophysis (which bears the rib articulation) faces posterolaterally. In SMNS 16980 the diapophysis seems to face laterally only. There is also some difference in the shape of the transverse process in the two cervicals. In the Berlin cervical the process and articulation are oblong and oriented with the long axis in a vertical plane, while in SMNS 16980 the long axis is vertical. Poor preservation in SMNS 16980 may account for this difference.

The transverse processes of cervicals 2–8 show a gradual change in position so that the succeeding vertebrae have the process slightly more posteriorly than the more anterior ones. In cervical 2, the process impinges on the central articular surface, in cervical 3 it is not so close to the articular face, while in cervical 4 the process is separated from it. In cervical 5 the transverse process approaches a midline position which it attains in cervical 6. Cervicals 7 and 8 do not really differ from cervical 6 in position.

In SMNS 16980 the diapophysis of the third cervical is definitely elongate with the long axis horizontal, further suggesting that the vertical position in the second cervical is anomalous. The cervicals with fused ribs have transverse processes that are nearly circular in cross section while the free rib cervicals (2–5) have more oblong transverse processes.

The ventral articulation of the cervical ribs would appear to be with a pair of unossified intercentra in cervicals 2–4 and probably 5. In these cervicals there is a space just anterior to the capitulum of the rib (when articulated with the transverse process). On the centrum this area is marked by a low ridge on the anterior and posterior ends of the centrum. This ridge ends in a beveled surface that faces anteroventrolaterally in the anterior part of the centrum and posteroventrolaterally posteriorly. The ridge is more prominent on the posterior end of the centrum. When the centra are articulated these ridges result in the formation of a wedge-shaped space that probably contained, either lost or unossified, a pair of intercentra. In cervicals 6–8 the capitulum of the fused rib is continuous with a bony process arising in this area. In *Meiolania* the intercentra lie in the same position as the wedge-shaped space in *Proganochelys.* Where the intercentra are not fused and/or missing in *Meiolania* there is a similar space and a ventral ridge results.

Proganochelys and *Meiolania* are the only turtles known with cervical ribs preserved although *Mesochelys* and *Kayentachelys* both have cervicals that have cervical rib articulation surfaces. The ribs in both *Proganochelys* and *Meiolania* are relatively flat and bladelike.

In *Proganochelys* the ribs are all about the same size, with that of cervical 2 being slightly longer than the rest. In *Meiolania* the ribs show a marked size decrease posteriorly. The rib of the second cervical is broad and long, the ribs of cervical 3 and 4 are about the same size but thinner than the cervical-2 rib. Cervicals 5 and 6 have ribs only about half the size of those on cervical four. The rib of cervical 7 is reduced to a spine that articulates only with the transverse process. The rib of cervical 8 is fused to the transverse process in *Meiolania* while in *Proganochelys* the ribs of cervicals 6–8 are fused. The fusions in *Proganochelys,* however, are of both rib heads so that a foramen results, except in cervical 8. The dorsal and ventral rib articulations are of equal size in *Proganochelys* but the dorsal one is distinctly larger in *Meiolania.* In *Meiolania* the ribs are slightly curved and concave posteromedially, but in *Proganochelys* they seem to be flat.

The fused ribs are preserved in SMNS 16980, the Berlin specimen, and SMNS 17204. All the fused ribs are cylindrical and posteriorly curved in contrast to the flat and straight free ribs. In the Berlin specimen the sixth cervical rib is slightly larger than the seventh, but in SMNS 16980 the sixth cervical rib is smaller than the seventh. The rib

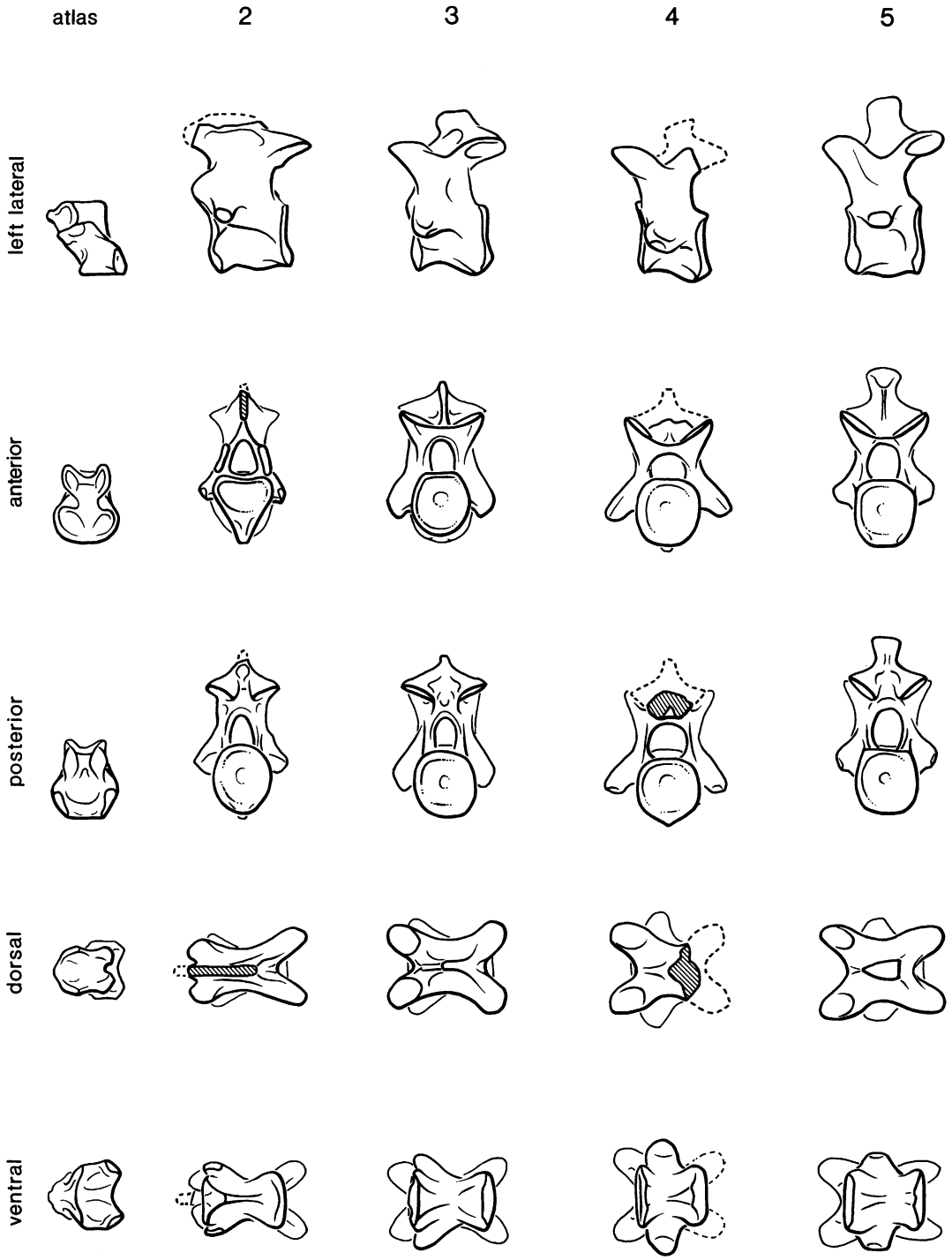

Fig. 111. *Proganochelys quenstedti,* SMNS 16980. Cervical vertebrae.

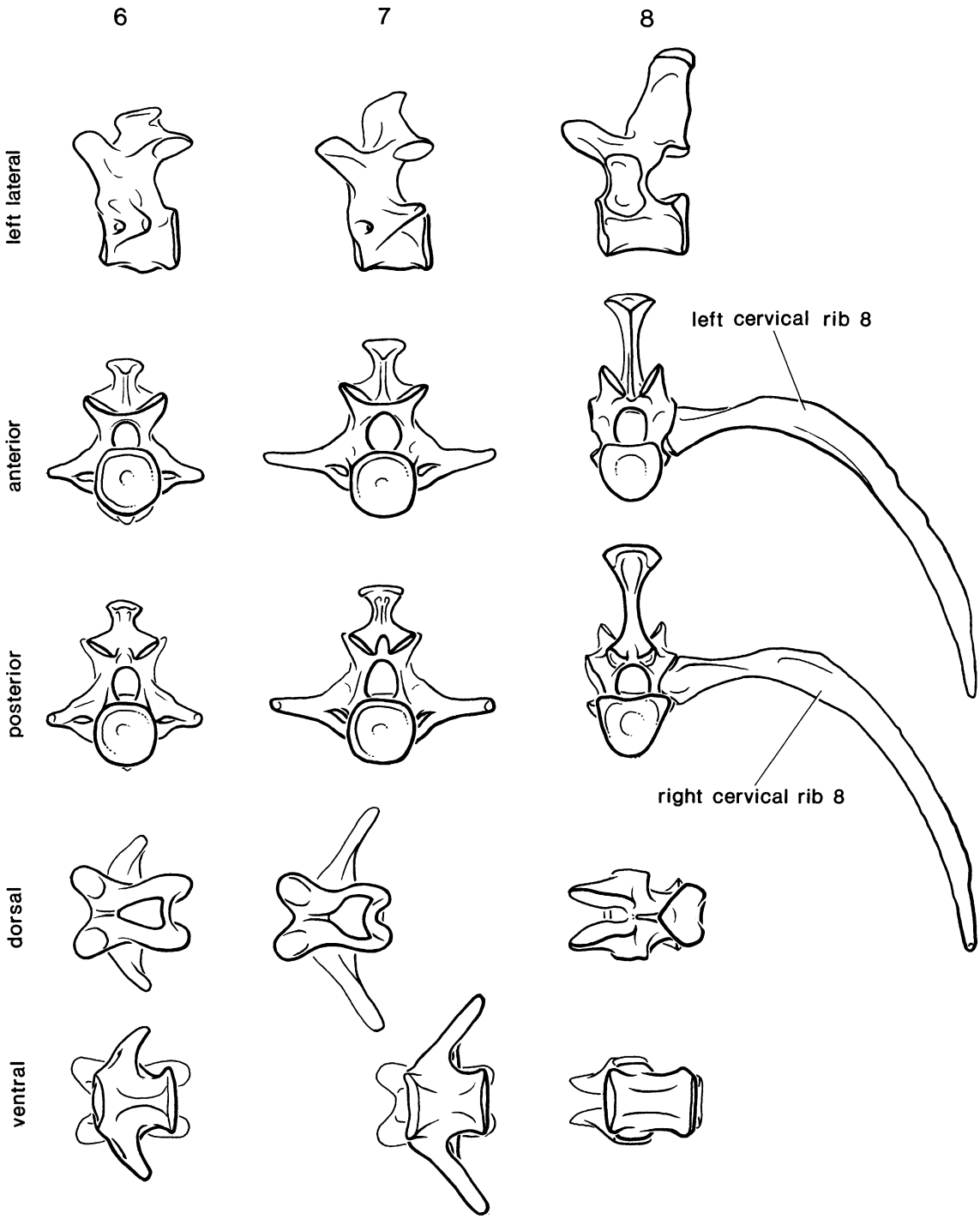

Fig. 111. Continued.

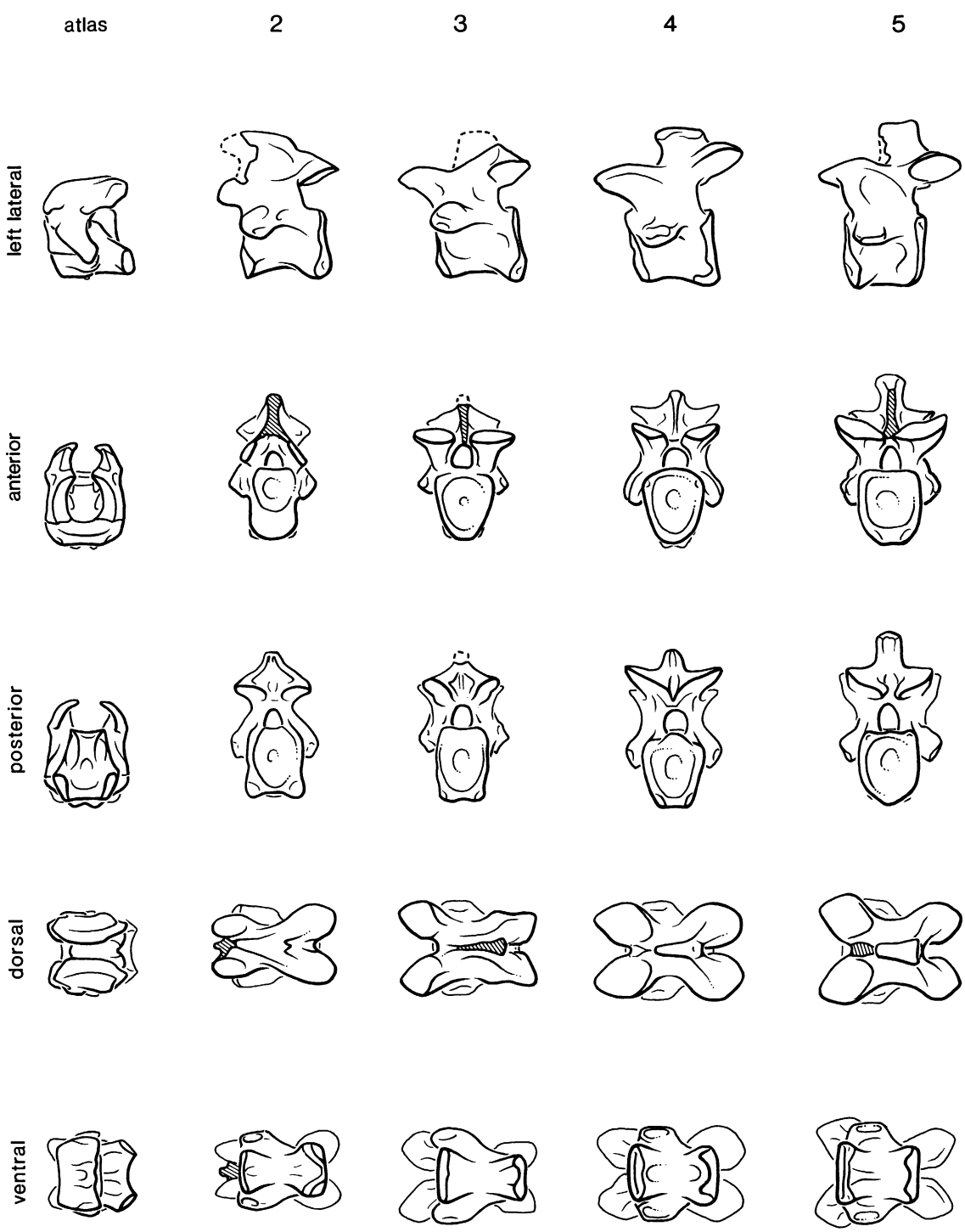

Fig. 112. *Proganochelys quenstedti,* MB 1910.45.2. Cervical vertebrae.

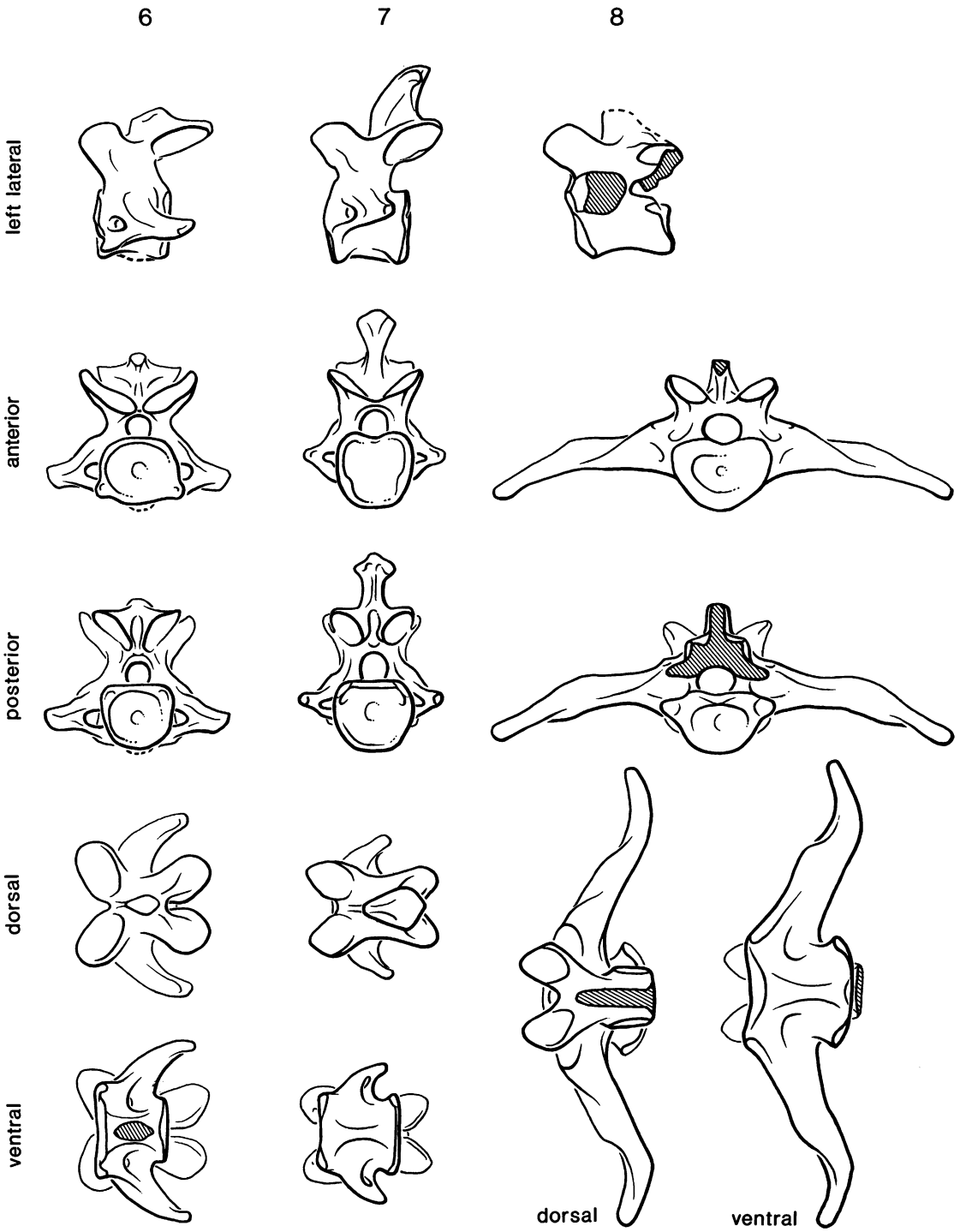

Fig. 112. Continued.

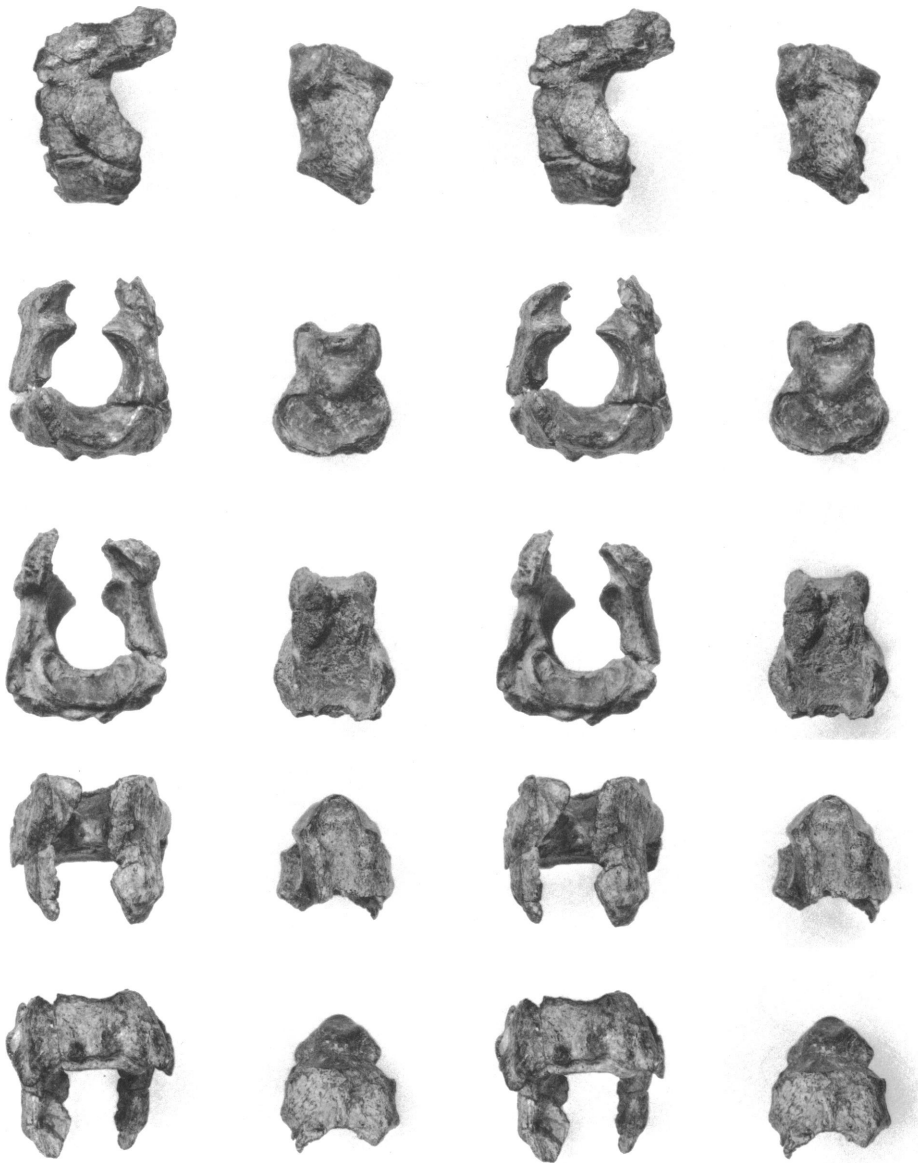

Fig. 113. *Proganochelys quenstedti,* MB 1910.45.2. Atlas, see Figure 112 for orientation and comparison with articulated atlas.

of cervical 6 has a strong curvature, not seen in cervical 7. The ventral articulation of the rib in cervical 6 is placed farther forward than the dorsal articulation. In neither specimen is there any indication of sutures separating the intercentra. The foramen formed between tuberculum and capitulum is oblong to triangular in shape.

The eighth cervical is preserved in both SMNS 16980 and the Berlin specimen (figs. 107, 108). In the Berlin specimen this vertebra has been distorted by dorsoventral

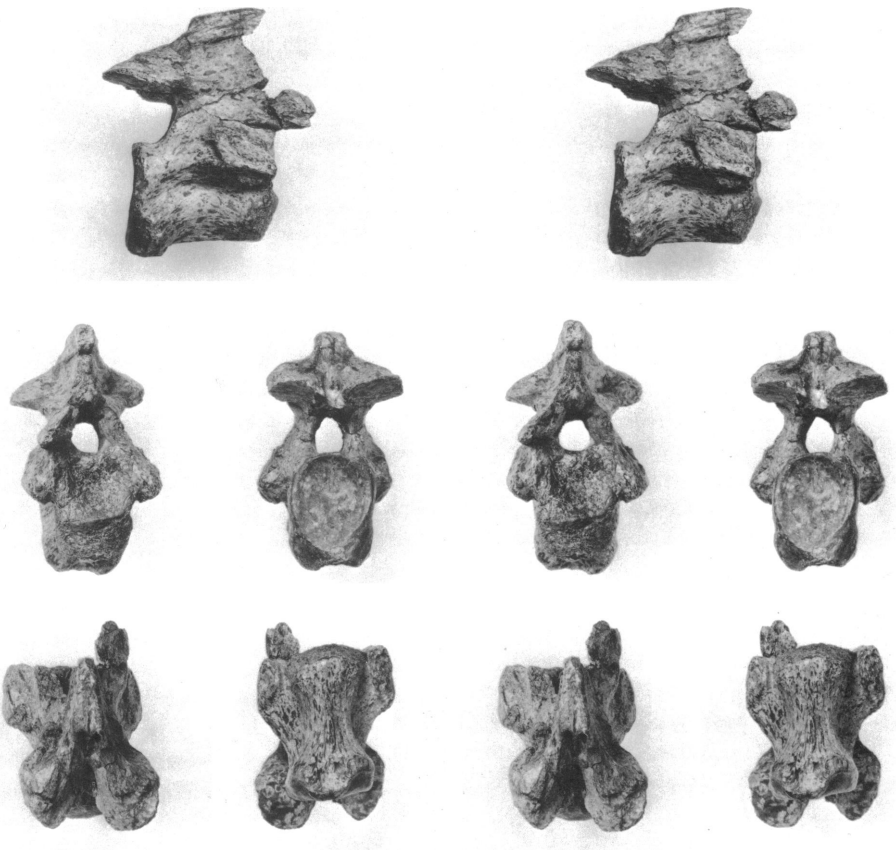

Fig. 114. *Proganochelys quenstedti,* MB 1910.45.2. Cervical 2, see Figure 112.

crushing, causing the centrum to be wider than long, which is probably not its original shape. This cervical differs from the others in having a tall neural spine that expands distally to fit into a depression in the carapace. The attachment is suturally fused in the Berlin specimen and disarticulated in SMNS 16980. (The figures of the eighth cervical in the Berlin specimen lack the top of the neural spine because it is broken off the cervical and still attached to the carapace; it is visible in fig. 82.) Other turtles may independently acquire cervical-carapace articulations, as in *Meiolania* and chelonioids, but no other turtles have a sutural attachment. This may be a *Proganochelys* autapomorphy or a primitive feature for turtles, but its absence in pleurodires, *Kayentachelys,* pleurosternids, baenids, and chelydrids argues that the generalized casichelydian condition is without an articulation.

The anterior central articulation of the eighth cervical is very much the same as in the other cervicals, a shallow concavity. The posterior central articulation, however, is platycoelous and would appear to have had little or no movement. Similarly, the prezygapophyses are as in the more anterior cervicals but the postzygapophyses are much smaller and very close to each other near the midline. The neural arch-centrum attachment is about the same width as the centrum in the more anterior cervicals, but in the eighth cervical this area is narrower as the result of a posterior excavation. The eighth cervical has large ribs that attach relatively high on the vertebra, on the area connecting centrum and neural arch.

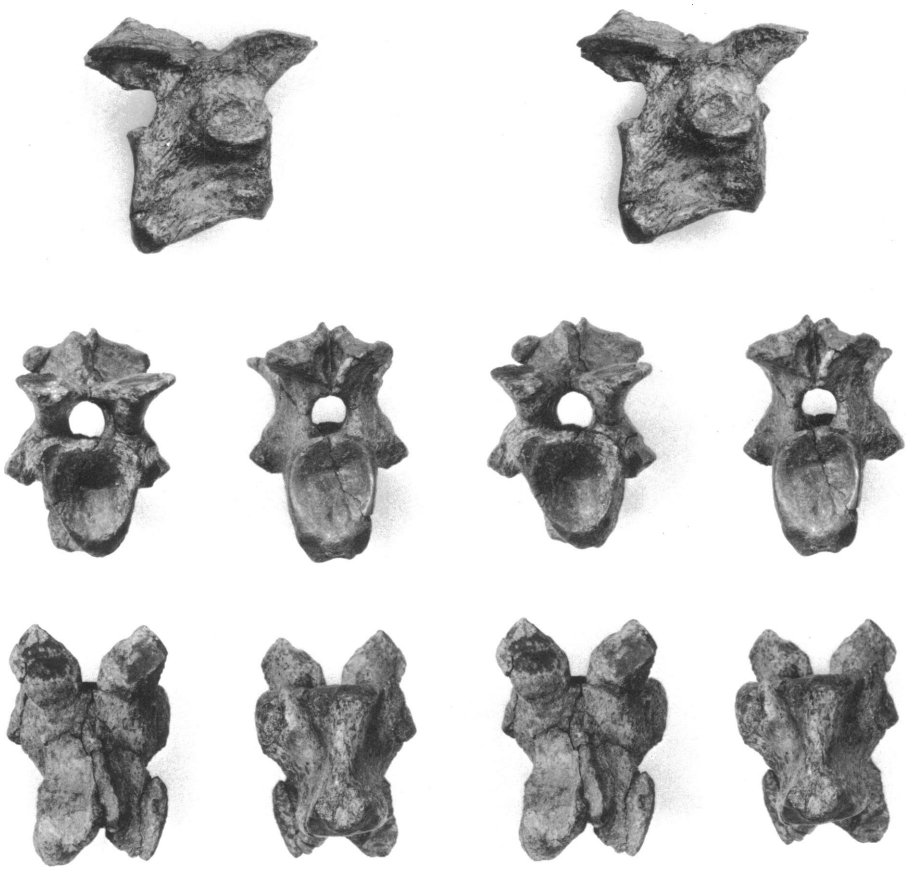

Fig. 115. *Proganochelys quenstedti,* MB 1910.45.2. Cervical 3, see Figure 112.

The centrum of the eighth cervical has very large ribs, much larger than the other cervical ribs and differing in having a single head rather than being bicipital as in cervicals 2–7. The ribs are very different in SMNS 16980 and the Berlin specimen. In SMNS 16980 the ribs are thin and flat dorsoventrally, lying in a flat plane at right angles to the midline. They curve ventrally and are attached to the centrum by an open suture. In the Berlin specimen the ribs are thick, much shorter, and extend laterally with only a slight downturn. They are fused to the centrum with no sign of a suture. The Berlin ribs are thick and stout medially but thin laterally where a curve is formed, concave anteriorly. This curved section lies directly behind the dorsal process of the scapula.

The differences between the eighth cervicals in the two specimens are hard to interpret. Some features, such as the open suture and generally thin appearance in SMNS 16980, can be ascribed to growth but the orientation and shape differences could be individual variation or taxonomic distinction.

CAUDALS
(table 14, figs. 125–132)

The three Trossingen specimens, SMNS 16980, SMNS 17203, and SMNS 17204, have what appear to be complete tails, while none of the other *Proganochelys* specimens have any caudals. SMNS 17204 (fig. 132) has a complete and articulated tail that has been prepared so that the osteoderms are in situ.

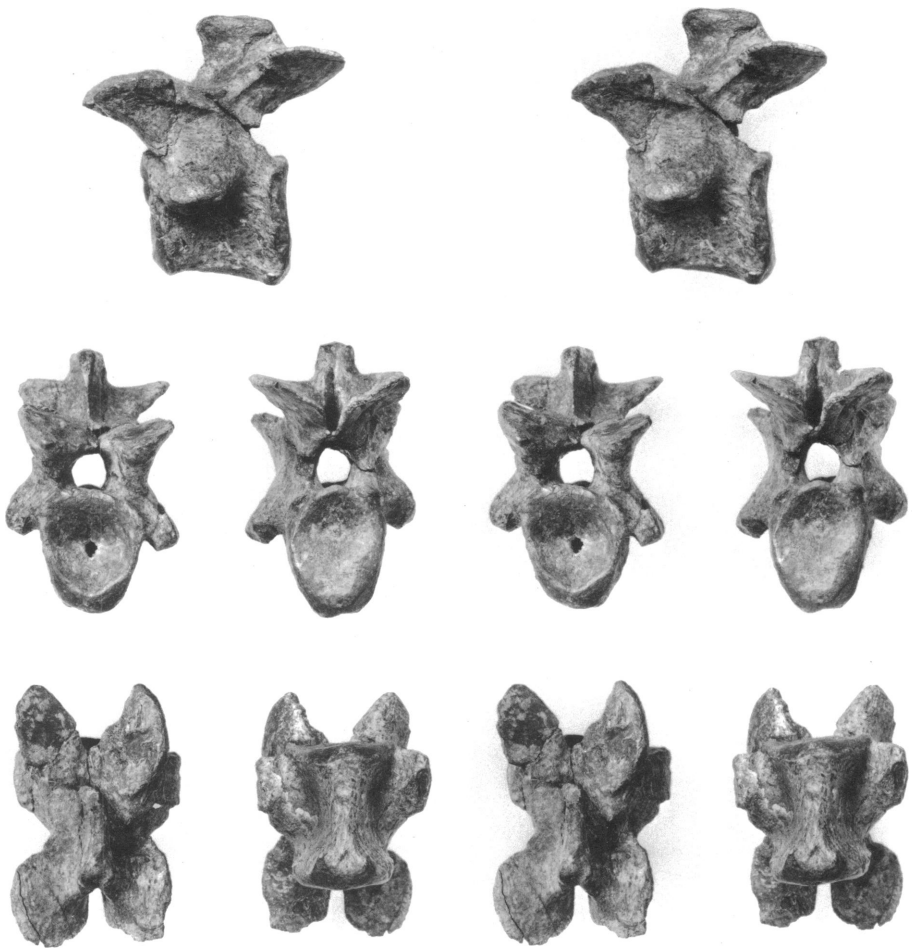

Fig. 116. *Proganochelys quenstedti,* MB 1910.45.2. Cervical 4, see Figure 112.

SMNS 16980 has had all of its caudals, chevrons, and osteoderms disarticulated and is the basis for the figures of the individual caudals (figs. 125–128). The caudals of SMNS 16980 have been identified by comparison with SMNS 17204. The tail of SMNS 17203 is not as well preserved as the tail in the other two Trossingen specimens. There is more crushing and distortion, probably related to the young and less ossified nature of the specimen. Only in this specimen are all the neural arches separated from the centra.

The tail of *Proganochelys* ends in a dermal ossification or sheath referred to here as a tail club for convenience, not as a functional interpretation. The club grades into the dermal osteoderms so that there is a certain amount of ambiguity concerning the extent of the club and the number of caudal centra incorporated. Nonetheless, counts of the caudal centra anterior to the club are different in each specimen. In SMNS 17204 there are 13 caudals anterior to the tail club, in SMNS 16980 there are 14 caudals, and in SMNS 17203 there are 18. The tail club of SMNS 17203 is clearly less extensive than the other two and supposing incorporation of one or more sets of osteoderms would reduce the tail count to 15 or 16, more in line with the other two specimens.

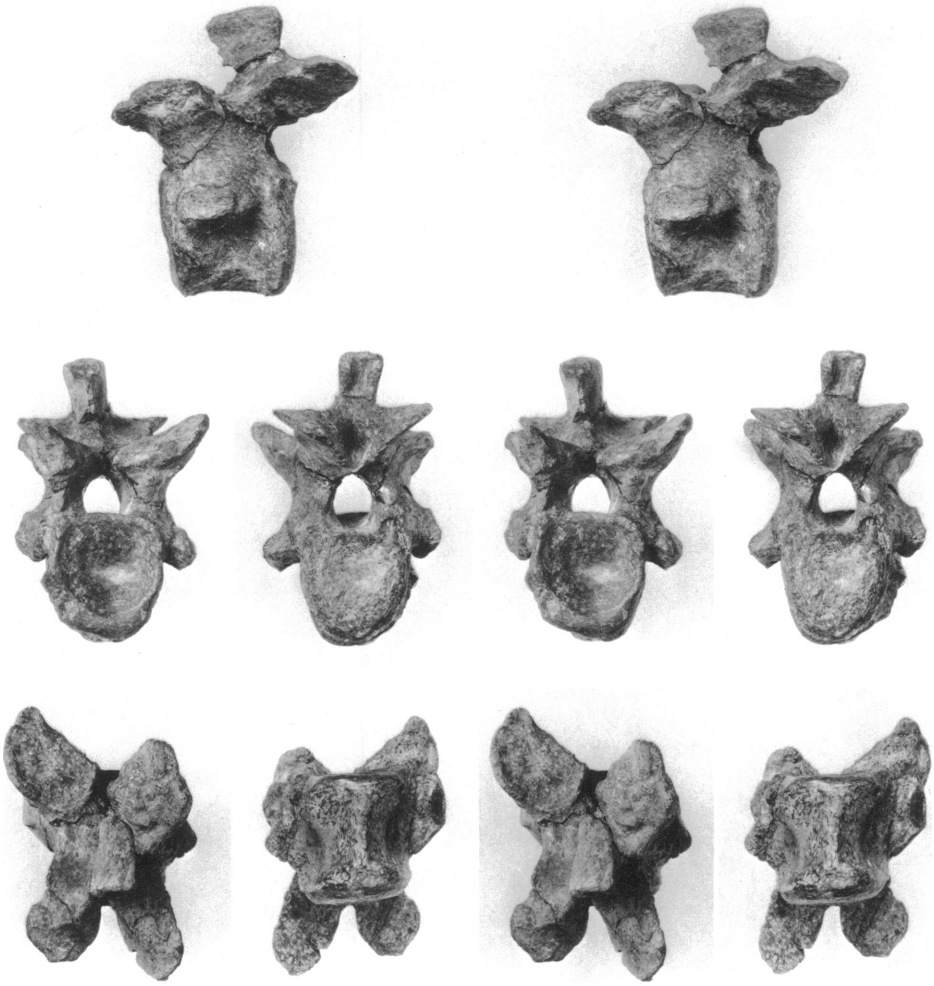

Fig. 117. *Proganochelys quenstedti,* MB 1910.45.2. Cervical 5, see Figure 112.

In SMNS 17204 the tail bones are in the same block as the shell up to caudal 3 where there is a break; all the remaining caudals and club are in a single piece. In SMNS 16980 caudals 1 through 9 are loose, and the remaining caudals and tail club are still in one piece connected by matrix. The tail of SMNS 17203 is separated into five pieces: caudals 1 and 2, caudals 3–7, caudals 8–12, caudals 13–16, and caudals 17 and 18 with the tail club. Except for caudals 10–14 incorporated with the tail club, SMNS 16980 has no osteoderms preserved in association with the loose caudals but in SMNS 17203 the osteoderm association has been maintained.

The caudals of *Proganochelys* are relatively short with very shallow, amphicoelous central articulations similar to the cervicals. The neural arches extend for nearly the length of the centrum. There is only a low ridge on the midline; a well-developed neural spine is absent. The zygapophyses lie well separated from the midline with curved articulations so that the prezygapophyses face dorsally in their medial part and turn medially on their dorsal part.

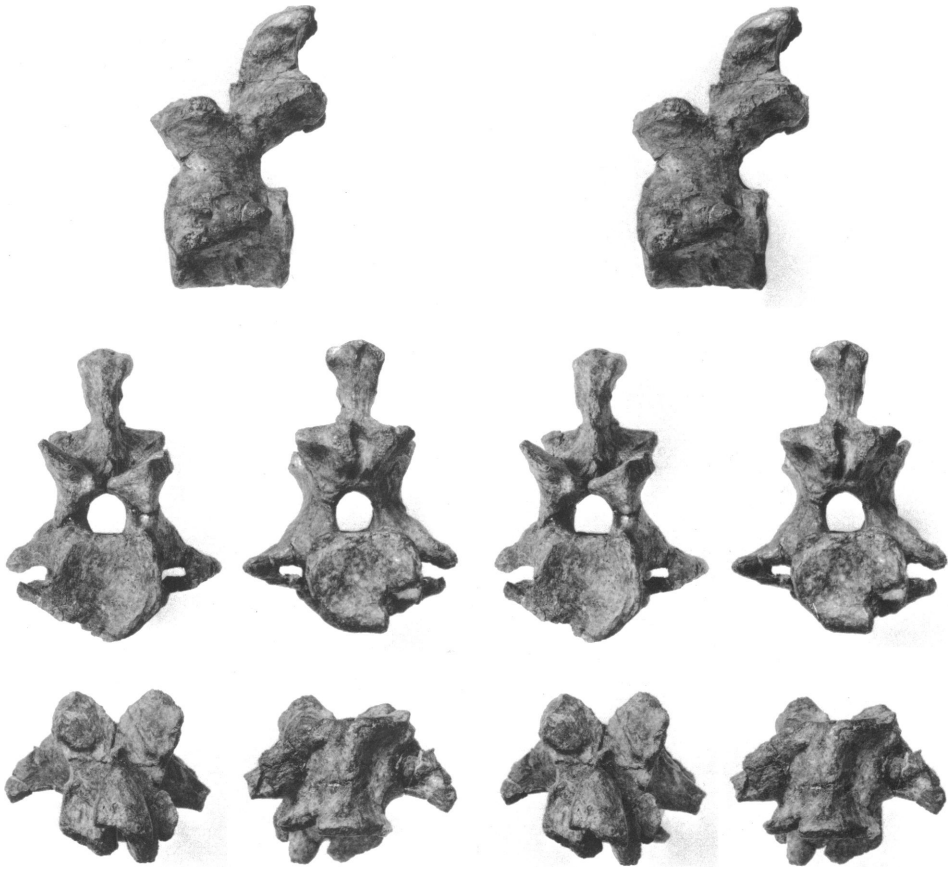

Fig. 118. *Proganochelys quenstedti,* MB 1910.45.2. Cervical 6, see Figure 112.

The transverse processes are relatively long, decreasing in length and thickness posteriorly but always well developed. The first caudal has particularly broad and flat transverse processes in comparison to the more posterior caudals. Well-developed transverse processes appear to be primitive for Casichelydia but in *Captorhinus* only the anterior caudals have them.

The chevrons or haemal arches begin on the third caudal and are attached to posteroventral paired ridges by means of open sutures. The more posterior chevrons are expanded distally.

The caudals of *Proganochelys* are large anteriorly and somewhat shorter, but they do not exhibit the degree of regional differentiation usually seen in turtles. The caudals are higher than long anteriorly and become equidimensional posteriorly with the transverse spines relatively shorter.

The caudal osteoderms are best seen in SMNS 17204 (fig. 132). The dorsal osteoderms consist of three spikes, or triads, one on the midline and one on each side, connected by a strap of bone. The triad arrangement is peculiar to the tail of *Proganochelys*; none of the other osteoderms are in sets of three. There are six sets of triads on the tail of SMNS 17204, evenly distributed from the carapace to the tail club. The first three are about the same size while the succeeding three decrease in size. The triads shift in position so that the anterior ones are nearly transverse

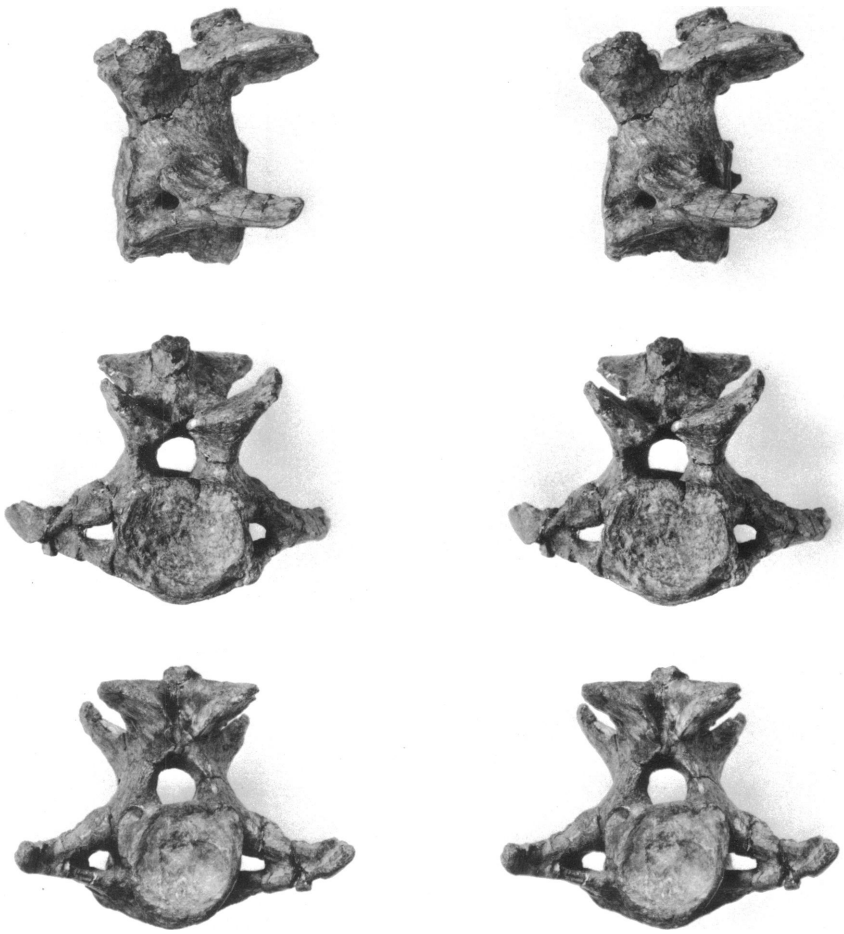

Fig. 119. *Proganochelys quenstedti,* MB 1910.45.2. Cervical 7, see Figure 112.

and the more posterior ones are skewed. This may be natural because some of the triads are not bilaterally symmetrical—the left spine can be larger than the right. Similarly, the triads still articulated with the posterior caudals of SMNS 16980 are not strictly symmetrical either in position or shape. Other, smaller osteoderms occur irregularly along the flanks of the tail and bases of the triads.

The only comparable elements in other turtles are the tail rings of *Meiolania* (Gaffney, 1985b). However, these semicircular structures almost surround the tail and have a strict symmetry consisting of two pairs of low spikes rather than the triads seen in *Proganochelys.*

The tail club is preserved in all three Trossingen specimens and is similar in all of them. It seems to consist of three sets of triads fused together and surrounded by a ground mass of bone. The spikes become less symmetrical and lower posteriorly, ending in what appears to be broken bone in all three tail clubs. Contrary to expectations, the tail club of SMNS 16980 is slightly more robust than the other two, although SMNS 17204 is longer than SMNS 17203.

As with the tail osteoderms, the tail club

Fig. 119. Continued.

of *Meiolania* has a different symmetry from that of *Proganochelys* (Gaffney, 1985b). The club in *Meiolania platyceps* has four sets of two pairs of low spikes in contrast to the three-fold symmetry of *Proganochelys*. Ventrally the solid bone surface of the tail club is covered by a series of C-shaped scales, about two to a vertebral segment. These are similar to laterally elongate osteoderms found loose more anteriorly.

SHOULDER GIRDLE
(table 15, figs. 133–138)

The scapula and coracoid are preserved in good condition on both sides of SMNS 16980 and on the left side of the Berlin specimen, MB 1910.45.2. A disarticulated scapula and coracoid are preserved in less satisfactory condition on the left side of SMNS 17203. In this specimen the dorsal process of the scapula has been pushed through the carapace and the coracoid is separated from the scapula along the suture.

Earlier reports of a cleithrum in *Proganochelys* (Jaekel, 1918a; Romer 1956; Gaffney, 1984; Gaffney and Meeker, 1983; Gaffney et al., 1987) are incorrect. The element thought to be a cleithrum is the dorsal process of the epiplastron (see Epiplastron).

SCAPULA
(fig. 135)

The scapula of *Proganochelys* (fig. 135) consists of an anterodorsal process, a triangular, ventromedial prong (acromial process), and a relatively horizontal central plate bearing the glenoid fossa laterally. When the entire scapulocoracoid is oriented with the flat plate of the coracoid and scapula horizontal, the dorsal scapular process on both sides of SMNS 16980 is at an angle of about 45° with the horizontal. In the Berlin specimen (fig. 136) in which the scapula is not noticeably crushed or distorted, the dorsal scapular process is closer to the vertical and it is hard to determine objectively which is correct, or if both are. If the scapulocoracoid were oriented with the flat plate tilted as in figure 136, then the dorsal scapular process would be vertical. In SMNS 17203 the dorsal process of the scapula is vertical and at right angles to the main body of the scapula, but

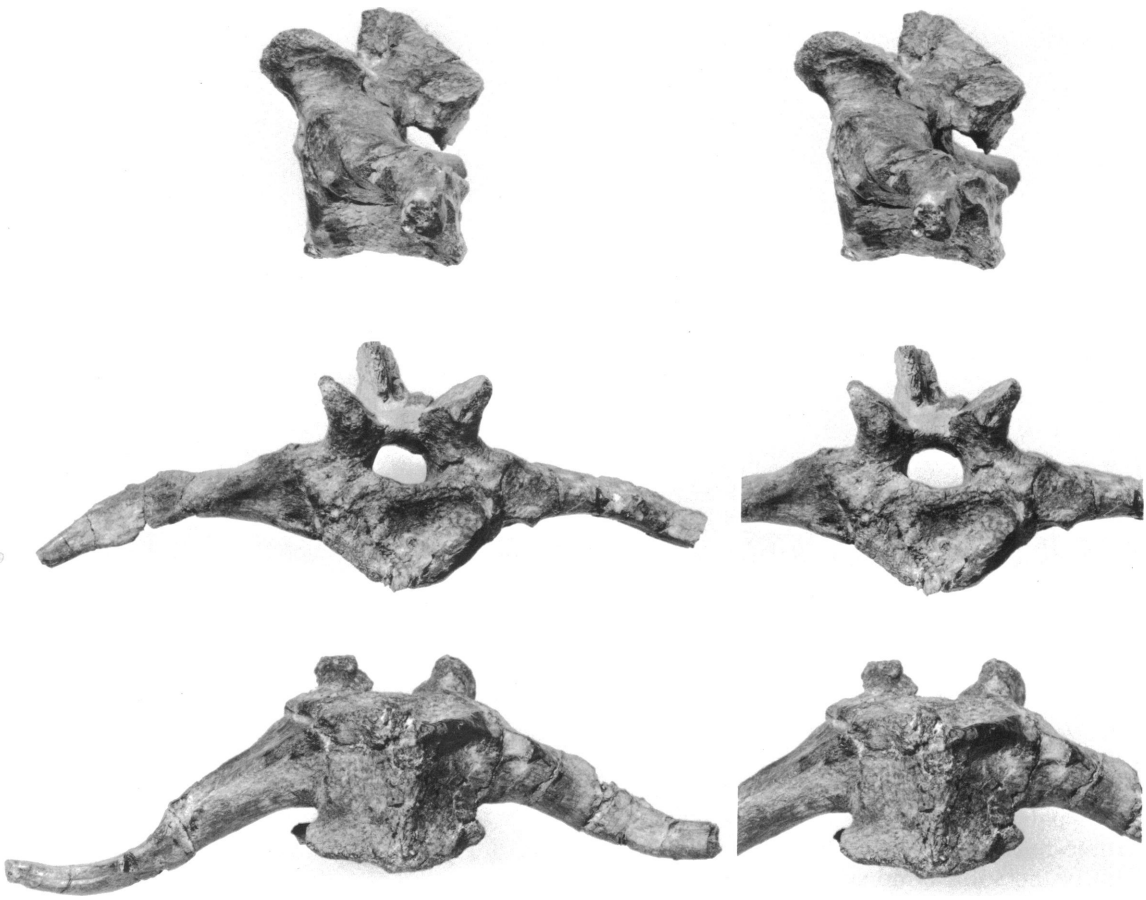

Fig. 120. *Proganochelys quenstedti,* MB 1910.45.2. Cervical 8, see Figure 112.

this specimen has been subjected to extensive crushing and the position may not be as in life. The problem of the orientation of this process is related to the position of the dorsal process of the epiplastron and is discussed under Epiplastron. The dorsal scapular process in casichelydians varies in its orientation but tends to be vertical or inclined anterodorsally so the difference in orientation compared with *Proganochelys* is not great.

The dorsal scapular process in *Proganochelys* is an oval column, somewhat more irregular than the generally smooth, parallel-sided scapular process in most casichelydians. There are poorly defined, longitudinal ridges and grooves on the scapular process of *Proganochelys* that seem to be related to the close approximation of the dorsal process of the epiplastron or the eighth cervical rib. Jaekel (1918a: figs. 17, 28; repeated here as fig. 80) shows the "cleithrum" (=dorsal process of epiplastron) lying along the anterior part of the dorsal scapular process with a shallow groove on this surface. The distal end of the process is expanded and slightly mushroom-shaped in SMNS 17203, a probable result of preservational damage. On both sides of SMNS 16980 the scapular process ends in a rounded surface with a small oval concavity that appears to have been finished in cartilage. In the Berlin scapula the dorsal process terminates in what seems to be a natural,

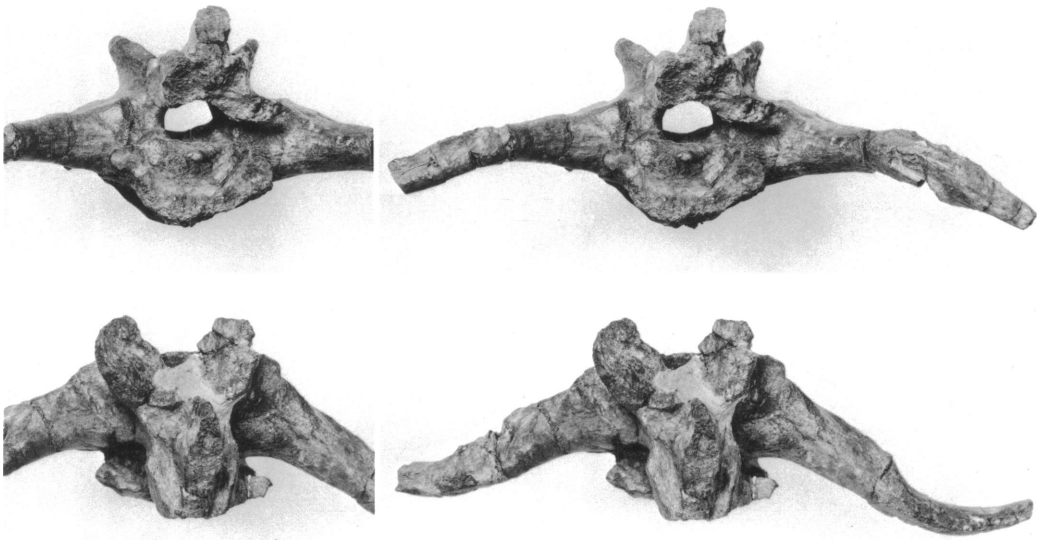

Fig. 120. Continued.

finished surface, and there is no evidence for Jaekel's (1918a) suprascapula (fig. 80). The anterior surface of the scapular tip has a shallow, curved depression that could be for the articulation of the dorsal process of the epiplastron.

The contrast between the dorsal process of the scapula of generalized amniotes and turtles is great (figs. 137, 138). *Proganochelys* and all other turtles have a columnar dorsal process while other amniotes have a flat blade. The flat blade of generalized amniotes provides a large area for muscle insertion and much of this is between the pectoral girdle and the vertebral column while in turtles the pectoral girdle is attached to the shell by more direct articulations rather than by muscles.

The posterior half of the scapula in *Proganochelys* is a roughly horizontal plate bearing the acetabulum posterolaterally, the base of the dorsal process anterodorsally, and the acromial process anteroventromedially. The acromial process, best seen in the Berlin specimen and the right scapula of SMNS 16980, is a triangular prong that has a broad base and narrows ventromedially with an acute termination that apparently articulates with the plastron. The process is essentially formed by three ridges: a horizontal ridge continuous with the main plate of the scapula and coracoid, an anterodorsal ridge which is a web extending from the base of the dorsal process, and a ventral ridge running from the medial margin of the glenoid fossa and separating the ventral surface of the scapula into an anteroventral surface and a posterior surface.

The coracoid or supracoracoid foramen (Romer, 1956) in *Proganochelys* is formed by both scapula and coracoid and lies in the suture between both bones. The presumed homolog is formed entirely in the posterior part of the scapula (anterior coracoid, see below) of *Captorhinus* and other generalized amniotes. Due to the extensive medial excavation of bone in casichelydians, a coracoid foramen is absent in all other turtles.

The acromial process of turtles takes its name from the acromion of mammals, but it is not homologous and has little similarity in the two groups. A different name for this structure in turtles would be best but the term is deeply imbedded in the literature. In any case, the "acromial" process is a chelonian synapomorphy and present in *Proganochelys* and all turtles. In casichelydians the acromial process of the scapula is a long, columnar

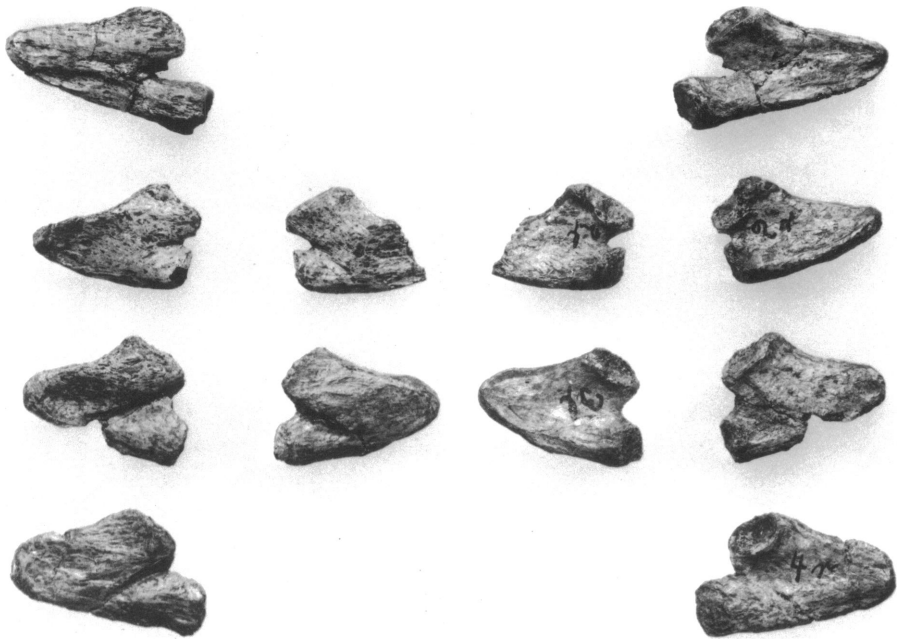

Fig. 121. *Proganochelys quenstedti,* SMNS 16980. Cervical ribs. Two left-hand columns are lateral views; two right-hand columns are medial views. Articulation with particular cervical centra is not known.

extension attaching very near the glenoid so that the scapula is essentially an L-shaped bone. In *Captorhinus* and generalized amniotes there is no ventromedial extension of the scapula and the bone does not extend ventral to the level of the glenoid fossa. *Proganochelys* might be considered morphologically intermediate between the primitive amniote condition and casichelydians, because the acromial process is clearly an extension continuous with the horizontal part of the scapula. The casichelydian condition completely lacks a horizontal plate.

The only suture visible in the scapulocoracoid of *Proganochelys* is a clear one separating the scapula and the coracoid and dividing the glenoid. Nonetheless, there is evidence that the scapula of *Proganochelys* (and all other turtles) contains the anterior coracoid of generalized tetrapods and that the suture seen is really the one between the anterior and posterior coracoid. Topological comparisons between *Proganochelys* and tetrapods with a generalized pectoral girdle having discrete coracoid elements (fig. 138) suggest that the anterior coracoid is incorporated in the scapula of *Proganochelys.* Using the glenoid fossa, the anterior coracoid-posterior coracoid suture, and the coracoid (supracoracoid) foramen as landmarks, the acromial process region of the scapula in *Proganochelys* is most similar topologically to the anterior coracoid of generalized tetrapods. The coracoid foramen in *Proganochelys* lies in the suture while in other forms, such as *Labidosaurus* and *Dimetrodon,* it lies in the anterior coracoid but near the suture with the posterior coracoid. Further evidence comes from a specimen of *Captorhinus* figured by Holmes (1977: fig. 4). Adult *Captorhinus* show no sutures in the scapulocoracoid but the apparently immature specimen figured by Holmes shows three elements: an anterior coracoid partially fused with the scapula and a posterior coracoid completely separated by a suture going through the glenoid. The acromial process of turtles also retains the clavicle-interclavicle contact of the generalized

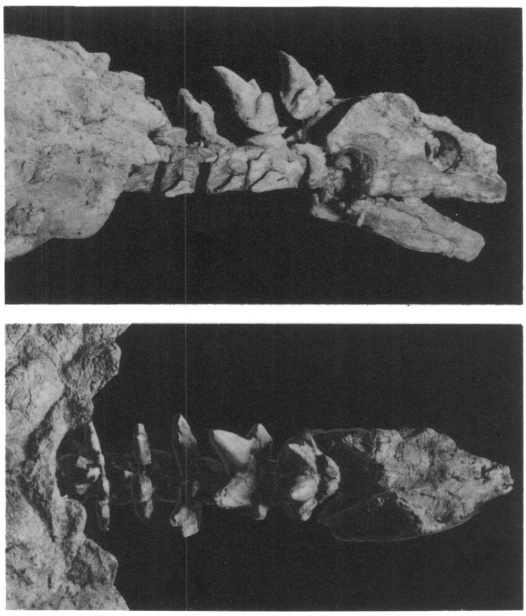

Fig. 122. *Proganochelys quenstedti,* MB 1910.45.2. Specimen as mounted in MB showing positions of cervical osteoderms. The basis for this arrangement is not definitely known. See Jaekel (1918a).

Fig. 123. *Proganochelys quenstedti,* anterior views of dermal ossicles from dorsal surface of neck (see Figure 98). Upper two ossicles are SMNS 16980, lower ossicle is probably SMNS 17203; see text for discussion.

amniote by articulating with the epiplastron-entoplastron of the shell. Further suggestive, but not definitive, evidence comes from the attachment of the supracoracoideus muscle on the anterior coracoid of generalized amniotes (Romer, 1922; Holmes, 1977) and on the acromial process of turtles (Walker, 1973). Therefore, the scapula of turtles is probably homologous to the scapula plus anterior coracoid of generalized amniotes and the coracoid of turtles is homologous to the posterior coracoid in the primitive amniote condition.

The glenoid fossa of *Proganochelys* is formed by the scapula anteriorly and the coracoid posteriorly. It is an ovoid concavity facing ventrolaterally for the articulation of the head of the humerus. In *Captorhinus* and generalized amniotes the glenoid has the "screw-shape" described in the literature (Romer, 1922; Miner, 1925; Romer, 1956; Holmes, 1977). *Proganochelys* has a slight torsion but in general it clearly is similar to the relatively simple glenoid of turtles. The consequence of these differences would appear to suggest that the humeral movements in *Proganochelys* were more like those of casichelydians than of generalized amniotes.

Coracoid

The coracoid of *Proganochelys* is a broad, flat plate contacting the scapula anteriorly, having subparallel medial and lateral margins and a curved posterior border. The medial edge is thinner than the lateral but in general the coracoid is of uniform thickness. In comparison to that of *Labidosaurus* and

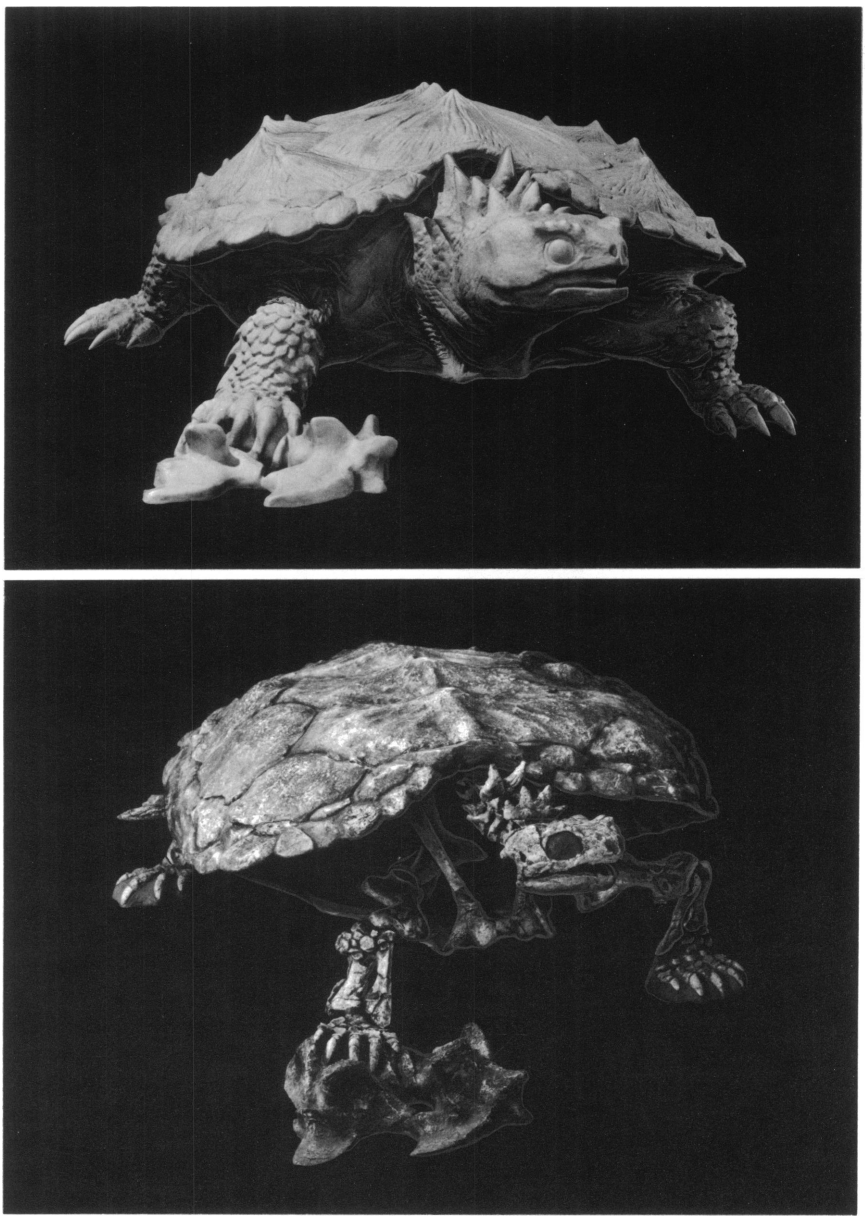

Fig. 124. *Proganochelys quenstedti,* anterior views. Upper, life restoration made at half life size; lower, cast of articulated skeleton of SMNS 16980, showing orientation and placement of dermal ossicles overlying neck.

Dimetrodon the coracoid of *Proganochelys* is much more extensive posteriorly in relation to the glenoid and scapula contact. In the primitive amniote condition the coracoid does not usually extend posteriorly very far beyond the glenoid fossa, but in *Proganochelys* the coracoid has a substantial posterior blade. Casichelydians, however, differ significantly from *Proganochelys* in having a coracoid with a narrow neck close to the

TABLE 14
Comparison of Caudal Vertebrae

	Captorhinus	*Proganochelys*	Casichelydia
Central articulations	Amphicoelous, notochordal	Amphicoelous, shallow	Amphicoelous, shallow
Neural spines	High and narrow	Very low	Moderate
Chevrons	Present, well developed	Present, well developed	Present, well developed
Number of caudals	Estimated at 60+	13–16	30+
Caudal osteoderms	Absent	Present	Absent
Transverse processes	Present only on anterior caudals	Well developed on all caudals	Well developed on anterior caudals
Tail club	Absent	Present	Absent

glenoid and the orientation of the neck and distal blade is posteromedial rather than posterior as in *Proganochelys*. The degree and shape of the distal blade of the coracoid vary considerably in casichelydians where it may be straight and narrow (*Podocnemis*), curved and broad (trionychids), or short and flared (testudinids).

The scapulocoracoid in casichelydians is distinctive among tetrapods in its triradiate shape, analyzed by Walker (1971) as functioning as a truss distributing the shell forces to the limbs. *Proganochelys* has a scapulocoracoid that is essentially a horizontal blade with a dorsal process and is not obviously triradiate. However, it can be readily interpreted as functioning in the same way as the triradiate casichelydian scapulocoracoid. The dorsal process articulates with the carapace as in casichelydians (and/or with the dorsal process of the epiplastron which in turn articulates with the carapace). The ventral plate has a well-developed acromial process for the more anterior plastral articulation and the coracoid blade provides the more posterior plastral articulation, again as in casichelydians.

PELVIC GIRDLE
(table 16, figs. 139–147)

Ilium

The pelvis is present in all five *Proganochelys* specimens, SMNS 16980, SMNS 17203, SMNS 17204, SMNS 15759, and the Berlin specimen. In SMNS 15759 only the ventral plate of the pelvis along with the hypoischia (fig. 145) is preserved. The pelvis in the Berlin specimen (fig. 141) figured by Jaekel (1918a) and repeated in many review works, is badly distorted by anteroposterior crushing, resulting in a pelvis that is unnaturally high and narrow in lateral view. SMNS 17204 (fig. 88) has a pelvis in situ articulated with the shell and hind limbs. It is only visible ventrally but presumably it is complete. In its visible areas it is the most complete pelvis available and the size of the thyroid fenestrae is based on this specimen. SMNS 17203 has the three bones of the left pelvis disarticulated and free of matrix (fig. 142), while the right pelvis is disarticulated and in situ on the ventral surface of the carapace providing limited information. SMNS 16980 has a complete pelvis with sacral ribs (fig. 139) free of matrix and is the basis of the description due to its accessibility and relative completeness. It is not as well preserved as SMNS 17204, however, and the thyroid fenestrae and areas of the pubic and ischiac plate have been restored during preparation.

The pelvis of an adult *Proganochelys* probably was completely fused because pelvic sutures have been seen only in the juvenile SMNS 17203. SMNS 16980 has sacral rib-pelvis sutures but none are visible within the pelvis, even in the acetabulum where they are usually persistent in turtles.

There are two sacral ribs and vertebrae in *Proganochelys* (fig. 139) as in *Captorhinus* (Fox and Bowman, 1966; Heaton and Reisz, 1980) and casichelydians. Also as in these taxa, the first sacral rib is much larger than the second. In *Proganochelys* the ribs are

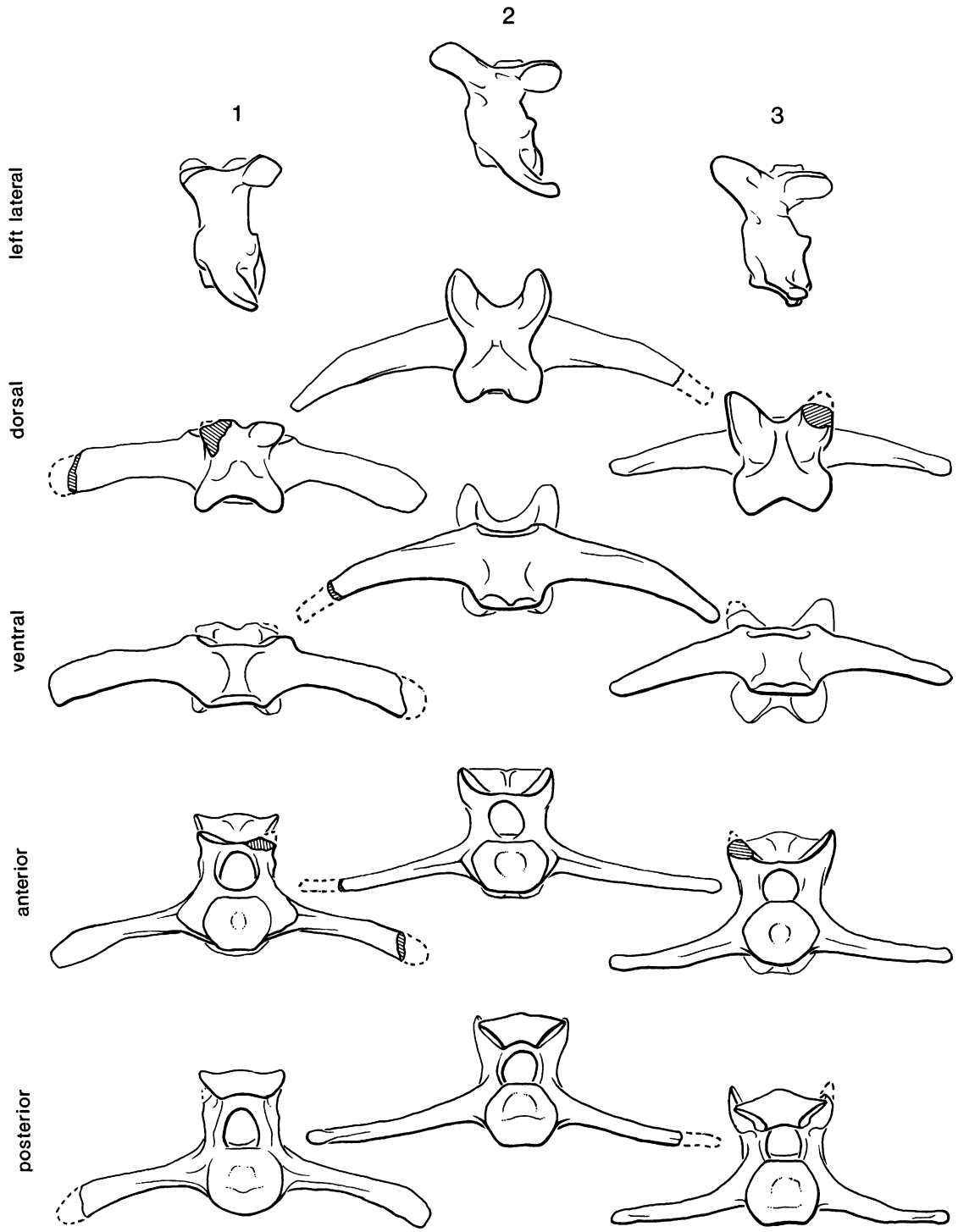

Fig. 125. *Proganochelys quenstedti,* SMNS 16980. Caudal vertebrae 1–3.

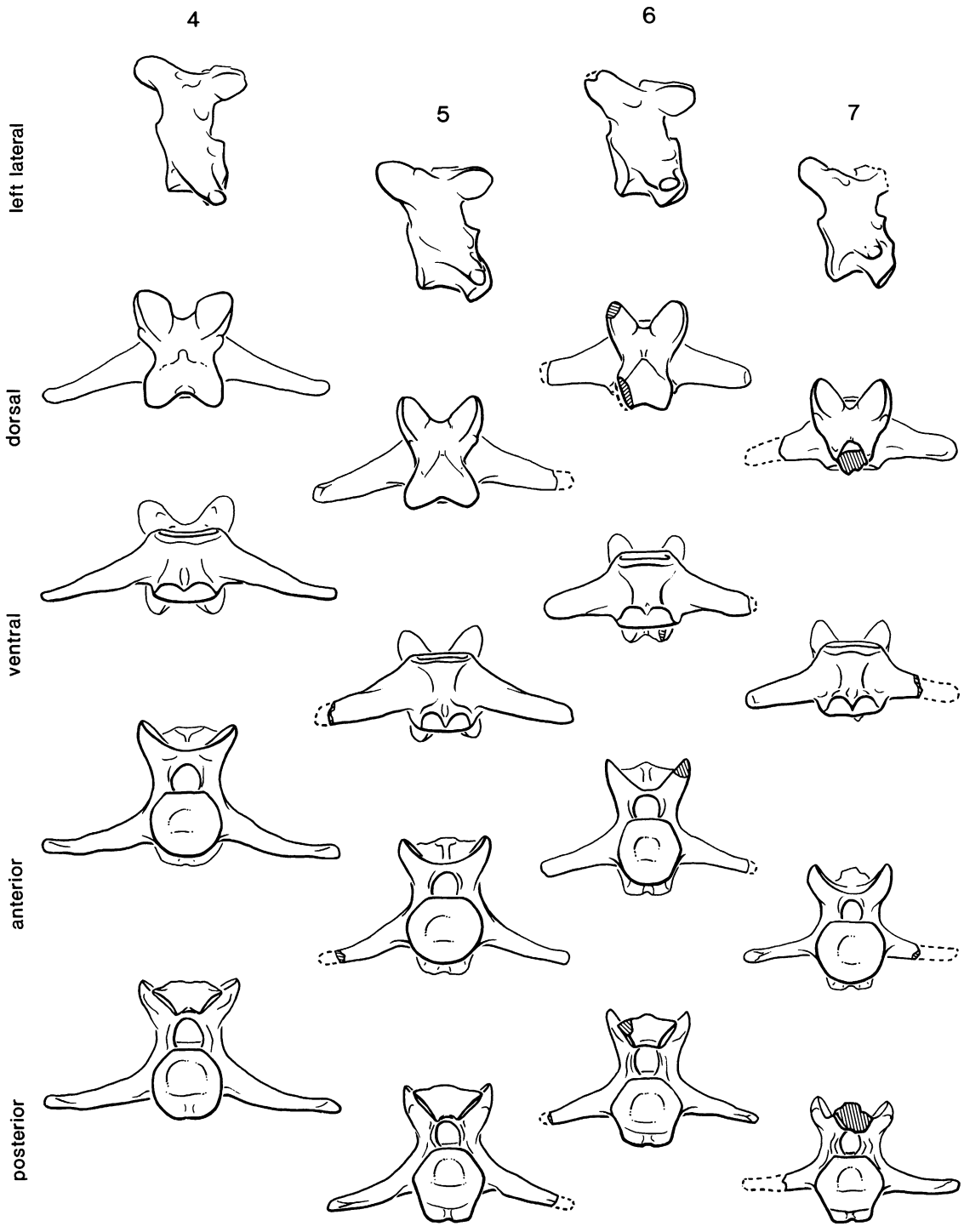

Fig. 126. *Proganochelys quenstedti,* SMNS 16980. Caudal vertebrae 4–7.

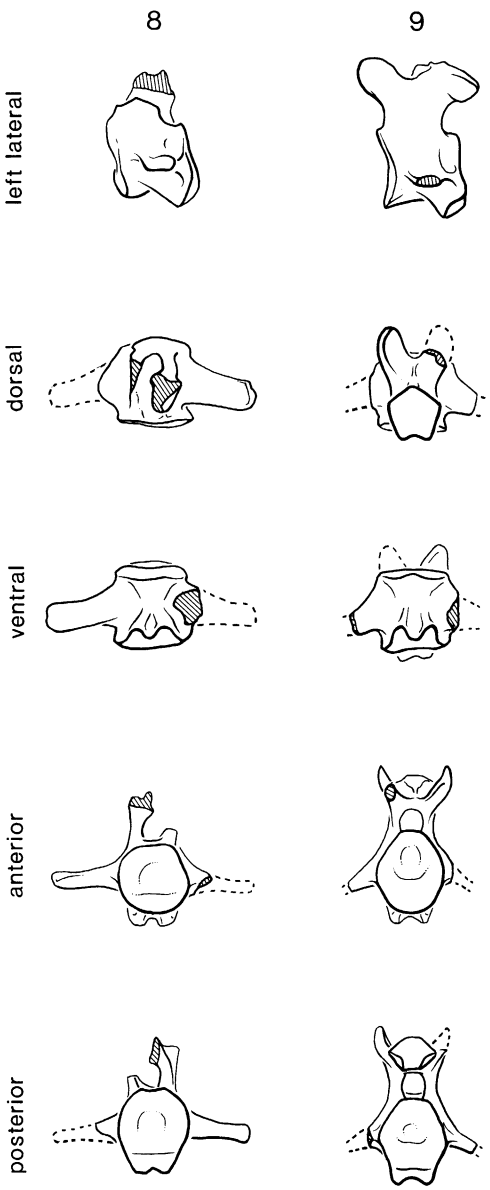

Fig. 127. *Proganochelys quenstedti,* SMNS 16980. Caudal vertebrae 8 and 9.

tightly attached distally to the medial surface of the ilium, with a large, oval space separating the ribs. The anterior articulation of the centrum of the first sacral is concave as in other turtles and receives the convex centrum of the last thoracic vertebra. The contact between first and second sacral centra is flat and synarthritic, also as in other turtles. The posterior articulation of the second centrum is convex with a small concavity in its center; this central articulation varies among Casichelydia. In *Captorhinus* all the central articulations are amphicoelous and notochordal.

The sacral zygapophyses are inclined at a steep, nearly vertical angle, and nearly meet ventrally in *Proganochelys.* They are very close together, closer than in the cervicals or caudals. This pattern of closely approximated sacral zygapophyses can be seen in casichelydians but *Captorhinus* has sacral zygapophyses that are much further apart.

In casichelydians the neural spines of the sacrals are usually attached to the carapace by cartilage or connective tissue rather than by suture, and this seems to be the case in *Proganochelys.* The neural spines in *Proganochelys* are distinctly developed, and higher than in most casichelydians but comparable to those of *Captorhinus.*

The ilium of *Proganochelys* is a relatively massive element with an expanded dorsal portion different from that of *Captorhinus* and other turtles (figs. 143–144). In casichelydians the ilium is a relatively high structure, extending dorsally or posterodorsally as a column from the acetabulum and expanding distally to varying degrees (Zug, 1971). The pelvis of *Captorhinus* is only partially described in the literature (Fox and Bowman, 1966; Heaton and Reisz, 1980) and I have relied on the descriptions of *Labidosaurus* (Broili, 1904) and primitive pelycosaurs (Romer and Price, 1940), as well as *Seymouria* (White, 1939) for information on the pelvis in generalized amniotes. The ilium of generalized amniotes is a long, posterodorsally directed spine that bears the sacral rib articulations medially and may become dorsally expanded to a varying extent (*Captorhinus, Labidosaurus*). *Petrolacosaurus* (Reisz, 1981) and primitive pelycosaurs (Romer and Price, 1940; Reisz, 1980) have the narrow ilium seen in protorothyrids (Carroll, 1969), strongly suggesting that the primitive condition for diapsids and synapsids is the narrow ilium seen in protorothyrids and that the slightly expanded ilium of captorhinids is a synapomorphy with turtles.

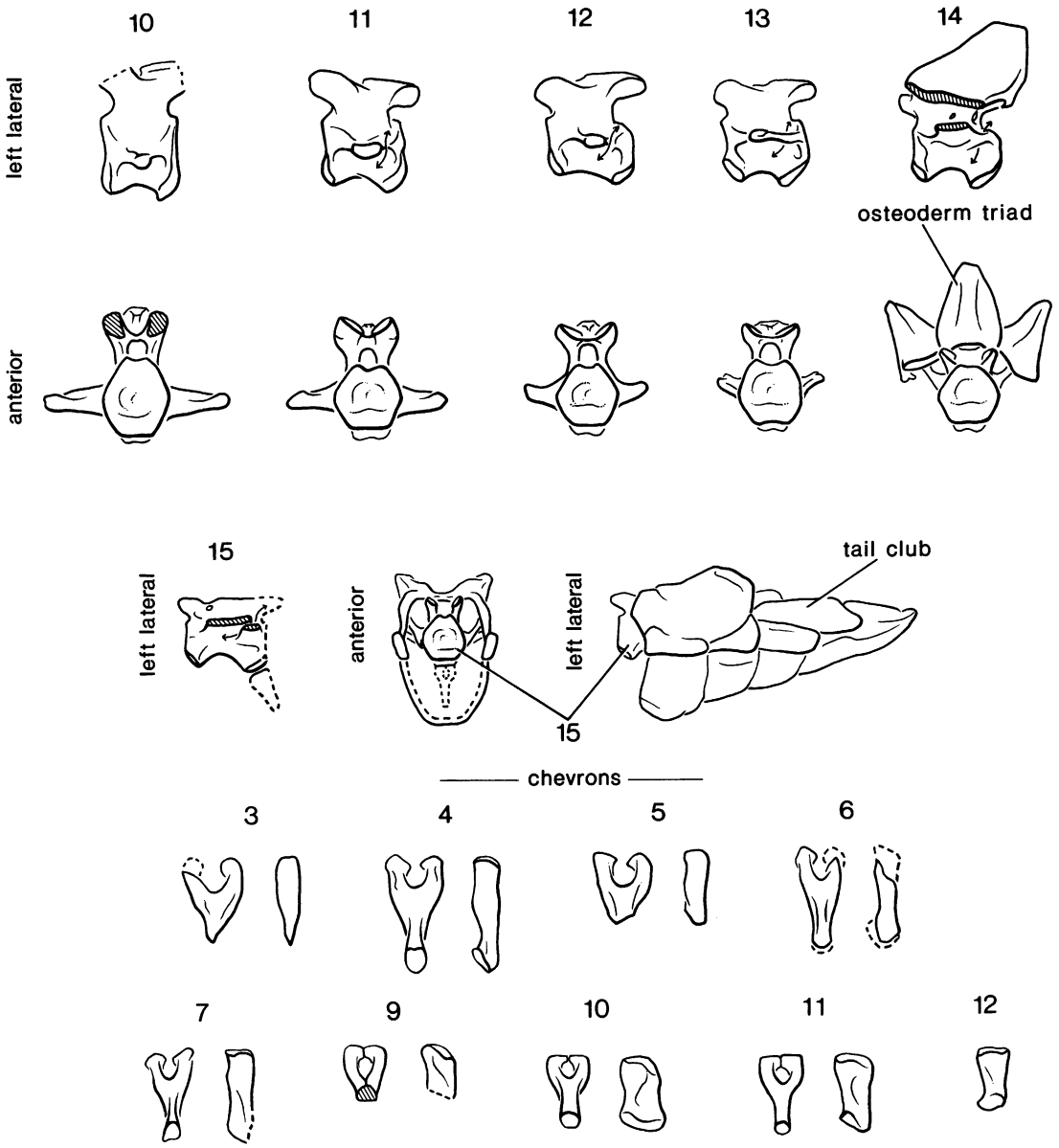

Fig. 128. *Proganochelys quenstedti,* SMNS 16980. Caudal vertebrae 10–15, tail club, and chevrons.

In *Proganochelys* the dorsal part of the ilium is greatly expanded anteroposteriorly, even more than in casichelydians. Anterodorsally the ilium of *Proganochelys* is enlarged into a rounded process bearing the large sacral rib medially and an oval, raised tubercle dorsally. The tubercle contacts similar size tubercles on the carapace in what seems to be an unsutured, moveable articulation. The articular tubercles are seen on the Berlin specimen and SMNS 16980 but not on SMNS 17203, presumably due to immaturity, but also possibly damage.

The dorsal portion of the ilium of *Proganochelys* narrows posteriorly to end in a posteriorly directed spine extending back from

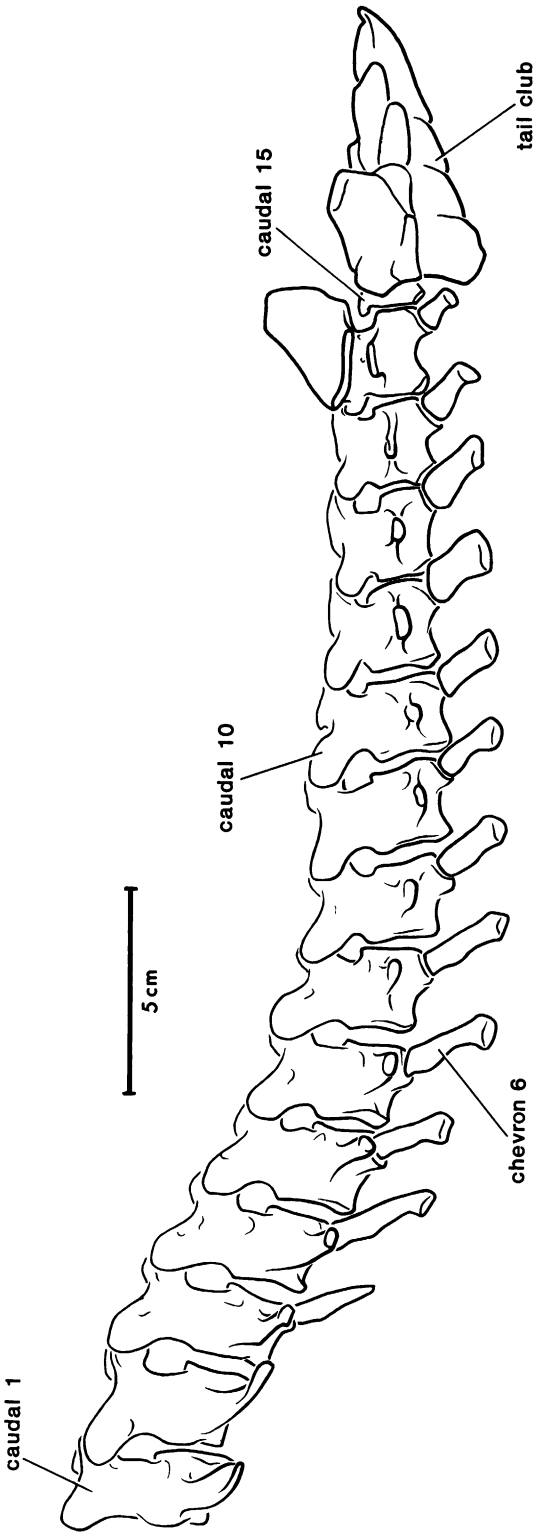

Fig. 129. *Proganochelys quenstedti*, SMNS 16980. Articulated tail in lateral view. All unattached osteoderms removed.

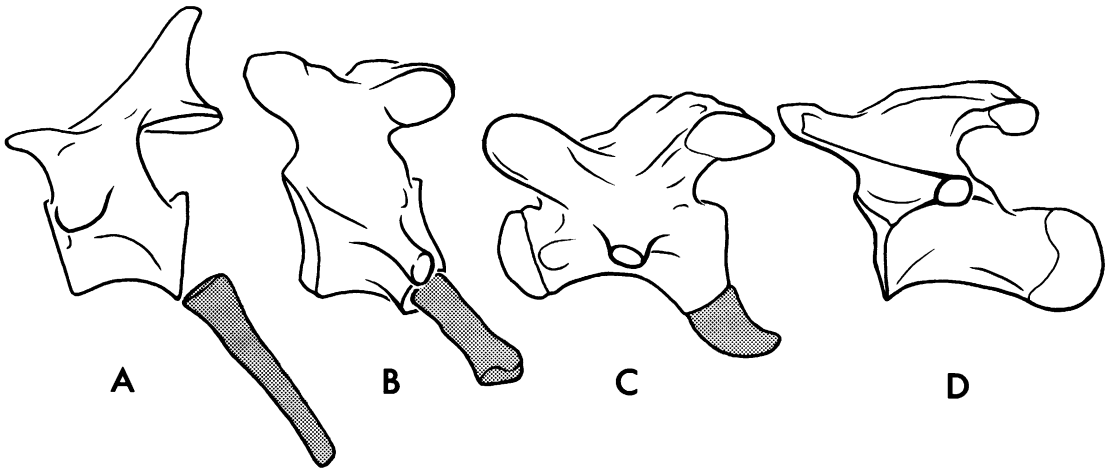

Fig. 130. Comparisons of fifth caudal vertebra. Anterior to the left, haemal spines stippled. **A,** *Captorhinus* sp., from Heaton and Reisz (1980) and AMNH 19393, 19395. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Macroclemys temmincki,* AMNH 58251. **D,** *Podocnemis expansa,* AMNH 62947.

the main region of the ilium. This ilial process tapers posteriorly to end in a blunt projection, oval in cross section. The medial surface of the ilium articulates with the sacral ribs along the dorsal edge of the ilium in *Proganochelys* and casichelydians, and this region would then seem to be homologous in both. The great dorsal extension of the ilium in casichelydians would thus result from a posterodorsal elongation of the neck between sacral articulation and acetabulum. This elongated neck is a casichelydian synapomorphy. The Berlin specimen is crushed anteroposteriorly giving it the appearance of a more "normal" turtle pelvis, and this, unfortunately, is the specimen that has been repeatedly figured in review works (such as Carroll, 1988, figs. 10–25).

In SMNS 17203 the sutures in the acetabulum can be seen. As in other tetrapods this concavity for the articulation of the femoral head is made up of the ilium, pubis, and ischium meeting in a tripartite, Y-shaped suture. The three bones equally form the acetabulum. The acetabulum of *Proganochelys* differs from that of other turtles and most generalized amniotes in being a very solid, relatively deep concavity with well-formed margins all around its circumference. The bone around the acetabulum appears swollen, so that the areas supporting the acetabulum are thicker than the other parts of the pelvis. In general, the acetabulum of all turtles, *Proganochelys* and casichelydians, tends to be better developed than in generalized amniotes, such as *Captorhinus.*

Pubis

The pubis in *Proganochelys* forms the anteroventral third of the pelvis from the acetabulum to the lateral pubic process. As in other tetrapods, the pubis meets the ilium posterodorsally and the ischium posteroventrally. Good sutures are only seen in SMNS 17203. The pubis of *Proganochelys* is a curved plate that forms the anterior half of the pelvis in ventral view. On the midline the two pubes meet to form a small epipubic process, similar in size to the ossified (not the calcified cartilage extension) epipubis seen in many casichelydians. Some other turtles, such as baenids (Hay, 1908), however, have a large ossified epipubic process, but this does not occur in *Proganochelys.* On the ventral midline *Proganochelys* has a low ridge where the pubes and ischia meet.

Labidosaurus (Broili, 1904) has an indentation where the pubes meet on the midline; *Seymouria* (White, 1939) has a slight anterior extension, and the condition in *Captorhinus* (based on AMNH specimens) appears to be similar. The development of an epipubic process would appear to be a chelonian synapomorphy.

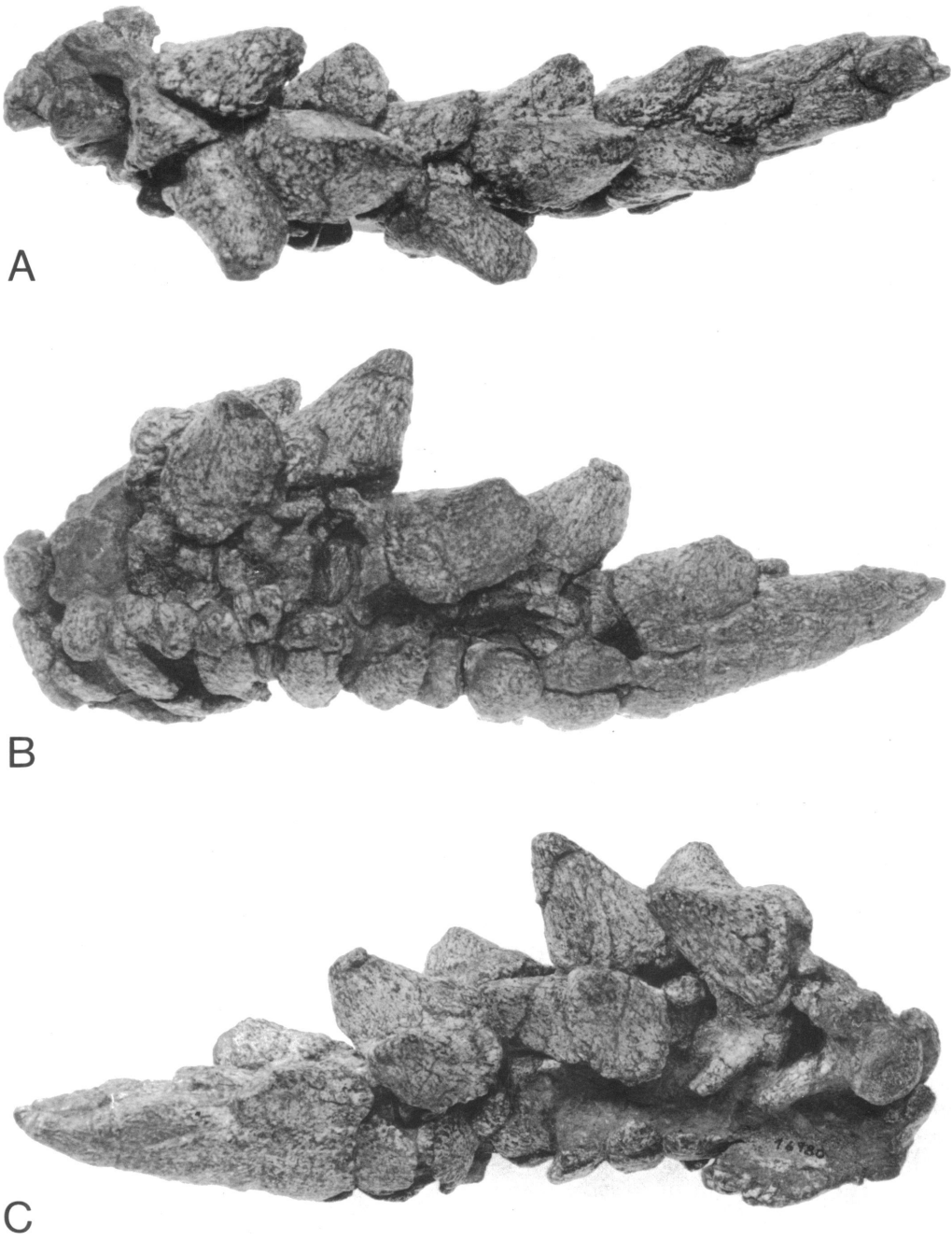

Fig. 131. *Proganochelys quenstedti,* SMNS 16980. Tail club; fine stipple are caudal vertebrae; coarse stipple are chevrons.

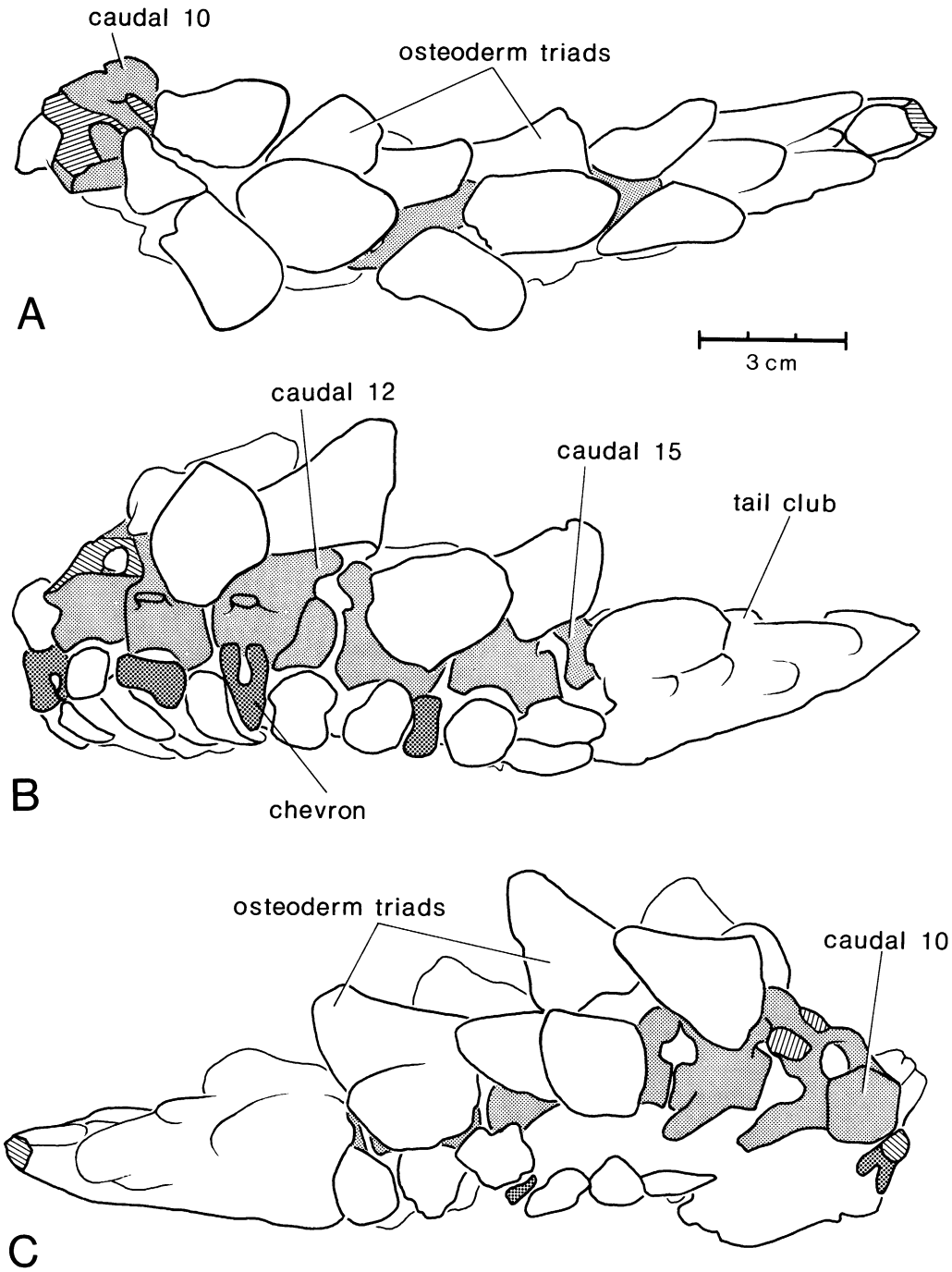

Fig. 131. Continued.

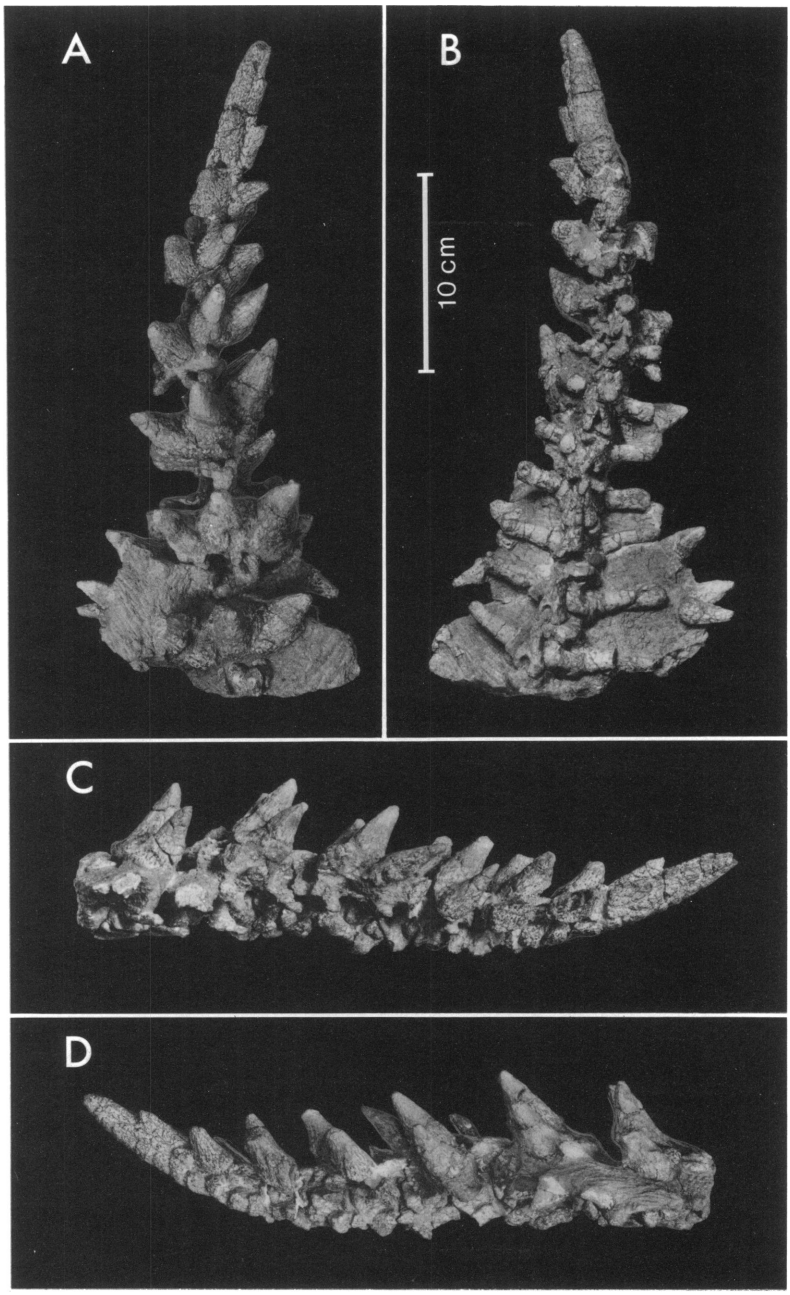

Fig. 132. *Proganochelys quenstedti,* SMNS 17204. Articulated caudal vertebrae and osteoderms. **A,** dorsal; **B,** ventral; **C,** left lateral; **D,** right lateral.

The ventral part of the pubis is a curved plate, concave dorsally, with an anteroventrolateral process (the lateral pubic process) that meets the plastron. Distally there is a smooth, oval foot that articulates with an oval concavity on the plastron. The articulation seems to be a moveable one; a suture is not present. This type of articulation is similar

TABLE 15
Comparison of Shoulder Girdle

	Captorhinus	*Proganochelys*	Casichelydia
Clavicle and interclavicle	Ventral part of shoulder girdle	Part of plastron	Part of plastron
Interclavicle (entoplastron) relatively large and with strong median stem	Yes	Yes	No
Interclavicle (entoplastron) arrowshaped with distinct posterolateral process	No	Yes	Yes
Dorsal process of scapula	Broad, thin blade	Narrow columnar process	Narrow columnar process
Anterodorsal articulation of scapula with dorsal process of epiplastron (=clavicle)	Present	Present	Absent
Acromial process of scapula	Absent	Short, triangular	Long, columnar
Anterior coracoid	Discrete ossification	Fused with scapula	Fused with scapula
Glenoid fossa	"Screw-shaped"	Concave	Concave
Coracoid shape	Flat plate without posterior extension	Flat plate with posterior extension	Columnar with variable posteromedial expansion
Coracoid foramen	Formed by scapula	Formed by scapula and coracoid	Absent

to one seen in generalized cryptodires, such as baenids and pleurosternids, where an articulation facet persists. The epipubic process and the lateral pubic process in *Proganochelys* reach anteriorly to about the same extent.

In generalized amniotes the obturator vein penetrates the pubis through the obturator foramen, a small hole ventral to and slightly ahead of the acetabulum. In casichelydians the obturator foramen is included in a very large opening, the thyroid fenestra, that is formed by the pubis and ischium and may be merged at the midline or only separated by cartilage. In *Proganochelys* this region is completely preserved only in SMNS 17204; the other specimens have lost bone in this area, thereby enlarging the foramen. SMNS 16980 (fig. 139) has breaks in this area and unnaturally large fenestrae were restored during preparation. In SMNS 17204 (fig. 88) it can be seen that *Proganochelys* has a small foramen (not the large thyroid fenestra of casichelydians), which is in the position of the obturator foramen of generalized amniotes.

Ischium

The ischium in *Proganochelys,* as in other tetrapods, forms the posteroventral third of the pelvis. It is a curved plate, concave dorsally, with an indistinct posteroventral enlargement, the lateral ischial tuberosity. The contact between pubis and ischium on the ventral plate of the pelvis is not preserved in any of the specimens. The disarticulated pubis and ischium of SMNS 17203 is broken along the contact area where the bones are thinner.

The most prominent feature of the ischium is a large, rounded tubercle on the midline of the ventral surface. This tubercle was posterior to the posterior margin of the plastron as can be seen in SMNS 17204 and SMNS 16980 (the latter by articulating the lateral pubic processes with contact areas on the plastron). In other turtles with small plastra, such as chelydrids, the ischia are also posterior to the plastron. The tubercle is not developed in SMNS 17203, presumably due to

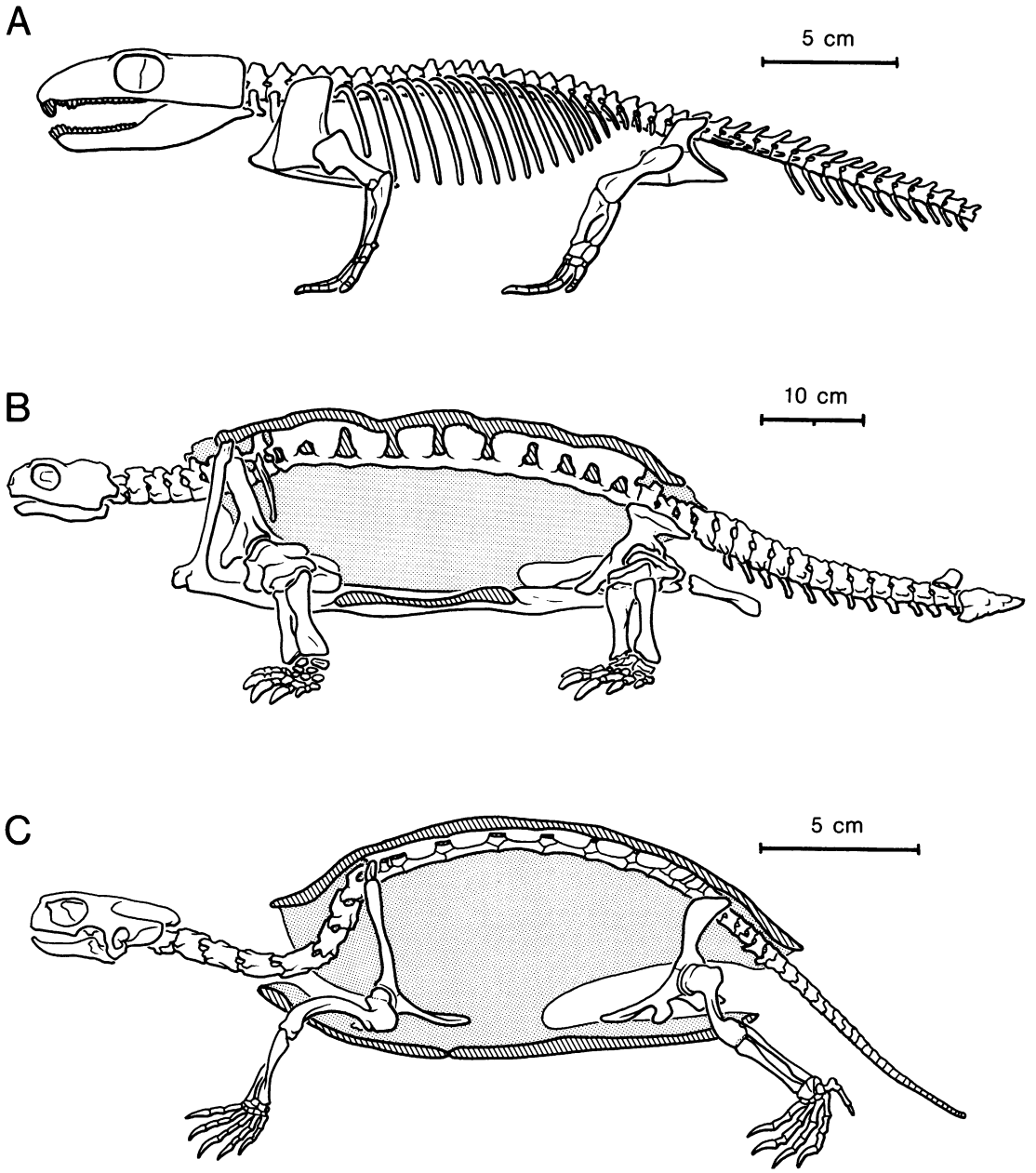

Fig. 133. Comparison of turtles and a primitive amniote. The two turtles have the shell (but no other skeletal elements) sectioned parasagittally, just to the left of the midline. **A,** *Captorhinus* sp., Early Permian, from Heaton and Reisz (1980), distal portion of tail deleted. **B,** *Proganochelys quenstedti,* SMNS 16980, Late Triassic. **C,** *Emys orbicularis,* from Bojanus (1819) and specimens, Recent.

the immaturity of this specimen. In the Berlin pelvis the tubercle is present but the pelvis lacks its posterior part and the break goes through the tubercle so that the posterior half of it and the ischia are missing. The ischial tubercle is roughly mushroom-shaped, the

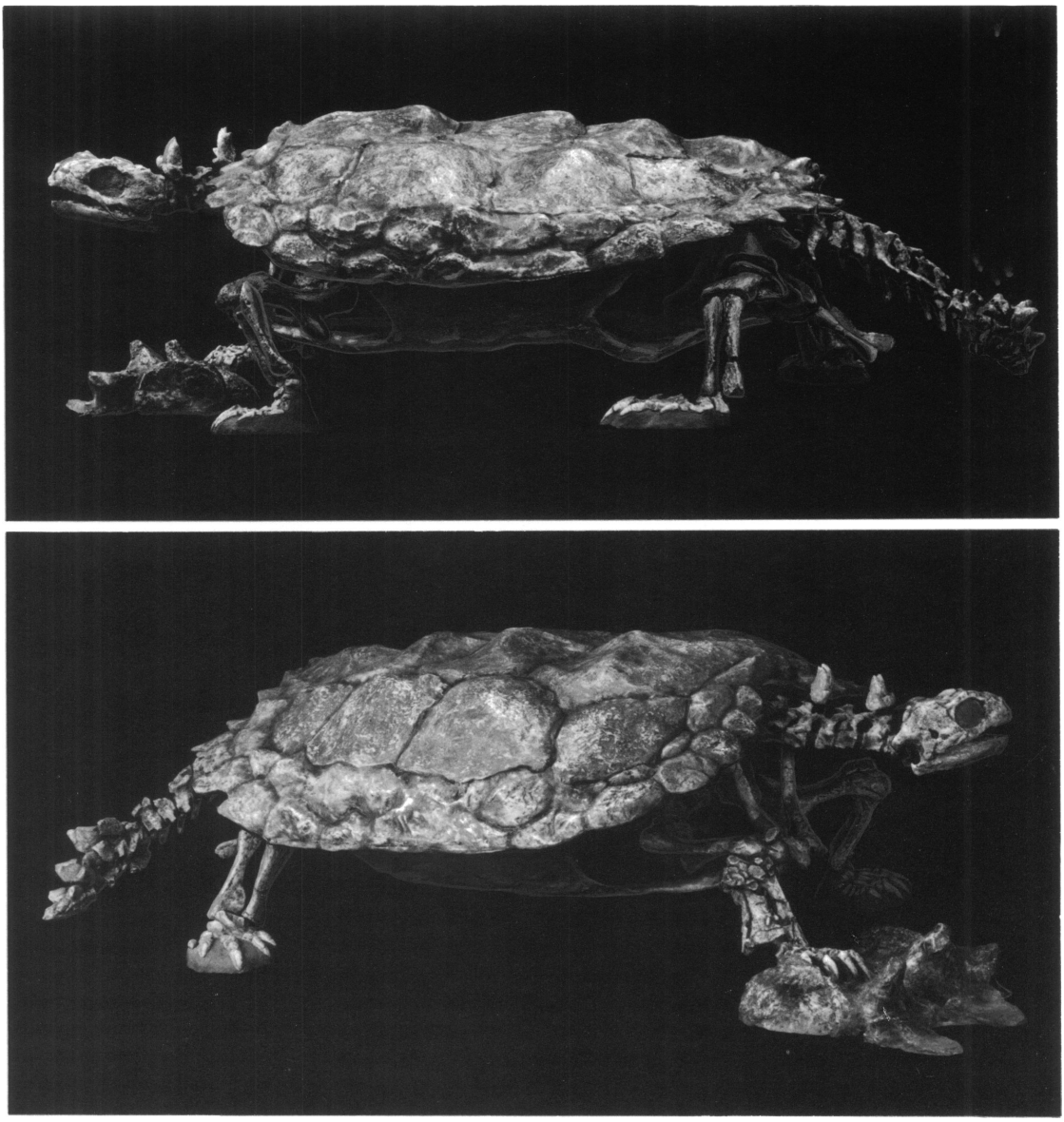

Fig. 134. *Proganochelys quenstedti,* cast of SMNS 16980. Lateral views of mounted skeleton.

ventral part being separated from the main plate of the ischia by a constriction. The tubercle is rounded but irregular in shape and is of about the same size in SMNS 17204 and SMNS 16980.

The posterior limits of the ischia differ in SMNS 16980 and SMNS 17204 (figs. 88, 139). In SMNS 16980 the ischia end at the ischial tuberosity while in SMNS 17204 they continue posterior to it. This is not due to differences in position of the tuberosity because the relations to other features of the pelvis are the same. The posterior ischial margin in SMNS 16980 has shallow, paired concavities; in SMNS 17204, however, the posterior ischial margin consists of paired convexities with a shallow midline indentation. The lateral ischial process in SMNS

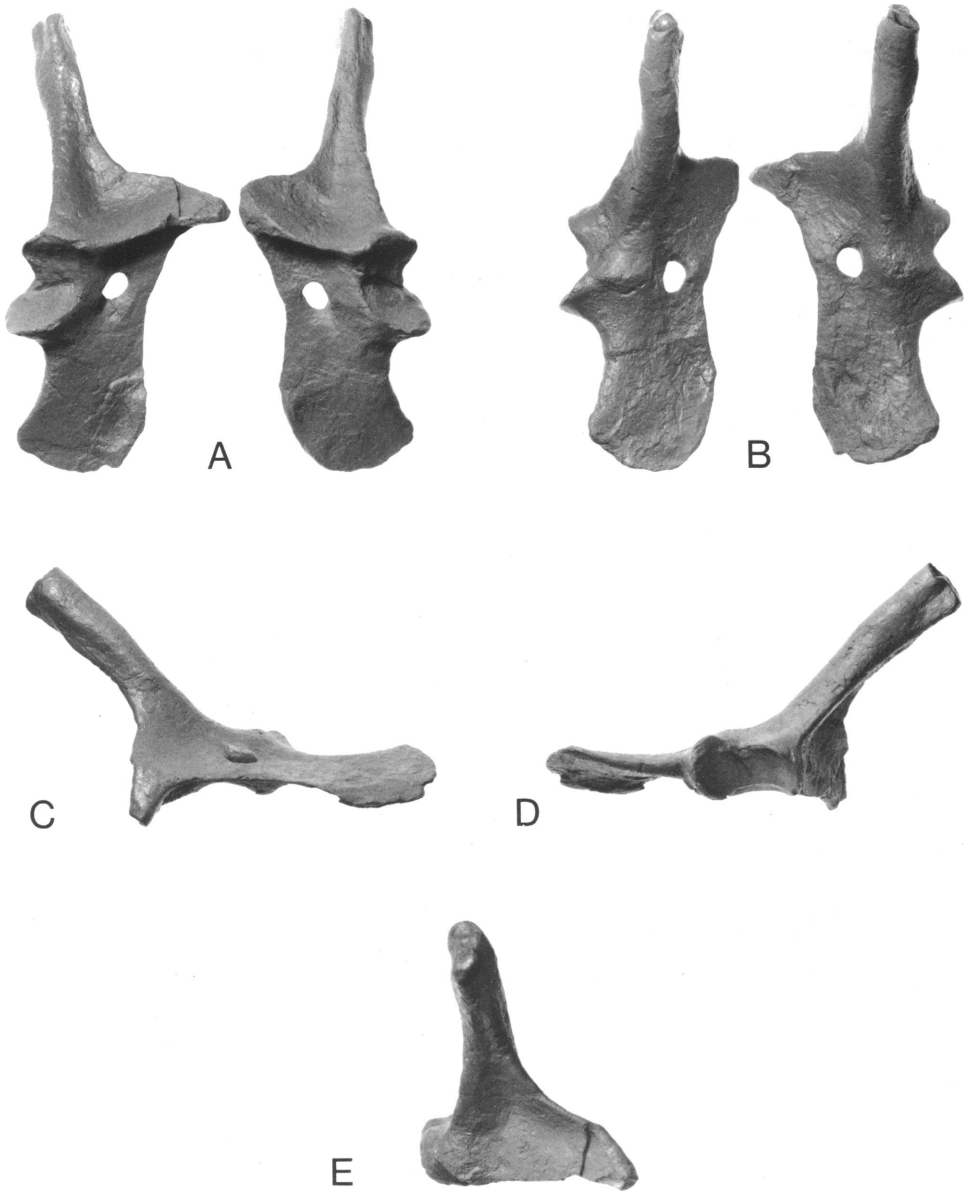

Fig. 135. *Proganochelys quenstedti,* cast of SMNS 16980. Scapula-coracoid. **A,** right and left in ventral view; **B,** right and left in dorsal view; **C,** right in medial view; **D,** right in lateral view; **E,** right in anterior view.

17204 is a rounded obtuse corner with little similarity to that of other turtles. This difference in the ischium of *Proganochelys* appears to be related to the hypoischium which articulates on the posterodorsal margin of the ischium. It is likely that this area is more cartilaginous in SMNS 16980 and reflects its immaturity with respect to SMNS 17204.

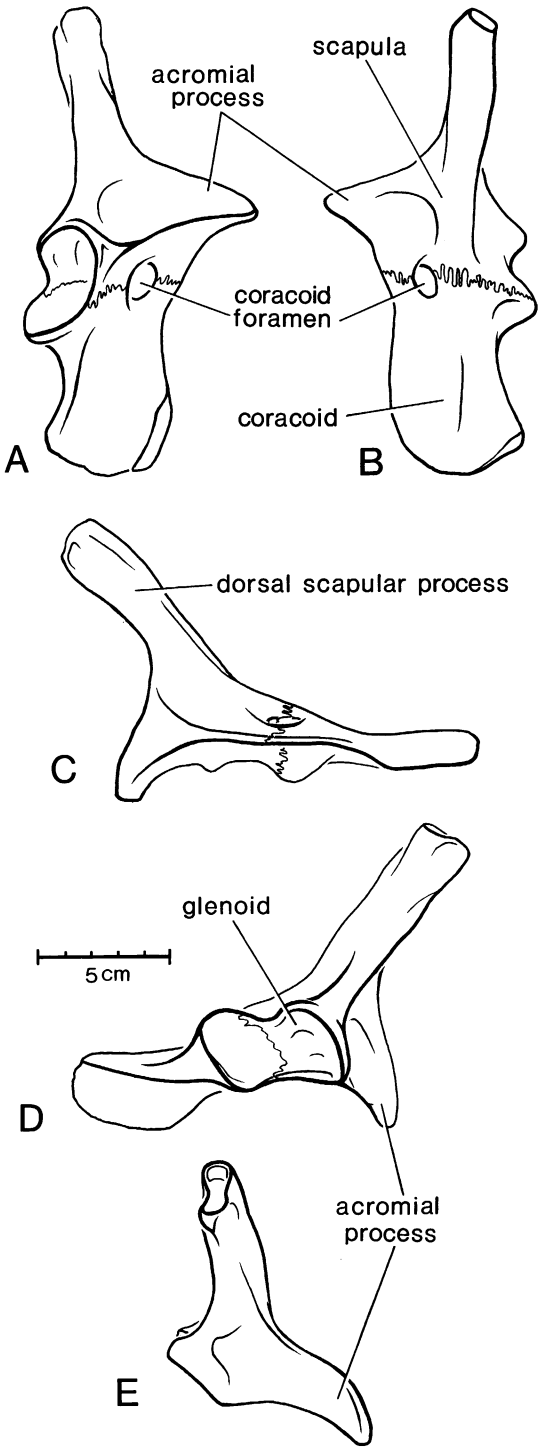

Fig. 135. Continued.

There is also the possibility that this a sexual difference although there is no recent analog.

It would appear that, given the posterior overhang of the pelvis in *Proganochelys* and the lack of an ischial-plastron articulation in it and in some casichelydians, the presence of an ischial-plastron contact in pleurodires and other groups of cryptodires may be independently acquired within the Casichelydia.

The ischium of generalized amniotes is a broad, curved plate, extending posteriorly to a greater extent than in turtles, including *Proganochelys*. Casichelydians, however, are advanced over *Proganochelys* in having a smaller ischium, considerably abbreviated by the anterior enlargement of the thyroid fenestra and the posterior reduction of the ischium. The result is that in most casichelydians the ischium is more rod- or trusslike than platelike.

Hypoischium

Four of the *Proganochelys* specimens have postpelvic ossifications that apparently lie in the plane of the ventral plate of the pelvis and articulate with the ischia. In two of the specimens these ossifications are single; in the other two they are paired. In SMNS 17204 (fig. 88) there is a single, bilaterally symmetrical plate preserved in situ, articulating with the ischia. A nearly identical plate is associated with SMNS 16980 (fig. 146) and assumed to have the same relationship with the pelvis. In SMNS 15759 (fig. 145) there is a pair of plates articulating in situ with a pelvis, and, a pair of similar plates in SMNS 17203 (fig. 145) are assumed to be the same as in SMNS 15759. The similarity of the ossifications to structures termed by various authors (see below) the "hypoischium" is not great enough to conclude that the elements are homologous, but the term is nonetheless used here because of its descriptive aptness and because the elements termed hypoischium in the literature are certainly the closest things to the structure in *Proganochelys*. These structures are not known in extinct amniotes nor in any other turtles. The single type of hypoischium is described first, then the paired form.

The single form of the hypoischium of *Pro-*

Fig. 136. *Proganochelys quenstedti,* MB 1910.45.2. Left scapula-coracoid. Left, lateral view; right, anterior view.

ganochelys (fig. 146) is a flat, triangular plate lying horizontally behind the ischia with its apex pointed anteriorly. Anterolaterally the plate is thickened into paired protuberances that end in ovoid concavities, which in SMNS 17204 articulate with the posterodorsal margin of the ischia. In SMNS 17204 these protuberances are much thicker and more extensive than in SMNS 16980. In SMNS 16980 the hypoischium is relatively flat anteriorly but in SMNS 17204 the thickened areas are larger and a narrow trough is formed anteriorly on the ventral surface. In SMNS 17204 the hypoischium does not articulate directly on the ischia and presumably varying amounts of cartilage intervened. The pelvis of SMNS 16980 shows no articular surface and the surface does not mirror that of the hypoischium so that a fair amount of cartilage must have been present, particularly in front of the protuberances. Between the protuberances is a thinner, pointed process on the midline. All of the anterior margin of the hypoischium is unfinished, supporting the idea that it ended in cartilage.

Posterolaterally the single hypoischium has paired processes that become thinner posteriorly and curl slightly at the tips. These processes are absent in SMNS 17204 due to breakage. As I interpret the orientation in SMNS 16980 the posterolateral processes twist so that the lateral edge is turned ventrally and the medial edge is turned dorsally.

The position of the hypoischium in SMNS 17204 (fig. 88) is unambiguous as preserved in situ but offers some difficulties when interpreted as a living animal. The articulation between the hypoischium and the ischia is extremely close and posteriorly the hypoischium lies on the ventral edge of the caudal vertebrae which in this region has chevrons and wide transverse processes. If this was true

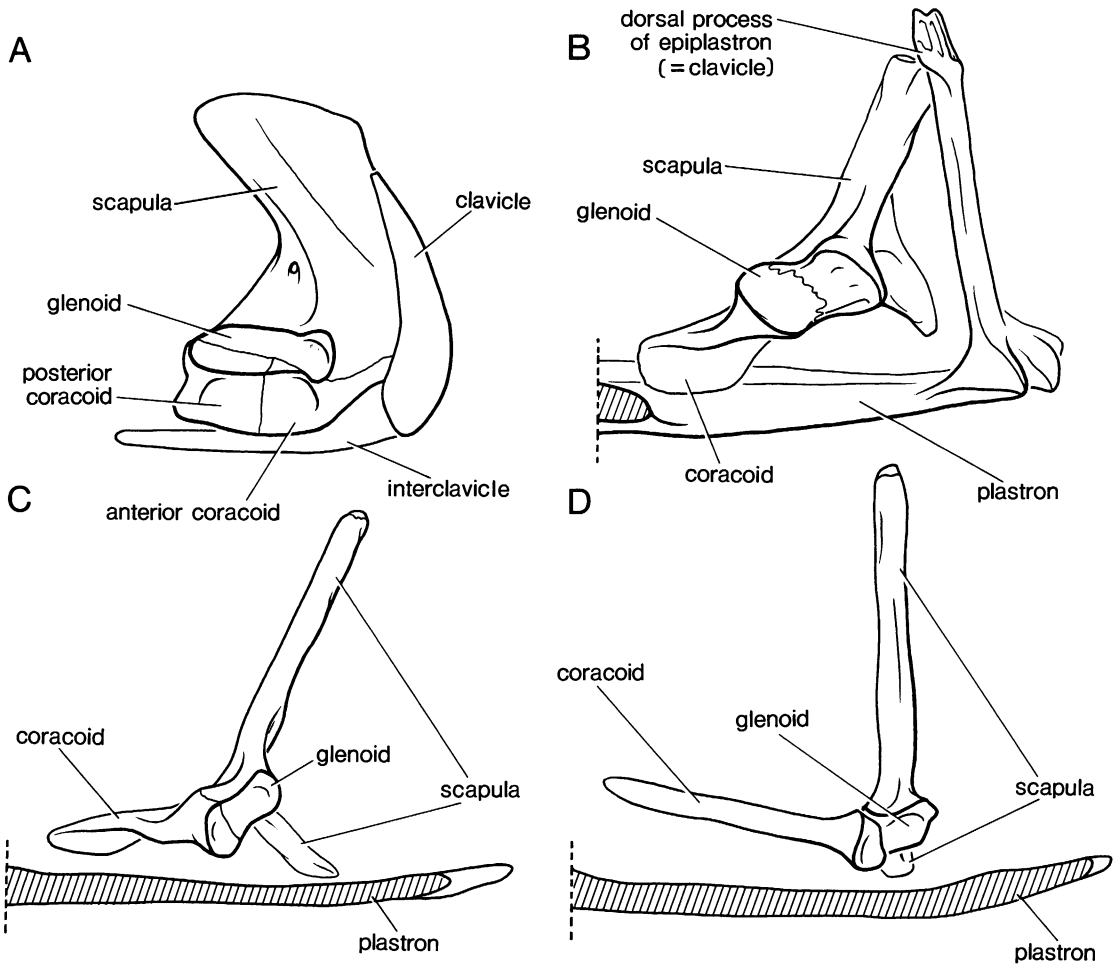

Fig. 137. Comparisons of right shoulder girdles in lateral view; anterior to the right. **A,** *Captorhinus* sp., from Holmes (1977) and specimens. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Macroclemys temmincki,* AMNH 36602. **D,** *Podocnemis expansa,* AMNH 62947.

in life, where did the poor bastard have its cloaca and associated structures? There is a median cleft between the paired hypoischiadic protuberances and the median notch of the ischia that could have held a small cloaca, but its opening would have been unexpandable and would have prevented egg laying. The cloaca could have been placed more posteriorly, between the hypoischium and the caudals if it is assumed that the posterior end of the hypoischium was much more ventrally oriented in life.

Most living turtles have very short tails, with the cloacal opening within or under the carapacial margin, but in males the tail may be longer with the opening at the very end, beyond the carapacial margin. The only living turtles with tails comparable in length to *Proganochelys* are the chelydrids. The cloaca in female chelydrids is within or just under the carapacial margin while in males it is usually beyond the shell margin but not at the end of the tail.

In SMNS 15759 (fig. 145) and SMNS 17203 the hypoischium is a paired structure consisting of the two flat triangular bones lying side by side. SMNS 15759 has the ventral plate of the pelvis, below the acetabulum, preserved with the anterior halves of the two triangular bones in place. As preserved, the

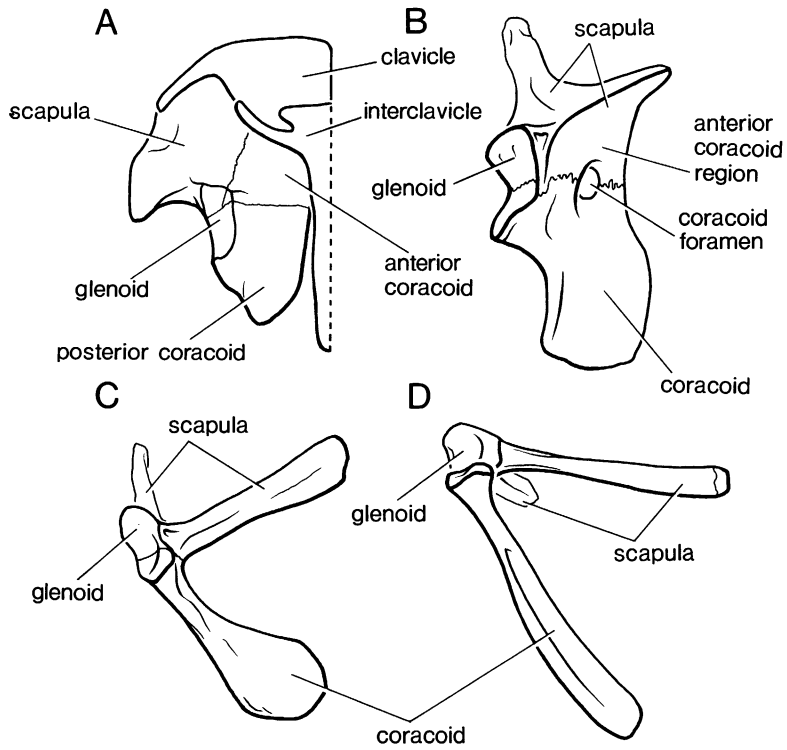

Fig. 138. Comparisons of right shoulder girdles in ventral view; anterior to top of page. **A,** *Captorhinus* sp., from Holmes (1977) and specimens. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Macroclemys temmincki,* AMNH 36602. **D,** *Podocnemis expansa,* AMNH 62947. In B, C, and D the clavicle (epiplastron) and interclavicle (entoplastron) are deleted for clarity.

anterior edge of the hypoischia (the base of the triangle) lies directly against the posterior margin of the ischia with no space for intervening cartilage. In SMNS 15759 the base of the right hypoischium overlies the left one. This arrangement strongly contradicts the possibility that the cloaca went through here. The paired ossifications of SMNS 15759 and SMNS 17203 must be considered comparable with the paired protuberance of SMNS 16980 and SMNS 17204 but the position and type of attachment and lack of fusion (even with contact) are significant differences. The size of the partial shell, skull, pelvis, and paired hypoischia in SMNS 15759 is greater than in SMNS 16980, so it is unlikely that the paired forms are ontogenetic predecessors of the single. The best guess is that the paired bones are in females and the condition is sexual (so that the egg can get through).

Peters (1964: 161) has this to say about the term "hypoischium":

> A cartilaginous or bony rod posteriorly directed from the symphysis of the ischia. It is usually single but can be paired. In some lizards it has a "V" or "Y" shape, and apparently acts as a support for the cloacal wall. According to the studies of Mehnert [1891] . . . , the hypoischium arises as a knob of cells on the embryonic ischium, and is thus originally paired, but Camp [1923] . . . , suggests that the hypoischium is a continuation of the ligament at the symphysis of the ischia, and is originally single, arising as a calcareous deposit in the ligament. If both hypotheses are correct, then there are two different structures designated as the hypoischium. Syn.: cloacal cartilage (cartilago cloacalis), hypoischial cartilage.

From my own examination of Mehnert (1891) and Camp (1923), Peters' account is a good summary. The hypoischium of lizards is figured in those two papers as well as in Noble (1921), who also showed paired clo-

TABLE 16
Comparison of Pelvis

	Captorhinus	*Proganochelys*	Casichelydia
Dorsal portion of ilium	Slightly expanded (*Labidosaurus*)	Greatly expanded	Expanded
Posterodorsal elongation of neck of ilium	Absent	Absent	Present
Acetabulum with well-formed margins on all edges	No	Yes	Yes
Distinct epipubic process	Absent (*Labidosaurus*)	Present	Present
Lateral pubic process	Indistinct (*Labidosaurus*)	Well-defined, articulates with plastron	Same as in *Proganochelys*
Obturator foramen	Small, in posterior part of pubis (*Labidosaurus*)	Small, in posterior part of pubis	Large thyroid fenestra, formed by pubis and ischium
Lateral ischial process	Broad, blunt	Small, indistinct	Narrow, well developed
Large ventral tubercles on ischium	Absent	Present	Absent
Posterior extent of ischium	More	Less	Less
Plate-like ischium	Yes	Yes	No
Separate, ossified hypoischium	Absent	Present	Absent

acal bones occurring in the same species that has a single, midline hypoischium, so they are presumably not the same thing in lizards. Turtles are not known to have a postpelvic ossification, but Romer (1956: 320) referred to turtles having ". . . small accessory ossifications develop in the epipubic and hypoischiadic regions . . ." and to a hypoischium as a small, posteriorly directed, median projection. Guibé (1970: 68–69) described and figured a "hypoischion" for *Sphenodon* but this is in cartilage.

It would seem, then, from the literature that calling the postpelvic ossification in *Proganochelys* a hypoischium would be consistent with previous authors, at least with regard to the positional similarities. It is hard to see that all these structures are homologous, occurring so far only in lepidosaurs and one turtle. There is no suggestion of sexual differentiation in the lizard paired versus single ossification (although I wonder if this was investigated) as may very well be the case in *Proganochelys*. In conclusion, the closest comparison of the postpelvic bones in *Proganochelys* is clearly with the hypoischium/hypoischia of lizards. Nonetheless, they would appear to be another autapomorphy for *Proganochelys* with no apparent functional or phylogenetic relation to other turtles or to generalized amniotes.

FORELIMBS
(table 17, figs. 148–151)

HUMERUS

The best humeri are in SMNS 16980, both right and left. They are cracked and flattened to an unknown extent but they preserve more morphology than any other specimen (fig. 150). The left humerus of SMNS 17203 (fig. 151) seems to have its original curvature and this has been added to SMNS 16980 to produce the reconstructed humerus in fig. 148. SMNS 17203 lacks much of the proximal articular detail, presumably because it is a juvenile, and its distal end is damaged. SMNS 17204 has both humeri but they are poorly preserved, although the right provides some information on the ventral surface. The orientation of the humerus and the morphologic terms are those used by Walker (1973).

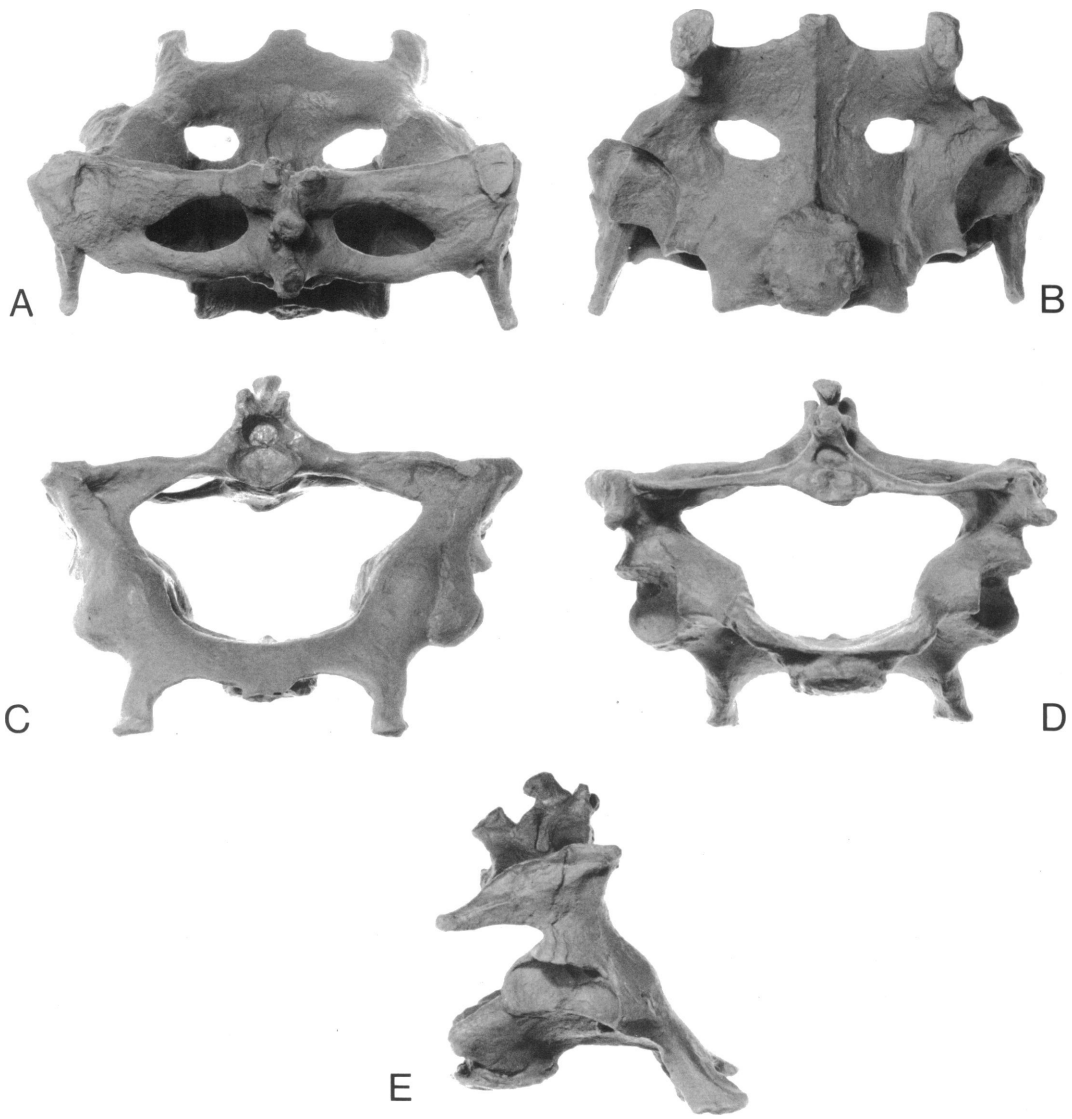

Fig. 139. *Proganochelys quenstedti,* SMNS 16980. Cast of pelvis. **A,** dorsal; **B,** ventral; **C,** anterior; **D,** posterior; **E,** lateral. Thyroid fenestrae are enlarged as a result of breakage. See Figure 144.

The humerus of *Proganochelys* is similar to that in other turtles: the proximal and distal expansions are in nearly the same plane and the shaft has a sigmoidal curve in anterior (preaxial) or posterior (postaxial) view. *Captorhinus* and generalized amniotes (Romer, 1956; Holmes, 1977) have a humerus with the expansions at right angles to each other and the shaft is straight. The proximal articulation surface or head of the humerus is roughly hemispherical in *Proganochelys* but it varies from a true hemisphere in being wider anteroposteriorly than deep. Casichelydians, particularly the more generalized forms, tend to have a head that has more than the 180° of curvature seen in *Proganochelys.* The

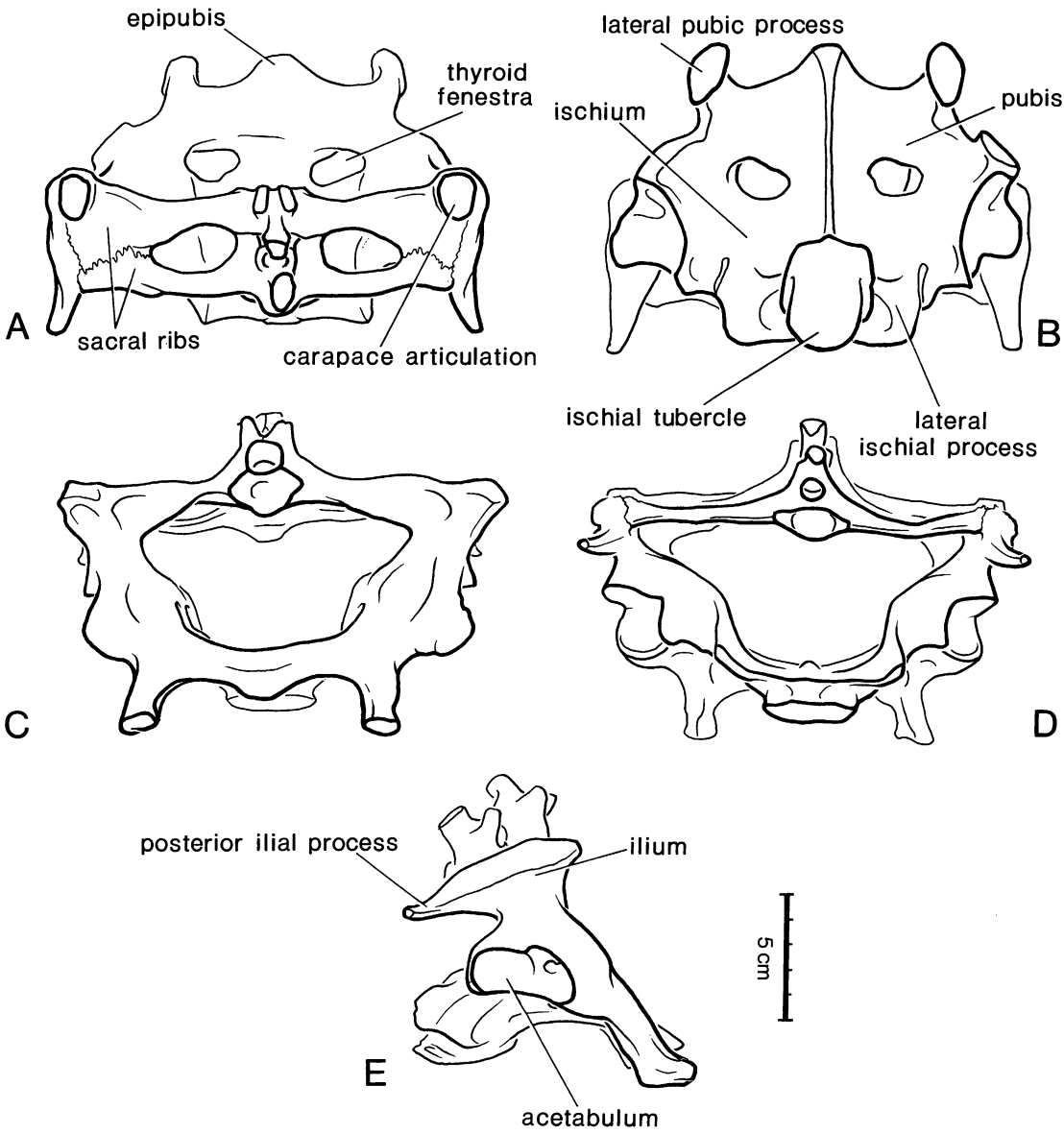

Fig. 139. Continued.

anterior (preaxial) margin of the proximal articulation surface has a distinct shelf or shoulder (fig. 149) that occurs in many cryptodires and is absent in pleurodires. Pleurodires generally have a more rounded, equidimensional hemisphere for the articulation surface than cryptodires, and the absence of a shoulder appears to be a pleurodire synapomorphy. *Captorhinus* and generalized amniotes have a proximal humeral articulation that differs significantly from turtles. The articulation surface in these forms is not separated off the main body of the humerus as a distinct head as in turtles, and the surface has a curved, straplike shape (Miner, 1925; Romer, 1956; Holmes, 1977; and references) rather than a hemisphere shape.

The proximal expansions of the *Progan-*

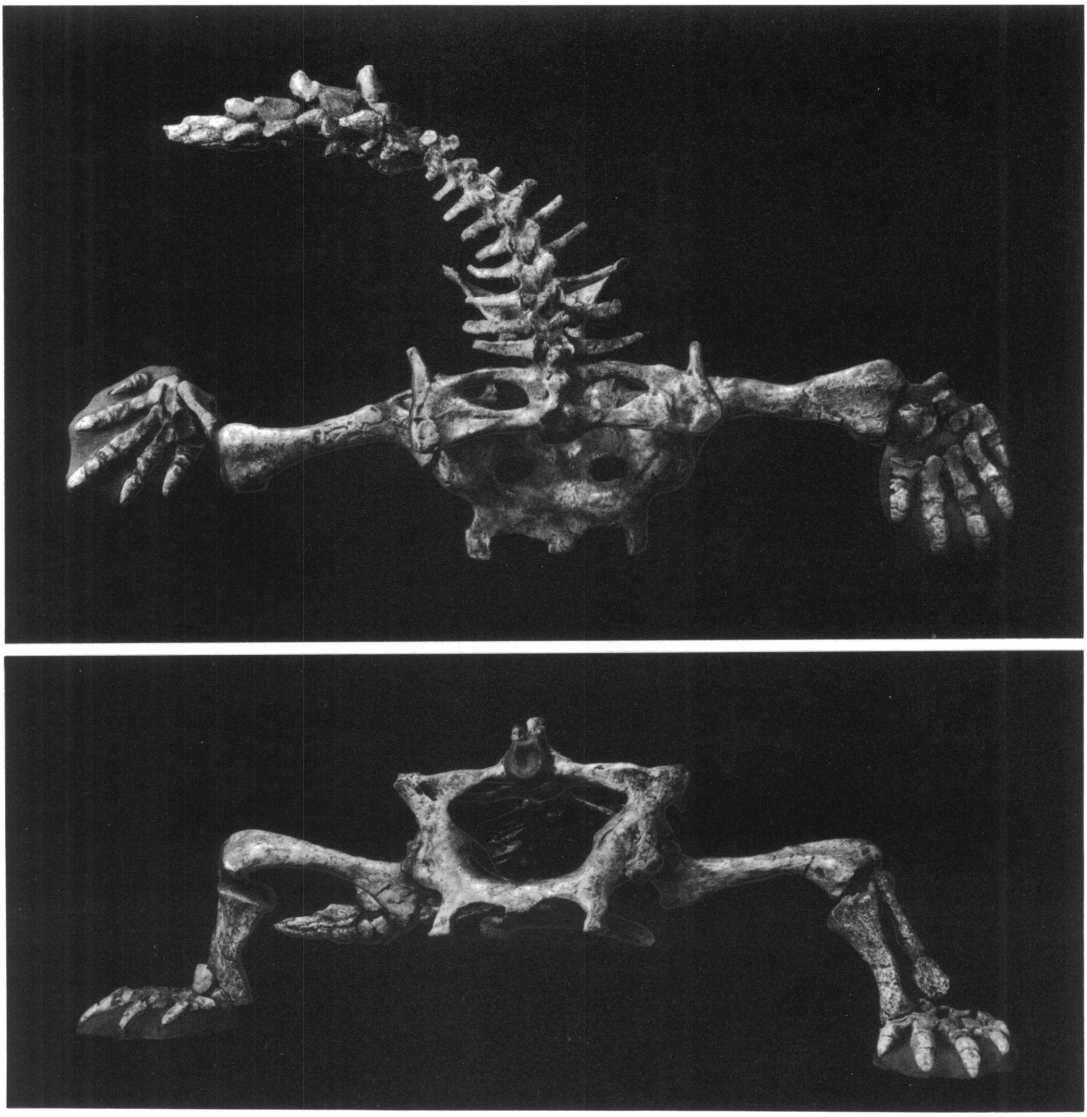

Fig. 140. *Proganochelys quenstedti,* cast of SMNS 16980. Hind limbs, pelvis, and tail. Upper, dorsal view; lower, anterior view.

ochelys humerus are roughly equal in size; following Walker (1973), the anterior (preaxial) one is termed the lateral process and the posterior (postaxial) one is the medial process and between them is the intertubercular fossa. In most pleurodires the processes are also of roughly equal size, while in most cryptodires the lateral process is smaller than the medial process. The lateral process is essentially continuous with the deltopectoral crest, the latter area being distinct from the lateral process only in some chelonioids. In *Captorhinus* and generalized amniotes the proximal expansion of the humerus must be rotated 90° with respect to the distal expansion in order to compare this area with that of turtles. The lateral and medial processes hardly exist in generalized amniotes but a strong deltopectoral process extends from the base of the proximal expansion. In *Progan-*

Fig. 141. *Proganochelys quenstedti,* MB 1910.45.3. Pelvis and right femoral head.

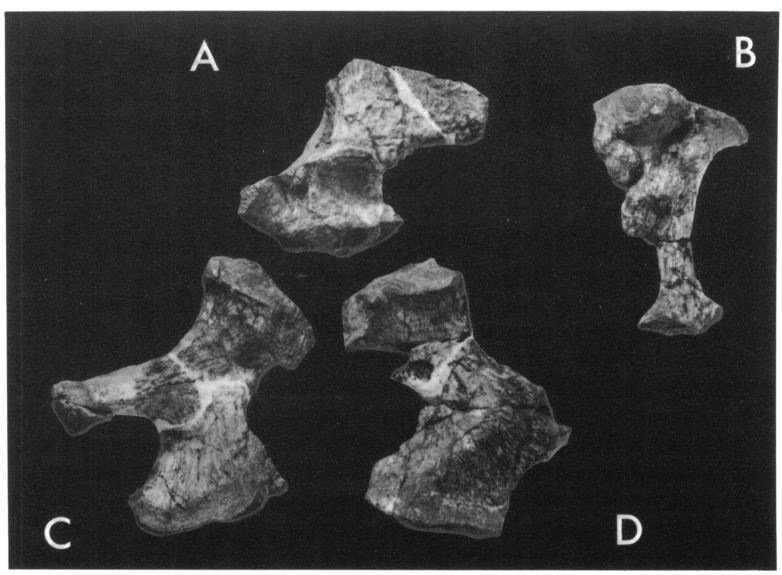

Fig. 142. *Proganochelys quenstedti,* SMNS 17203. Left pelvis. **A,** ilium; **B,** first and second left sacral ribs; **C,** pubis; **D,** ischium.

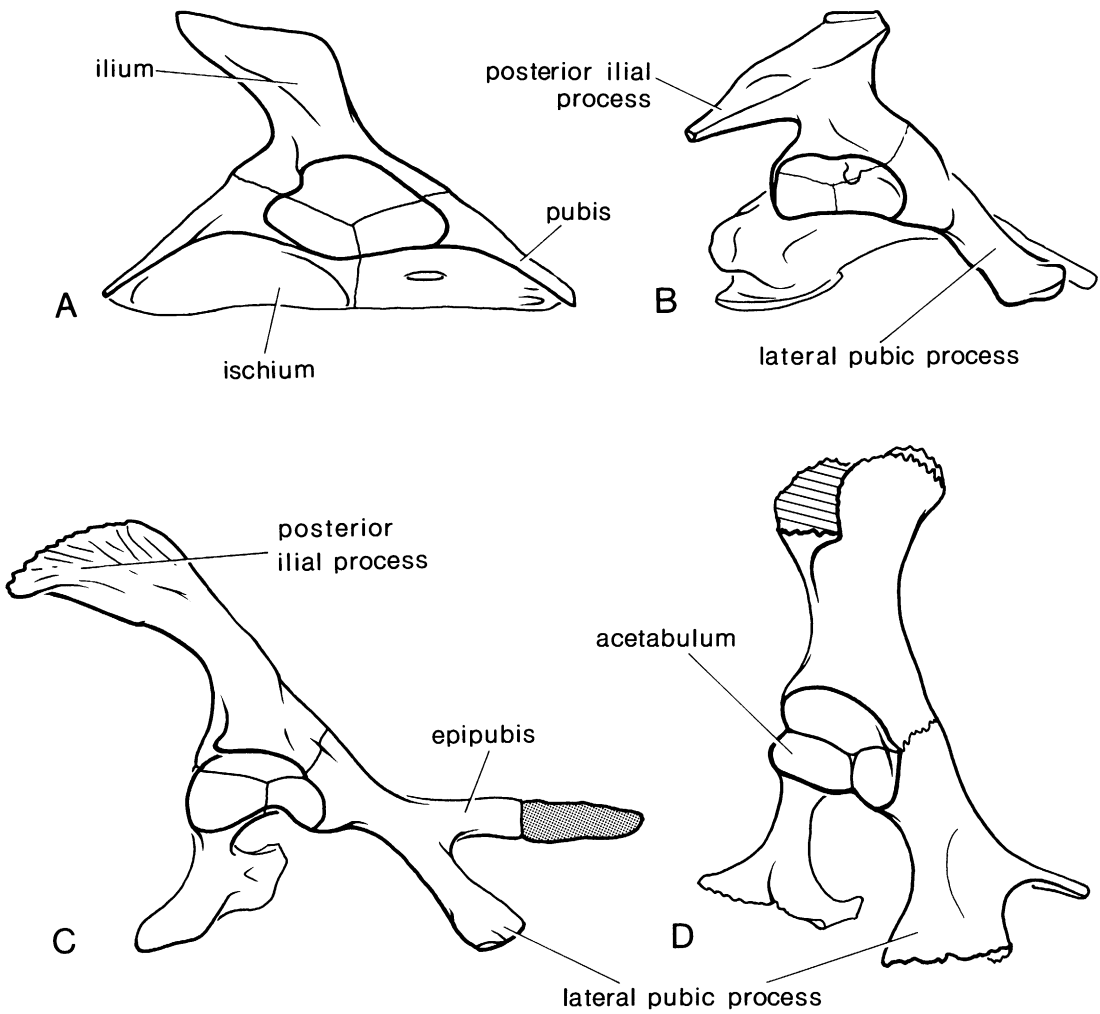

Fig. 143. Comparisons of pelves in lateral view. **A,** *Captorhinus* from Heaton and Reisz (1980) and specimens; **B,** *Proganochelys quenstedti,* SMNS 16980; **C,** *Macroclemys temmincki,* AMNH 58251; **D,** *Podocnemis expansa,* AMNH 62947.

ochelys the lateral process is separated from the head by a notch, giving the lateral process a proximally directed eminence while the medial process is connected with the head by a web of bone. The area around the base of the lateral process, the deltopectoral crest, is expanded and thicker than the proximal part of the process.

The intertubercular fossa of *Proganochelys* is a C-shaped concavity similar in size and shape to that of other turtles. There is no comparable structure in generalized amniotes although the posteroventral surface of *Captorhinus* (Holmes, 1977) is somewhat concave and apparently bears the coracobranchialis brevis as does the intertubercular fossa of turtles (Walker, 1973).

The shaft of the humerus in *Proganochelys* is very similar to that in other turtles, exhibiting the sigmoidal curve typical of turtles (except many chelonioids), although not to the extent seen in testudinids. As mentioned above, the plane of the distal expansion in *Captorhinus* and generalized amniotes is at

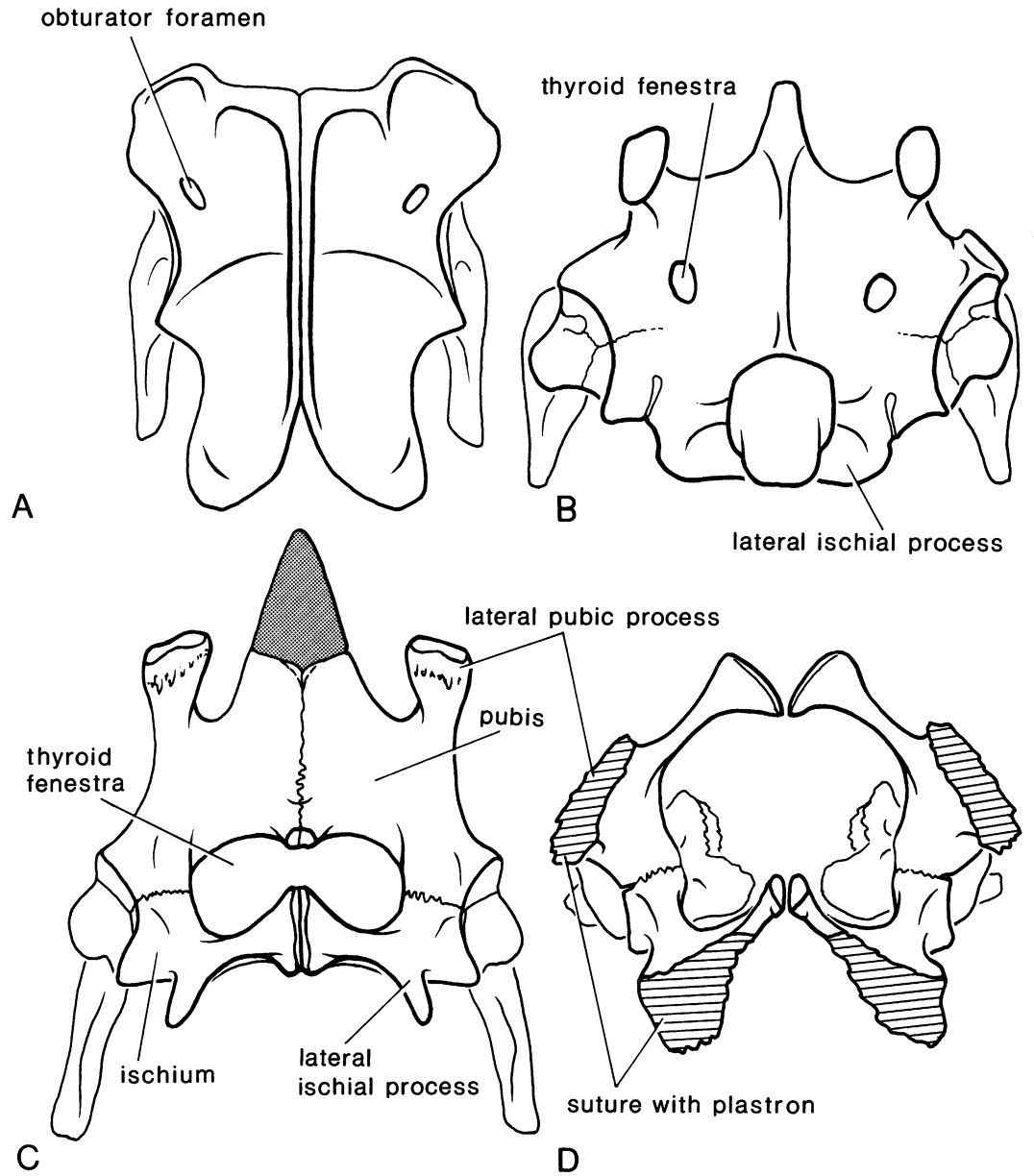

Fig. 144. Comparisons of pelves in ventral view. **A,** *Labidosaurus hamatus* (after Broili, 1904); **B,** *Proganochelys quenstedti,* SMNS 16980 and 17204; **C,** *Macroclemys temmincki,* AMNH 58251; **D,** *Podocnemis expansa,* AMNH 62947.

90° to the plane of the proximal expansion, while in turtles they are nearly in the same plane. There is some variation and the anterior (preaxial) distal expansion is usually slightly (5–10°) more dorsal than the posterior, although commonly there is no difference. *Proganochelys,* however, appears to have a twist in this direction of about 25°. There is some difficulty in assessing the degree of this twist because all the *Proganoche-*

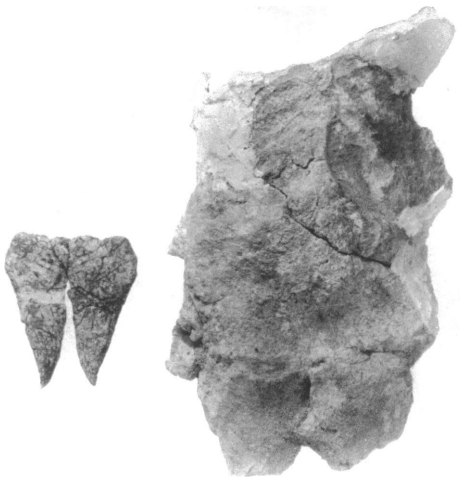

Fig. 145. *Proganochelys quenstedti.* Hypoischia. SMNS 17203, paired hypoischia in ventral view; SMNS 15759, pubis and ischium with anterior portions of paired hypoischia articulated in situ along posterior margin of ischia. See Figures 88, 146, 147.

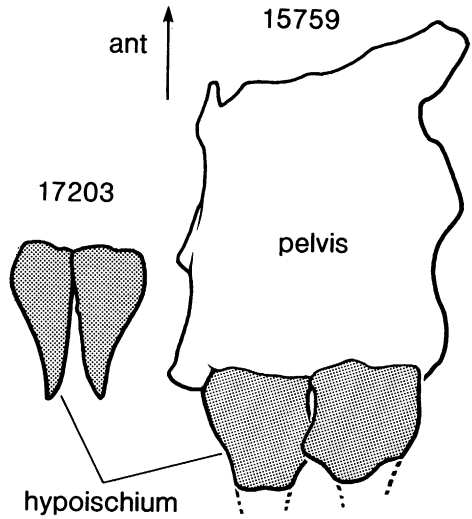

Fig. 145. Continued.

lys humeri are deformed or damaged. Both right and left humeri of SMNS 16980 have twists of the same magnitude and they appear to have been flattened somewhat, reducing the degree of twist. It is likely that, despite the difficulty of quantification, *Proganochelys* has slightly more twisted humeral expansions than casichelydians do, but not to the degree seen in generalized amniotes.

The distal end of the humerus in *Proganochelys* has the typical chelonian double condyle, made up of the radial articulation (capitellum) anteriorly and the ulnar articulation

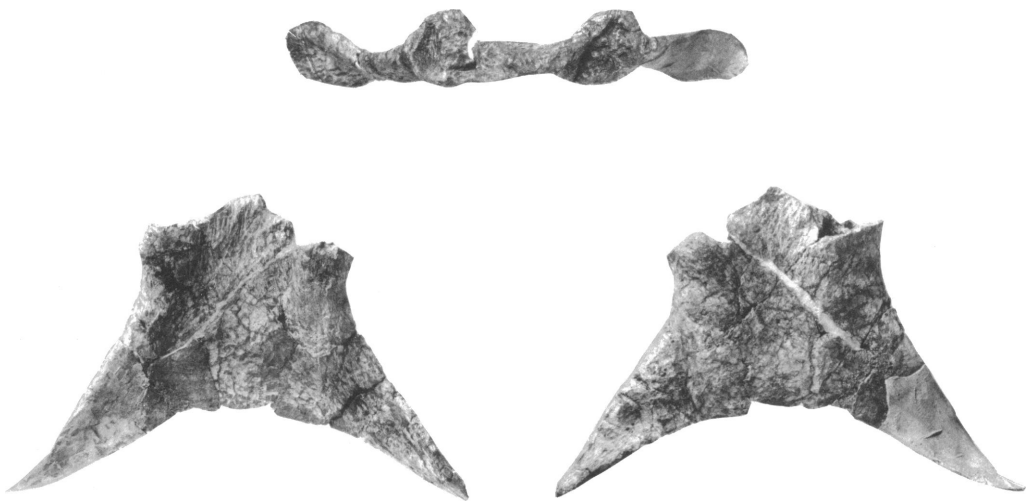

Fig. 146. *Proganochelys quenstedti,* SMNS 16980. Unpaired hypoischium. Top, anterior view; lower left, ventral view; lower right, dorsal view. See Figures 88, 147.

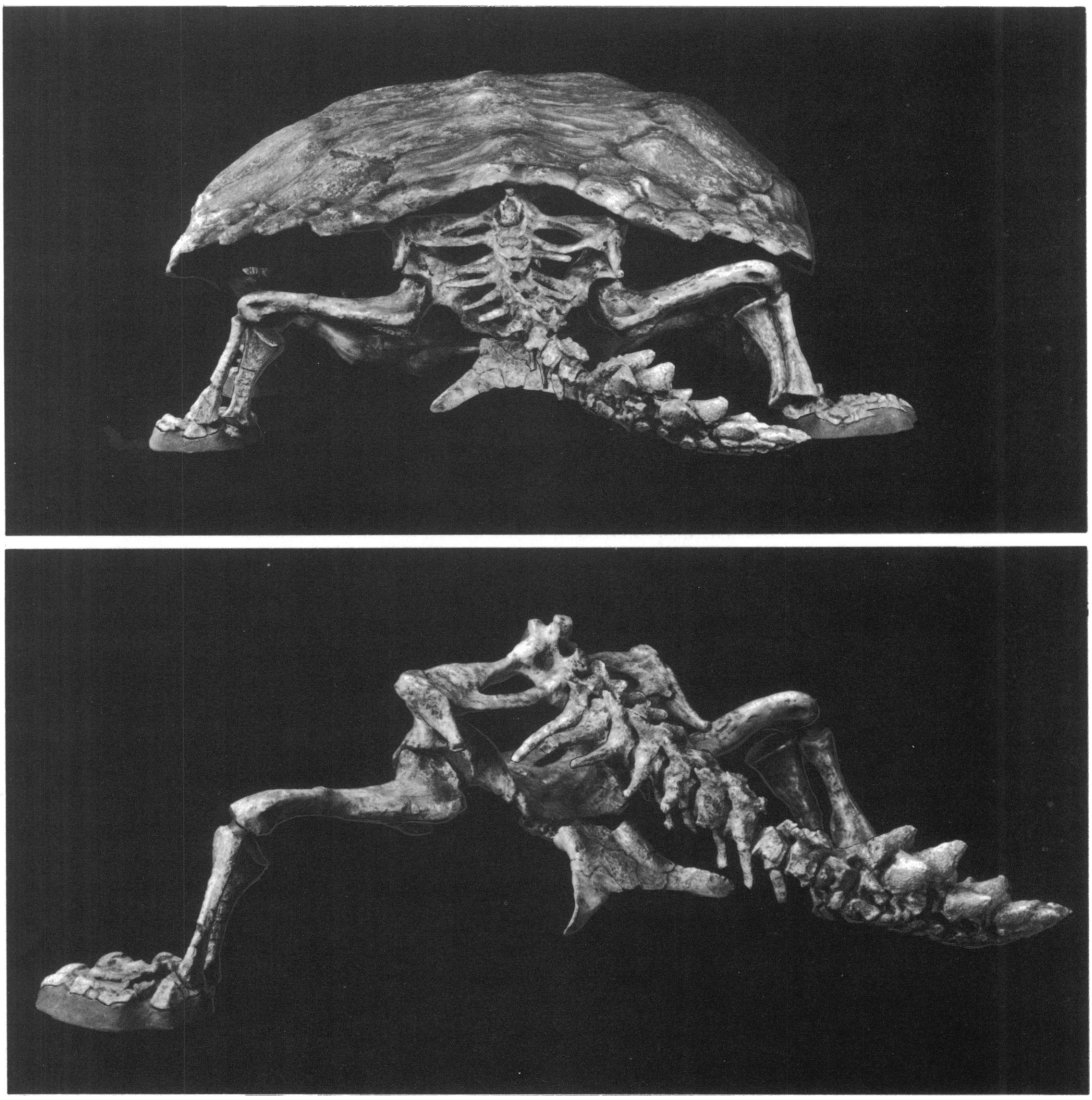

Fig. 147. *Proganochelys quenstedti,* cast of SMNS 16980. Upper, posterior view of mounted skeleton; tail is deflected to right. Lower, articulated hind limbs, pelvis, and tail vertebrae. Note position of hypoischium in both figures. See Figure 88.

(trochlea) posteriorly. In *Proganochelys* and other turtles these articulations are oval convexities separated by a shallow groove. The generalized amniote condition, seen in *Captorhinus,* differs markedly. The capitellum is a well-developed hemisphere, convex ventrally with very little distal exposure. The trochlea is a curved articular surface running from the ventral surface distally. The cup-shaped radial articulation fits directly ventral to the capitellum and the curved ulnar articulation wraps around the trochlea. In *Proganochelys* and other turtles, the epipodial articulations are nearly the same shape, the ulnar articulation is between the two condyles, and the combined articular surface has a more distal orientation (i.e., the antebrachium is not at right angles to the humerus as in

TABLE 17
Comparison of Humerus

	Captorhinus	*Proganochelys*	Casichelydia
Proximal and distal expansion of humerus	At right angles	Nearly in the same plane	Nearly in the same plane
Humeral shaft with sigmoidal curve	No, straight	Yes	Yes
Proximal articulation surface (head) of humerus	Curved, strap-shaped	Hemispherical	Hemispherical, but usually greater curvature than in *Proganochelys*
Shoulder on proximal articulation surface of humerus	Absent	Present	Present in cryptodires, absent in pleurodires
Lateral and medial processes of humerus	Absent, except for deltopectoral crest	Present	Present
Intertubercular fossa of humerus	Absent	Present	Present
Distal ulnar-radial articulation of humerus	Well-defined hemisphere (radius), strap-shaped trochlea (ulna)	Low, double condyle	Low, double condyle
Entepicondyle of humerus	Large	Small	Small
Ectepicondyle of humerus	Small (but large in other generalized amniotes)	Small	Small
Ectepicondylar foramen	Absent (but present in some generalized amniotes)	Present	Present (cartilaginous in some)
Entepicondylar foramen	Present	Absent	Absent
Supinator process	Absent (but present in other generalized amniotes)	Absent	Absent

Captorhinus). The ulna of *Proganochelys* and other turtles lacks the proximal process that extends around the humerus and articulates on the trochlea. The epipodial articulation of *Proganochelys* seems to differ from that of other turtles only in being slightly more ventrally oriented and similar to *Captorhinus*. As in other turtles, the capitellum is slightly larger than the trochlear condyle in *Proganochelys*.

Generalized amniotes (fig. 149) usually have conspicuous distal expansions, the epicondyles, on either side of the epipodial articulations. The entepicondyle projects posteriorly, usually bearing most of the forearm flexors while the ectepicondyle projects anteriorly bearing the forearm extensors. *Proganochelys* agrees with other turtles in having a small entepicondyle, only a slight swelling posterior to the epipodial articulation. In *Captorhinus* and other generalized amniotes the entepicondyle is very large and bears a considerable surface for flexor attachment. On the anterior edge, the ectepicondyle of most generalized amniotes is also large and this appears to be the primitive amniote condition. *Captorhinus* and turtles have a small ectepicondyle, although *Captorhinus* does have a short distal projection absent in turtles. This may be a captorhinid-turtle synapomorphy, because a relatively large ectepicondyle is common in generalized diapsids and synapsids. However, this feature is not consistent in all the groups mentioned, and judging intermediate conditions is difficult.

Proganochelys has a well-formed and large ectepicondylar foramen that penetrates the ectepicondyle from the dorsal surface, extending distoventrally to emerge on the ventral surface just anterior to the ulnar articulation margin. The foramen is well preserved in the right and left humeri of SMNS 16980,

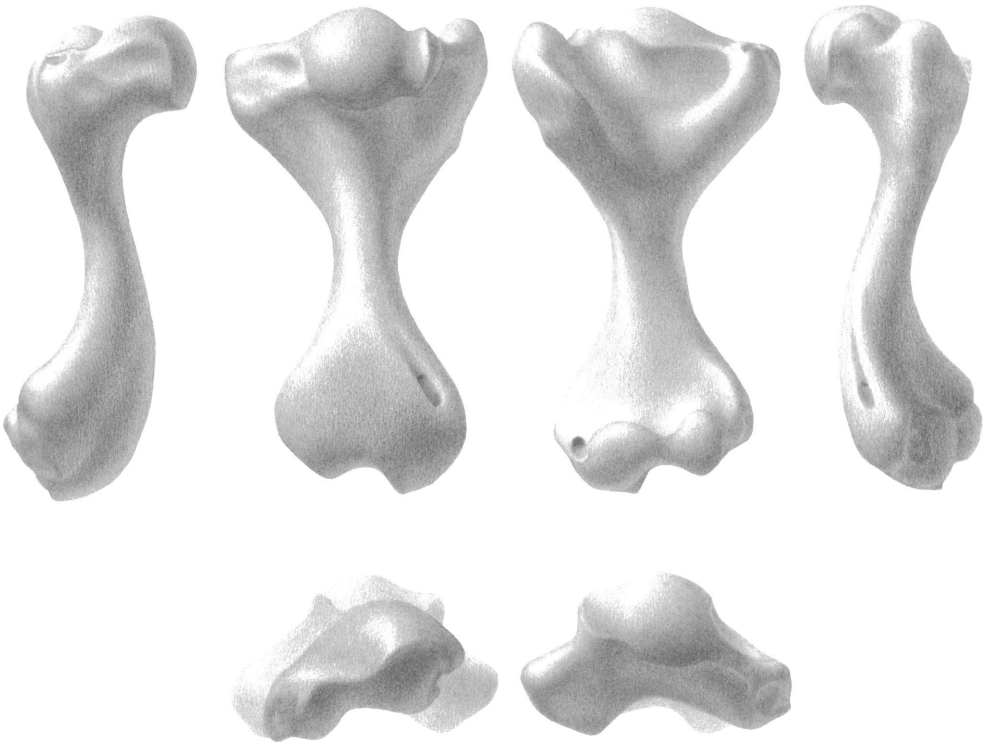

Fig. 148. *Proganochelys quenstedti,* SMNS 16980. Right humerus. Top row (left to right), posterior, dorsal, ventral, anterior; lower row (left to right), distal, proximal.

on which this description is based. As in other turtles, the opening on the dorsal surface is at the end of a groove extending distoanteriorly along the shaft of the humerus. In many turtles the foramen is only a groove. The ectepicondylar foramen is absent in *Captorhinus.* Also lacking in this form is the supinator process, usually the more distal margin of the foramen. Turtles also lack a supinator process but they have the foramen. The distribution of the ectepicondylar foramen is not systematically regular at higher taxonomic levels. It is absent in all captorhinids and protorothyrids, many diapsids, some pelycosaurs, and some therapsids. There does not appear to be systematic significance in its pattern at this level, although its presence many be a chelonian synapomorphy.

The entepicondylar foramen, very prominent in captorhinids, synapsids, and some diapsids, is absent in all turtles, including *Proganochelys.* Again, this may be a chelonian synapomorphy, but it is absent in many apparently unrelated groups (Romer, 1956).

Radius
(table 18, figs. 151–155)

The radius is best preserved in SMNS 16980 where both right and left radii are present. The left radius has been completely freed of matrix although it was originally articulated with the ulna and osteoderms (fig. 153), in an obviously disturbed position, such that ulna and radius were at an angle to each other rather than parallel. The right radius is also articulated with the right ulna and this relationship has been maintained (fig. 153), as it is close to the presumed life position. The radii in SMNS 16980 are better preserved than in the other *Proganochelys* specimens and have been the primary basis for the figures (fig. 154) of the radius, but they still leave something to be desired. Both bones have

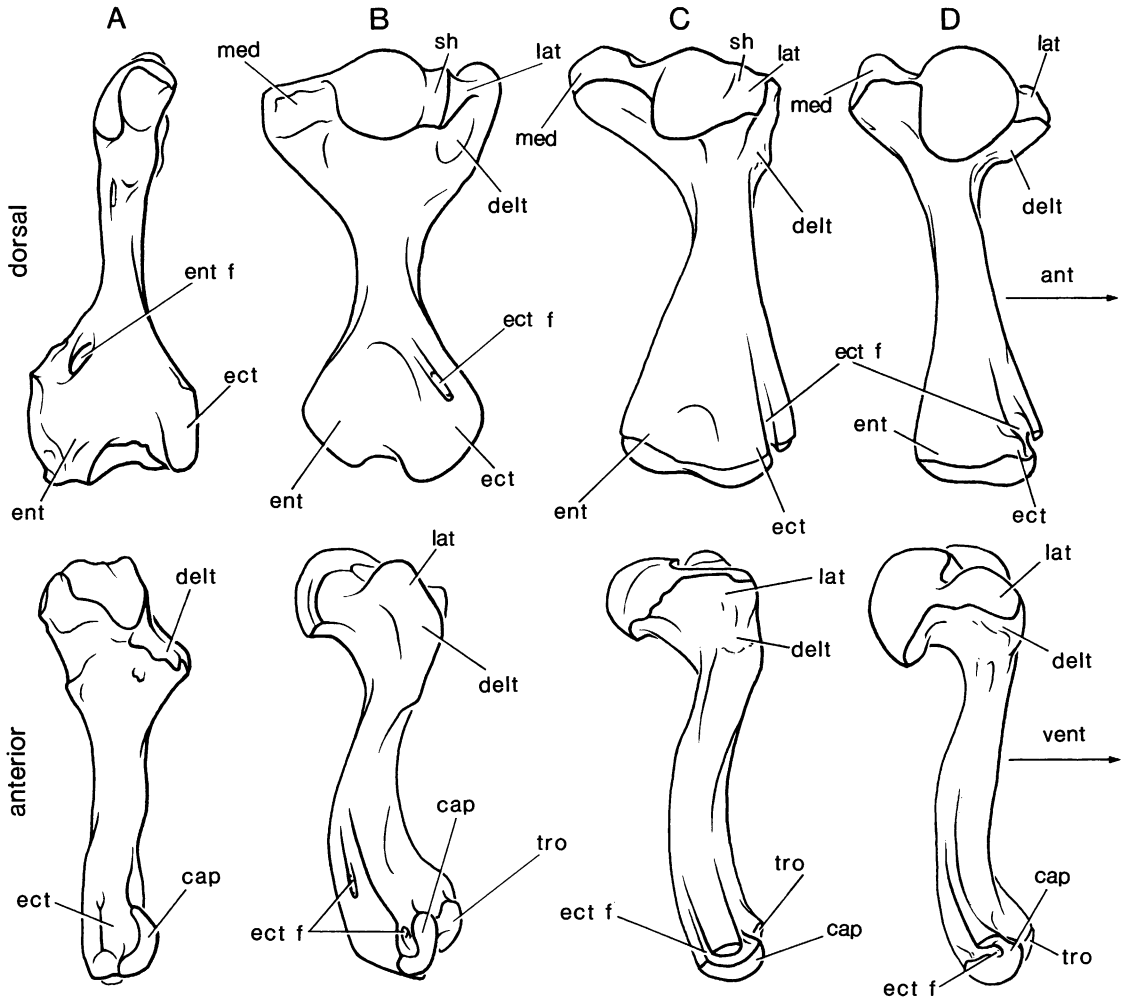

Fig. 149. Comparisons of right humeri. Upper row, dorsal views; anterior to right. Lower row, anterior views, ventral to right. **A,** *Captorhinus* sp., after Holmes (1977) and AMNH 19370–19373. **B,** *Proganochelys quenstedti,* SMNS 16980. **C,** *Macroclemys temmincki,* AMNH 1118 (comparative anatomy collection). **D,** *Podocnemis expansa,* AMNH 62947. Abbreviations: **ant,** anterior direction; **cap,** capitellum; **delt,** deltopectoral crest; **ect,** ectepicondyle; **ect f,** ectepicondylar foramen; **ent,** entepicondyle; **ent f,** entepicondylar foramen; **lat,** lateral process; **med,** medial process; **sh,** shoulder; **tro,** trochlea; **vent,** ventral direction.

minute fractures causing distortion of the shape and loss of fine surface detail. The fact that each radius has been distorted differently can be seen in the lengths of the radii of SMNS 16980: the right radius is 90 mm long while the left is 83 mm long, yet neither has large, obvious cracks. Figure 154 is based more on the left radius because it seems to have fewer cracks and internal inconsistencies than the right radius.

SMNS 17203 has the right radius preserved in articulation with the ulna, but its morphology is largely obscured by the osteoderms which cover it ventrally and the carapace to which it is attached dorsally.

SMNS 17203 (fig. 151) has a left radius

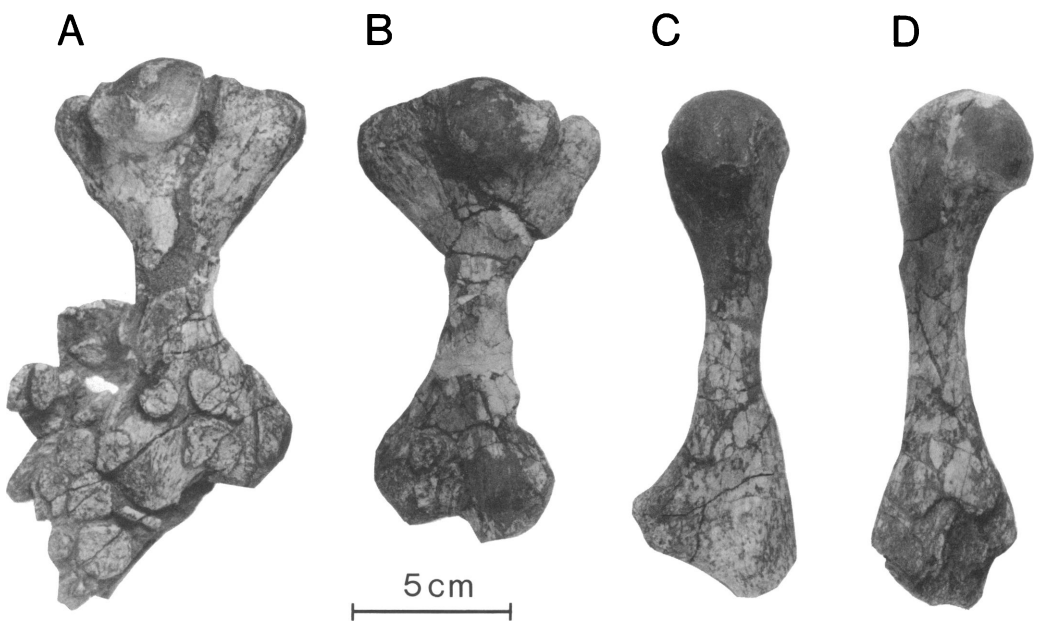

Fig. 150. *Proganochelys quenstedti,* SMNS 16980. **A,** left humerus; **B,** right humerus; **C,** left femur; **D,** right femur.

and ulna preserved in articulation in what appears to be close to a life position, along with some osteoderms. The preservation condition of the radii in SMNS 17203 and SMNS 17204 is comparable to that of SMNS 16980 but slightly poorer due to softer bone and more cracking.

The radius of turtles (fig. 155) does not show much variation in morphology, except for the swimming forms, chelonioids, trionychids, and *Carettochelys*; there is a relatively consistent morphology within turtles (Walker, 1973). *Proganochelys* readily fits into the pattern of typical chelonian radial morphology.

The proximal end of the radius of *Proganochelys* is circular in cross section and only slightly larger than at the midsection, while the distal end is expanded in the mediolateral plane. The proximal articulation surface articulates with the humerus and is ovoid and slightly concave, falling off along its rounded edges. The lateral part of the margin contacts the ulna. This region is very similar in *Proganochelys* and other turtles (fig. 155), such as *Podocnemis* and *Macroclemys,* as well as baenids and *Meiolania.* In *Captorhinus* the proximal end of the radius is more oval in cross section but the other features are generally similar.

Just distal to the humeral articulation surface, the shaft of the radius in *Proganochelys* has a short ridge or swelling laterodorsally. Most turtles have a ridge or rugosity here, as in *Proganochelys,* and Haines (1946) showed that it is the attachment site of the superior radio-ulnar ligament, a short band that fixes ulna and radius together proximally. *Captorhinus* (Holmes, 1977) has no such swelling or rugosity in this area. More distally there is a similar rugosity on the laterodorsal edge of the distal expansion in *Proganochelys,* also presumably for the radio-ulnar ligament as in living casichelydians. Thus, it seems likely that the radius and ulna of *Proganochelys* had limited movement with respect to each other—in contrast to the condition in lizards and lissamphibians (Haines, 1946) and, presumably, *Captorhinus.*

The shaft of the radius in *Proganochelys* is relatively stout as in some testudinids but not as thick as in cheloniids. It is slightly thicker

TABLE 18
Comparison of Radius and Ulna

	Captorhinus	*Proganochelys*	Casichelydia
Distal expansion on radius	Absent	Present	Present
Distal articulation surface of radius at right angles to longitudinal axis of forelimb	Yes	No	No
Olecranon of ulna large and well developed	Yes	No, but larger than Casichelydia	No
Humeral articulation surface of ulna	Faces medially more than dorsally	Faces dorsally	Faces dorsally
Humeral articulation surface close to bicipital tubercle of ulna	Yes	No, separated proximally	No, separated proximally
Distal end of ulna with distinct torsion compared with proximal expansion	No, both ends in same plane	Yes	Yes
Rugosities on distal and proximal opposing surfaces of radius and ulna for radio-ulnar ligament	Absent	Present	Present

than in *Macroclemys* and thinner than in *Meiolania.* There is a low ridge running down the shaft that appears to be in the vicinity of the separation between the tractor radii and the extensor radialus intermedius (Walker, 1973) and which occasionally occurs in other turtles.

Distally, the radius of *Proganochelys* is expanded mediolaterally with the lateral part of the expansion more extensive so that the radius is asymmetrical in dorsal and ventral view. This distinctive shape of the radius is found in most turtles except the groups highly adapted for swimming. *Captorhinus* has a slight distal expansion but it is quite different from the chelonian radius in being relatively long and narrow with slight proximal and distal extensions.

The distal articulating surface on the radius in *Proganochelys* is elongate and slopes lateroproximally so that the articulation with the carpus is not at right angles to the longitudinal axis of the forelimb. In *Captorhinus* this articulation surface is at right angles to the longitudinal axis of the forelimb. In *Proganochelys* it is at right angles to the longitudinal axis of the forelimb and is convex and slightly more protuberant medially than laterally. The degree to which the radius articulates with the intermedium and with the medial part of the ulna varies in turtles. Although it is not possible to be sure, it is likely that in *Proganochelys* the radius and ulna barely contact each other proximal to the intermedium. This is most closely approached by the articulated right forearm of SMNS 16980 in which the radius and ulna seem only slightly displaced from life position (fig. 153).

Ulna
(table 18, figs. 151–153, 156–157)

Both right and left ulnae are preserved in SMNS 16980, a left ulna is present in SMNS 17203, and a right ulna is present in SMNS 17204. The ulnae of SMNS 16980 are the best preserved; the left one is freed of matrix while the right is in articulation with the radius. The ulna of SMNS 17203 (fig. 151) is partially obscured by the radius and osteoderms, while the ulna of SMNS 17204 (fig. 152) is extensively obscured by osteoderms and the carapace. Even though 16980 has the best ulnae these are still somewhat distorted and damaged by postmortem fracturing. The partially reconstructed figure 156 is based primarily on the left side of SMNS 16980 with some information from the more poorly preserved right side.

The ulna in *Proganochelys* is generally similar in proportion to the ulna of casichelydians and *Captorhinus* (fig. 157). Highly aquatic turtles have a modified ulna (Walker, 1973) but most turtles have a consistent ulnar shape.

Proximally, the ulna of *Proganochelys* is

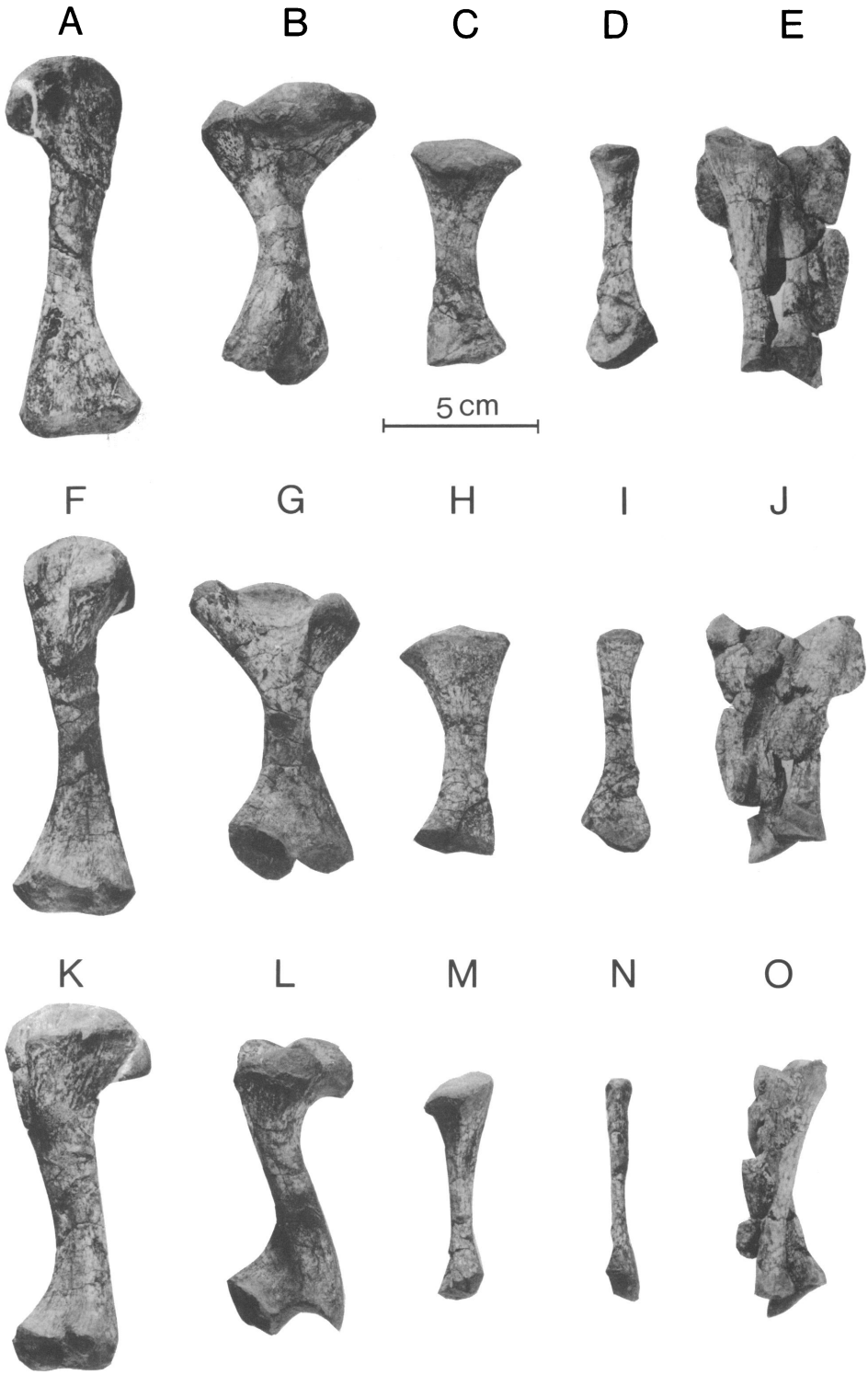

Fig. 151. *Proganochelys quenstedti,* SMNS 17203. **A, F, K,** left femur; **B, G, L,** right humerus; **C, H, M,** left tibia; **D, I, N,** left fibula; **E, J, O,** right radius and ulna with osteoderms.

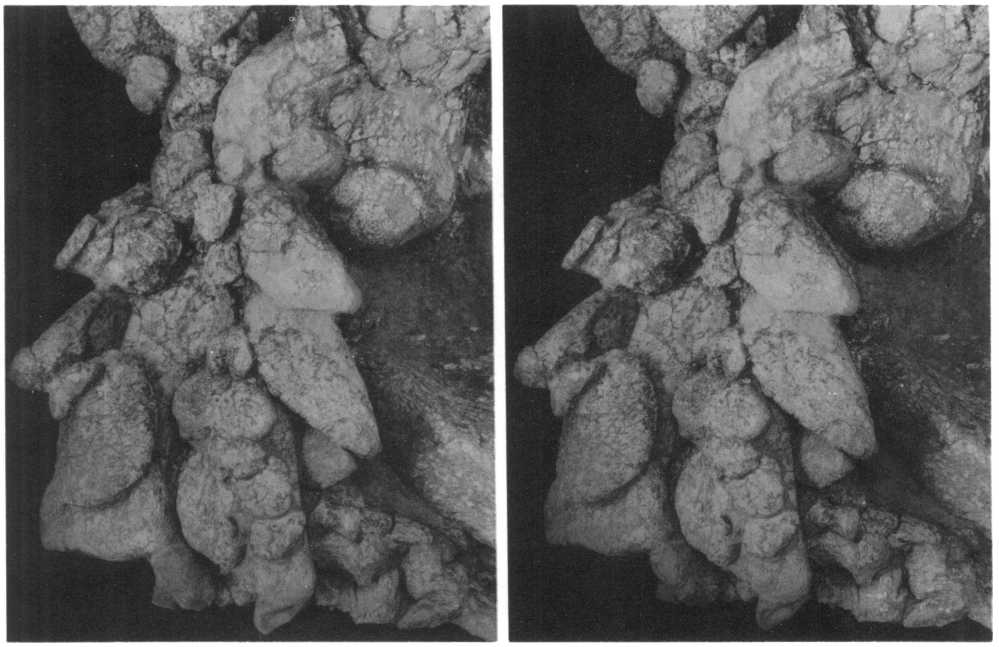

Fig. 152. *Proganochelys quenstedti,* SMNS 17204. Right forearm in ventral view, showing osteoderms covering humerus, radius, and ulna. See Figure 88.

dominated by the olecranon on its proximodorsal margin. The olecranon is a proximally directed process which bears the attachment for the triceps muscle-ligament system. In casichelydians the olecranon is only slightly developed; it does rise above the humeral articulation surface but not to the extent seen in many amniotes, even generalized ones, such as *Captorhinus.* In *Captorhinus* (Holmes, 1977), the olecranon is a large, rounded process, slightly larger in circumference than the ulnar shaft. In *Proganochelys* the olecranon is smaller, nearly the size of the olecranon in those casichelydians in which it is best developed. There is, however, no difficulty in identifying the *Proganochelys* olecranon as belonging to the casichelydian pattern, because the triceps attachment area is significantly smaller in *Proganochelys* and casichelydians than it is in *Captorhinus.* This may possibly be related to the tendency on the part of turtles to walk with the elbow joint relatively fixed and not requiring the degree of extension seen in other amniotes, which in turn appears to be a limitation on locomotion imposed by the shell.

The proximal articular surface of the ulna is usually a compound curved surface, the sigmoid notch of Romer (1956). In *Captorhinus* (Holmes, 1977), the surface forms an arc of roughly 130° while in *Proganochelys* it is 100° or less, and in casichelydians it is usually considered less than 100°, being nearly flat in some turtles. In *Captorhinus* the articular surface faces medially more than it faces dorsally while in *Proganochelys* and other turtles it faces dorsally with a medial tilt.

About one-third of the distance down the ulnar shaft from its proximal end, the ulnae of *Captorhinus, Proganochelys,* and most casichelydians have a small rugosity, the bicipital tubercle (Walker, 1973) for the attachment of the biceps profundus. The position of this tubercle is about the same in relation to the length of the shaft in *Captorhinus* and turtles, including *Proganochelys.* The sigmoid notch and the enlargement of the head to bear the articulation, however, are more distal in *Captorhinus* so that the bicipital tubercle lies very close to the articulation surface and on the proximal enlarge-

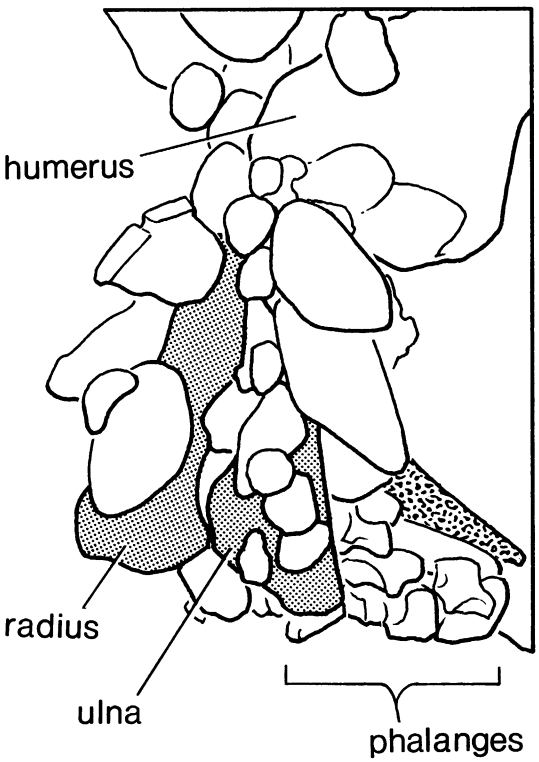

Fig. 152. Continued.

ment of the ulna. In *Proganochelys* and other turtles the proximal enlargement bearing the sigmoid notch is distinctly more proximal than in *Captorhinus,* resulting in a bicipital tubercle that is separated from the proximal enlargement.

The sigmoid notch may be divided into two articulation areas, although they are broadly continuous and separated by a low ridge. In *Captorhinus* these features are more distinct than in turtles: the larger, semicircular area faces proximomedially and the smaller, arcuate surface faces dorsomedially. They are separated by a low ridge labeled by Holmes (1977: fig. 9) "helical ridge on proximal ulnar articulation surface." In *Captorhinus* there are two very different articular surfaces on the humerus: the hemispherical capitulum, the central part of which articulates with the radius, and the groove or "trochlea" (Romer, 1956: fig. 163; Holmes, 1977: fig. 8) into which fits the helical ridge of Holmes. Thus, the smaller, arcuate articular surface articulates on the side of the humeral capitulum while the larger, hemispherical articular surface articulates with the broadly curved surface dorsal to the trochlea of the humerus. In *Proganochelys* and other turtles the distal articulations of the humerus are quite different from the hemisphere and trochlea of *Captorhinus* but the homologous articular surfaces can be identified (see Humerus). On the ulna the low ridge separating the two articular surfaces can be made out. The ridge articulating with the humeral trochlea separates two surfaces roughly the same in area rather than smaller dorsal and larger ventral surfaces. In *Proganochelys* the orientation of the surfaces also differs; both face proximally with a slight tilt dorsally and ventrally on either side of the ridge.

Distally, the shaft of the ulna in *Proganochelys* is flattened dorsoventrally, as in *Captorhinus* and most turtles, and is bowed concave ventrally. The lateral margin of the ulna in *Proganochelys* comes to an acute edge, also seen in other turtles and to a slight extent in *Captorhinus.* The medial edge is semicircular to nearly flat and forms the thickest part of the shaft. On the dorsal surface, between the bicipital tubercle and the proximal articulation surface, is a low ridge that forms the dorsomedial margin of the surface of the ulna that is opposite the radius. The radio-ulnar surfaces are apposed here but only come in contact along the lip of the articulation surface. The radio-ulnar ligaments described by Haines (1946) presumably attached along this ridge. This ridge is strongly developed and prominent in *Proganochelys* but it is usually less developed in other turtles and barely discernible in *Captorhinus.*

The shaft of the ulna in *Proganochelys* is narrowest about two-thirds of the distance from the proximal to the distal end, and this is similar in *Captorhinus* and casichelydians. At about this position along the shaft the wide dimension of the ulna twists to produce a noticeable torsion of the distal width compared with the proximal width. This is present in casichelydians as well but not in *Captorhinus.*

The carpal articulation surface of the ulna is quite similar in *Proganochelys,* casichelydians, and *Captorhinus.* It is strap-shaped and curved, facing distally with the medial portion facing medially to some extent. The ulna

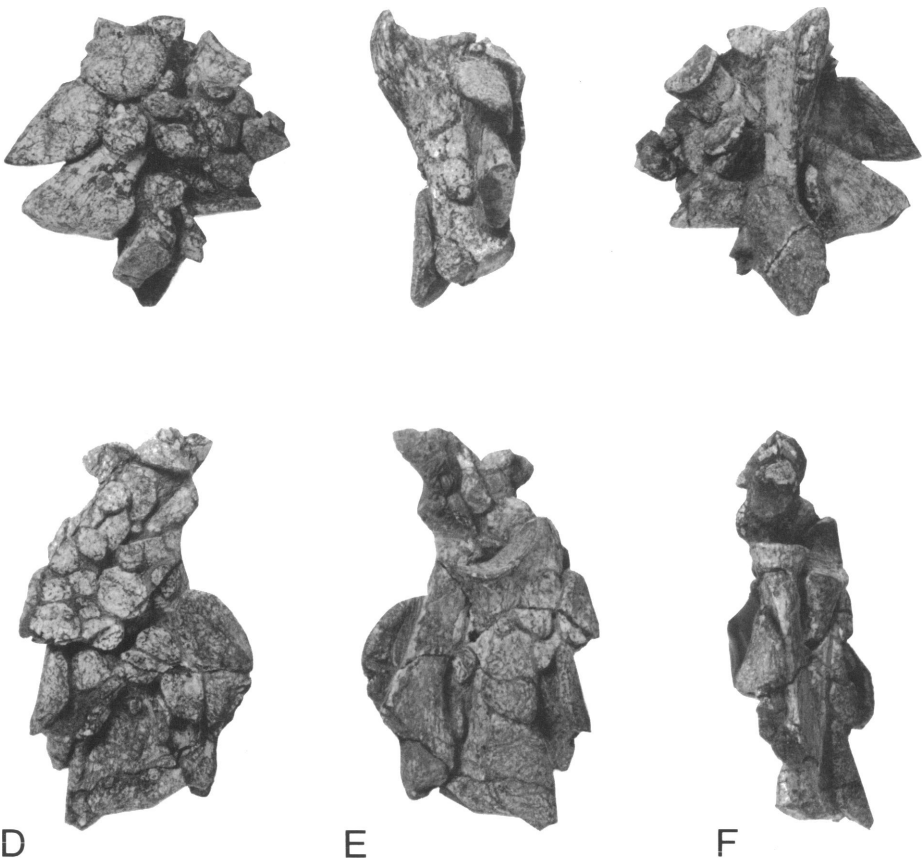

Fig. 153. *Proganochelys quenstedti,* SMNS 16980. **A–C,** left ulna and radius; **D–F,** right ulna and radius. A, distal view of ulna, dorsal view of radius; B, ventral view of ulna, distal view of radius; C, lateral view of ulna, ventral view of radius; D, dorsal view of radius and ulna; E, ventral view of radius and ulna; F, medial view of radius and ulna.

contacts the ulnare and the intermedium; its possible contacts with the radius are discussed under that bone.

The ulna of SMNS 17203 (fig. 151) differs from the ulnae of SMNS 16980 in almost completely lacking the olecranon and in being thinner. These differences, along with many other differences in the skeleton, are presumed to be the result of the juvenile nature of SMNS 17203, a topic discussed elsewhere.

Carpus and Manus
(tables 19, 20, figs. 158–162)

The left carpus of SMNS 16980 is the best preserved *Proganochelys* carpus (table 19), although there are serious problems that prevent a complete understanding of the structure. A photograph published by Berckhemer (1938: pl. 4) shows the anterior half of the skeleton of SMNS 16980, minus the carapace. In this photograph (reproduced here as fig. 98) the skeleton is articulated as discovered in situ; subsequently most of the bones were prepared free of the matrix and their relationships to each other lost. Neither the original of this photograph nor any other data concerning the relative position of elements has been located. The left manus is shown in the Berckhemer photograph to be articulated in a more or less natural position, with the digits strongly flexed and retracted over the metacarpals. Most of the carpus appears to be present and articulated. The entire forelimb seems to be complete and not seriously disturbed by postmortem processes. Some

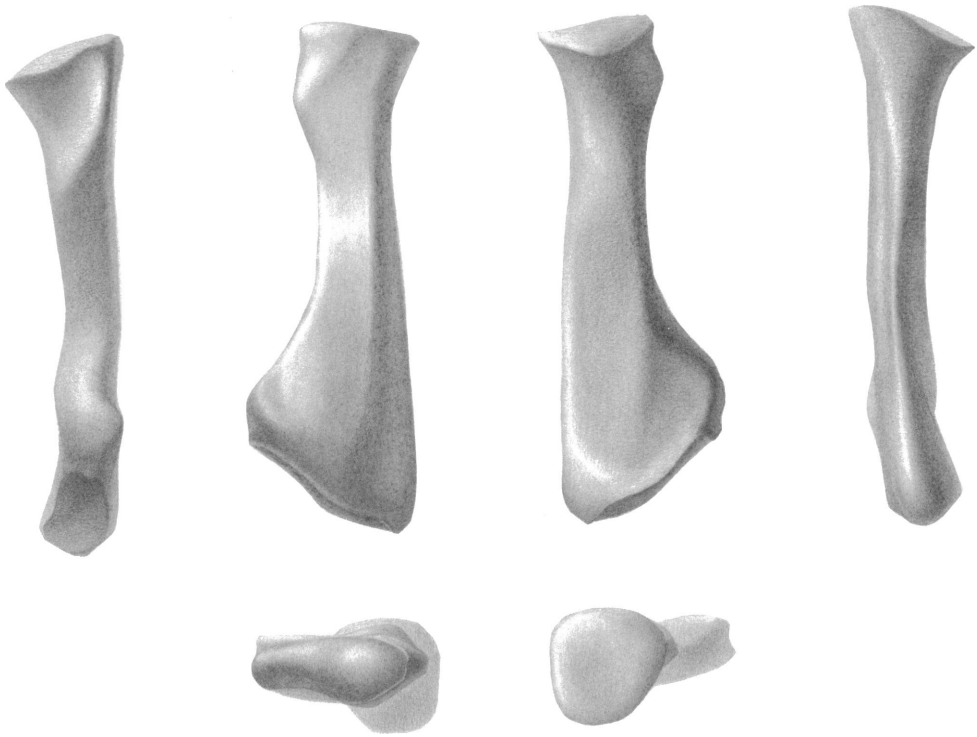

Fig. 154. *Proganochelys quenstedti,* SMNS 16980. Right radius. Top row (left to right), lateral, dorsal, ventral, medial; lower row (left to right), distal, proximal.

time after this photograph was taken and before 1979, when this study began, the left carpus (as well as the rest of the skeleton) was partially disarticulated and some elements were rearticulated in positions different from those in the Berckhemer figure. The lateral portion of the carpus with three metacarpals and six carpals was still articulated in matrix (fig. 159), but the remaining elements had been removed and mixed with other carpal and tarsal elements from the right side and from SMNS 17203. During the course of this study, the articulated carpal elements have been prepared further, the incorrectly rearticulated bones removed, and an effort made to reassemble the carpus based on the Berckhemer figure. Unfortunately, this has been only partially successful and some of the results are open to more than one interpretation. The Beckhemer figure was published in a coarse screen size and details of the carpus lack good definition. Also, the right manus, which is now almost completely disarticulated, was probably articulated originally, but it does not appear in the Berckhemer photograph, making identification of the right carpal elements difficult as well. My reconstruction of the *Proganochelys* forefoot appears in figure 160.

The left forefoot of SMNS 16980 (fig. 159) is best understood by beginning the description with the elements that are most certain of identification. The lateral three metacarpals are articulated, along with other carpal and digital elements, and they can be associated with two metacarpals, articulated with each other, by means of the Berckhemer figure. This gives the complete set of metacarpals I–V along with most of the digits associated with each metacarpal. Metacarpal I has the ventral process of the basal phalange articulating with it but the main body of the phalange and the ungual is missing.

The Berckhemer photograph shows a claw-like bone and possibly an associated phalange but these have not been located in the collection. Metacarpal I is now free of metacarpal II but in 1979 it was still attached in the

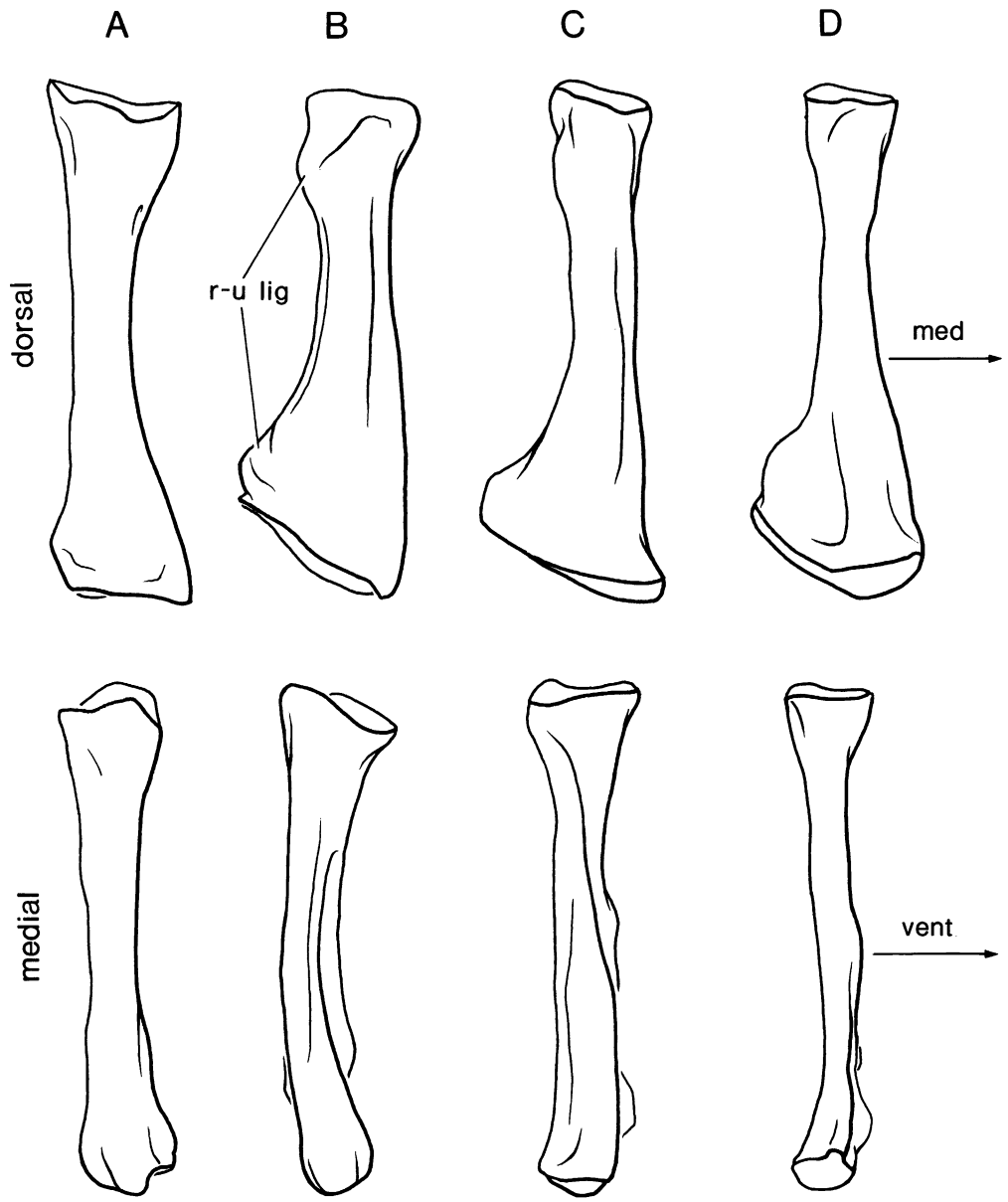

Fig. 155. Comparisons of right radii. Upper row, dorsal views; lower row, medial views. **A,** *Captorhinus* sp., after Holmes (1977) and AMNH 19376; **B,** *Proganochelys quenstedti,* SMNS 16980; **C,** *Macroclemys temmincki,* AMNH 58251; **D,** *Podocnemis expansa,* AMNH 62947. Abbreviations: **med,** medial direction; **r-u lig,** radio-ulnar ligament; **vent,** ventral direction.

same position seen in the Berkhemer figure. The second metacarpal has a phalange and ungual attached to it and these are flexed and retracted over the metacarpal, as are digits III and IV. Metacarpals III, IV, and V are articulated to each other so that III and IV are side by side but V is displaced proximally to the extent that the base of IV is adjacent to the distal articulation of metacarpal V. The fifth digit is roughly aligned with metacarpal

Fig. 156. *Proganochelys quenstedti,* SMNS 16980. Right ulna. Top row (left to right), lateral, dorsal, ventral, medial; lower row (left to right), distal, proximal.

V but both phalange and ungual are displaced from their natural position, the phalange lying too medial and the ungual lying too lateral for natural articulation. Thus, on the basis of the left manus of SMNS 16980 there is a complete set of metacarpals and digits with no ambiguity as to position. SMNS 15759, a nearly complete, articulated manus, confirms the arrangement and allows an accurate reconstruction of the right manus of SMNS 16980.

The articulated piece of forefoot of SMNS 16980 that contains the left digits and metacarpals III–V also has the most articulated carpals, but there is some question about their identifications. As I interpret this group of elements, there are three distal carpals, two centralia, the ulnare, and two sesamoids. The sesamoids are identifiable because they are thin ovals of porous bone on the surface of the carpus, not penetrating into the main body. The three distal carpals lie in a curved line adjacent to the line of metacarpals but there is enough disturbance to prevent a one-to-one identification of each distal carpal with its adjacent metacarpal. It is most likely that the three distal carpals are II–IV rather than III–V, as are the metacarpals. Examination of the Berckhemer photograph shows one distal carpal directly behind digit I and just lateral to it is the first distal carpal in the articulated piece. There does not appear to be any room for a distal carpal between them. If this is distal carpal II then, as preserved in this specimen, it contacts metacarpal III as well as metacarpal II. The next distal carpal moving laterally is quite convincing as belonging to metacarpal III. However, nearly all of it contacts metacarpal III and it does not contact metacarpal IV. The third distal

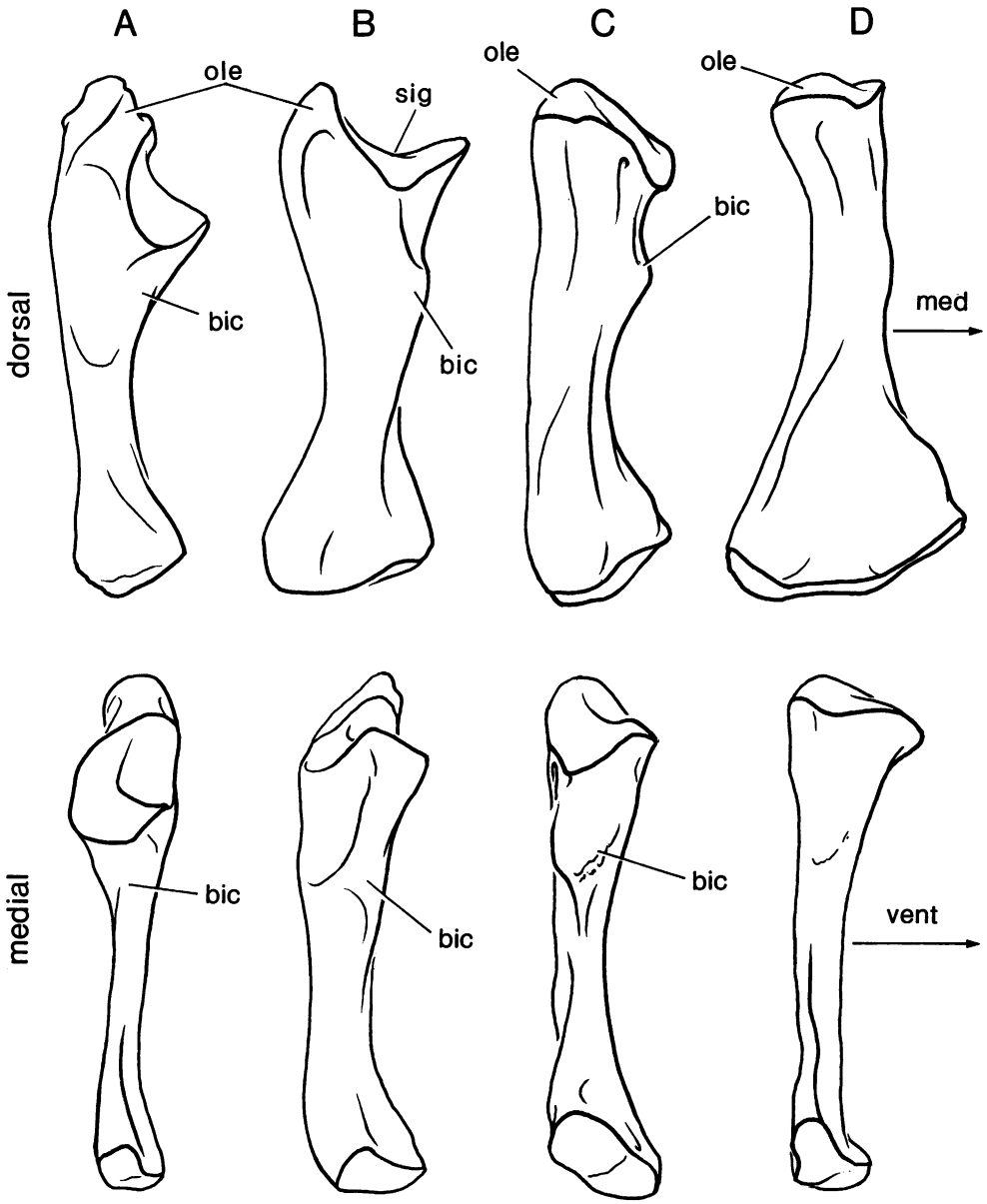

Fig. 157. Comparisons of right ulnae. Upper row, dorsal views; lower row, medial views. **A,** *Captorhinus* sp., after Holmes (1977) and AMNH 19374, 19375; **B,** *Proganochelys quenstedti,* SMNS 16980; **C,** *Macroclemys temmincki,* AMNH 58251; **D,** *Podocnemis expansa,* AMNH 62947. Abbreviations: **bic,** bicipital tendon attachment; **med,** medial direction; **ole,** olecranon; **sig,** sigmoid notch; **vent,** ventral direction.

carpal is separated from metacarpal IV by the sesamoid and matrix, and it contacts metacarpal V. However, the lateral region of the carpus is disturbed with metacarpal V being pushed medially and the ulnare twisted in the plane of the carpus. My favored interpretation is that this is distal carpal IV, but not in its premortem position. The Berck-

TABLE 19
Preserved Material of Carpus and Manus

	SMNS 16980	SMNS 17203	SMNS 17204	SMNS 15759	MB 1910.45.2
Ulnare	R, L	? L	–	–	–
Intermedium	R, L	? L	–	–	–
Radiale	–	? L	–	–	–
Medial centrale	R, L	–	–	–	–
Lateral centrale	L	–	–	–	–
Distal carpal 1	–	–	–	R	–
Distal carpal 2	? R, L	–	–	–	–
Distal carpal 3	? R, L	–	–	–	–
Distal carpal 4	L	–	–	R	–
Distal carpal 5	? R	–	–	R	–
Metacarpal I	R, L	L	–	R	–
Metacarpal II	R, L	? L	–	R	–
Metacarpal III	R, L	? L	–	R	–
Metacarpal IV	R, L	–	–	R	–
Metacarpal V	R, L	–	–	R	–
Phalanx I	R, L	–	–	R	–
Phalanx II	R, L	–	?	R	–
Phalanx III	R, L	–	?	R	–
Phalanx IV	R, L	–	–	R	–
Phalanx V	R, L	–	–	R	–
Ungual I	R	–	–	R	–
Ungual II	R, L	–	?	R	–
Ungual III	R, L	–	?	R	–
Ungual IV	R, L	–	–	R	–
Ungual V	R, L	–	–	R	–

hemer photograph only shows four distal carpals clearly and they seem to be I–IV. My interpretation would require V to have been either not present in *Proganochelys* or lost before 1938.

It is at this point that the right carpus of SMNS 16980 and SMNS 15759 (fig. 158) become useful. The right carpus has a complete digit V with metacarpal articulated and two carpal bones, one of which looks very much like the ulnare of the left carpus and the other is clearly a distal tarsal articulating much more directly with the base of metacarpal V than the distal carpal close to metacarpal V on the left carpus. SMNS 15759 has only three distal carpals preserved, but these are clearly I, IV, and V, strongly arguing that *Proganochelys* had five distal carpals. Therefore, it is most likely that the left carpus of SMNS 16980 has four carpals preserved, I–IV, and that distal carpal V is missing as a result of postmortem factors. The distal carpal I seen in the Berckhemer photograph cannot be identified specifically in the group of loose mesopodials in the SMNS collection, but it is likely that one of them is that bone.

In the section of articulated carpals from the left carpus of SMNS 16980 (fig. 159), there are four bones proximal to the three distal carpals identified above. One of these, on the ventral surface, is a thin oval, identified as a sesamoid, while the other two are interpreted as two centralia and the ulnare. Of these, the ulnare is most certain; it lies proximal to the distal carpals and centralia at the lateral edge of the carpus and distal to the ulna. The ulnare, however, is not in its life position; the element has been rotated 90° so that it is now perpendicular to the plane of the carpus and the articulating surfaces face dorsally and ventrally rather than proximally and distally. The ulna is also disturbed so that the surface normally articulating with the ulnare faces dorsally rather than distally.

TABLE 20
Comparison of Manus and Carpus

	Captorhinus	*Proganochelys*	Casichelydia
Pisiform	Present	Absent, probably as a result of postmortem damage	Present
Ulnare	Flat, constricted in center	Deep, ovoid	Variable, flat and deep, but never constricted
Foramen formed by ulnare and intermedium	Present	Absent	Absent
Intermedium elongate proximodistally	Yes	No	No (except in cheloniids)
Radiale	Large and bearing most of the radial articulation	Probably absent	Small or absent, bearing little if any radial articulation
Centralia in manus	Two present, lateral and medial	Two present, lateral and medial	Varies from one to ?three, primitively two, lateral and medial
Distal carpals	Flat, five	Ovoid, five	Variable, from flat to ovoid, five or less due to fusion
Metacarpal 1	Similar to other metacarpals	Shorter and more robust than other metacarpals	Variable, but primitive condition as in *Proganochelys*
Overlapping metacarpal bases	Absent	Present	Usually present, but variable
Digital formula of manus	2-3-4-5-3	2-2-2-2-2	Usually 2-3-3-3-3
Digital length in manus	Long	Short	Usually long
Proximal phalanx with strong ventral process	Absent	Present	Primitively present but variable
Sesamoids	In flexor tendons	In extensor tendons	Absent

There is no pisiform identifiable. Distal to the ulnare lies what appear to be two centralia. They are closely apposed to each other, the lateral one being constricted in its center and fitting the ovoid medial centrale. Given the lack of natural articulation, at least in the lateral portion of this carpus, this identification cannot be considered definitive. The Berckhemer photograph, however, shows only one element missing from the proximal carpals and this is the intermedium, readily identified among the dissociated bones. In contrast to the other carpals, the intermedium is trapezoidal in shape, with a diagnostic outline that can be matched with the Berckhemer photograph and restored to its original position. In the Berckhemer photograph there is no sign of a radiale (or a pisiform) but the ulnare and intermedium appear to be in their expected positions.

As mentioned above, the intermedium in the Berckhemer photograph has a distinctive shape and the collection of dissociated elements contains what appears to the right and left intermedia of SMNS 16980. Comparison with other turtles, such as *Macroclemys,* supports this identification.

The right manus of SMNS 16980 consists of five digits, I–III, and V being articulated within the digit, while IV is disarticulated but all were found together in the same box. Each digit consists of an ungual, phalanx, and metacarpal. Digit V also has two carpals attached to the proximal articulation of the metacarpal. The carpal in direct contact with the metacarpal appears to be the ulnare rotated distally from its life position and the other carpal appears to be distal carpal V, although it is possible that it is distal carpal IV. In the collection of dissociated elements

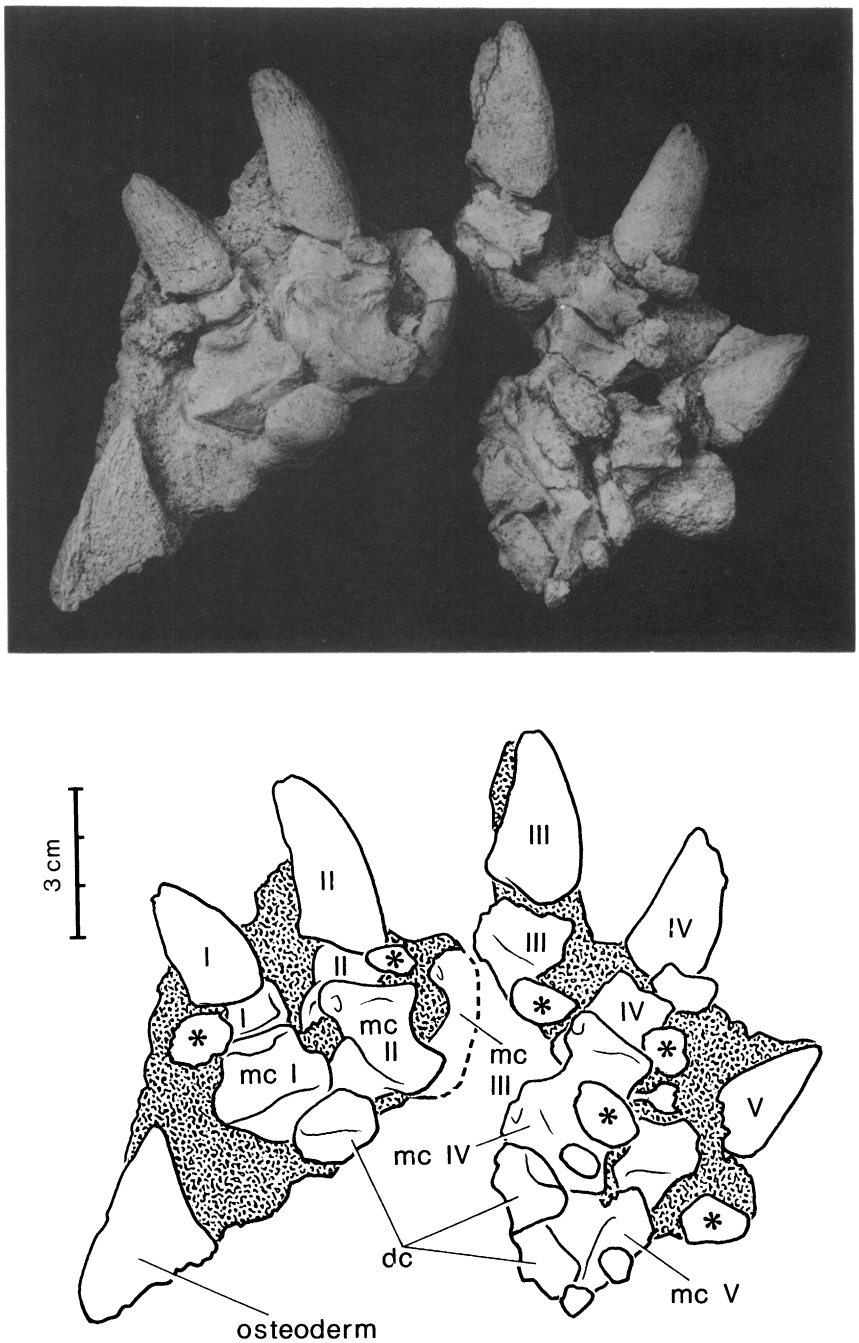

Fig. 158. *Proganochelys quenstedti,* SMNS 15759. Right manus in dorsal view. The specimen is preserved in situ in two pieces with no contact. Abbreviations: **dc,** distal carpal; **mc,** metacarpal. Asterisk (*) indicates sesamoids.

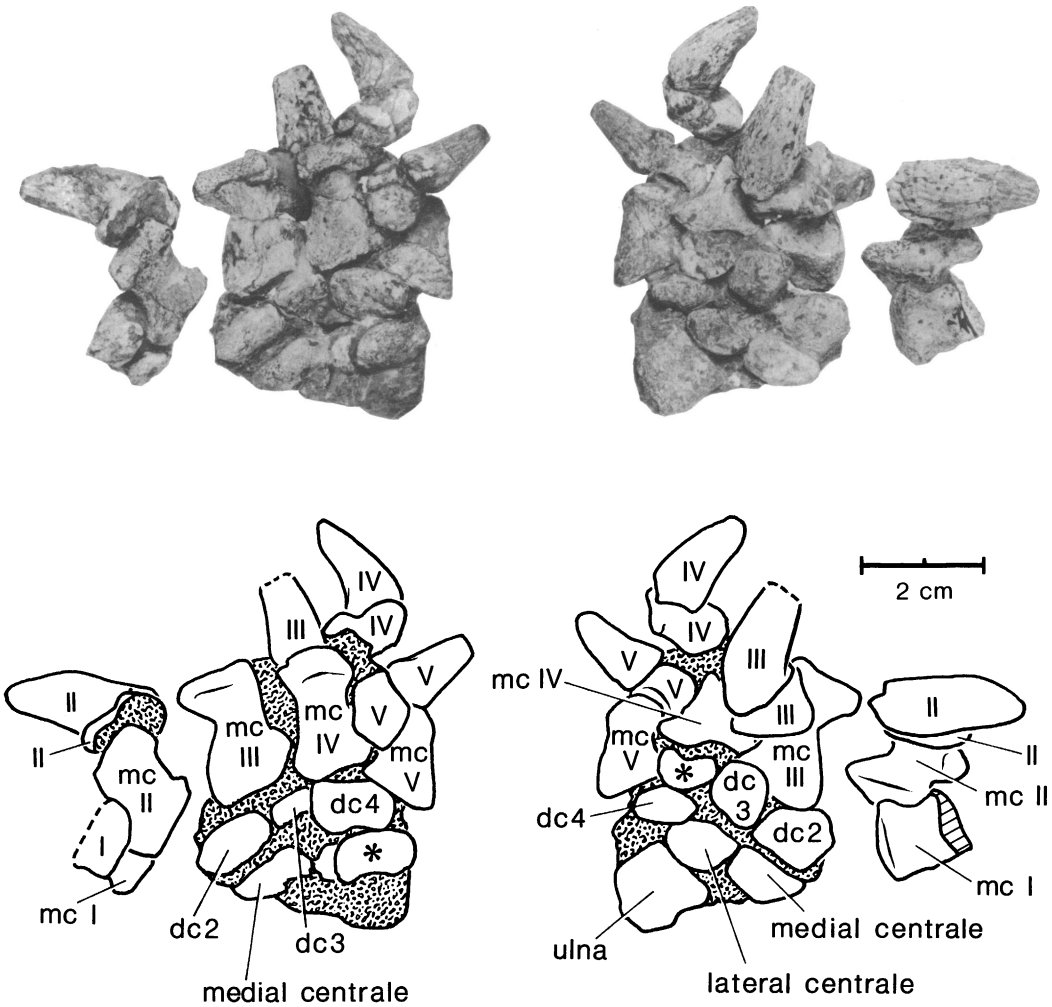

Fig. 159. *Proganochelys quenstedti,* SMNS 16980. Left manus in ventral (left) and dorsal (right) views. This is the same left manus in the Berckhemer (1938) photograph (fig. 98). Note that the digits have been disarticulated and rearranged. See text for discussion. Abbreviations: **dc,** distal carpal; **mc,** metacarpal; **ses,** sesamoid. Asterisk (*) indicates osteoderm.

there is a lateral centrale and a right intermedium, most likely belonging to this carpus, and four of what appear to be distal carpals. Two of these are articulated and could possibly be distal carpals II and III of the right carpus. The remaining two are less well preserved and could be distal carpals or centralia. The lateral centrale of *Proganochelys* is a distinctive element because it is narrow in the middle and is readily identifiable. It seems likely, then, that the right carpus of SMNS 16980 was originally at least as complete as the left and possibly articulated.

SMNS 15759 provides an articulated right manus that consists of all five digits but only a few carpals (fig. 158). Digits I, II, and IV are complete, with ungual, phalanx, and metacarpal, while digits III and V are missing portions of the metacarpals. Only three bones of the carpus are preserved, distal carpals I, IV, and V. None of these is complete; all are missing at least some of the proximal portion.

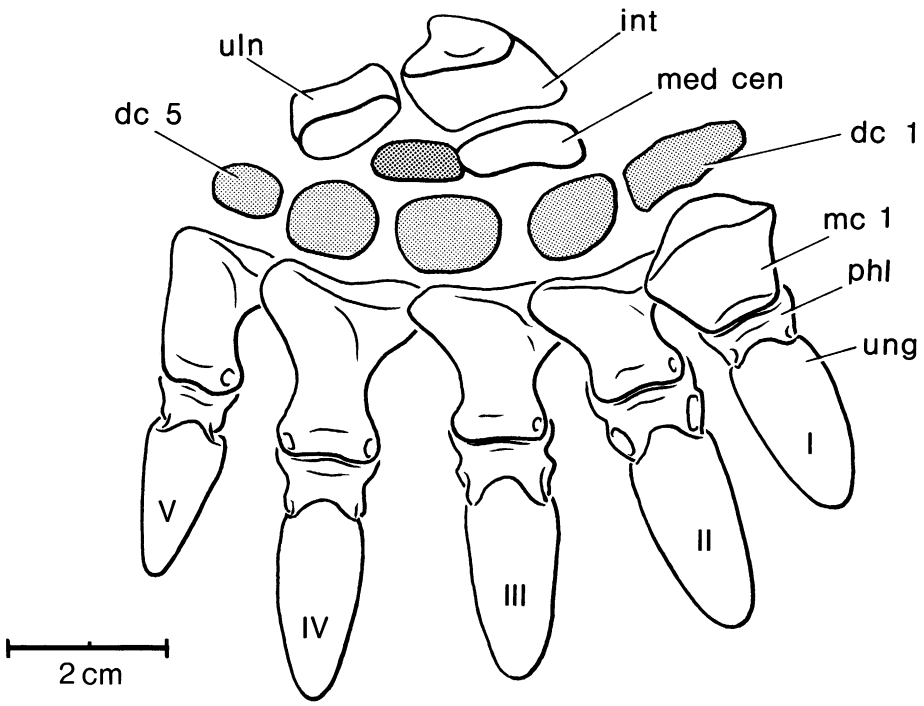

Fig. 160. *Proganochelys quenstedti.* Dorsal view of right manus and carpus, partially restored, based on SMNS 16980 and SMNS 15759. Abbreviations: **dc,** distal centrale; **int,** intermedium; **mc,** metacarpal; **med cen,** medial centrale; **phl,** phalanx; **uln,** ulnare; **ung,** ungual. Lateral centrale is in heavy stipple, distal carpals are in light stipple.

Among the collection of loose elements there are some unguals that are too small to belong to SMNS 16980 or SMNS 17204 and probably are referrable to the manus or pes of SMNS 17203. In this collection, small, irregular mesopodiallike nodules might also belong to SMNS 17203. SMNS 17204 has no left forelimb but much of the right forelimb is present, articulated onto the ventral surface of the shell. Most of the limb is poorly preserved and covered with osteoderms but two unguals are recognizable. Neither SMNS 17203 nor SMNS 17204 supplies any information used in the description of the *Proganochelys* manus.

Although the carpus of *Proganochelys* is not perfectly known, many of its characteristics are determinable and allow comparison with other turtles and other amniotes. There are five distal carpals as in most other turtles and proximally there are four carpals that can be definitely determined. Many turtles have four or five proximal carpals, while *Captorhinus* and apparently baenids, have six. These differences will be discussed below.

The pisiform is the most lateral of the proximal carpals and usually lies laterally to the ulnare and just distal to the ulna. It occurs in *Captorhinus* (Holmes, 1977) and apparently all turtles (Rabl, 1903) but it cannot be identified in *Proganochelys.* The lateral portion of the carpus is preserved in situ in the left carpus of SMNS 16980 and the right carpus of SMNS 15759 but both specimens seem to be incomplete laterally. In SMNS 15759 the preserved area terminates distal to the expected position of a pisiform. In SMNS 16980 the area can only be extrapolated from the photograph in Berckhemer (1938) described above, and a pisiform does not seem to be present. However, distal carpal V is also missing in this specimen and the ulnare and ulna are disturbed and not in their life positions; this combined with the supposition

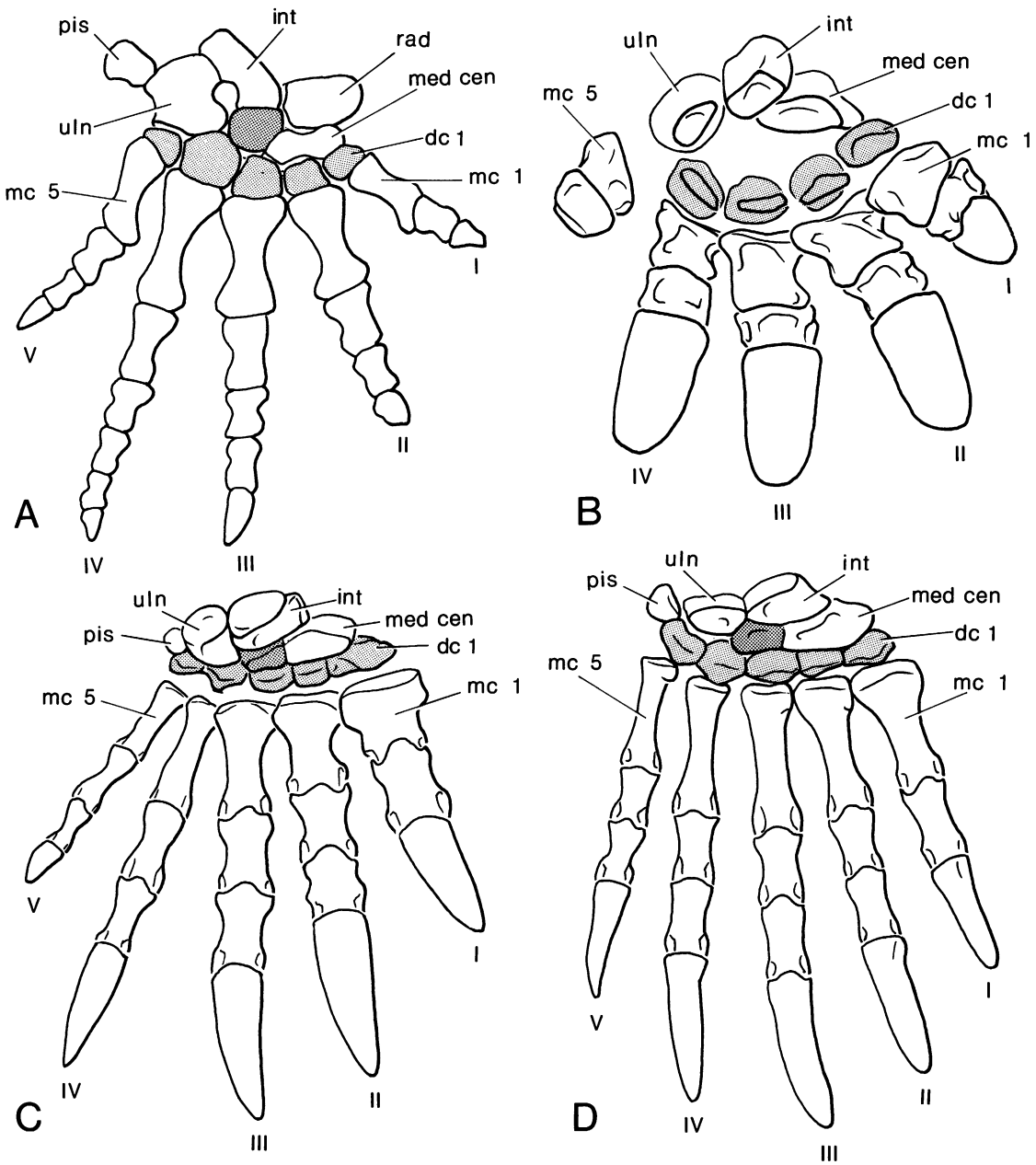

Fig. 161. Comparison of right maniacs in dorsal view. **A,** *Captorhinus* sp., from Heaton and Reisz (1986); **B,** *Meiolania platyceps,* Australian Museum F57984; **C,** *Macroclemys temmincki,* AMNH 58251 and 36602; **D,** *Podocnemis expansa,* AMNH 62947. Abbreviations: **dc,** distal carpal; **int,** intermedium; **mc,** metacarpal; **med cen,** medial centrale; **pis,** pisiform; **rad,** radiale; **uln,** ulnare. Distal carpals are indicated by light stipple; lateral centrale is indicated by heavy stipple.

that a pisiform could be easily mistaken for an osteoderm (many of which were removed during pre-1979 preparation) suggests that the pisiform may not have been absent in life.

Moving medially, the ulnare is present in situ in both carpi of SMNS 16980, but it does not seem to be in its life position on either side. In the left carpus the ulnare is rotated

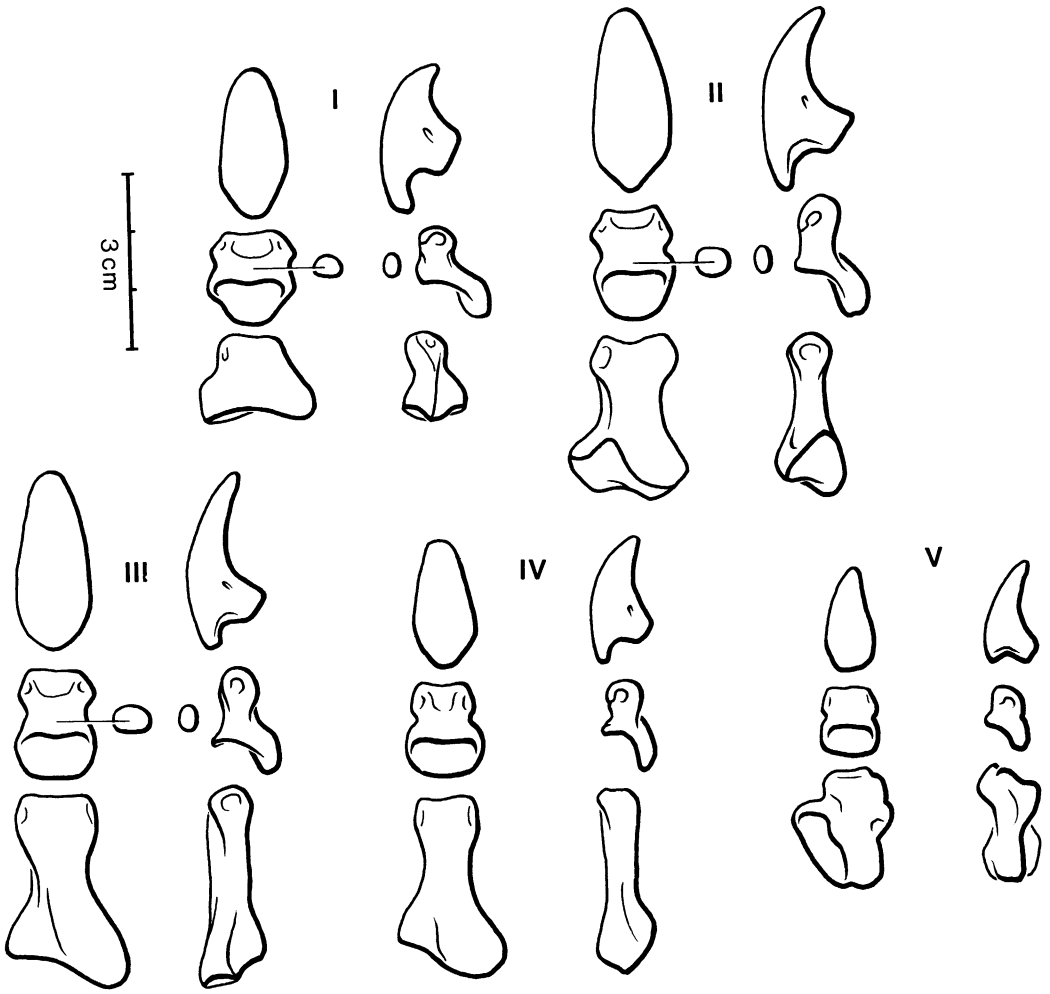

Fig. 162. *Proganochelys quenstedti,* SMNS 16980 (using information from right and left as well as from SMNS 15759) digits of right manus. Each digit is figured disarticulated in dorsal (left) and lateral (right) views. Sesamoid bones are indicated; in the dorsal views the sesamoid is displaced with a leader showing its correct position.

90° so that its articular surfaces face dorsally and ventrally but its relative position in the carpus appears correct. It is just distal to the ulna and proximal to the distal carpals IV (and V if restored) laterally and the lateral centrale medially. The intermedium lies medially and slightly proximal to the ulnare. This position is consistent with that in *Captorhinus* and other turtles generally. The right carpus has the ulnare oriented correctly but it is too far anterior and just adjacent to distal carpal V. The ulnare in *Proganochelys* is roughly the shape of an oval cylinder with its axis dorsoventral so that it is oval in dorsal and ventral view. Although the articular surfaces are broadly curved with no distinct facets, there is a broadened area facing proximally to articulate with the ulna. In dorsal or ventral view this ulnar surface may be considered the base of a triangle with a smaller articular surface facing medially and distally for the lateral centrale, and another surface facing laterally and distally for the distal carpals. The dorsal and ventral surfaces are slightly depressed concavities, as is often the case in the nonarticulating surfaces of mesopodials covered only by dermis. The ulnare of *Proganochelys* differs from that bone in

Captorhinus and many cryptodires, such as *Trachemys* and *Chelydra,* in being thicker in its dorsoventral dimensions than in its other dimensions. *Captorhinus* and many turtles have generally flat and platelike proximal carpals. Pleurodires, such as *Meiolania,* have ulnares, as well as the other proximal carpals, that are thicker and more ovoid, as in *Proganochelys.* Among the various turtles that I have compared with *Proganochelys,* the ulnare is most similar to, and differs only slightly from, the ulnare of fully grown specimens of *Podocnemis expansa.* I conclude, then, that the ulnare of *Proganochelys* is consistent with what would be expected in the sister group of Casichelydia.

The intermedium of *Proganochelys* is known only from two disarticulated elements that I have identified as the right and left intermedia of SMNS 16980 on the basis of comparisons with other turtles, but primarily on the photograph in Berckhemer (1938) of the articulated left carpus of SMNS 16980. In contrast to the other carpals in *Proganochelys,* the intermedium is a trapezoidal, blocklike element with relatively well-defined articular surfaces. It is the largest carpal in *Proganochelys* and has a broad, transverse surface facing proximally. As in other turtles, at least the lateral portion of the surface is for articulation with the ulna; the extent is not determinable precisely, but appears to be about one-half, based on the Berckhemer photograph and rearticulation of the carpus. Laterally, there is a smaller, flat surface facing the ulnare proximally and the lateral centrale distally. This face and the margin parallel to it are the short sides of the trapezoidal intermedium with the proximal and distal surfaces being the long sides. The angle between the proximal and lateral surfaces is acute (as is the angle between the distal and medial surfaces) while the angle between the lateral and distal surfaces is obtuse (as is the angle between the proximal and medial surfaces).

The distal surface apparently articulates closely with the medial centrale and is slightly concave toward that bone. While the other three surfaces are approximately at right angles to the plane of the carpus, the medial surface is inclined dorsally, resulting in a wedge-shaped outline in proximal or distal view. While the ventral surface is slightly concave but generally parallel to the plantar surface of the carpus, the dorsal surface is formed in two planes, a more lateral surface, slightly concave and roughly parallel to the plane of the carpus, and a more medial surface that faces dorsomedially. This dorsomedial surface appears to be an articular surface but what it might articulate with is hard to imagine, unless the radius rotated over this surface during flexion. Turtle intermedia are usually roughly flat but variably thickened for the ulnar articulation, although not to the extent seen in *Proganochelys. Chelydra* and *Macroclemys* are very similar to *Proganochelys* in the size and shape of the intermedium and the degree of medial tapering. In these recent taxa, however, the radial articulation is a small but transverse facet lying at right angles to the plane of the carpus, rather than inclined as in *Proganochelys.*

In turtles the shape of the intermedium is closely related to the degree to which the distal ends of the radius and ulna contact each other or are separated by a space, usually filled by the intermedium. Even if one excepts the diverse conditions found in trionychids, testudinids, and cheloniids, it is still difficult to see a consistent systematic pattern for this feature. Rather, the shape of the intermedium differs widely among turtles and the condition in *Proganochelys* does not aid in sorting this out. Based on the morphology of the opposing surfaces and the in situ positions, the radius and ulna of *Proganochelys* seem to have been in close contact with each other, proximally and distally, although not to the extent seen in some testudinids.

It is convenient to compare both ulnare and intermedium of *Captorhinus* with these bones in *Proganochelys* and other turtles. Holmes (1977) has described and figured these elements which may now be considered well known in *Captorhinus.* Both bones are platelike and relatively flat, in contrast to *Proganochelys,* and the whole carpus is a tighter-fitting structure with closely apposed articular surfaces in contrast to the looser arrangement in *Proganochelys.* The ulnare of *Captorhinus* is constricted in the middle of its proximodistal axis, the medial constriction forming the lateral half of a round open-

ing which has its medial half formed by the intermedium. Turtles lack this foramenlike opening and lack a wasp-waisted ulnare. As in turtles, the distal articulation of the ulna of *Captorhinus* articulates with the ulnare laterally and the intermedium medially. The intermedium of *Captorhinus,* however, differs from that of turtles in being relatively elongate in the direction of the limb axis, while turtles, however variable the intermedium may be, have an intermedium that is blocklike, ovoid, or tapered, but not elongate.

The centralia in the carpus of *Proganochelys* are readily homologized with the two centralia in *Captorhinus* (fig. 161). They are cylindrical on the dorsoventral axis and oval in dorsal and ventral view. The medial centrale is similar in shape to the ulnare, with broadly convex, curved articular surfaces. The lateral centrale, however, has a distinctive shape; in articular view it is hourglass-shaped with a constricted center. The oval dorsal and ventral surfaces, parallel to the plane of the carpus, are slightly concave and are connected by the constricted main body of the bone. The ventral surface is significantly smaller in size than the dorsal surface so that a ventrally directed taper is superimposed on the constriction. As a result of this constricted shape, the lateral centrale fits more closely to the surrounding carpals, and in the partially articulated left carpus of SMNS 16980 it is tightly pressed against the medial centrale. The relations of the lateral centrale to the other carpals is nearly the same in *Proganochelys* and *Captorhinus.* Distally the lateral centrale is bordered by distal carpal 3, laterodistally by distal carpal 4, lateroproximally by the ulnare, and proximally by the intermedium. There is a difference in that *Captorhinus* has a medial contact with the radiale proximomedially and the lateral centrale distomedially, while in *Proganochelys* the medial centrale is directly medial and there is no possibility of a radiale contact (even if one was present) because of the medial-intermedial contact. The medial centrale in *Proganochelys* appears to be relatively smaller in size than that in *Captorhinus,* so that in *Proganochelys* the distal articulation of the medial centrale is with distal carpal 2 and less than half of distal carpal 3, while in *Captorhinus* the medial centrale has broad contacts with distal carpals 1 and 3 as well as 2. In *Captorhinus* the lateral and medial centralia are slightly offset with the medial centrale being more distal, while in *Proganochelys* they are aligned transversely. Conclusions about homologies between the centralia of *Captorhinus* and *Proganochelys* are straightforward: the two centralia of *Proganochelys* are very similar to the medial and lateral centralia of *Captorhinus.* Conclusions about homologies between *Proganochelys* and other turtles, however, are less clear. In most turtles (Rabl, 1910) the carpus has either two discrete central ossifications, two ossifications partially or entirely fusing during life, or one ossification. When discrete, the lateral centrale is similar in position to the lateral centrale of *Proganochelys* in being equidimensional and being surrounded by distal carpals 3 and 4, the ulnare, the intermedium, and the presumed medial centrale. The more medial element, however, differs in many cases from the medial centrale of *Proganochelys* in being medially elongate and usually bearing an articulation surface for the radius. Rabl (1910) termed this element a fused radiale and medial centrale. In some forms, such as *Chelus,* however, the element may not be elongate and it looks very similar to the medial centrale of *Proganochelys.* Bramble (1982) has homologized this element with the medial centrale of *Captorhinus,* and I think the condition in *Proganochelys* supports this hypothesis.

There is no evidence of a radiale in *Proganochelys.* Despite the fact that I have argued above that the absence of a pisiform in specimens of *Proganochelys* did not necessarily mean that it was absent in life, I think it is likely that the radiale in *Proganochelys* was either absent or very small. First of all, the region of the pisiform is disturbed in the best specimen of *Proganochelys* while there is no particular indication of disturbance on the medial margin of the left carpus in SMNS 16980, where the radiale would be expected. This area was disarticulated before 1979 but the Berckhemer photograph (fig. 98) clearly shows no ossification that could be a radiale. Secondly, the collection of unidentified, disarticulated mesopodials has carpals but none

that are suggestive of a presumed radiale. Lastly, the restored articulation of the carpus (fig. 160) allows little room for a well-developed radiale, so that, if present, it would be comparatively small (and easily lost).

Comparison of this area in the *Captorhinus* carpus with *Proganochelys* and other turtles is also helpful. In *Captorhinus* the well-developed radiale has a proximolateral articulation with the intermedium so that the intermedium and radius barely contact, if at all. In *Proganochelys* and many other turtles, the intermedium contacts the ulna rather than the radiale as in *Captorhinus,* suggesting that the radiale is either absent as a definitive element or it is in a significantly different position in turtles. Therefore, even though the material does not allow a definitive conclusion, it is very likely that the radiale was either small or absent in *Proganochelys.* A small and laterally placed or absent radiale can be considered a chelonian synapomorphy. The shape and relations of the radiale in pelycosaurs (Reisz, 1980) and the primitive diapsid, *Petrolacosaurus* (Reisz, 1981), are very similar to *Captorhinus* and can by hypothesized as the primitive amniote condition.

One of the more interesting controversies in the carpal literature centers on the presence or absence of a radiale in turtles (see Burke and Alberch, 1985, and references). Now that the carpus of *Captorhinus* is well known (Holmes, 1977), it is no longer necessary to rely on comparisons with a "generalized" tetrapod such as *Eryops* or living lissamphibians. This is particularly fortunate in view of the fact that temnospondyls and lissamphibians are characterized as having only four digits in the manus, a condition that is probably synapomorphic for temnospondyls + lissamphibians and that may have consequences for other carpal features. The carpus of *Captorhinus* (fig. 161) has six elements proximal to the distal carpals and I accept Holmes' identification of these elements: pisiform, ulnare, intermedium, and radiale in the most proximal row, and lateral centrale and medial centrale for the two elements in the more distal row. There seems little difficulty in concluding that the standard identifications in such works as Rabl (1910), Romer (1956), Bramble (1982), and Burke and Alberch (1985) of the pisiform, ulnare, and intermedium in turtles are homologous with the same-named elements in Holmes' description of *Captorhinus.* Rather the difficulties arise with the radiale and centralia. Rabl (1910), who did the most extensive study of the mesopodium in turtles, considered the radiale to be present in nearly all turtles but usually fused (except in cheloniids) with at least one centrale. Three later authors (Bramble, 1982; Burke and Alberch, 1985) have argued that the fused radiale plus centrale of Rabl only consists of centralia and that the radiale is either absent during development and in the adults of almost all turtles (Burke and Alberch, 1985), or present developmentally but ossified in only some cryptodiran and pleurodiran taxa (Bramble, 1982). Rabl (1910) reported this element as the "accessorium" and also showed that it occurs sporadically in cryptodires and pleurodires. Burke and Alberch (1985) identified this element as a centrale based on developmental criteria.

Although *Proganochelys* aids in this dispute only by showing that two centralia were present and the radiale was either absent or very small, the question of the homology of the "accessorium" and the presence or absence of a minute radiale in turtles is not helped. There is, however, little evidence for a fusion of the radiale with either medial or lateral centralia, and it is clear that all turtles lack a well-developed radiale of the generalized amniote pattern.

There are five distal carpals in *Proganochelys,* as in other turtles and in *Captorhinus,* and they are generally ovoid, rounded elements, not tightly fitting either to themselves or to the metacarpals. In *Captorhinus* and many turtles, the distal carpals are more tight-fitting with flat articular surfaces but the *Proganochelys* condition does occur in other turtles, such as *Meiolania* and some pleurodires. The first distal carpal is not complete in SMNS 15759 but it appears to differ from the other distal carpals in being flatter and broader, much as in other turtles, such as *Chelydra.* The second and third distal carpals are very similar. They are rounded, ovoid elements with a broad base, tapering dorsally to a conical tip, with a smoothly concave distal surface. Distal carpal IV is similar but the dorsal end of the cone ends in a small,

flattened surface, parallel to the plane of the carpus. Distal carpal V is also incompletely known but appears similar to the distal carpal IV, only smaller. The distal carpals appear to have slightly offset contacts with their respective metacarpals, rather than being directly aligned as in most other turtles and *Captorhinus,* but this may be a preservational artifact. The conical-tapered shape of the distal carpals indicates that *Proganochelys* had a plantigrade stance in the forefoot (Auffenberg, 1966), similar to such turtles as chelydrids and pelomedusids. The closest similarity of the distal carpals in *Proganochelys* is with *Podocnemis*; the primary difference is that these bones in *Podocnemis* are fitted more closely to each other than in *Proganochelys.*

The metacarpals in *Proganochelys* are robust, relatively short elements, slightly shorter than in *Captorhinus* and generally comparable to chelydrids. They are, however, more elongate than in *Meiolania* and testudinids. The first metacarpal in *Proganochelys* is relatively short and broad, distinctly different from the other metacarpals. The proximal articulation is rounded on the edges but otherwise flat. The articulation surface is borne on an expanded base that is thicker and broader than the rest of the bone. Proximally the first metacarpal tapers with a slight convexity on each side in dorsal view and a marked constriction in thickness. The distal articulation surface is thicker than the middle and bears a uniformly rounded, cylindrical area for the proximal phalanx. In *Captorhinus* the metacarpals are very similar to each other and this differentiation of metacarpal morphology seems to be common in turtles. *Macroclemys* has a metacarpal I that is very similar to that of *Proganochelys* in morphology and degree of differentiation from the other metacarpals. It differs from the *Proganochelys* metacarpal primarily in having the distal articulation surface divided by a groove for the reception of a ridge on the proximal phalanx. This condition is common in Casichelydia but not found in either *Captorhinus* or *Proganochelys.*

Metacarpals II–IV are similar in shape, having a fairly broad base, a distinct constriction midway along the length, and an expansion distally from the phalanx articulation. The metacarpals increase in length from I to IV with V being shorter—about the same length as II. This size differentiation is not unusual in turtles, and is the same in *Macroclemys* and *Chelydra* and very similar to the condition in *Captorhinus.* Metacarpal V differs from metacarpals II–IV because the lateral margin is virtually straight, rather than concave as in II–IV.

The metacarpals of *Proganochelys* have small articular facets on their expanded bases for the articulation of the adjacent metacarpal. This articulation is a broadly overlapping one as can be seen in SMNS 15759 and SMNS 16980. The more medial metacarpal overlaps onto the more lateral one with the result that metacarpal I is not overlapped and metacarpal V does not do any overlapping. Viewing the proximal articulation surface of the metacarpals shows that the they are modified for this overlap by extending the proximal articulation surface and curving it to face dorsolaterally on metacarpals II–V. The ventromedial portion of the base in metacarpals I–IV articulates onto this area of each respective metacarpal. This sort of overlapping metacarpals does occur in other turtles, such as *Meiolania,* but rarely to the extent seen in *Proganochelys. Captorhinus* has hardly any overlap and the character, if synapomorphic for turtles, has been considerably reduced in most of them.

Proganochelys has only two phalanges in each digit in the manus. The proximal phalanx is very similar in all five digits of the manus, as well as the pes, and almost impossible to identify as to digit from disarticulated material. The proximal phalanx differs in size along the manus: phalanges I and V are smaller than the three central phalanges. The proximal phalanx has a proximal articulation surface that is quite large and occupies about half of the phalanx. This surface is curved, convex proximodorsally, and is formed largely by a proximally directed process that underlies the metacarpal and forms an attachment site for the flexor tendons. The main body of the phalanx is broader than deep, and blocklike, with a slight constriction in its center, both in dorsoventral and proximodistal views. *Captorhinus* and most turtles have a relatively flat proximal articulation surface on the proximal phalanx but chelydrids have a fairly well-developed ven-

tral process similar to that of *Proganochelys*. The lateral and medial edges of the distal end of the proximal phalanx have small concavities for ligament attachment, as in many tetrapods.

The ungual phalanges of *Proganochelys* (fig. 162) are distinctly clawlike, blunt in comparison to those of chelydrids and emydids, but more acute than in *Meiolania* and testudinids. They are roughly three times longer than wide at the base with a well-formed proximal articulation facing directly proximally and a ventrally thickened edge but without a strong ventral process as in the proximal phalanx. The proximal part of the ungual is equidimensional in proximal view but the bone becomes thinner anteriorly and is slightly recurved, concave ventrally, and convex dorsally. The unguals of *Proganochelys* are comparable to those in other turtles, although more robust than in most, but they are quite different from those in *Captorhinus*, which are conical and smaller than the more proximal phalanges.

Proganochelys has a manus (and pes) digital formula of 2-2-2-2-2; in *Captorhinus* it is 2-3-4-5-3, and the most common chelonian formula is 2-3-3-3-3. Baenids (Russell, 1934) also have 2-3-3-3-3 and the general occurrence of this formula in pleurodires as well argues that it is probably primitive at the level of Casichelydia. The *Proganochelys* condition is best interpreted as autapomorphic for that genus and independently acquired by *Meiolania* as a second instance and by testudinids as a third instance.

HINDLIMBS
(table 21, figs. 150, 151, 163, 164)

FEMUR

The femur of *Proganochelys* is preserved on both sides in SMNS 16980 (fig. 150) but the distal end is badly damaged in the right femur and distorted in the left. In SMNS 17204 (fig. 87) both femora are preserved in articulation and remain attached to the carapace. The left femur in this specimen is intact but not well preserved while the right is the best preserved femur among the available *Proganochelys* specimens. This femur, visible in its anterior and ventral aspects, has provided much of the information in the composite drawing (fig. 163). SMNS 17203 also has both femora in relatively good condition; the right one (figs. 101, 102) is still in articulation with the rest of the limb while the left is disarticulated (fig. 151). Jaekel (1918a: figs. 19, 20; pl. 3B) described a pelvis and right femoral head (fig. 141) of another individual of "*Stegochelys dux*" from Halberstadt.

The femur of *Proganochelys* is a cylindrical bone, expanded at either end and arched dorsally. Its overall morphology is similar to that of other turtles, particularly *Macroclemys*. Proximally its most prominent feature is the pelvic articulation surface or femoral head. In *Captorhinus* and other generalized amniotes (fig. 164), the acetabular articulation surface faces proximally primarily, and, although curved, is roughly at right angles to the long axis of the femur. In all turtles, including *Proganochelys*, the articulation surface is borne on a head that consists of a dorsal projection inclined away from the long axis of the femur. The femoral head of turtles does not reach the right angle inclination with a constricted neck as seen in mammals, but it is distinctly inclined in contrast to the primitive amniote condition.

In proximal view the femoral head of *Proganochelys* is oval, narrower than long, but not as narrow as in *Captorhinus* and other generalized amniotes. In casichelydians the head is wider and there is usually a more extensive articular surface than in *Proganochelys*. In Zug's (1971) study of the cryptodiran hind limb, he determined that a circular-spherical head is associated with walking, either terrestrial or bottom walking. The elongate head of *Proganochelys* is consistent with forms categorized as freshwater swimming, such as batagurines or even emydines (except *Terrapene*).

In addition to a dorsally inclined femoral head, the acetabular articulation surface in turtles has a greater degree of curvature as seen in anteroposterior view, than in generalized amniotes. In *Captorhinus* the surface is curved more than in some extinct forms, such as primitive pelycosaurs, but less than in any turtle. *Proganochelys* has a curvature of roughly a right angle, more than in *Captorhinus* but less than in other turtles.

TABLE 21
Comparison of Femur

	Captorhinus	*Proganochelys*	Casichelydia
Articulation surface of femur with acetabulum	Faces directly proximal, not inclined	On distinct, dorsally inclined head	On distinct, dorsally inclined head, developed to a variable extent
Shape of femoral head in proximal view	Narrow, width about ½ length	Narrow, but wider than in *Captorhinus*	Narrow to circular, but more extensive than in *Proganochelys*
Degree of curvature of femoral head in anteroposterior view	Slight, but greater than in some generalized amniotes such as *Ophiacodon*	Greater than in *Captorhinus*, but less than in Casichelydia	Variable, but greater than in *Proganochelys*, nearly spherical in some
Trochanter minor	Distinct, thumblike projection	Distinct, but connected to femoral head	Variable, but primitively as in *Proganochelys*
Trochanter major	Barely distinct from femoral head	Distinct from femoral head, but connected by web of bone	Usually free of femoral head to variable extent, primitively as in *Proganochelys*
Intertrochanteric fossa	Shallow concavity compared with turtles	Deeper and better defined than in *Captorhinus*	Variable, but primitively as in *Proganochelys*
Femoral shaft	Straight	Arched dorsally	Arched dorsally
Fourth trochanter	Present	Absent	Absent
Low ridge on posteroventral margin of femoral shaft	Absent	Present	Absent
Intercondylar fossa on dorsal surface of distal end of femur	Present	Absent	Absent
Posterior (fibula) condyle with distinctive ventral ridge	Present	Absent	Absent
Anterior and posterior condyles	Posterior condyle larger	Posterior condyle slightly larger but of nearly equal size	Equal in size or as in *Proganochelys*

The proximal end of the femur in *Proganochelys* is expanded by the development of two variably defined processes or trochanters: the trochanter minor (of Walker's usage, 1973; also termed the internal or lesser trochanter). In *Captorhinus* (Fox and Bowman, 1966) the trochanter minor is a thumblike projection separated from the femoral head with its axis aligned proximally and slightly anterior. In other generalized tetrapods, the trochanter minor is only a low, rugose ridge. At present, the distribution of this feature is not clear but the presence of a distinct trochanter minor appears to be a synapomorphy at some level, low in the amniote cladogram. *Proganochelys* and other turtles have definitive trochanters minor although in some groups, such as testudinids and advanced cheloniids, the process is completely joined to the head and trochanter major by webs of bone. In *Proganochelys* and most turtles the trochanter minor is a flange of bone connected with the femoral head and not a separate process as in *Captorhinus*. The difference would appear to be the relatively greater size of the trochanter in turtles. The position and shape of the trochanter minor in *Proganochelys* is very similar to *Macroclemys* differing only in the greater thickness of the projection in *Proganochelys*.

The trochanter major is poorly defined in *Captorhinus*; the acetabular articular surface

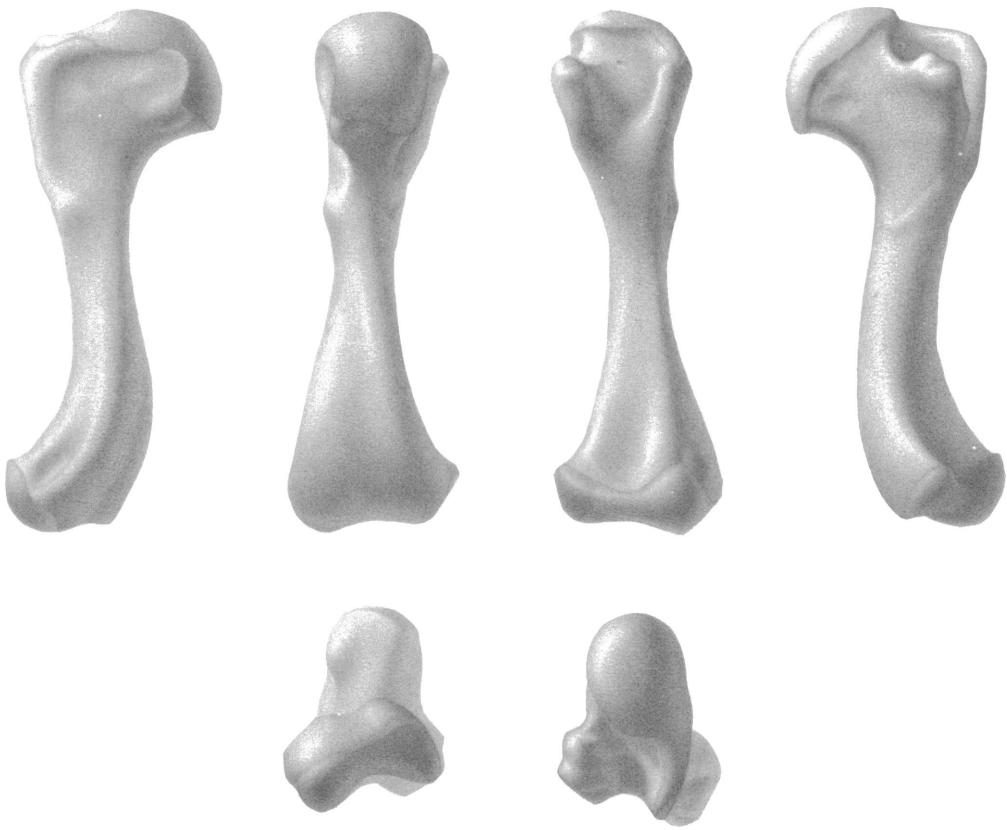

Fig. 163. *Proganochelys quenstedti,* composite of SMNS 16980 and SMNS 17204, right femur. Top row (left to right), posterior, dorsal, ventral, anterior; lower row (left to right), distal, proximal.

of the femoral head is contiguous with the trochanter. In *Proganochelys* and casicheloydians, primitively the trochanter major, although connected to the head by a web of bone, is more differentiated than in *Captorhinus* and generalized amniotes. *Proganochelys* does not differ significantly from baenids and other generalized turtles in the size and shape of the trochanter major.

The intertrochanteric fossa is a ventrally and proximally open concavity that is formed anteriorly by the trochanter minor and posteriorly by the trochanter major and is, in consequence, related to the development of those structures. In *Captorhinus* and generalized amniotes the fossa is broad, relatively shallow, and not well defined. In *Proganochelys* the fossa is narrower, relatively deep, and well defined by the ridges supporting the two trochanters. The intertrochanteric fossa of *Proganochelys* is most similar in size and shape to such forms as *Macroclemys* and *Pseudemys,* differing from those of batagurines in being deeper. Pleurodires tend to have shallow to absent intertrochanteric fossae because the trochanters are more in a line with the head rather than being ventral to the head, while testudinids and cheloniids have a fossa closed ventrally and only open proximally.

The femoral shaft of *Proganochelys* is arched or bowed dorsally as in other turtles but in contrast to the straight shaft of *Captorhinus* and generalized amniotes. *Captorhinus* and generalized amniotes have a ridge or rugosity on the anteroventral surface of the shaft, the fourth trochanter, that is absent in turtles. There is no sign of a rugosity in this position in *Proganochelys* but there is a distinct ridge a little less than halfway along the shaft from the head on the posteroventral

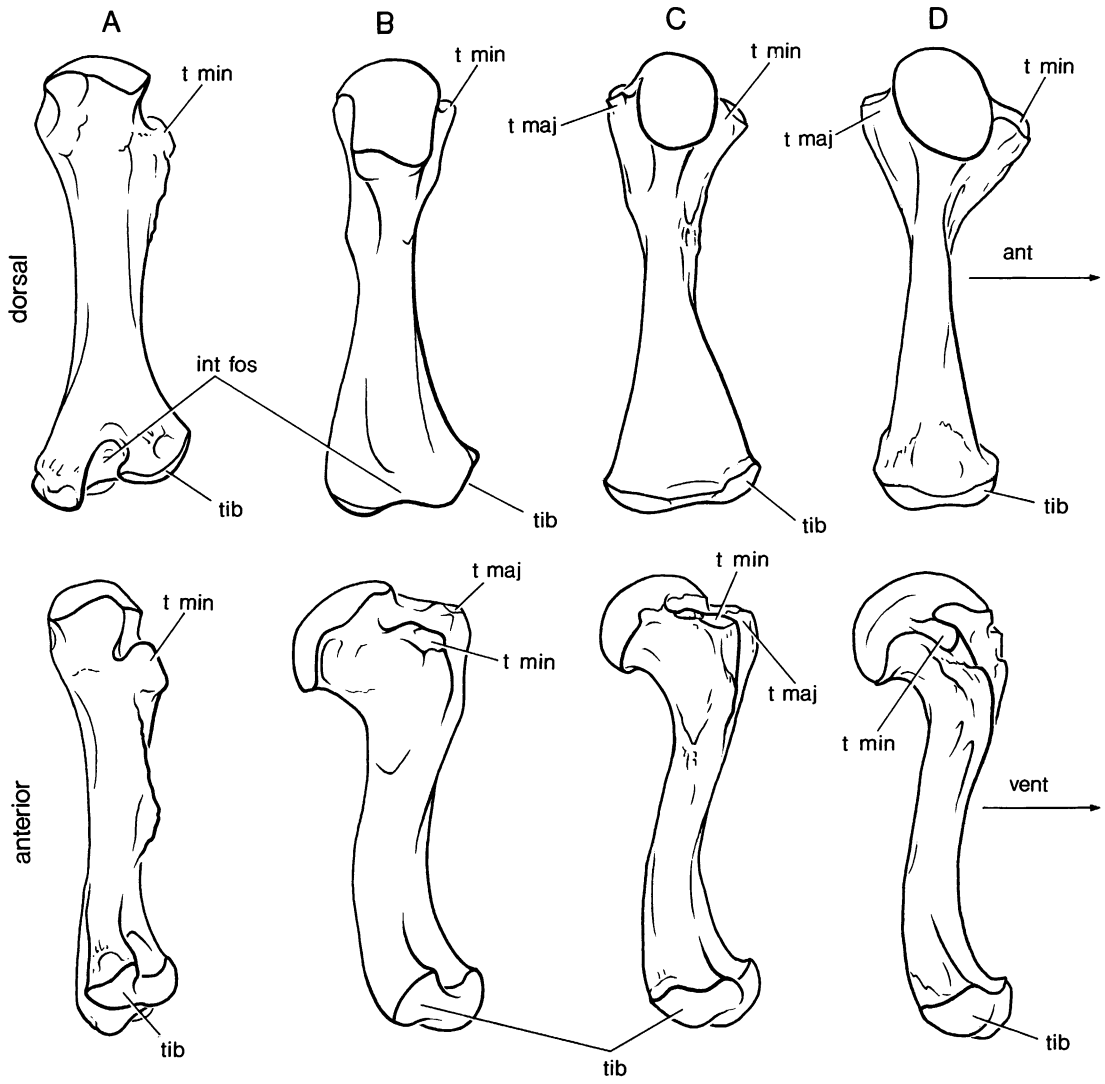

Fig. 164. Comparisons of right femora. Upper row, dorsal views; lower row, anterior views. **A,** *Captorhinus* sp., AMNH 19377–19380; **B,** *Proganochelys quenstedti,* SMNS 16980; **C,** *Macroclemys temmincki,* AMNH 58251; **D,** *Podocnemis expansa,* AMNH 62947. Abbreviations: **ant,** anterior direction; **int fos,** intercondylar fossa; **tib,** tibial articulation area; **t maj,** trochanter major; **t min,** trochanter minor; **vent,** ventral direction.

margin. This ridge seems to be absent in all other turtles but its presence in *Proganochelys* is clearly visible on both femora of SMNS 16980 and particularly the well-preserved right femur of SMNS 17304. Of all the features seen in the femur of *Proganochelys,* this is the only character that I interpret as autapomorphic and not primitive for turtles.

The distal end of the femur in *Proganochelys* and other turtles consists of two poorly differentiated condyles, an anterior one bearing the anterior part of the tibial articulation and a posterior one bearing the rest of the tibial articulation and, on its posterior margin, the fibular articulation. In *Captorhinus* and generalized amniotes these condyles are usually separated, particularly dorsally, by a deep trough, the intercondylar fossa. In

TABLE 22
Comparison of Tibia and Fibula

	Captorhinus	*Proganochelys*	Casichelydia
Well-developed ridge for patellar tendon attachment to tibia	Present	Absent	Absent
Distal end of tibia with close-fitting articulation for astragalocalcaneum	Absent	Present	Present
Fibula bowed away from tibia	Yes	No, straight	No, straight
Proximal end of fibula	Moderately expanded	Slightly expanded	Slightly to not expanded

Proganochelys and casichelydians this fossa is effectively absent; only a low depression separates the condyles dorsally and a slight constriction of the articular surface ventrally. In *Captorhinus* and primitive amniotes the two condyles are unequal in size: the posterior condyle is larger and bears a stout ridge ventrally. In *Proganochelys* and other turtles the condyles are nearly equal, the posterior one being barely larger than the anterior condyle. In *Proganochelys* and other turtles the distal articulation surface is a smooth area with the condyles blending into each other while in *Captorhinus* and generalized amniotes the condyles are discrete. *Proganochelys* has a well-developed fibular epicondyle jutting posteriorly from the base of the posterior condyle. On the ventral surface of the fibular epicondyle there is a posteroventrally opening concavity just proximal to the margin of the articular surface. Most turtles have some depression developed here but the one in *Proganochelys* seems to be more defined than in other turtles. *Captorhinus* has a fibular epicondyle in the form of a ridge on the posterior surface.

Tibia
(table 22, figs. 151, 165–167)

The tibia of *Proganochelys* is best preserved in SMNS 17204 where it is present on both sides but only the left side is prepared for study (fig. 166). The left tibia of SMNS 16980 is the next best specimen, and the drawing (fig. 166) is based on these two bones. The right tibia of SMNS 17204 (figs. 87, 88) is still in situ beneath the osteoderms and attached to the shell. The right tibia of SMNS 16980 is represented only by the distal third of the bone; the rest is missing. Both right and left tibiae of SMNS 17203 are preserved; the left is free (fig. 151) while the right remains in situ (figs. 101, 102). Both, however, lack some features of the larger, presumably adult, specimens and they have not contributed to the drawing.

The tibia in *Proganochelys* is a relatively stout element, very wide proximally, and tapering distally. In proportions it is more massive than in most casichelydians except testudinids and is similar to that of *Captorhinus* (fig. 167). Turtles do not show much variation in tibial morphology, varying primarily in length versus width. The tibia of *Captorhinus* is described briefly by Fox and Bowman (1966) and their figures can be supplemented by those in Heaton and Reisz (1980) but more useful comparative figures are those of primitive pelycosaurs, quite similar to *Captorhinus* in limb morphology, in Romer and Price (1940: 239).

Proximally, the tibia of *Proganochelys* is expanded to more than twice the width of the shaft at its narrowest point. The expansion forms the proximal half. This degree of width is comparable to that of the proximal end in *Captorhinus* but it is greater than in most turtles, *Meiolania* and some testudinids being exceptions. The proximal articular surface is not well preserved in any of the *Proganochelys* specimens, but it seems comparable to those turtles that have a shallow, medial concavity for the medial condyle of the femur and a convex, lateral area for the trough between the condyles. *Captorhinus* has a generally flat articular surface, although it is partially divided for the femoral condyles also.

The patellar tendon attachment site (the cnemial crest of Fox and Bowman, 1966) in *Captorhinus* is a prominent ridge dividing the tibial head into two areas in dorsal view. This

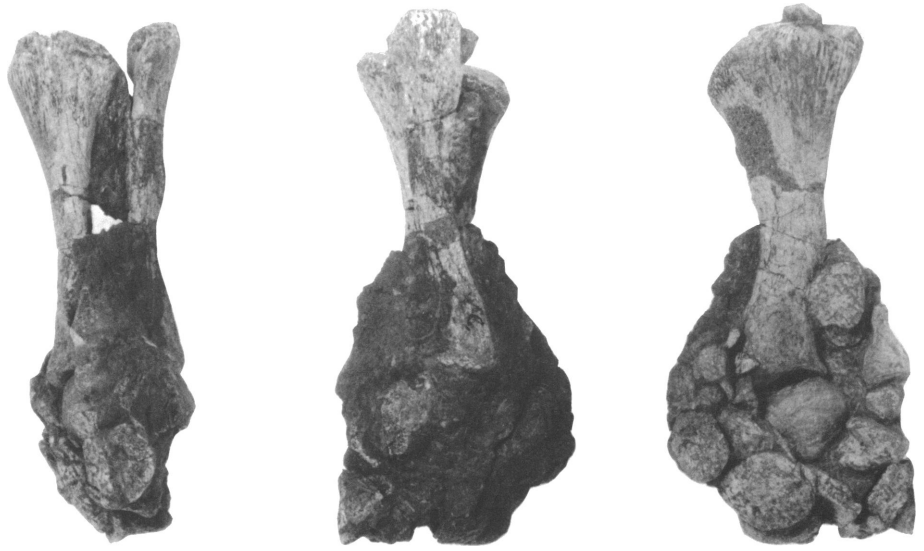

Fig. 165. *Proganochelys quenstedti,* SMNS 16980. Left tibia, fibula, and partial tarsus. Left, lateral view; center, posterior view; right, anterior view. Orientations are only approximate.

area is identifiable in *Proganochelys* and other turtles as a rugose area on the anterior surface of the tibia, but a discrete ridge is not formed.

The shaft of the tibia in *Proganochelys* bows laterally in the direction of the fibula, rather than being straight or bowing away from the fibula as in other turtles and *Captorhinus*. At about two-thirds of the distance distally along the shaft of the ulna there is a low protuberance on the lateral margin in the direction of the fibula. A similar rugosity, but even better developed, occurs in *Meiolania,* and can be found in other turtles. In *Captorhinus* this appears to be comparable to a very thin ridge along the lateral margin.

On the ventral surface of the tibia in *Proganochelys,* just proximal to the margin of the distal articulation surface, is a pit and an adjacent convexity, the pit being medial to the convexity. Similar structures do not seem to occur in either *Captorhinus* or other turtles, and I do not know what they are.

The distal articulation surface on the tibia of *Proganochelys* has the distinctive chelonian shape of a medial dome and a lateral flat or slightly concave facet. This surface fits onto the astragalocalcaneum relatively tightly, not allowing a great deal of movement. The tarsal articulation surface of *Captorhinus* is relatively loose, presumably allowing more movement.

As in some of the other articular surfaces of the limbs in SMNS 16980, the distal tibial surface has the remnants of a bony rim that curls around the edge as if it were forming the margin of a cartilaginous sheet covering the articular surface. I have not seen anything exactly the same in recent turtle specimens.

SMNS 17203 has both tibia preserved (figs. 101, 102, 151) and they differ from the ones in SMNS 16980 and SMNS 17204 in being poorly defined at both ends and lacking the articular features. This is presumed to be a result of the hypothesized juvenile nature of this specimen.

Fibula
(table 22, figs. 151, 168–169)

The fibula is preserved, at least in part, on both sides of SMNS 17203 (figs. 101, 102, 151), SMNS 17204 (figs. 87, 88), and SMNS 16980. However, it is obscured by osteoderms and other elements on the right side of SMNS 17204, it is lacking the proximal two-thirds on the right side of SMNS 16980, and the morphology is not fully expressed in SMNS 17203. Therefore, figure 168 is based on the left fibula of SMNS 17204 and the left

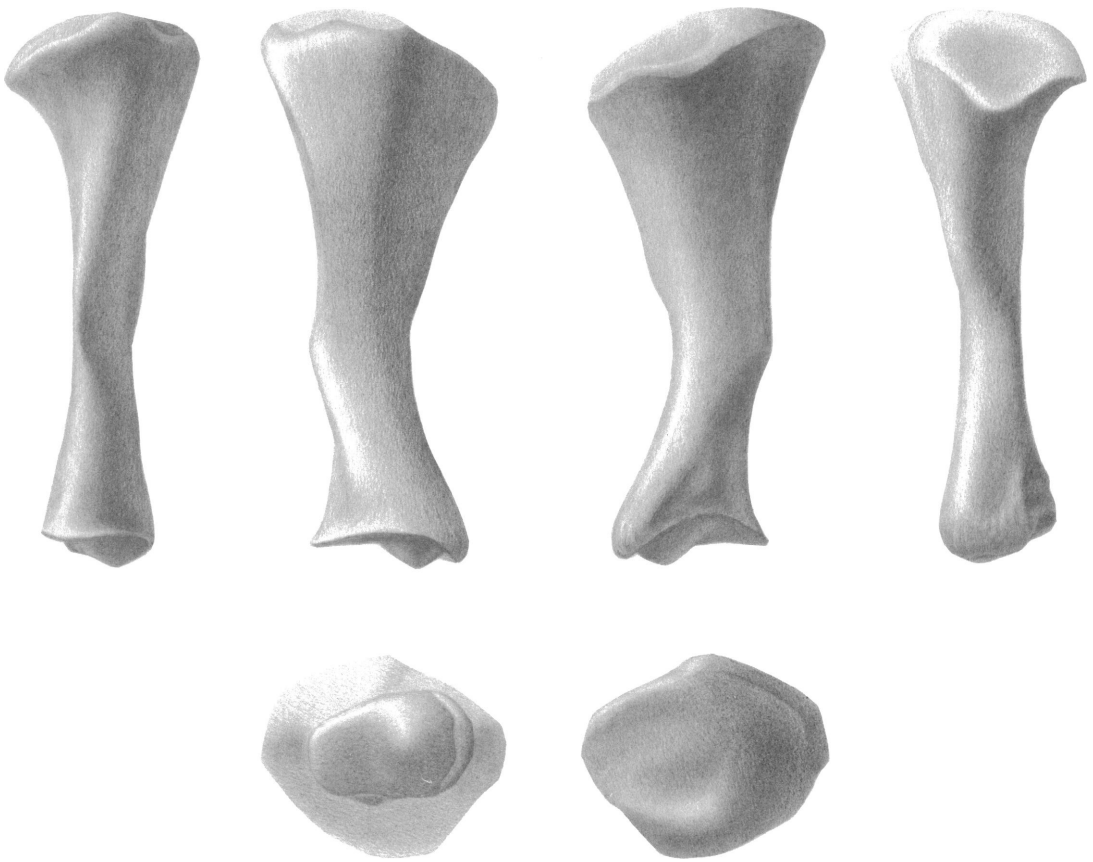

Fig. 166. *Proganochelys quenstedti.* Right tibia, composite of SMNS 16980 and SMNS 17204. Top row (left to right), lateral, dorsal, ventral, medial; lower row (left to right), distal, proximal.

fibula of SMNS 16980. SMNS 17204 has well-preserved articular surfaces but is damaged along the shaft, while SMNS 16980 has a good shaft but the articular surfaces (especially the proximal) are not as well preserved.

The fibula of turtles (fig. 169) is a consistently slender element with the distal end expanded and the proximal end only slightly larger than the shaft. *Proganochelys* readily fits the chelonian fibular pattern. The only description of the fibula in *Captorhinus* is in Fox and Bowman (1966: 47) and this can be supplemented by Heaton and Reisz (1980). The limbs of primitive pelycosaurs are very similar to those of *Captorhinus* and the figures of the fibula in Romer and Price (1940: 239) of *Ophiacodon* are useful comparisons.

The proximal end of the fibula in *Proganochelys* articulates on the side of the lateral condyle of the femur as in most generalized, nonmammalian amniotes (Haines, 1942). The articulation surface is angled ventroproximally to meet this articulation. The surface is broadly rounded in SMNS 17204, which appears to be undamaged, but concave in SMNS 16980, which may be the result of postmortem deterioration. The proximal head is enlarged dorsoventrally but it is smaller than the distal end and less than twice the width of the shaft. In *Captorhinus* (fig. 169) the proximal end is more than twice the width of the shaft but still narrower than the distal end. The proximal articulation surface in *Captorhinus* is flat and angled somewhat as in *Proganochelys.* The casichelydian fibula agrees closely with the proximal end of the

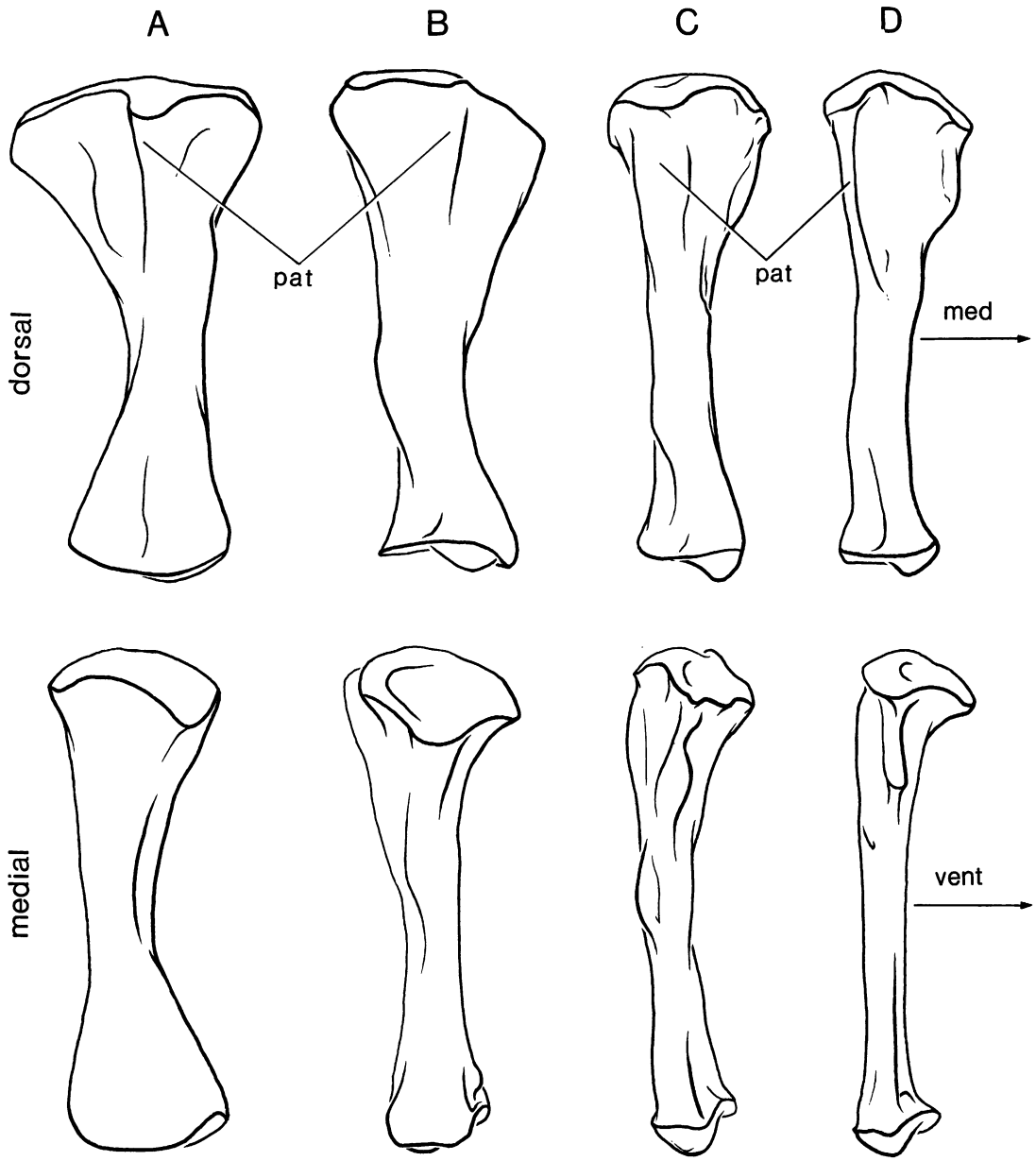

Fig. 167. Comparisons of right tibiae. Upper row, dorsal views; lower row, medial views. **A,** *Captorhinus* sp., AMNH 19383, 19384; **B,** *Proganochelys quenstedti,* SMNS 16980, 17204; **C,** *Macroclemys temmincki,* AMNH 58251; **D,** *Podocnemis expansa,* AMNH 62947. Abbreviations: **med,** medial direction; **pat,** patellar tendon attachment; **vent,** ventral direction.

fibula in *Proganochelys* but it generally has a more convex, rounded articular surface.

The shaft of the fibula is distinctively curved or bowed away from the tibia in *Captorhinus,* while it is straight in *Proganochelys* and other turtles. Although it is hard to be certain, it is likely that the fibula contacted the tibia proximally as in casichelydians and

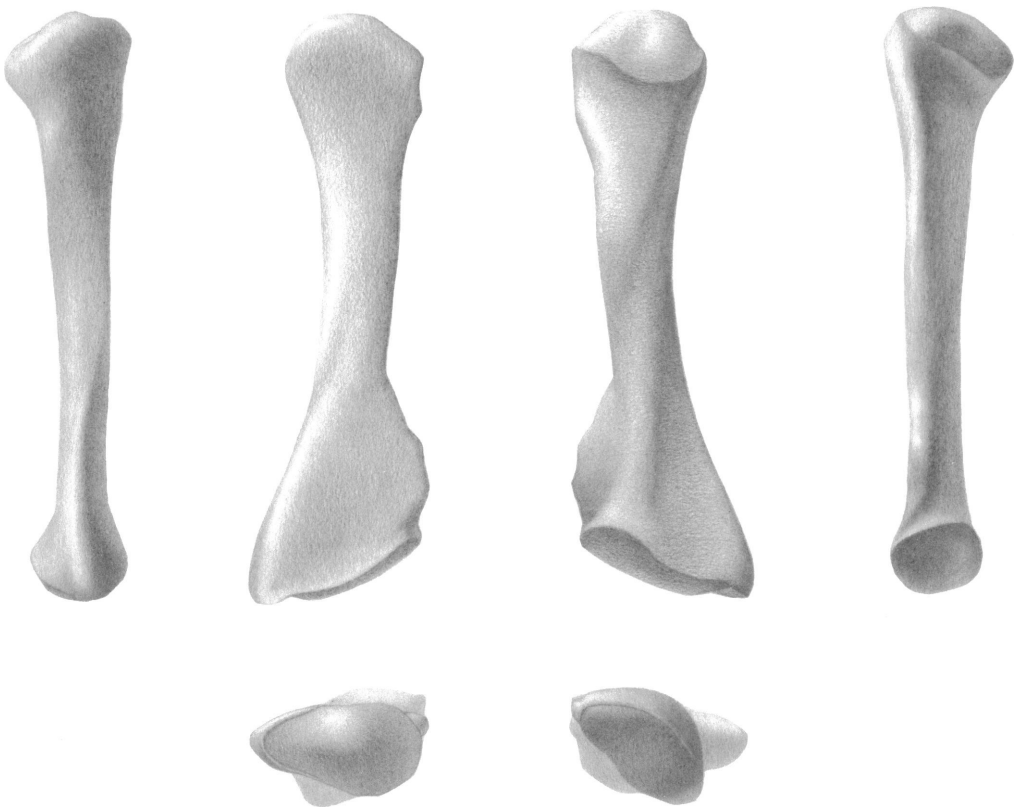

Fig. 168. *Proganochelys quenstedti,* SMNS 16980 and SMNS 17204. Right fibula. Top row (left to right), lateral, dorsal, ventral, medial; lower row (left to right), distal, proximal.

other amniotes. There are no specific rugosities that reflect this but some of the proximal rugosities on the shaft of the fibula in *Proganochelys* are similar to those in casichelydians.

Distally the fibula of *Proganochelys* is expanded and bears a wide astragalocalcaneal articulation surface. The plane of this expansion is twisted from the plane of the proximal expansion by about 30°. A similar torsion can be seen in the fibula of *Captorhinus* and most other turtles. The distal part of the fibula shaft in *Proganochelys* is flat on its dorsal side but there is a thickened ridge on the ventral side that ends at an expanded part of the distal articulation surface. The fibula fits closely onto the tarsus and bridges the contact between astragalus and calcaneum.

The fibula of SMNS 17203 (fig. 151) is similar to those of other *Proganochelys* specimens but has unfinished articular surfaces and is smaller in size—features presumably related to its juvenile nature.

Tarsus and Pes
(tables 23, 24, figs. 170–175)

Significant portions of the pes are preserved on both sides of SMNS 16980 (figs. 98, 172) and SMNS 17204 (figs. 87, 88). No identifiable elements of the pes of SMNS 17203 are available, although it is possbile that some of the unidentified disarticulated bones belong to that part of SMNS 17203.

The best preserved pes is in the left limb of SMNS 17204 (fig. 170). The entire hind limb is articulated in a tightly retracted position so that the limb is within the shell overhang and presses against the ventral surface of the carapace. The pes is brought dorsally so that the metatarsals lie parallel to and nearly touch the tibia and fibula. The pha-

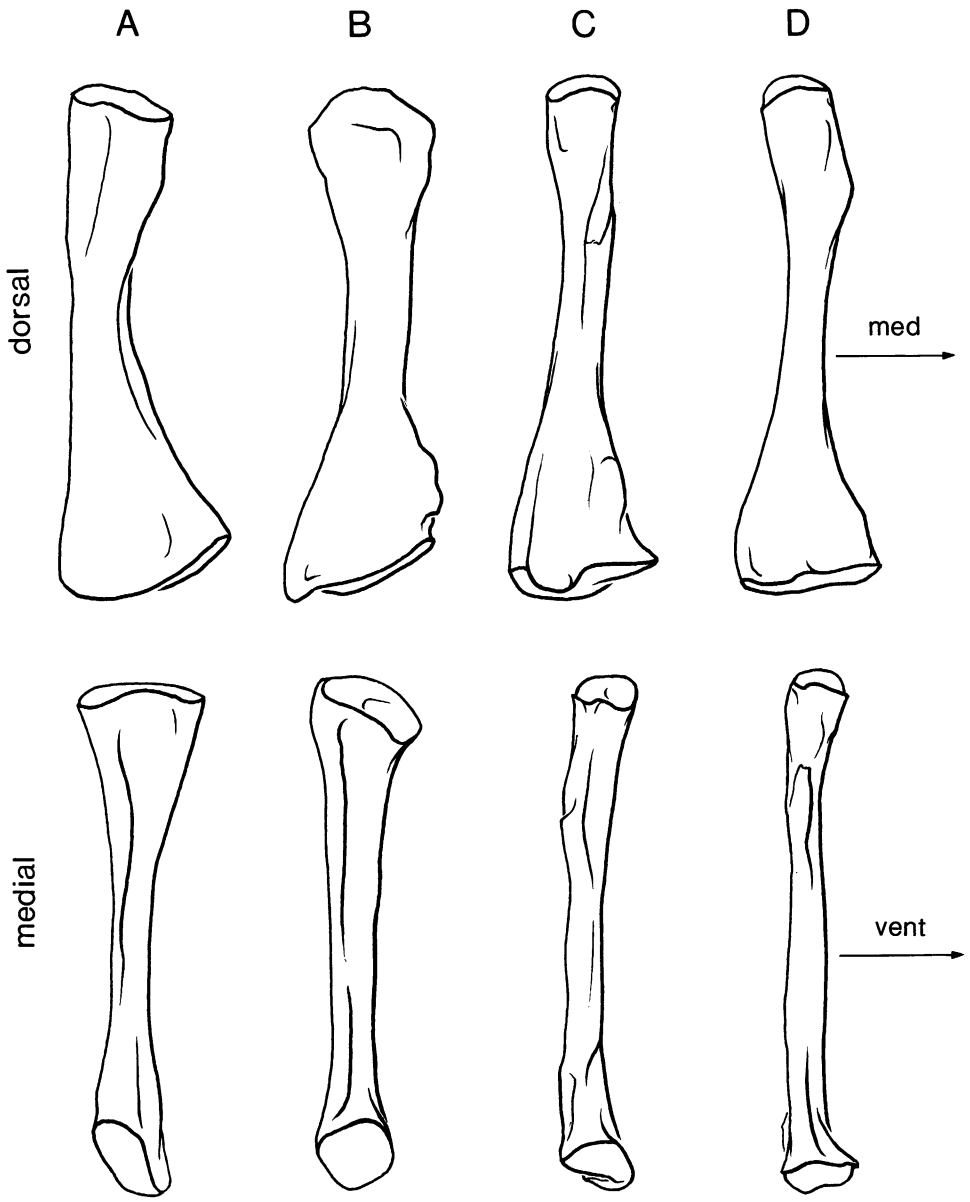

Fig. 169. Comparison of right fibulae. Upper row, dorsal views; lower row, medial views. **A,** *Captorhinus* sp., AMNH 19381, 19382; **B,** *Proganochelys quenstedti,* SMNS 16980, 17204; **C,** *Macroclemys temmincki,* AMNH 58251; **D,** *Podocnemis expansa,* AMNH 62947.

langes are tightly flexed with the unguals lying at right angles to the metatarsals. Before 1979 the pes was prepared but the major elements were not disarticulated. The extreme flexion of the pes, however, may have caused the distal tarsals 1–3 to be prominently exposed and they may have been removed with the sesamoids and osteoderms, nearly all of which were removed. In any case, distal tarsals 1–3 are missing from the pes. Distal tarsal 4

TABLE 23
Preserved Material of Tarsus and Pes

	SMNS 16980	SMNS 17203	SMNS 17204	SMNS 15759	MB 1910.45.2
Astragalocalcaneum	R, L	? R	L	–	–
Distal tarsal 1	? R	?	? R	–	–
Distal tarsal 2	–	?	R	–	–
Distal tarsal 3	R	–	–	–	–
Distal tarsal 4	R, L	–	L	–	–
Metatarsal I	R	–	R, L	–	–
Metatarsal II	R, L	–	R, L	–	–
Metatarsal III	R, L	–	R, L	–	–
Metatarsal IV	R, L	–	L	–	–
Metatarsal V	R	–	L	–	–
Phalanx I	R, L	–	R, L	–	–
Phalanx II	R, L	–	R, L	–	–
Phalanx III	R, L	–	R, L	–	–
Phalanx IV	R, L	–	? R, L	–	–
Phalanx V	–	–	L	–	–
Ungual I	R, L	–	R, L	–	–
Ungual II	R, L	–	R, L	–	–
Ungual III	R, L	–	R, L	–	–
Ungual IV	R	–	R, L	–	–
Ungual V	? R or L	–	R, L	–	–

was present at the beginning of this study in 1979 but it was missing in 1980 (photographs allow its position to be known). The flexion of the hind foot and pes is consistent with its being caused by postmortem muscle contraction, as may be the case in the forelimb of SMNS 16980.

In SMNS 17204 the astragalus is separated from the calcaneum by matrix that appears to be filling a suture. The astragalus and calcaneum are tightly attached by suture in the two tarsi of SMNS 16980 and it is likely that this was the case in SMNS 17204. In this specimen the contact area between these bones is eroded and the two elements barely contact each other. When in situ, the bones were offset with respect to each other and separated more than in life. The astragalocalcaneum in SMNS 17204 in situ (fig. 171) is oriented so that the distal surface, normally articulating with the distal tarsals, is facing ventrally (with respect to the shell of SMNS 17204) while the metatarsals are facing distally (or anteriorly with respect to the shell). The distal tarsal 4 lies just lateral to the astragalus and, as a result of the flexion, ventral to the calcaneum. Lateral to distal tarsal 4 is the fifth metatarsal, a fan-shaped element very different from the other metatarsals but quite similar to the hooked metatarsal V of other turtles (Rabl, 1910).

Metatarsals I to IV of SMNS 17204 are articulated in situ in very nearly their presumed life position. The metatarsal bases overlap strongly and their axes are roughly parallel. The base of metatarsal V, however, has been rotated medially causing its axis to extend laterally rather than distally. Its articulation surface, however, still is in articulation with distal tarsal 5. The phalanx is still barely in articulation with the fifth metatarsal, being bent dorsally at more than 90°. The ungual of the fifth digit is not articulated at the distal surface of the phalanx but lies on the medial edge of the phalanx.

The digits I–IV have one phalanx and one ungual and these are in articulation and flexed at about 90° to the plane of the metatarsals. This would appear to be the maximum degree of flexion possible naturally.

TABLE 24
Comparison of Tarsus and Pes

	Captorhinus	*Proganochelys*	Casichelydia
Astragalus and calcaneum articulation	Separate elements, loosely articulated	Tightly sutured	Tightly sutured
Astragalus and centrale articulation	Separate elements, loosely articulated	Presumably fused, sutures not apparent	Sutural contact apparent
Astragalus	Plate-like, with triangular outline	Cuboid	Cuboid
Tibia-astragalus contact	Loose, ill-defined	Tight fitting	Tight fitting
Tripartite suture in astragalus	Present	Absent	Absent
Astragalo-calcaneal foramen	Present	Absent	Absent
Calcaneum	Platelike with semicircular outline	Cubical	Cubical
Size of astragalus and calcaneum in proximodistal plane	Elongate	Compressed	Compressed
Size of calcaneum versus astragalus	Equal	Calcaneum much smaller than astragalus	Calcaneum much smaller than astragalus
Semicircular concavity on astragalocalcaneum for articulation of distal tarsal 4	Absent	Present	Present
Well-developed plantar swelling on astragalus	Absent	Present	Present
Free centrale	Present	Absent	Absent
Number of distal tarsals	Five	Four	Four (less due to fusion)
Outline of distal tarsal 4	Pentagonal	Circular	Generally circular
Distal tarsal 5	Present	Absent	Absent
Mesotarsal joint	Presumed limited mobility	Greater mobility than *Captorhinus*	Variable, but less primitively as in *Proganochelys*
Tarsometatarsal joint	Presumably greater mobility than mesotarsal joint	Mobility as in *Captorhinus* or greater	Variable, but primitively as in *Proganochelys*
Crurotarsal joint	Considerable potential mobility	Limited mobility	Limited mobility
Sesamoids	In flexor tendons (at least in manus)	In extensor tendons	Absent
Distal tarsal 4 with well-developed metatarsal V contact	Absent	Present	Present
Strongly overlapping metatarsal bases	Absent	Present	Primitively present, but variable
Hooked or "L" shaped metatarsal V	Absent	Present	Present
Digital formula of pes	2-3-4-5-4	2-2-2-2-2	Variable but 2-3-3-3-3/2 most common
Digit V	Larger than I, same as II	Much smaller than I–IV	Much smaller than I–IV
Claw on ungual V	Probably present	Present	Absent

Fig. 170. *Proganochelys quenstedti,* SMNS 17204. Left hind foot in ventral view; see Figure 173 for orientation. Abbreviations: **ast,** astragalus; **mt,** metatarsal; **ost,** osteoderm; **tib,** tibia. Asterisk (*) indicates sesamoid.

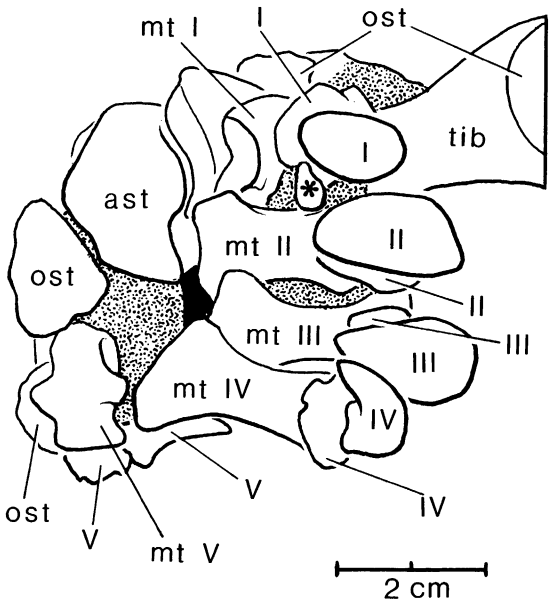

Fig. 170. Continued.

The right pes of SMNS 17204 (figs. 87, 88) is not as well preserved as the left pes; it is retracted and lies against the ventral surface of the carapace and is articulated with the rest of the right hind limb. The proximal ends of the tibia and fibula are close to the distal end of the femur but are not in life position. The fibula lies between the pes and the carapace with the distal end of the tibia completely covered by pes and fibula. The pes is tightly flexed with respect to the epipodials; the tibia is also pushed into the pes, disarticulating the first digit and medial tarsals. The proximal portion of the pes is a mass of osteoderms. The astragalocalcaneum is not visible but it may be present beneath the osteoderms.

The only tarsal bones identifiable in the right pes of SMNS 17204 are two distal tarsals that lie near the base of the metatarsals I and II. Neither of these bones are prepared free of matrix and this identification is based on their position and general shape, both suspect in a foot that is not well preserved. Presumed distal tarsal I is separated from metatarsal V by the tibia which enters the tarsus here. Only three metatarsals, I–III, are apparent, and these are roughly parallel to each other in approximate life position. However, their long axis orientation with respect to each other is twisted. Digit I has its ungual and phalanx in contact with each other and metatarsal I, but the bones are rotated out of their presumed life positions. Digit II has the phalanx overlapping the metatarsal ventrally but its ungual is correctly articulated. In digit III

the metatarsal is nearly in contact with ungual III and the intervening phalanx appears to be pushed laterally and completely disarticulated. Metatarsals IV and V are not identifiable and seem to be missing, while the digits associated with them are disarticulated. There are two phalanges lying lateral to metatarsal III and these are presumably III and IV, although one could be missing and V could be present. However, this is unlikely as digit V is smaller than the others present. The more medial phalanx is likely to be III and the other IV. The ungual of IV lies with its distal apex aimed medially into the pes with its articulation surface exposed laterally. Its apex contacts both of the disarticulated phalanges. The ungual of V is lying proximolateral to metatarsal III and can be identified because of its small size.

The right pes of SMNS 16980 is the better preserved of the two and retains more tarsal elements in their life positions. The astragalocalcaneum is well preserved but rotated dorsally with its proximal (fibular and tibial) surface facing more distally than would be natural in life. This flexion has pushed the distal tarsals somewhat ventrally and covered distal tarsal 3 from dorsal view. The distal ends of the tibia and fibula are retained in situ and show the extreme flexion of the tarsus. Instead of being at right angles or greater than right angles, the tibia and fibula are bent forward to lie in nearly the same plane as the metatarsals. The effects of this extreme flexion are evenly distributed among the various joints, and the original, life positions of most of the elements are fairly clear.

The right tarsus of SMNS 16980 is the only *Proganochelys* tarsus to preserve more than one distal tarsal in situ. Distal tarsals 3 and 4 are preserved with distal tarsal 4 in contact with the astragalocalcaneum, metatarsals III–IV, and distal tarsal 3. The astragalocalcaneum is rotated so that the distal tarsal 3 is hidden by it in dorsal view. Ventrally, distal tarsal 3 lies directly behind metatarsal III and contacts it. There is no indication of distal tarsal 2. The position where it should lie is open and free of matrix, suggesting that the element may have been removed during earlier preparation. Digit I is somewhat displaced, but near the proximal articulation surface of metatarsal I is an oblong of bone that is probably the first distal tarsal. As preserved, it lies ventral to the tightly flexed tibia and is rotated medially away from its presumed position.

All five metatarsals are preserved in the right pes of SMNS 16980 with only the fifth somewhat shifted from its presumed life position. Metatarsal V, as preserved, lies underneath both the base of metatarsal IV and distal tarsal 4 rather than in the same plane. Metatarsals I–IV have strongly overlapping bases and appear to be in life position. Metatarsal I is somewhat damaged and not well preserved. Digit V is missing (although the ungual may be one of the small unguals in the collection of disarticulated elements) but the remaining digits are present. These digits were apparently removed from their in situ positions and rearticulated before 1979 using glue and plaster. Even after further cleaning and preparation, these elements are not well preserved, having more cracks and poorer bone than is usual in the Trossingen specimens. The left pes of SMNS 16980 as examined in 1979 was in two pieces, both consisting of in situ assemblages but not having any contacts or other indications of their respective orientations. Both of these have been prepared further, revealing the elements involved. The peculiar relation of these two pieces is enhanced by the fact that the distal piece (fig. 172) is an articulated set of four digits, not far from the presumed life positions, while the proximal grouping has a properly articulated tibia and fibula with an astragalocalcaneum that is close to life position but the more distal part of the tarsus is a confused mixture of osteoderms/sesamoids showing considerable postmortem disturbance. There is no sign of the metatarsals or metatarsal fragments missing from the distal piece and no indication of their orientation. It is difficult to see how the articulated digits relate to the badly disturbed tarsus.

The astragalocalcaneum in the left pes of SMNS 16980 lacks the lateral end of the calcaneal portion which ends in a clear break. The broken end of the calcaneum seems to be a fragment pushed proximally and lying along the shaft of the tibia. When prepared

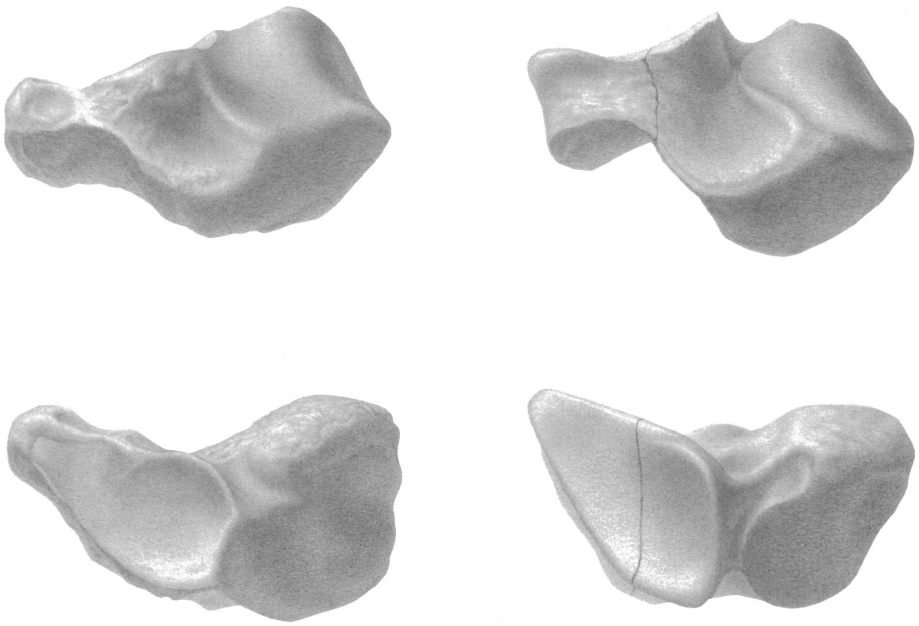

Fig. 171. Right astragalus-calcaneum. **A, C,** *Meiolania platyceps,* Australian Museum, F 57984; **B, D,** *Proganochelys quenstedti,* SMNS 17204 (left, reversed). A, B, anterior views; C, D, dorsal (proximal) views.

free of matrix, this piece approximates but does not fit exactly onto the break; nonetheless, it seems to be the end of the calcaneum. This astragalocalcaneum seems to show a clearer fusion line between astragalus and calcaneum than the right astragalocalcaneum. The only other identifiable tarsal in this pes is the distal tarsal 4. This element lies displaced from its articulation surface and instead lies on the distal plantar expansion of the astragalus. Nonetheless, it is the best preserved *Proganochelys* distal tarsal 4 and has been prepared off the astragalus and cleaned. The rest of the proximal piece of the tarsus consists of many flat overlapping ovals of bone, more porous than the tarsal elements, that appear to be osteoderms rather than sesamoids.

The distal piece containing the left hind digits of SMNS 16980 (fig. 172) has been prepared leaving the elements articulated in situ but with most of the matrix removed. This piece contains metatarsals II–IV and a very small part of I, phalanges I–IV, and unguals I–II. One of the small unguals in the collection of disarticulated elements may be the fifth ungual of this foot. The digits, although articulated, have been subjected to medial-lateral pressure and the pes is distorted to lie more in a dorsoventral than horizontal plane. The unguals of digits I–III are flexed at right angles to the phalanges and metacarpals, as in the left pes of SMNS 17204. Metacarpal II is most dorsal, with III below and slightly lateral to it and IV (lacking its ungual with its phalanx) below the other metacarpals and lateral to the unguals. Digits I and II have sesamoids in articulation.

The pes of *Proganochelys* (figs. 173, 175) consists of the astragalocalcaneum, four distal tarsals, five metatarsals, and a digital formula of 2-2-2-2-2. Except for the digital formula, the pes agrees with the expected primitive pattern for casichelydians.

The tarsus of *Proganochelys* has a single, large proximal element divided by a suture. This element consists of astragalus and calcaneum as demonstrated in the literature, and based on the fact that its compound nature is revealed in such living turtles as pleuro-

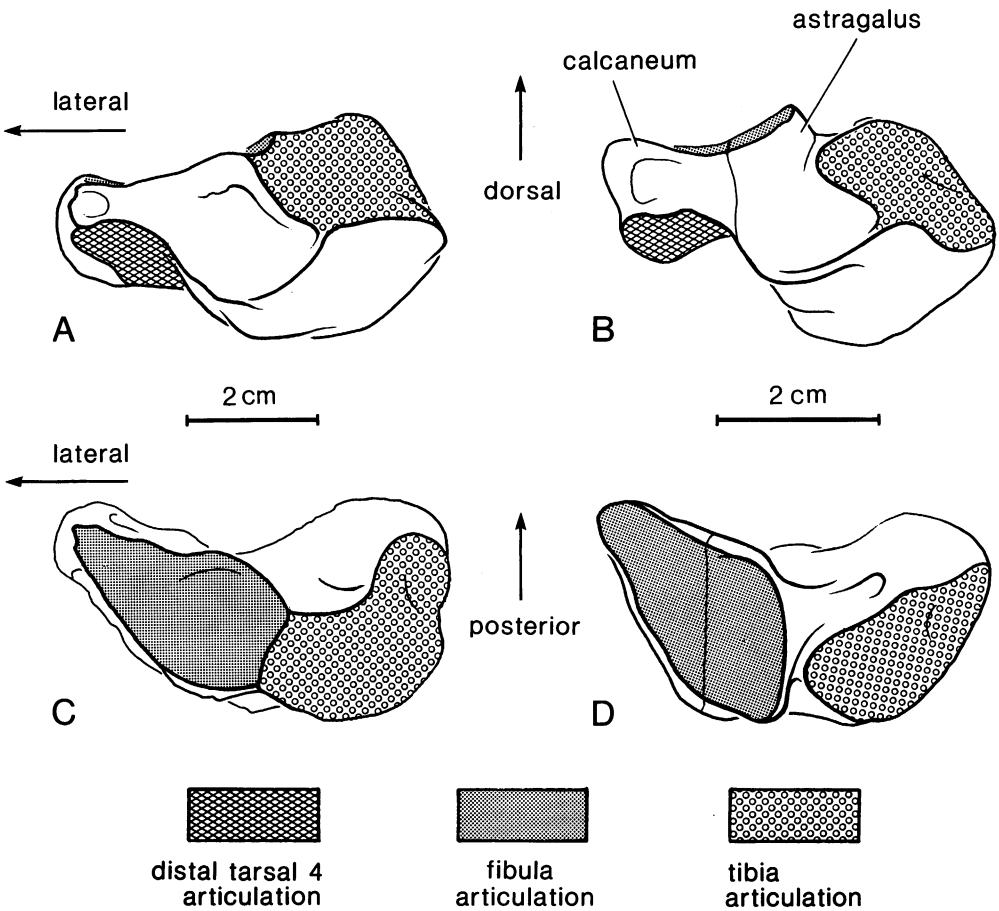

Fig. 171. Continued.

dires and chelydrids. These bones are preserved in the left tarsus of SMNS 17204 and both tarsi of SMNS 16980.

The astragalus of amniotes has a large literature concerned with its development and adult comparative morphology. In living turtles, Rabl's (1910) work showed that three ossifications may be variably involved with the astragalus. The largest ossification, "tibiointermedium" of Rabl, bears the tibial articulation and the medial half of the fibular articulation, and is usually called the astragalus based on its presumed homology with the mammalian astragalus. In some turtles, such as chelydrids, cheloniids, and pleurodires, there is an element lateral to the astragalus that rarely may be free or may occasionally be separated by a suture or partial fusion. This element is usually identified as the calcaneum or fibulare. In most adult cryptodires there is no indication of a suture or fusion between this element and the astragalus. In chelydrids and pleurodires there is evidence of a third element, on the distal surface of the astragalus, and this has been identified as a centrale (Rabl, 1910). Based on the systematic position of these living turtles, i.e., chelydrids as the sister group of all living cryptodires, and pleurodires as the sister group to all cryptodires, it would be expected that *Proganochelys* should have these elements distinctly separated by sutures if not entirely free. Such is not the case. In *Proganochelys* the astragalus and calcaneum are separate ossifications tightly sutured together but there is no clear evidence for a centrale. However,

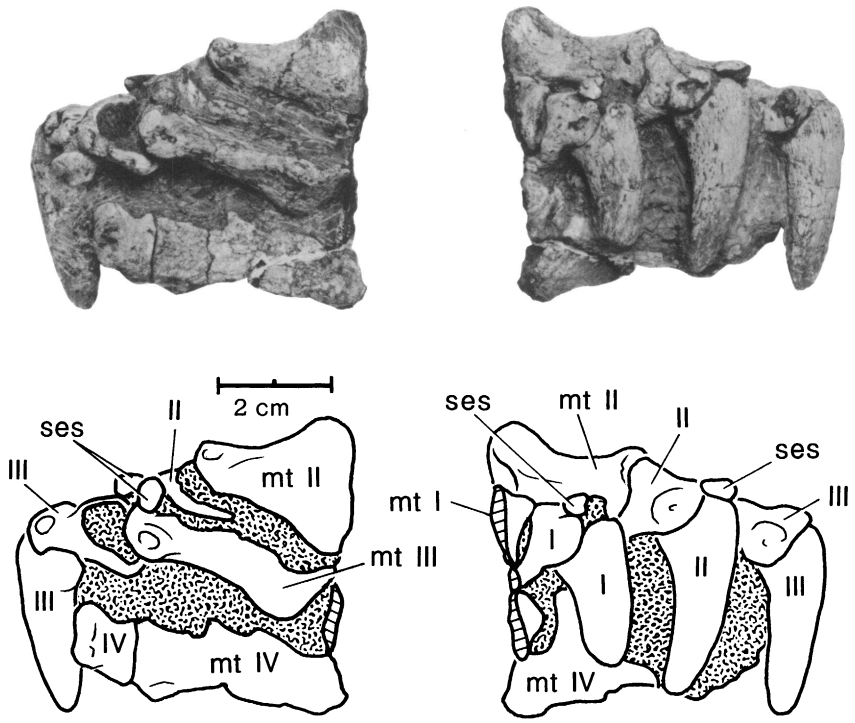

Fig. 172. *Proganochelys quenstedti,* SMNS 16980. Partial left pes in situ articulation. Left, ventromedial view; right, dorsolateral view. Abbreviations: **mt,** metatarsal; **ses,** sesamoid.

the preservation is not good enough to completely rule out the possibility of a suture in this area but a well-defined, separate ossification is not present, suggesting that the centrale is completely fused to the astragalus. In summary, then, *Proganochelys* has a single, proximal tarsal element showing a prominent calcaneum-astragalus suture but without a prominent centrale-astragalus suture or fusion zone.

Other extinct turtle groups provide some perspective on the systematic significance of the astragalar fusion lines. Baenids have a fused astragalocalcaneum (Russell, 1934; Case, 1939; Hay, 1908) with variably expressed sutures or fusion lines. Case's specimens of *Plesiobaena antigua* (University of Michigan, Museum of Paleontology 20480) shows the chelydridlike fusion zone between astragalus and calcaneum but no suture. The centrale-astragalus contact is not clear on either side. A *Eubaena cephalica* (UCMP 10717, brought to my attention by Dr. David Archibald and described in his Ph.D. thesis, 1977) has a well-preserved tarsus showing the astragalus-calcaneum fusion zone and a partially separated suture between the astragalus and centrale. *Dinochelys whitei* (Dinosaur National Monument 986; Gaffney, 1979b), a generalized cryptodire of undetermined relationships, consists of a shell with some limb elements. The pes of this specimen clearly shows a sutured centrale and a partially fused calcaneum-astragalus. These extinct taxa indicate that the condition seen in chelydrids and pleurodires is the plesiomorphic pattern at least for casichelydians. *Proganochelys* differs from this only with regard to the centrale. The significance of this difference is probably not great, as in chelydrids and the pleurodires I have examined; the degree of expression of the centrale-astragalus fusion zone or suture seems much more variable than the calcaneum-astragalus fusion zone. The interesting aspect of all this is that in terms of astragalar fusion, *Proganochelys* has the same general-

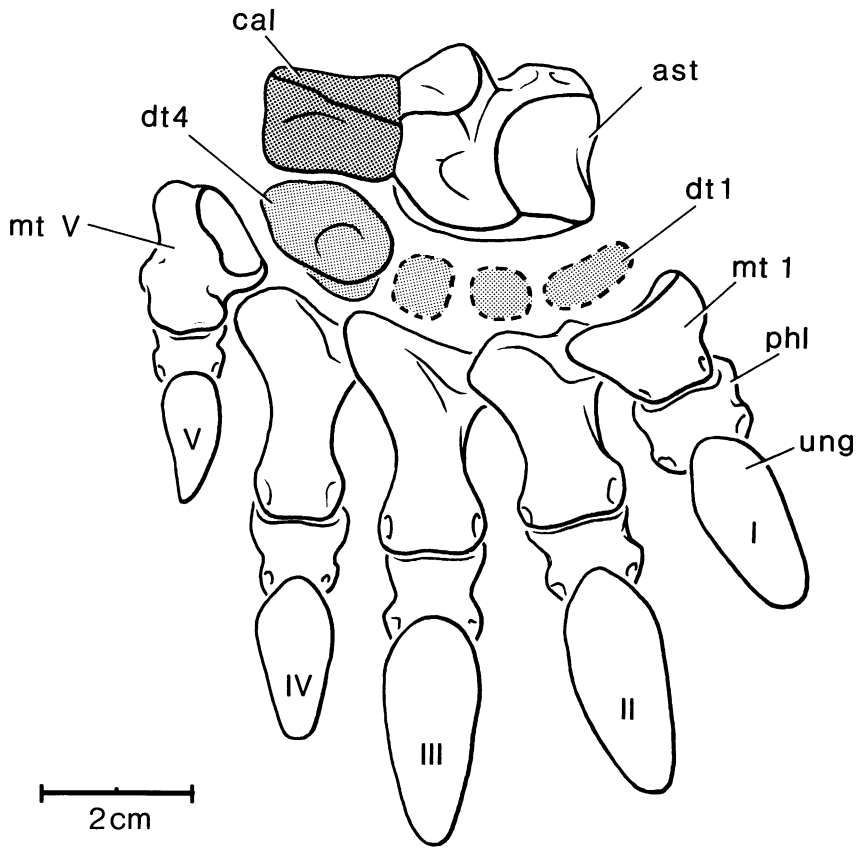

Fig. 173. *Proganochelys quenstedti.* Dorsal view of restored right pes and tarsus, based on the left pes of SMNS 17204 with additions from SMNS 16980. Dashed distal tarsals 1–3 are based on ossifications present in SMNS 16980 but not definitely determinable as to position; see text. Abbreviations: **ast,** astragalus; **cal,** calcaneum; **dt,** distal tarsal; **mt,** metatarsal; **phl,** phalanx; **ung,** ungual. Calcaneum is in heavy stipple; distal tarsals are in light stipple.

ized condition as Recent turtles and does not retain features of more generalized amniotes such as *Captorhinus.*

The shape of the astragalocalcaneum of *Proganochelys* is very similar to that bone in casichelydians. There is not much variation in the shape of the astragalocalcaneum in turtles (Rabl, 1910; Zug, 1971). It is an irregular blocklike element, tapering laterally. Figure 171 compares the astragalocalcaneum in *Proganochelys* and *Meiolania. Meiolania* (Gaffney, 1983) is a primitive eucryptodire that, although derived and peculiar in other areas of its morphology, has a typical cryptodiran astragalocalcaneum, quite similar to that of baenids and chelydrids.

As in all turtles, the proximal portion of the astragalus in *Proganochelys* is an articulation surface for the tibia medially and part of the fibula laterally. The tibial surface is curved and somewhat saddle-shaped with a low, central ridge that fits the trough of the distal surface of the tibia. This morphology occurs in nearly all turtles. The tibial articular surface is nearly equidimensional in *Proganochelys* (and *Meiolania*), differing slightly from those of most eucryptodires and baenids in which the lateromedial dimension is usually greater. Laterally the astragalus bears the medial half of the fibular articulation surface and the calcaneum the lateral half. As in most turtles, this surface is almost twice as

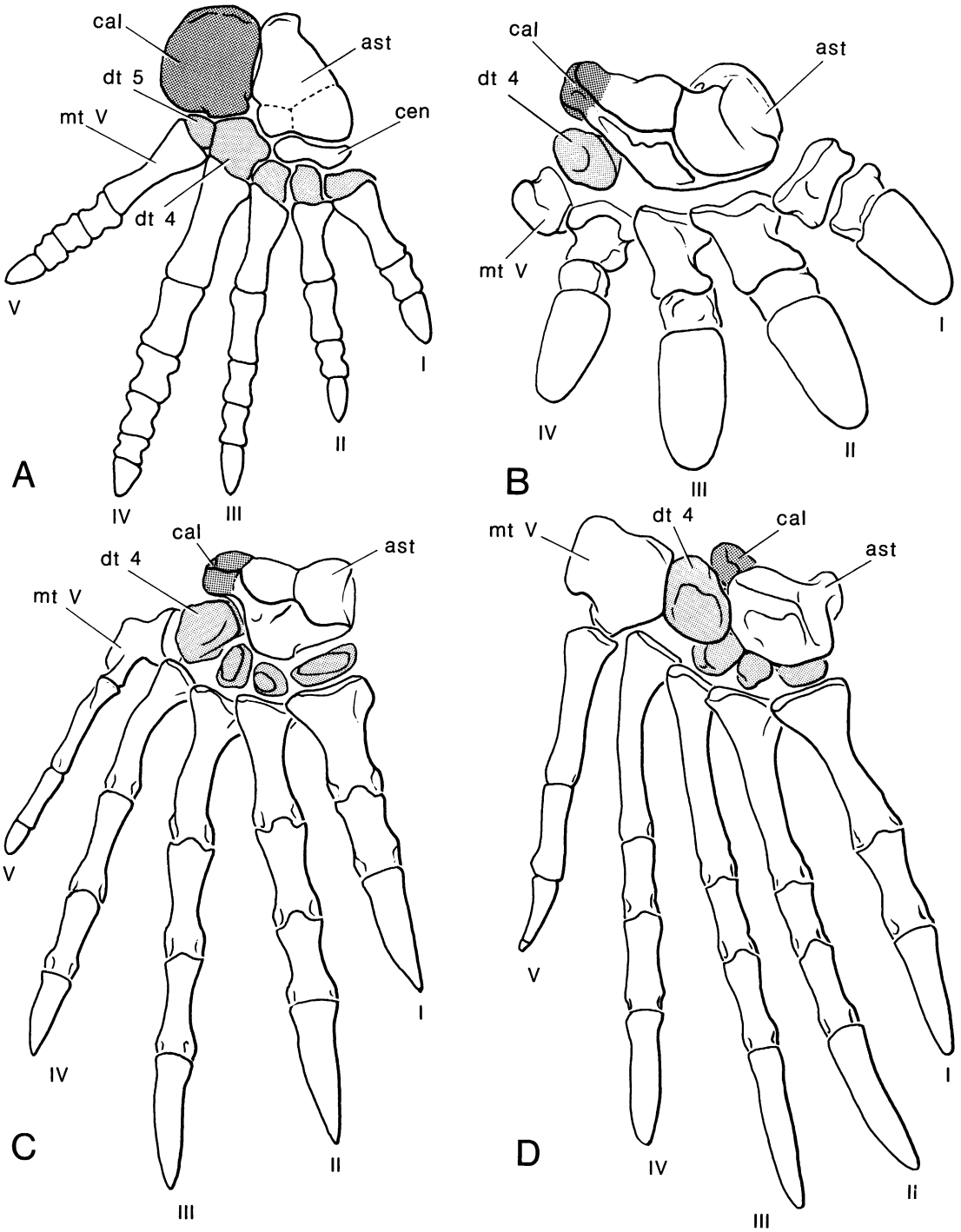

Fig. 174. Comparison of right pedes in dorsal view. **A,** *Captorhinus* sp., from Heaton and Reisz (1986); **B,** *Meiolania platyceps,* Australian Museum F 57984 (distal tarsals 1–3 not known); **C,** *Macroclemys temmincki,* AMNH 58251 and 36602; **D,** *Podocnemis expansa,* AMNH 62947. Abbreviations: **ast,** astragalus; **cal,** calcaneum; **dt,** distal tarsal; **mt,** metatarsal. Calcaneum is in heavy stipple, distal tarsals are in light stipple.

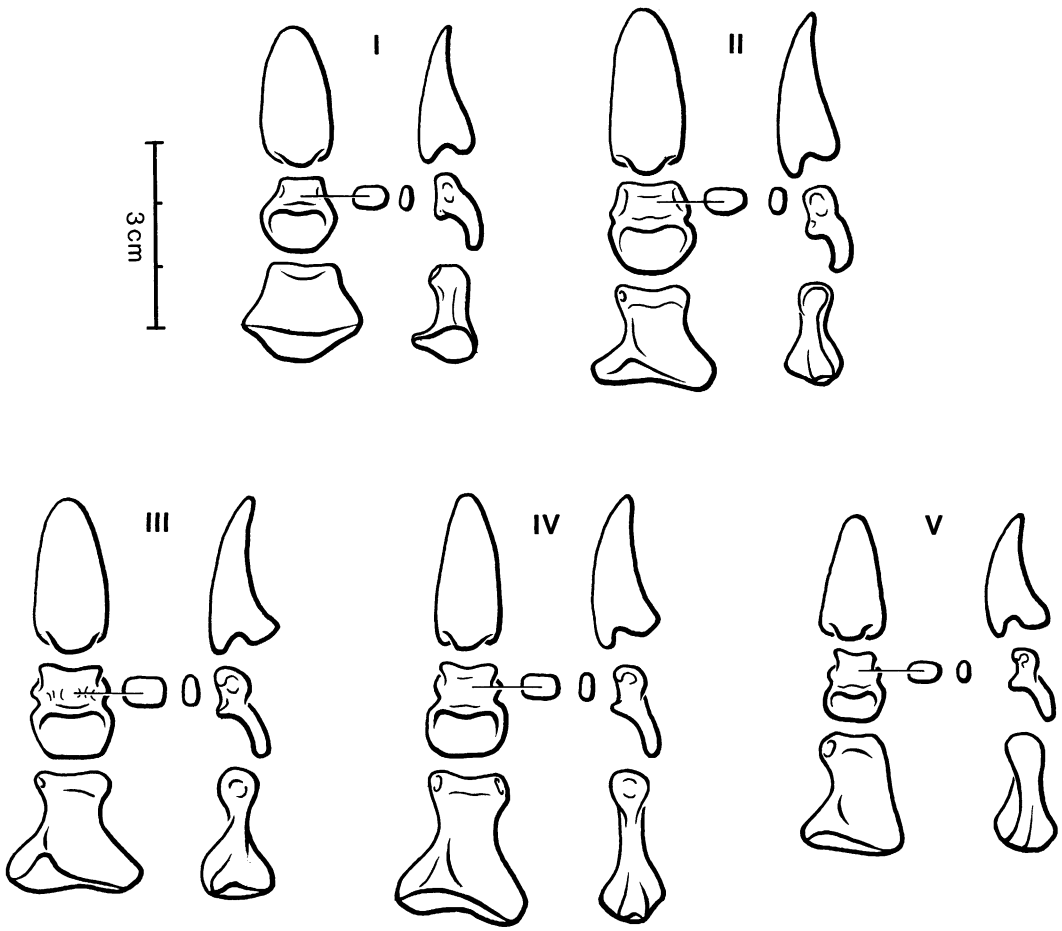

Fig. 175. *Proganochelys quenstedti,* SMNS 17204 (left side reversed with additions from SMNS 16980). Digits of right pes. Each digit is figured disarticulated in dorsal (left) and lateral (right) views. Sesamoid bones are indicated; in the dorsal views the sesamoid is displaced with a leader showing its correct position.

long (lateromedially) as it is deep (anteroposteriorly). The surface is broadly concave, tapering laterally in proximal view. The tibial surface faces anteroproximomedially while the fibular surface faces proximally. In many turtles, as in *Meiolania* and chelydrids, the tibial and fibular articulation surfaces meet to a variable extent forming a ridge. This is correlated with the degree to which the distal ends of the tibia and fibula contact each other. In *Proganochelys* and many other cryptodires and pleurodires, the tibia and fibula do not meet distally and the astragalar articulation surfaces for each bone are separated by a narrow trough. There seems to be little systematic pattern in this feature; it occurs sporadically within various families.

As in most Recent turtles (Schaeffer, 1941), movement at the crurotarsal joint appears to be limited in *Proganochelys.* The opposing joint surfaces fit as in most Recent turtles, although not to the extent seen in testudinids and certainly tighter than in trionychids and cheloniids. There is no indication in *Proganochelys* of a tarsal joint pattern significantly different from that seen in living casichelydians.

Distally the astragalus of *Proganochelys* and most other turtles has a distally convex swelling that forms part of the plantar surface of the foot. This is particularly well developed in *Proganochelys* and is similar to the extent seen in *Macroclemys* and *Chelydra.* This swelling seems to be better developed in plan-

tigrade turtles than in digitigrade or unguligrade ones. The plantar swelling is more medial on the astragalocalcaneum and laterally the element is significantly thinner, about half the thickness in a proximodorsal direction. This is due to the excavation of the distolateral part of the astragalocalcaneum to receive the fourth distal tarsal and it occurs in nearly all turtles. The excavation is semicircular with a slightly concave surface.

Comparison of the astragalus and calcaneum in *Proganochelys* and *Captorhinus* (fig. 174) is not much different from comparing *Captorhinus* with any turtle. The tarsus of *Captorhinus* (Peabody, 1951; Fox and Bowman, 1966; Heaton and Reisz, 1986) differs significantly from that of *Proganochelys* and other turtles. The astragalus of *Captorhinus* is a relatively thin, platelike element that is roughly triangular rather than being irregular and cuboid as in turtles. In *Proganochelys* and other turtles the tibia has a relatively tight fitting articulation with the astragalus while in *Captorhinus* the tibia has a loose articulation indicating a mobile crurotarsal joint, which is absent in turtles. The astragalus of *Captorhinus* has a set of sutures indicating fusion from three elements (Peabody, 1951; Romer, 1956) while these sutures are absent in *Proganochelys* and other turtles. The calcaneum and astragalus of *Captorhinus* have a relatively loose articulation while in *Proganochelys* they are tightly sutured or fused as in nearly all turtles. The astragalus and calcaneum of *Captorhinus* are very large in the proximodistal plane while in *Proganochelys* and other turtles they are compressed and much less extensive in this plane. There is a distinct foramen formed between the astragalus and calcaneum in *Captorhinus* but not in turtles. The calcaneum in *Captorhinus* is as large as the astragalus and particularly expanded laterally in contrast to *Proganochelys* and other turtles where it is smaller than the astragalus and ends laterally at the lateral margin of the fibular articulation. The astragalocalcaneum of *Proganochelys* and other turtles is modified for the articulation of the circular fourth distal tarsal, but in *Captorhinus* the fourth distal tarsal has a simple contact. Lastly, *Proganochelys* and most turtles have a well-developed plantar swelling on the astragalus and this is absent in *Captorhinus*.

Aside from the dubious possibility of a fused centale on the astragalus, there are no centralia in *Proganochelys*. The tarsal material is not as good as it might be and the distal tarsals are not well preserved in any specimen, but it is very unlikely that centralia, particularly of the sort seen in *Captorhinus*, were present. *Captorhinus* has a single, elongate ossification, identified by Peabody (1951) as centrales one and two fused, lying distal to the astragalus. This element, in whole or part, is presumably homologous to the single central ossification seen fused or sutured in chelydrids, pleurodires, and baenids.

The distal tarsals of *Proganochelys* (fig. 173) appear to be four in number, as in casichelydians. Distal tarsal 1 is not well preserved but seems to be ovoid and nodular, similar in size and shape to distal tarsal 3. Distal tarsal 2 is based on a speculative identification but it looks like distal tarsal 3 also. Distal tarsal 3 is an irregular, ovoid nodule, not bilobate or constricted as in chelydrids. Distal tarsals 1–3 lie approximately behind their respective metatarsals; their more precise relations and contacts cannot be determined.

Distal tarsal 4 (fig. 174) is distinctive in turtles because it is usually a circular element that is larger than the other distal tarsals and fits into a curved recess in the astragalocalcaneum (fig. 171). Distal tarsal 4 in most turtles also articulates with metatarsals III, IV, and V as well as distal tarsal 3. In *Proganochelys* distal tarsal 4 is the same as in casichelydians in morphology and contacts. SMNS 16980 has both distal tarsals 4 well preserved and one is in articulation on the right side. The bone is oval in anterior view and is roughly equidimensional when viewed proximally or distally. The anterior surface is a shallow concavity roughly paralleling the plane of the foot. In many casichelydians distal tarsal 4 is roughly cylindrical, with the posterior surface parallel to the anterior and the sides roughly forming the cylinder. In *Proganochelys,* distal tarsal 4 is more irregular; the posterior surface is a pendant tubercle extending distally with a broad trough proximally. This morphology is probably not primitive for turtles as it tends to occur in

the more aquatic emydids and some pleurodires. The distal tarsal 4 of *Captorhinus* is a five-sided plate having relatively tighter articulations with surrounding elements compared with turtles. Distal tarsal 4 is larger than the others in *Captorhinus* as in turtles, but it does not have a well-developed fifth metatarsal contact nor the circular articulation with the astragalus and calcaneum. As in other aspects of the pes, the distal tarsals of *Proganochelys* agree with those of other turtles and are not intermediate or similar to more generalized amniotes.

The metatarsals of *Proganochelys* are relatively large, robust elements in comparison to the metatarsals of most turtles. They are somewhat more robust than in *Macroclemys* but of generally similar size and shape. The metatarsals increase in length from I to III and then decrease to V. The distal articulations are rounded and cylindrical with only a slight indication of a median groove rather than a distinct groove as in most casichelydians. Most turtle metatarsals are relatively long and slender; pleurodires and baenids have this condition and it would appear to be generalized for casichelydians. The more robust metatarsals of *Proganochelys* are similar to *Macroclemys* and *Meiolania,* however, rather than testudinids. In testudinids the metatarsals are shorter and have generally flat articulation surfaces. Metatarsal I in *Proganochelys* is a very stubby element, about one-half the length of metatarsal II and wider than long. It is asymmetrical and expanded laterally at its base to overlap metatarsal II. A very short metatarsal I also occurs in testudinids, but rarely in other turtles. Metatarsals II–IV are similar to each other, only varying in length. The proximal articulation is curved to flat and slightly irregular. Distally, the articulation is cylindrical and through about 300° of curvature. The base of each more medial metatarsal strongly overlaps the more lateral metatarsal. The bases are expanded and have articular facets for this overlap. A strong overlap is found in baenids and chelydrids but is not common among turtles.

The fifth metatarsal of turtles is a peculiarly shaped element, usually characterized as "hooked" and very different from the other metatarsals. The fifth metatarsal of *Proganochelys* is roughly L-shaped and much flatter than the others. The bone is curved concave ventrally, and has a large, oval articular surface medially for the fourth distal tarsal. This articular surface is shallowly concave and faces medially and slightly proximodorsally. Distally there is an articulation for phalanx V, which is flatter and not as well formed as the phalanx articulations on the other metatarsals. The fifth metatarsal of *Proganochelys* is not particularly the same as in other turtles; some have a more angular L shape while others, as in baenids, have a more equidimensional plate shape.

The peculiar shape of the fifth metatarsal in turtles combined with the absence of a fifth distal tarsal has at times led to the identification of metatarsal V as a distal tarsal (Hoffman, 1890; Boulenger, 1889; Case, 1939; as referred to by Zug, 1971, and Archibald, Ph.D. thesis), resulting in a lower phalangeal count. A somewhat similar fifth metatarsal occurs in many living and fossil nonmammalian amniotes and has given support to the use of a hooked fifth metatarsal as a character consistent with Goodrich's "Sauropsida" (see Gaffney, 1980, for references and discussion). The absence of a hooked fifth metatarsal in *Petrolacosaurus,* the hypothesized sister taxon to the Diapsida (Reisz, 1981), however, argues against this interpretation. Nonetheless, the presence of one in *Proganochelys* shows that this character occurs in all turtles and may be an independently acquired chelonian synapomorphy.

Captorhinus (Heaton and Reisz, 1986) has metatarsals that differ from those of turtles in lacking basal overlap and the marked differentiation of metatarsals I and V. Metatarsal V in *Captorhinus* has the same morphology as the other metatarsals and articulates with the fifth distal tarsal, absent in turtles.

Proganochelys has a phalangeal formula of 2-2-2-2-2 while the presumed generalized condition in turtles is 2-3-3-3-3. Zug (1971) reviewed the variation of phalangeal formulas in turtles and showed that the testudinids come closest to the *Proganochelys* formula with 2-2-2-2-1 or 0 as a common pattern. *Captorhinus* (Heaton and Reisz, 1986) has a phalangeal formula of 2-3-4-5-4 and this is likely to be the plesiomorphic am-

niote condition. As in the manus, the phalangeal formula of *Proganochelys* is best interpreted as an autapomorphy of that taxon.

It is interesting to note that *Meiolania* differs from *Proganochelys* in apparently having a formula of 2-2-2-2-0 with the fifth metatarsal block-shaped rather than hooked and L-shaped (figs. 173, 174).

The proximal phalanx in the five digits of the *Proganochelys* pes is very similar to that bone in the manus. There is a strong ventral process forming the ventral part of the metatarsal articulation; such processes can be seen in *Macroclemys* and some other living turtles. The strength of this process and the well-developed, cylindrical concavity of the articular surface differ markedly in testudinids with reduced digits, which generally have less extensive articular surfaces. Phalanges I–IV differ slightly in size and development of the ventral process but phalanx V is less than half the size of the others.

The unguals of *Proganochelys* are all curved, clawlike elements, similar to the manal unguals but more robust and deeper. The unguals have more curvature than those of most other turtles and have well-developed flexor attachment tubercles on the ventral surface. At the point of these tubercles the unguals are about as deep as they are wide, but distally they flatten with the dorsal surface more convex than the ventral. The unguals of *Proganochelys* vary in size, II and III being the largest, I and IV being smaller, and ungual V being the smallest. The entire digit V is much smaller than the other pedal digits, a disparity seen in other turtles and not paralleled in the manus of *Proganochelys.* The very small fifth digit in *Proganochelys* and other turtles is different from the pattern in *Captorhinus* in which V is larger than I and about the same as II (Heaton and Reisz, 1986) and may be interpreted as a chelonian synapomorphy.

Although digit V is small in *Proganochelys* the ungual is fully developed and would appear to have had a claw as in the other digits. Zug (1971) and Walker (1973) stated that all living turtles lack a claw on digit V, and examination of baenids suggests that this is true of them also, so that the absence of a claw on the fifth digit may be a casichelydian synapomorphy.

The joint surfaces and tarsal element morphology in *Proganochelys* are consistent with mobile, functional mesotarsal and tarsometatarsal joints as described by Zug (1971) for living nonmarine cryptodires. Also in common with living turtles is the relatively less mobile crurotarsal joint. It is impossible to determine the actual degree of movement in the tarsus of *Captorhinus* but comparison of the flat-sided tarsals lying in one plane with the curved and well-developed articular surfaces on the three-dimensional tarsal of *Proganochelys* and other turtles strongly suggests that turtles have greater degrees of controlled mobility in the tarsus.

SESAMOIDS AND OSTEODERMS
(figs. 158, 159, 162, 170, 172, 175)

Proganochelys is unusual in having what are interpreted as sesamoid ossifications in the extensor tendons of the digits. In the forefoot these ossifications are best seen in SMNS 15759, a partially complete, articulated manus (fig. 158). In this specimen there are nodules of bone lying dorsal to and slightly to one side of the medial phalanx in all five digits. These nodules are ovoid and dense in contrast to the osteoderms which tend to be flat or conical and porous. Nonetheless, it is difficult to be entirely sure of the identification but it is likely that more sesamoids have been misidentified as osteoderms than vice versa. Sesamoids are also found in situ in digit II of the right manus and digits I and II of the left pes (fig. 172).

In all of the specimens the sesamoids are either slightly displaced from life position and/or somewhat damaged by preparation. Presumably there were more present in the other digits but may have been prepared off. In life, sesamoids seem to have been directly dorsal to the medial phalanx, between the ungual and metatarsal or metacarpal (figs. 162, 175). This would be the position of the distal end of the ligament from the extensor digitorum breves (Zug, 1971; Walker, 1973).

In turtles, the only other sesamoid reported is the os transiliens in the adductor musculature of some testudinids (Ray, 1959; Haines, 1969). Haines (ibid.) reviewed the distribution and structure of reptilian sesamoids and there are no reports of sesamoids in the dig-

ital extensor system of any reptiles. Lizards are known with sesamoids in the palmar aponeurosis of the flexor system and the report of Holmes (1977) of sesamoids on the ventral surface of the digits in *Captorhinus* would appear to be an example of this, rather than a feature comparable to *Proganochelys*. Haines (1969) also reviewed the function of sesamoids and a number of hypotheses might explain the *Proganochelys* condition.

SYSTEMATIC SIGNIFICANCE OF VARIATION AMONG THE *PROGANOCHELYS* SPECIMENS

The differences among specimens of *Proganochelys* have been described in the context of morphology earlier, but it is worthwhile assessing these differences in the context of possible taxonomic hypotheses. Table 25 lists the principal differences among the specimens. The type of *Proganochelys quenstedti* is not included because it is a steinkern or internal mold and none of these features can be seen on it. The size of the steinkern agrees with a carapace length of roughly 50 cm, so it does not differ drastically from the larger of the specimens with bone preserved.

Size differences (discussed earlier) among the six specimens are interpreted as consistent with growth differences within a species. The carapace lengths do not form a bimodal distribution and would be difficult to use as taxonomic criteria in any case.

The cranial scalation pattern is a feature that is diagnostic of some living turtle species, particularly pelomedusids. The three *Proganochelys* skulls show a relatively great range of differences when compared to such Recent species. However, the differences form an overlapping rather than discrete pattern. The Berlin skull and SMNS 16980 have low supraorbital scales, which are high and well developed in SMNS 15759; but SMNS 15759 agrees with the Berlin skull and differs from SMNS 16980 in lacking the nasal-frontal scale and in having a long scale 6. The significance of these differences is not clear.

The labial ridge differences can be interpreted as individual variation, based on my own observation of Recent turtles, such as chelydrids and cheloniids. However, the much shallower lower jaws may be related to growth as well as individual variation. The triturating surface width is probably also growth related, but SMNS 15759 has been crushed to make its lower jaws narrower than before burial.

The only shell difference seen among the few specimens that have comparable areas of shell preserved is the presence/absence of marginal scale 1. This is within the degree and kind of variation seen in the shell scales of Recent turtles, and can be interpreted as individual variation.

The cervical vertebrae of SMNS 16980 are smaller than the cervicals of the other three specimens that preserve them, but because SMNS 16980 is a smaller individual, this is consistent with a growth hypothesis. However, the shape of the rib of the eighth cervical has differences that cannot easily be ascribed to growth. This rib is preserved in only two specimens, MB 1910.45.2 and SMNS 16980 (fig. 108 and following), and it is quite different in them. In MB 1910.45.2 the rib is fused to the centrum and in shape it is thick and short with a curved distal end. In SMNS 16980 the rib is sutured to the centrum (possibly a growth difference), and is thin, long, and flat in the vertical plane. In my subjective assessment of all the differences among the *Proganochelys* specimens, this difference in the eighth cervical rib is the most inconsistent with a single species hypothesis.

The numbers of caudal verebrae differ in all three specimens that preserve them, and this appears to be related to the numbers of centra incorporated in the tail club. Recent turtles also have variable numbers of caudal centra but the distalmost centra become very small ossifications, quite subject to variation.

The postpelvic ossifications, here termed hypoischia, unique to *Proganochelys* among turtles, are single in two specimens and paired in two other specimens, and this does not correlate with size or presumed growth criteria. As speculated above, this may be a sex difference.

The cervical dermal osteoderms differ in the two specimens that preserve them. SMNS

TABLE 25
Features with Possible Systematic Significance Among Specimens of *Proganochelys*

	MB 1910.45.2	SMNS 16980	SMNS 17203	SMNS 17204	SMNS 10012	SMNS 15759
Midline carapace length (cm)	53.5	48.5	40.0*	51.0+*	60.0	59.0*
Supraorbital scales	Low	Low	—	—	—	High
Cranial scale five	Absent?	Present	—	—	—	Present
Cranial scale six	Longer than wide	Wider than long	—	—	—	Longer than wide
Nasal-frontal scale	Present	Absent	—	—	—	Present
Labial ridges	Intermediate	Low	—	—	—	High
Lower jaw	Deep	Shallow	—	—	—	Deep
Triturating surface width	100%	54%	—	—	—	59%
Marginal one	Present	Absent	—	?present	—	—
Cervical vertebrae	Large	Small	—	Large	—	Large
Rib of cervical 8	Thick, short, fused	Thin, long, sutured	—	—	—	—
Numbers of caudals	—	14	18	13	—	—
Hypoischium	—	Single	Paired	Single	—	Paired
Neck osteoderms	3 single 2 paired	2 single	—	—	—	—

* estimated.

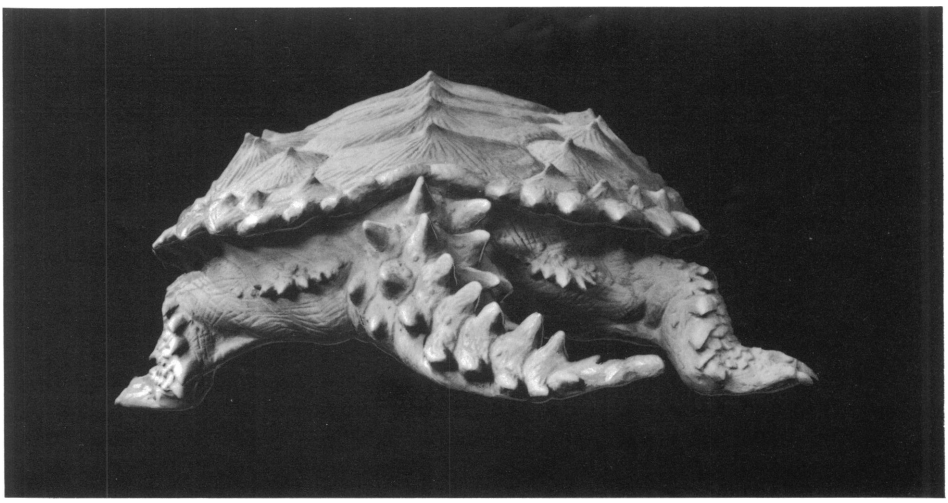

Fig. 176. *Proganochelys quenstedti.* Posterior view of ½ life size restoration.

16980 has two single ossifications while MB 1910.45.2 has five ossifications, three single and two paired. This may be an individual, sexual, or systematic variation.

Although six specimens are entered in table 25, only three are comparable in terms of preserved areas. Two of these, MB 1910.45.2 and SMNS 15759 have more features common to themselves than to the third, SMNS 16980. By intentionally discarding the overlapping features, one could make a case for two species, one consisting of MB 1910.45.2 plus SMNS 15759 and diagnosed by: cranial scale 6 longer than wide, nasal-frontal scale present, lower jaw deep, cervical rib 8 short and thick, five neck osteoderms. The other species would be only SMNS 16980 and diagnosed by: cranial scale 6 wider than long, nasal-frontal scale absent, lower jaw shallow, cervical rib 8 long and narrow, two neck osteoderms.

I feel that in the context of the limited number of specimens and the poor preservation of most, it would be difficult to maintain this assertion of two species. Furthermore, SMNS 16980 is clearly younger or in some relative way, less grown, than the other two specimens (see growth section earlier). Although some of these five features are not definitely known to be growth related in Recent turtles, it is possible that many of them were growth related in *Proganochelys.*

Therefore, although the presence of more than one taxon is possible among the six specimens, the hypothesis that is most consistent with the available evidence is that only one species is represented in the available specimens.

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