The Skeletal Morphology of the Cretaceous Cryptodiran Turtle, *Adocus,* and the Relationships of the Trionychoidea

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CONTENTS

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ABSTRACT

The osteology of the Cretaceous turtle, *Adocus,* is described, based on a nearly complete specimen from the Hell Creek Formation of Fallon County, Montana. An analysis of this morphology, combined with comparisons with all other fossil and living trionychoids, provides the basis for a phylogenetic analysis of the superfamily Trionychoidea, which consists of two large, monophyletic groups, the epifamilies Trionychoidae and Kinosternoidae. The epifamily Trionychoidae includes the sister families Trionychidae and Carettochelyidae; their sister-group, *Peltochelys*; the sister-group of those three taxa, the Nanhsiungchelyidae;

and the sister-group of those four taxa, the Adocidae. The epifamily Kinosternoidae includes the genus *Hoplochelys* as the sister-group to a monophyletic Kinosternidae; the possible sister-group to those two taxa, *Agomphus*; the sister-group to those three taxa, a restricted Dermatemydidae (including only *Baptemys* and *Dermatemys*); and the sister-group to those four taxa, *Emarginachelys.* The inclusion of fossils in this study results in a hypothesis for the relationships among the living families that is fundamentally different from that based on a previous study of the living families alone.

INTRODUCTION

During his short career, George Baur (1859–1898) proposed several hypotheses for relationships among turtles that were novel for the day but have proved over the years to be well supported. In contrast to Cope (1871), Dollo (1886), Boulenger (1889), and Lydekker (1889), he considered *Dermochelys* to be a derived chelonioid (Baur, 1889a) and not the sister-group to all living turtles (i.e., the Atheca). He challenged the ideas of Owen (1881) and Boulenger (1887b) and suggested that *Meiolania* was a cryptodiran turtle (Baur, 1889b). And he suggested that *Glyptops* should be placed in the family Pleurosternidae, close to the Baenidae (Baur, 1891a, 1891b). All of these ideas have recently been supported by attempts to develop complete phylogenetic hypotheses for turtles (Gaffney 1972, 1975, 1984; Gaffney and Meylan, 1988). Baur also recognized that Trionychi-

dae (his Trionychia) was "not an original, but a highly specialized group" and that it was related via the Carettochelyidae to staurotypine and kinosternine kinosternids and dermatemydids (Baur, 1891c). Thus he predicted the existence of the Trionychoidea of Gaffney (1975, 1984), a superfamily whose recognition is supported by the work of Albrecht (1967, 1976), McDowell (1961), and Meylan (1987).

The subject of this paper is the relationships of the members of the Trionychoidea based primarily on the study of a remarkable new fossil of *Adocus.* Although membership of living families in this superfamily is sufficiently established, there are two fundamentally different hypotheses for interrelationships among them (Gaffney, 1975, 1984; Meylan, 1987) and the inclusion of extinct forms has not been completely explored

(Hutchison and Bramble, 1981). A nearly complete and well-preserved specimen of the genus *Adocus* provides critical new data and the incentive for a detailed review of the relationships of fossil and living Trionychoidea.

The specimen described below (CCM 60-15) was made available through the generosity of Marshall Lambert of the Carter County Museum, Ekalaka, Montana. It was located and collected by his son, Brice, during the summer of 1961 from the Late Cretaceous (Lancian), Hell Creek Formation in the NW ¼ of Sec 32 T6N R60E, Fallon County, Montana (figs. 1, 2).

Details of the shell morphology of this specimen support its assignment to the genus *Adocus* of Cope (1868). The type species of Cope's *Adocus* is *Emys beatus* Leidy, 1865, based on fragmentary remains from the Cretaceous Greensands of New Jersey. Cope (1868) gave this species a new generic name, *Adocus,* and suggested that it resembled *Staurotypus* and *Dermatemys.* He later (Cope, 1870) coined the family name *Adocidae* for this new genus. He included the genera *Zygoramma* and *Homorophus* in this family, both of which appear to be synonyms of *Adocus.*

Wieland (1904) provided the first thorough description of the shell of *Adocus* based on Marsh's (1890) *Adocus punctatus.* Wieland also recognized the affinity of *Adocus* to *Dermatemys, Staurotypus,* and *Claudius.* Hay (1908a) first referred *Adocus* to the Dermatemydidae, and considered it the least modified member of the family. Gilmore (1919), who described five new species of *Adocus* from the Cretaceous-Tertiary boundary of New Mexico, considered *Adocus,* and also *Hoplochelys,* to be representatives of the Dermatemydidae. White (1972) reviewed the New Jersey Cretaceous Greensand specimens and considered them to represent a single species, *Adocus beatus,* but did not address the relationships of *Adocus.* Hutchison and Bramble (1981) included *Adocus* in the Dermatemydidae and considered the scale pattern of *Adocus* and a related form, *Ferganemys,* to represent the primitive condition for the family.

Several Old World paleontologists have
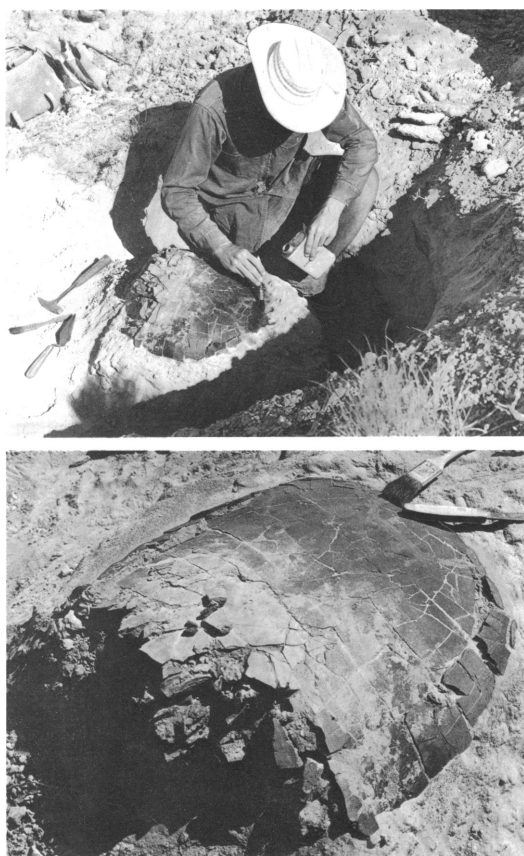
Fig. 1. Collecting the skeleton of *Adocus* sp. (Carter County Museum 60-15) in the Hell Creek Formation, Fallon County, Montana, 1961. Above, Brice Lambert exposing carapace; below, dorsal view of carapace in situ showing that the skeleton was found dorsal side up. (Photographs courtesy of Marshall Lambert, Carter County Museum)

recognized Cope's Adocidae. Mlynarski (1976) included *Adocus* in the family Dermatemydidae but recognized the subfamily Adocinae for *Adocus, Basilemys, Peishanemys,* and *Tretosternon* (which he considered a senior synonym of *Peltochelys,* but see Meylan, 1988). Nessov (1977, 1986) revised the Adocidae and added to it the Asian genera *Ferganemys* and *Shachemys.* Narmandakh (1985) interpreted the evidence provided by Khosatzky and Nessov (1977) as suggesting that the Adocidae be recognized as a taxon distinct from the Dermatemydidae. Although Narmandakh considers the question

Fig. 2.   Ventral view of the *Adocus* sp. skeleton (CCM 60-15) during preparation. Note articulated forelimbs, cervical series, and skull. (Photograph courtesy of Marshall Lambert, Carter County Museum)

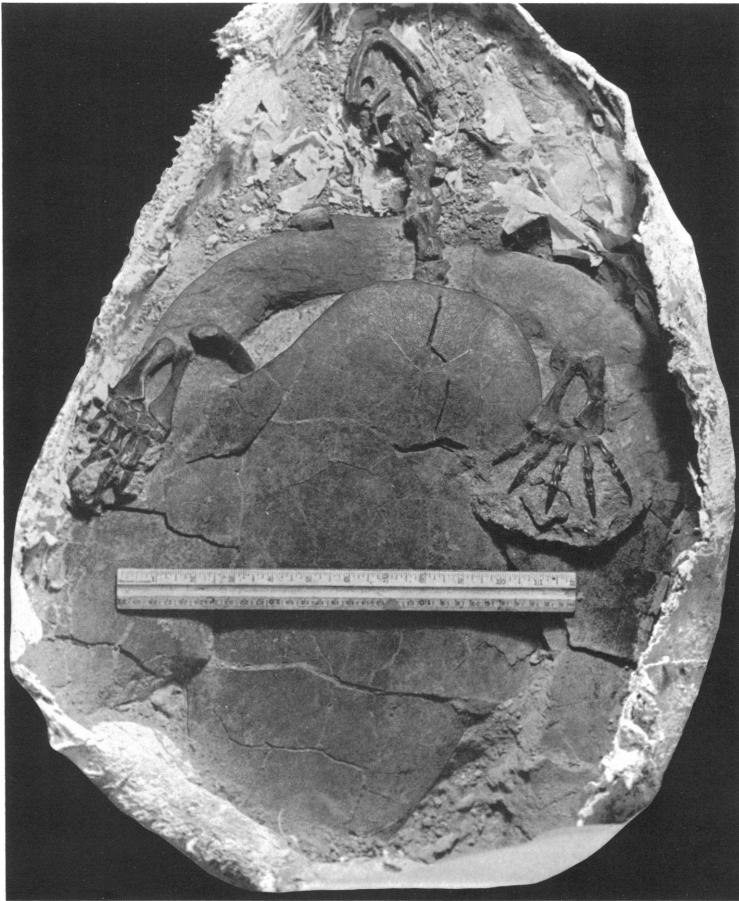incompletely resolved, he suggested that the Adocidae belong to the Testudinoidea rather than the Trionychoidea.

Gaffney and Meylan (1988) suggested a novel hypothesis of relationships for *Adocus*. This hypothesis, the subject of this paper, is that *Adocus* is part of an epifamily, Trionychoidae, which is the sister-group to the epifamily Kinosternoidae, and that together these two epifamilies make up the superfamily Trionychoidea.

MATERIALS AND METHODS

MATERIALS

This study is based primarily on specimens of fossil and Recent turtles, although in some cases we have had to use published descriptions. Our treatment of the systematics of the Trionychoidea extends to the generic level except for the clearly monophyletic families Trionychidae and Carettochelyidae which have been treated elsewhere (Meylan, 1987, 1988). The specimens on which we base our concepts of the basic taxa are listed below.

The genus *Agomphus* Cope, 1871, as currently recognized, may not be monophyletic. The species *Agomphus alabamensis* Gilmore, 1919, has features not present in the remaining species and some of these features are derived and shared with other genera (e.g., *Hoplochelys* and *Staurotypus*). The genus *Agomphus* is therefore included here exclusive of *A. alabamensis*. Our concept of *Agom-*

phus is based on the nearly complete shells of ANSP 15359 and NJSM 13753; the partial shells of AMNH 1478, 1479, and 1481; and descriptions of *Agomphus tardus* Wieland and *Agomphus masculinus* Wieland. All of this material is from the Cretaceous of New Jersey and may, in fact, represent a single species. The skull and nonshell postcrania of *Agomphus* are unknown.

Baptemys Leidy, 1870, has as its type *Baptemys wyomingensis* Leidy, 1870, from the Bridger Formation (ANSP 10074) which was examined. In addition we have studied the type specimens of *B. fluvatilus* (AMNH 4913) and *B. tricarinatus* (AMNH 6109); skulls of DMNH 511, USNM 13437, AMNH 5967, and YPM 3754; and the shells and other postcranial elements of USNM 5000, USNM 13437, USNM 13438, AMNH 5934, AMNH 5967, AMNH 6004, UCMP 45477, as well as the excellent descriptions and figures in Hay (1908a).

Dermatemys is represented by a single living species *Dermatemys mawii*, for which there is ample material. We studied the following specimens: BMNH 1911.1.28.1 (two specimens), BMNH 1984-1291, MCZ 85551, UF 29168, USNM 51072, USNM 66666, and USNM 66669. We also consulted descriptions and figures in Bienz (1895).

Our knowledge of *Emarginachelys* Whetstone, 1978, is based on reexamination of the type of *E. cretacea* (KU 23488) as well as Whetstone's (1978) description of this species which was originally referred to the Chelydridae.

Hoplochelys Hay, 1908, is included in our analyses on the basis of restudy of the excellent series of shells in the USNM including 6549 (type of *H. bicarinata* Hay, 1910), 8524, 5958 (type of *H. caelata* Hay, 1908b), 8641, 8643, 8525, 8553 (type of *H. elongata* Gilmore, 1919), 8608, 8609, 8527 (type of *H. laqueta* Gilmore, 1919), 8605, and 8646. The skull and nonshell postcrania of *Hoplochelys* are unknown.

The family Kinosternidae is included in analyses of cladistic relationship as two separate genera, *Staurotypus* and *Kinosternon*. *Kinosternon* is considered to include *Sternotherus*, following Seidel et al. (1986). Data for this family are based on the examination

of 7 *Staurotypus triporcatus*, 2 *Staurotypus salvini*, 12 *Claudius angustatus*, and 20 *Kinosternon* representing 12 different species.

The genus *Adocus* Cope, 1868, is included on the basis of CCM 60-15, the well-preserved specimen that is the focal point of this study. Additional skull data, especially for characters of the braincase, were taken from CM 3428. Other specimens examined include: AMNH 1204 (type of *A. substrictus*), AMNH 2528 (type of *A. pravus*), AMNH 1844 (type of *A. lacer*), AMNH 2260, USNM 6539 (type of *A. annexus*), USNM 8594 (type of *A. onerosa*), USNM 8650, USNM 8649, USNM 8613 (type of *A. bossi*), USNM 8577, USNM 8596 (type of *A. hesperius*), USNM 8593 (type of *A. kirtlandius*), AMNH 1844 (type of *A. lineolatus*), and AMNH 1204 (type of *A. substrictus*).

If one ignores the undiagnosable taxa, CCM 60-15 keys out to *Adocus punctatus* in the key provided by Hay (1908a) for North American species. *A. punctatus* is a junior synonym of *A. beatus*, the type species of the genus (White, 1972). The closest named species, stratigraphically and geographically, is *Adocus lineolatus* Cope (1874). However, the type of this species consists of a single costal and a partial pleural, and is not diagnostic.

Basilemys Hays, 1902, is included on the basis of restudy of AMNH 5448, NMC 8890, USNM 8804, and USNM 11084; NMC 376 and FMNH P12008, the type of *B. sinuosa* Riggs; and literature accounts of Riggs (1906), Hay (1908a), Langston (1956), and Estes et al. (1969).

Nanhsiungchelys Yeh, 1966, is included on the basis of the original description, as well as examination of the type and only described specimen of *N. wuchingensis*. A second specimen of *Nanhsiungchelys*, said to exist in the Natural History Museum of Shanghai, was not available.

The Carettochelyidae and Trionychidae are included using data published in our previous studies of the taxa (Meylan, 1985, 1987, 1988; Gaffney and Meylan, 1988).

METHODS

Phylogenetic Analysis Using Parsimony (PAUP; Swofford, 1984) was used to analyze

the morphological data. The complete data set (table 1) was examined using various combinations to find all equally parsimonious minimum-length trees. Analysis of the complete set of 15 terminal taxa and 48 characters was undertaken with characters 2, 22, 26, 27, 40, and 46 unordered. Use of the mulpars option and the swap = global or swap = alternate option indicates that there are nine equally parsimonious explanations for the observed character distribution (table 1). These shortest-length trees are 92 steps and have a consistency index of .641. These nine trees are identical except in their placement of the genera *Agomphus* and *Peltochelys,* two shell taxa. There are six alternative solutions for the relationships of *Agomphus* and four for *Peltochelys*. The choice of the solution cladogram (fig. 22) was made by an a posteriori weighting of characters. The solution chosen for *Peltochelys* is discussed in Meylan (1988); that for *Agomphus* is discussed below. If *Agomphus* and *Peltochelys* are deleted from the analysis, PAUP produces a single-solution cladogram of 88 steps, with a consistency of .670 and a topology for the remaining taxa identical to that shown in figure 22.

ABBREVIATIONS

AMNH   American Museum of Natural History
ANSP   Academy of Natural Sciences, Philadelphia
AUMP   Auburn University Museum of Paleontology
BMNH   British Museum of Natural History
CM   Carnegie Museum
CCM   Carter County Museum
DMNH   Denver Museum of Natural History
FMNH   Field Museum of Natural History
IRSNB   Natural History Museum of Belgium
JI   John Iverson (private collection to be deposited at UF)
KU   Museum of Natural History, University of Kansas
MCZ   Museum of Comparative Zoology, Harvard
NJSM   New Jersey State Museum
NMC   National Museum of Canada
UCMP   University of California Museum of Paleontology
UF   Florida State Museum, University of Florida
UNAM   Mexico University
USNM   U.S. National Museum
YPM   Yale Peabody Museum

DESCRIPTIONS OF *ADOCUS* WITH COMPARISONS TO OTHER MEMBERS OF THE TRIONYCHOIDEA

SKULL

Discussions of the skull morphology of *Adocus* are based on CCM 60-15 (figs. 3–5) and CM 3428. A thorough comparison of the skull of *Adocus* with *Baptemys* (based on DMNH 511, USNM 13437, AMNH 5967, and YPM 3754; fig. 6) and *Dermatemys* (fig. 7) is made throughout this section. Comparisons to other trionychoids and other cryptodires are made where they are important to understand the phylogenetic relationships among the Trionychoidea.

SKULL ROOF: The prefrontal is preserved in both *Adocus* skulls. The dorsal plate of this bone roofs the fossa nasalis and forms the anterior margin of the skull roof (fig. 4). There is no indication of nasal bones. The principal distinction of the dorsal plate of the prefrontal between *Adocus, Baptemys,* and *Dermatemys* is the orientation of the prefrontal-frontal suture. In *Adocus* the suture is transverse, whereas in *Baptemys* and *Dermatemys* it extends posterolaterally from the midline, reducing the degree of frontal exposure in the orbit. In all kinosternids and some specimens of *Dermatemys,* this prefrontal extension reaches the postorbital and excludes the frontal from exposure on the orbital margin. The suture orientation in *Dermatemys* is posterolateral in its medial half and transverse in its lateral half, usually allowing a small amount of frontal exposure in the orbit.

Adocus and *Baptemys* also differ in the shape of the external narial opening. The prefrontal of *Baptemys* extends anteriorly in relation to the dorsal process of the maxilla, resulting in a distinct lip, seen in many turtles. In *Adocus,* such an anterior projection of the prefrontal is absent and the narial opening lies in one plane and appears straight in lateral view. Anterolaterally the dorsal plate of the maxilla in *Adocus* and *Baptemys* sutures to the prefrontal as in most turtles.

The ventral process of the prefrontal is best seen in USNM 13437 and AMNH 5967 for *Baptemys* and CM 3428 for *Adocus.* This process forms the posterior wall of the fossa

TABLE 1
Data Matrix for Trionychoidea

	Adocus	Basilemys	Nanhsiungchelys	Peltochelys	Anosteira	Carettochelys	Lissemys	Trionyx	Emarginachelys	Baptemys	Dermatemys	Agomphus	Hoplochelys	Staurotypus	Kinosternon
1.	0	9	9	9	0	0	0	0	0	2	2	9	9	1	1
2.	0	9	9	9	9	1	1	1	0	2	2	9	9	2	2
3.	1	9	9	9	0	1	1	1	0	1	0	9	9	0	0
4.	0	9	9	9	9	1	1	1	1	1	1	9	9	1	1
5.	1	9	9	9	0	0	0	0	1	1	1	9	9	0	0
6.	0	9	9	9	0	0	0	0	0	1	1	9	9	0	0
7.	0	9	9	9	9	1	1	1	0	0	0	9	9	0	0
8.	0	9	0	9	9	1	1	1	0	0	0	9	9	1	0
9.	0	9	1	9	1	1	1	1	0	0	0	9	9	0	0
10.	0	9	1	9	1	1	1	1	0	0	0	9	9	0	0
11.	0	9	1	9	1	1	1	1	0	0	0	9	9	1	1
12.	0	9	1	9	1	1	1	1	0	0	0	9	9	0	0
13.	0	9	1	9	1	1	1	1	0	0	0	9	9	0	0
14.	0	9	0	9	1	1	1	1	1	1	1	9	9	1	1
15.	0	9	1	9	1	1	0	0	0	0	0	9	9	0	0
16.	0	9	9	9	0	0	0	0	0	0	0	9	9	1	1
17.	0	9	0	9	0	1	0	0	0	0	0	9	9	1	1
18.	1	9	9	9	9	1	1	1	9	0	0	9	9	0	0
19.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
20.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
21.	1	0	9	0	1	1	1	1	0	0	1	0	0	0	1
22.	0	0	9	1	1	1	2	2	0	0	0	0	0	1	1
23.	9	9	9	9	0	0	0	0	9	9	0	9	9	1	1
24.	0	0	9	9	0	0	0	0	0	1	1	0	0	0	0
25.	0	0	9	9	1	1	1	1	0	0	0	0	0	0	0
26.	0	9	9	9	9	1	2	2	0	9	0	9	9	1	1
27.	0	0	9	0	1	1	2	2	0	0	0	0	0	1	1
28.	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1
29.	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
30.	1	1	9	1	9	9	9	9	0	0	0	1	0	0	0
31.	0	0	1	0	9	9	9	9	1	1	1	1	1	1	1
32.	0	0	0	0	9	9	9	9	1	1	1	1	1	1	1
33.	1	1	1	0	9	9	9	9	9	9	9	9	9	9	9
34.	0	0	9	0	9	9	9	9	0	0	0	0	1	2	2
35.	0	2	9	1	9	9	9	9	1	1	0	2	1	2	2
36.	0	0	9	9	9	0	0	0	0	1	0	9	9	1	1
37.	0	1	1	9	9	0	0	1	0	0	1	9	9	0	0
38.	9	9	9	9	9	9	9	9	0	1	2	9	9	1	1
39.	1	1	9	9	9	1	1	1	0	0	0	9	9	0	0
40.	0	1	1	9	9	0	2	2	0	0	0	9	9	0	0
41.	0	0	9	1	1	1	0	0	0	0	0	0	0	0	0
42.	0	9	1	9	1	1	1	1	0	0	1	9	9	1	1
43.	1	9	9	9	9	1	1	1	9	0	0	9	9	0	0
44.	1	9	9	9	1	1	1	1	0	0	0	9	9	0	1
45.	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
46.	0	0	0	0	1	1	2	2	0	0	0	0	0	0	0
47.	2	1	9	0	9	9	9	9	0	0	0	0	0	0	0
48.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0

Fig. 3. Ventral view of *Adocus* sp. skull (CCM 60-15). Both cornu branchiale II and the lower jaw are shown in situ before preparation. (Photograph courtesy of Marshall Lambert, Carter County Museum)

nasalis and the lateral margin of the fissura ethmoidalis. The fissura is completely preserved only in one skull of *Baptemys* (AMNH 5967) and is partially broken in both *Adocus* skulls. *Dermatemys* has a distinct fissura ethmoidalis that is nearly circular in anterior view with a narrow ventral extension merging with the sulcus vomeri. In *Baptemys* the dorsal portion of the fissura is semicircular; the ventral limits are wide and merge gradually with the sulcus vomeri. The fissura ethmoidalis in the *Adocus* specimens, although incompletely preserved, appears to be similar to that of *Baptemys*, but wider.

The frontal is preserved in both skulls of *Adocus*. The contacts and general relations of the frontal are the same in *Adocus, Baptemys,*

and *Dermatemys*, except for the orientation of the frontal-prefrontal suture described above. The sulcus olfactorius is relatively wide and delimited by thick frontal ridges in all three genera. The frontal of kinosternids is distinctly smaller in comparison to *Adocus, Baptemys,* and *Dermatemys*. Its small size is apparently correlated with the large size and posterior extension of the prefrontal in kinosternids. In these three genera, the frontal sends a process anteriorly along the midline below the prefrontals to roof the fissura ethmoidalis. This process is reduced or absent in most kinosternids. The frontal morphology of these three genera is similar in ventral view to that figured for *Portlandemys* (see fig. 5 in Gaffney, 1976), except that the sulcus olfactorius is proportionately wider.

The parietal is preserved in both *Adocus* skulls. The relations and morphology of the dorsal plate of the parietal are very similar in *Adocus, Baptemys,* and *Dermatemys*. The parietal has a transverse suture with the frontal anteromedially, and a short suture with the postorbital anterolaterally. The dorsal portion of the parietal that covers the adductor musculature in the temporal fossa in chelonioids and baenids is absent in *Adocus, Baptemys,* and *Dermatemys*, as well as in kinosternids. *Adocus* has a rounded ridge that marks the edge of the temporal emargination. This ridge is absent in *Baptemys* and *Dermatemys*. Posteriorly, the parietal overlaps the supraoccipital and posterolaterally contacts the prootic. *Adocus* differs from *Baptemys* and *Dermatemys*, but is like the Trionychia, in possessing a lateral process of the parietal that supports the medial third of the processus trochlearis oticum (fig. 4B). In *Baptemys* and *Dermatemys* the parietal does not bear a significant portion of the processus trochlearis oticum and there is no lateral process.

The processus inferior parietalis forms the posterior margin of the foramen interorbitale and the side wall of the braincase. Its lower limits reach the foramen nervi trigemini and form complex contacts with the palatine and prootic. The descending process of the parietal in *Adocus, Baptemys,* and *Dermatemys* contacts a well-developed dorsal process of the palatine anteriorly, and forms a long, un-
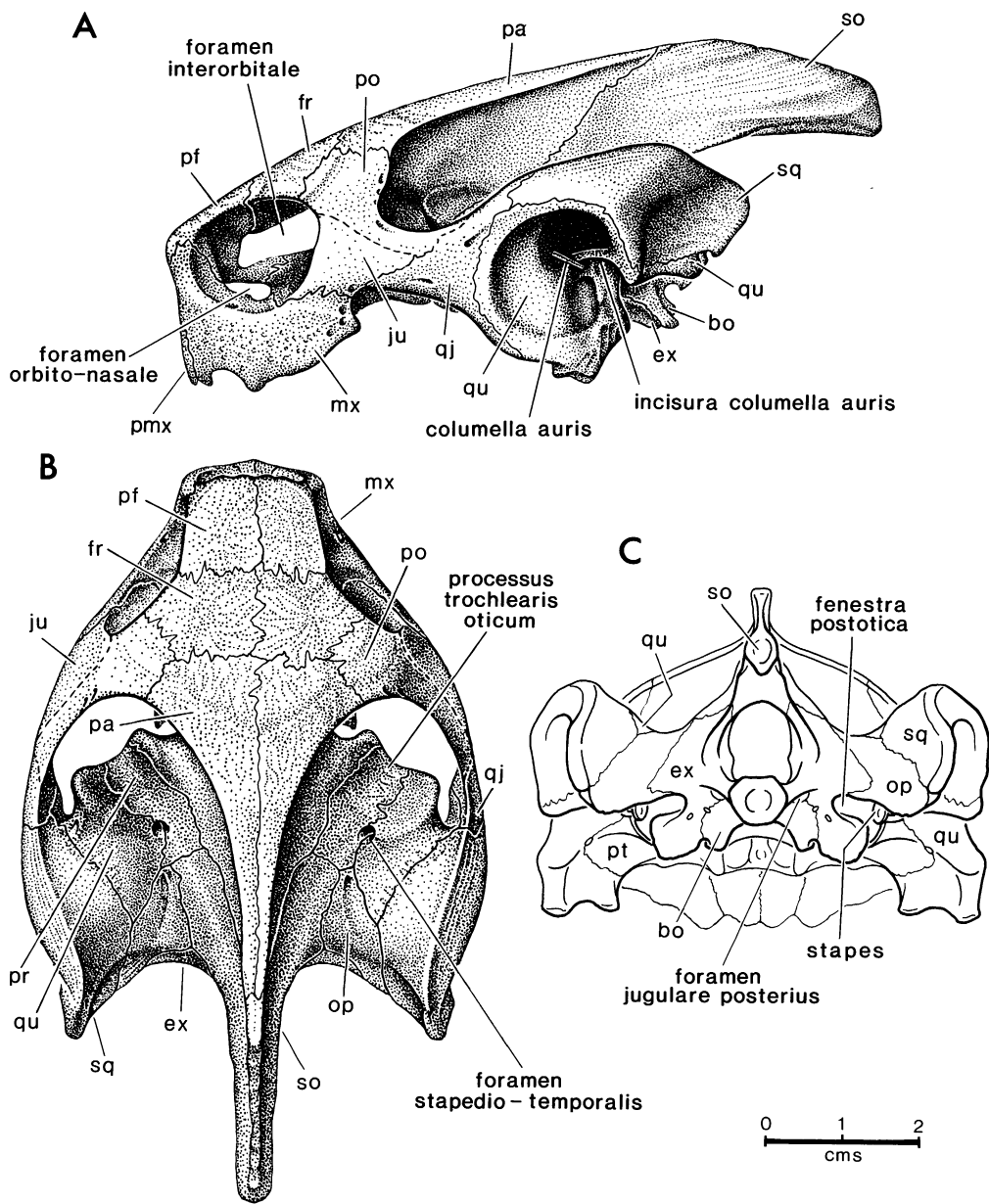
Fig. 4. Partially restored skull of *Adocus* sp. in (**A**) lateral, (**B**) dorsal, and (**C**) posterior views. Figure is based primarily on CCM 60-15 with additions from CM 3428. Abbreviations are: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pmx, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

even suture with the epipterygoid posteriorly. In *Dermatemys* the parietal forms the dorsal limits of the foramen nervi trigemini and sends a process ventrally along the anterior edge of the foramen. About half of the *Dermatemys* specimens examined also have a ventral parietal process along the postero-dorsal margin of the foramen. This dorsal
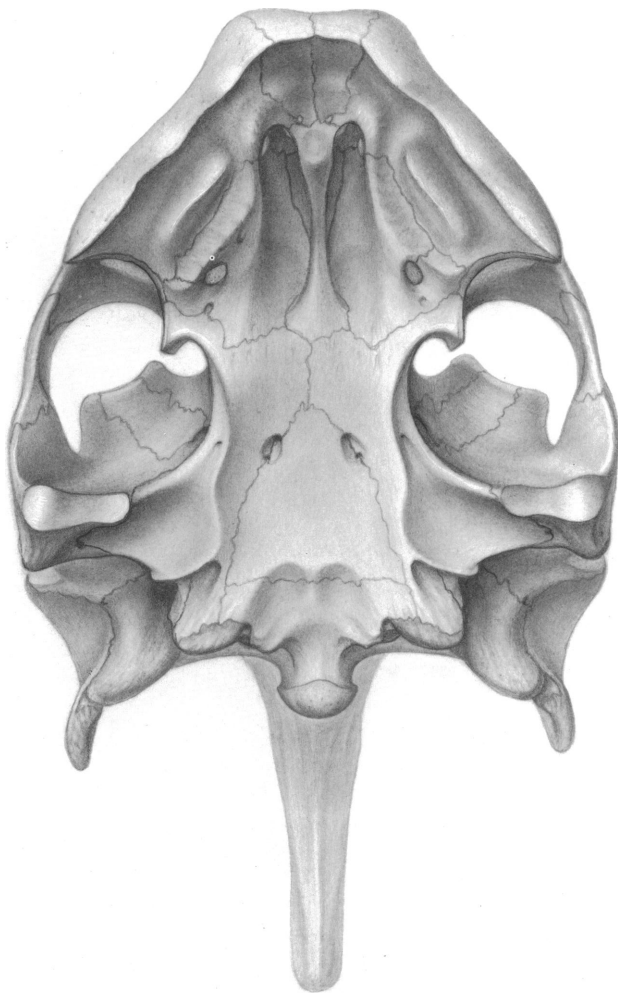
Fig. 5.   Skull of *Adocus* (CCM 60-15) in ventral view. Figure is based primarily on CCM 60-15 with additions from CM 3428.

process is definitely absent in *Baptemys* YPM 3754 and *Adocus* CCM 60-15. The anteroventral margin of the foramen nervi trigemini is poorly preserved in all specimens, but the epipterygoid appears to be the element that forms the anteroventral margin, and the parietal does not seem to have a ventral process in either *Adocus* or *Baptemys*.

Further variation of the parietal among trionychoids involves the orientation of the frontoparietal suture described above. In kinosternids (and some specimens of *Dermatemys*) the prefrontal extends posteriorly to

reach the postorbital and excludes the frontal from exposure on the orbital margin. In the Trionychia this frontoparietal suture is nearly transverse or trends posteromedially. The orientation of this suture in *Nanhsiungchelys* is not clear.

The postorbital is not entirely preserved in any of the *Adocus* specimens, but CCM 60-15 provides some useful information. The postorbital lies posterodorsal to the orbit and forms part of the orbital margin and part of the temporal margin in *Adocus, Baptemys,* and *Dermatemys*. In all three genera its con-
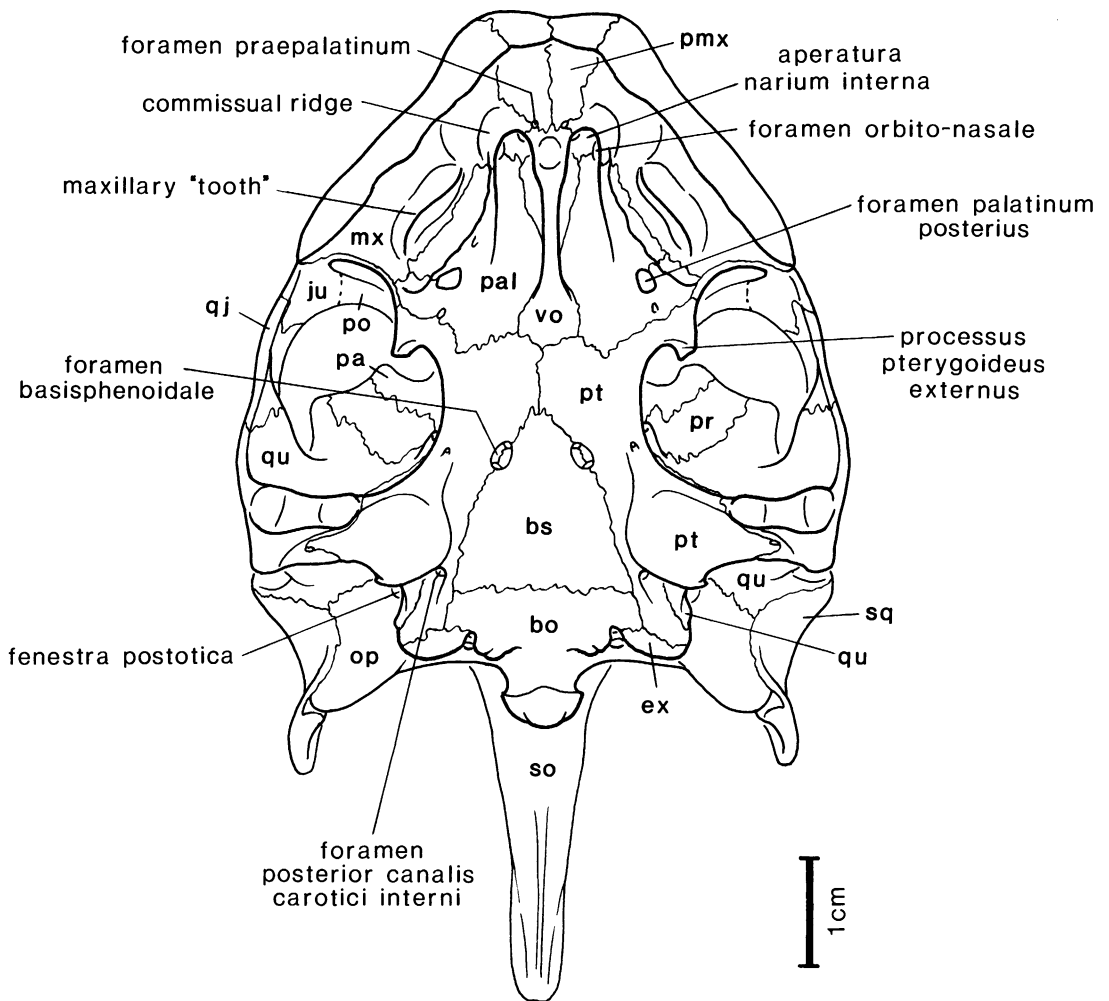
Fig. 5—*continued*. Key for figure 5. See figure 4 for abbreviations.

tacts are as follows: anteromedially with the frontal, posteromedially with the parietal, anteroventrally with the jugal, and posteroventrally with the quadratojugal. The size and relations of the postorbital agree in all three genera except that in *Adocus* the postorbital extends posteriorly above the quadratojugal more than in *Baptemys* or *Dermatemys*. It is possible that the postorbital extends posteriorly to contact the squamosal, although the more likely condition, in which the quadratojugal is exposed on the temporal margin, is used in figure 4A. The absence of postorbital-squamosal contact is a diagnostic fea-

ture of the Chelomacryptodira (Gaffney, 1984; Gaffney and Meylan, 1988).

The jugal is nearly intact in CCM 60-15; internal features are also visible in CM 3428. The jugal forms the posteroventral margin of the orbit and the extent of exposure in the orbit is about the same in *Adocus* as in *Baptemys* and *Dermatemys*. The jugal is also exposed ventrally where it forms part of the cheek emargination, but its shape varies among the three genera. Cheek emargination is most extensive in *Adocus*. The anterior part of the emargination forms a pocket in lateral view that is absent in the other two genera.
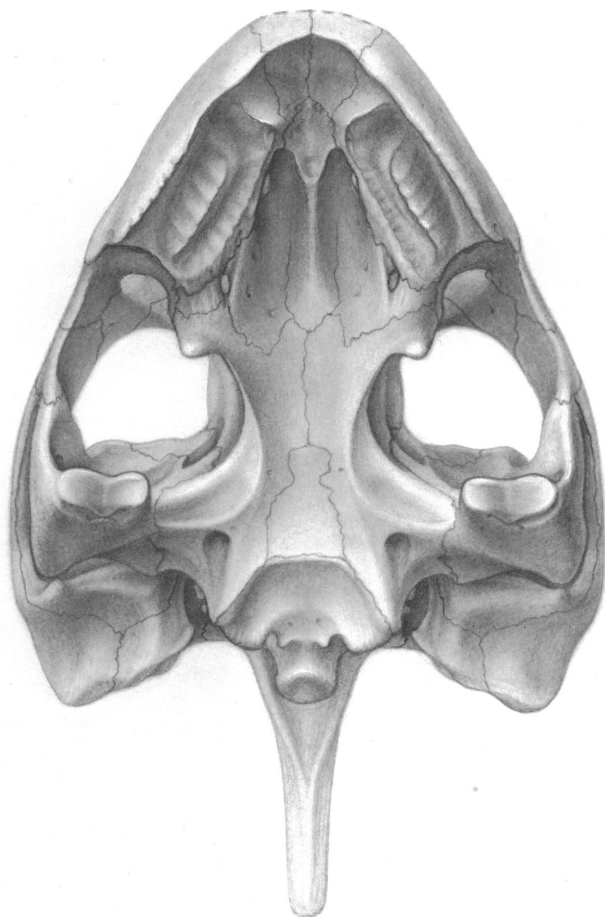
Fig. 6. Partially restored skull of *Baptemys* in ventral view. Figure is based on YPM 3758, with reference to DMNH 511.

The zygomatic arch is also thinnest in *Adocus,* but this is reflected more in the shape of the quadratojugal. The extent of cheek emargination is similar in *Baptemys* but is not as great posteriorly. In *Dermatemys* the cheek emargination is least extensive partly due to the ventral extension of the jugal bone. The posterior margin of the jugal in *Dermatemys* has a much greater contact area with the quadratojugal than in *Adocus* or *Baptemys.* The anterior contact with the maxilla is the same in the three genera.

Cheek emargination is present in chelydrids, testudinoids, and primitive chelonioids. Among trionychoids only *Adocus, Emargi-*nachelys, and *Baptemys* have cheek emargination that reaches anteriorly to the level of the orbit.

The medial process of the jugal extends on top of the maxilla and reaches the pterygoid just anterior to the processus pterygoideus externus. The medial process forms a dorsal ridge marking the posterior margin of the fossa orbitalis. This ridge is large and well developed in *Adocus,* somewhat less developed in *Baptemys,* and distinctly smaller in *Dermatemys.* Although the development of this ridge is quite variable among turtles, kinosternids have unusually large ones, even larger than in *Adocus.*
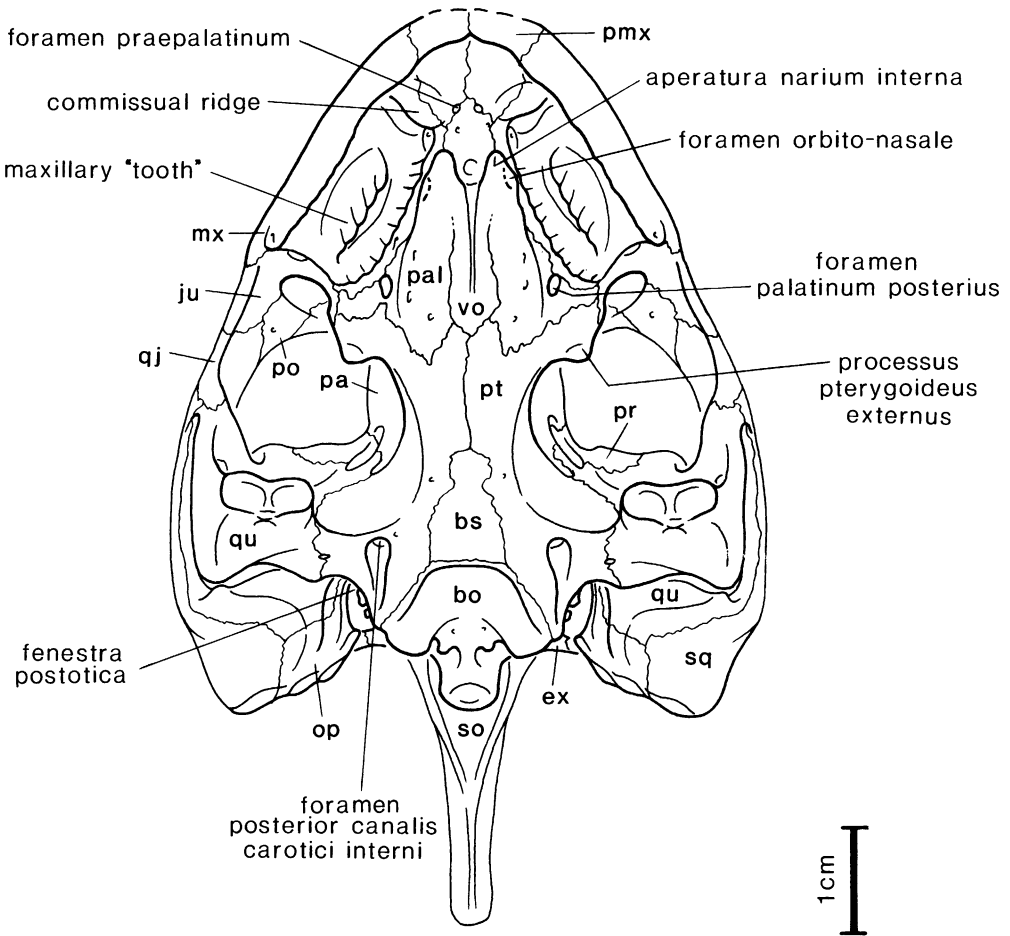
Fig. 6—*continued*. Key for figure 6. See figure 4 for abbreviations.

The quadratojugal is preserved in both *Adocus* skulls. It is a flat bone having a C-shaped contact with the quadrate posteriorly and meeting the postorbital anterodorsally and the jugal anteroventrally. *Dermatemys-Baptemys-Adocus* form a series in which the quadratojugal decreases in height along the cheek. *Adocus* has an anterior projection of the quadratojugal that is absent in both *Baptemys* and *Dermatemys*. *Carettochelys* and members of the Kinosternidae are unique in having contact between the maxilla and the quadratojugal. In a skull of either *Anosteira* or *Pseudanosteira* (FMNH PR 966), there is no such contact.

Significant portions of the squamosal are preserved in both *Adocus* skulls. The squamosal is a cone-shaped bone attached to the posterodorsal portion of the quadrate and forms the antrum postoticum. As in most turtles, it has contacts anteriorly with the quadratojugal and posteromedially with the opisthotic. It lacks any contact with the postorbital and does not participate in the skull roof as seen in some chelydrids, chelonioids, and baenids. The squamosals of *Dermatemys-Baptemys-Adocus* form a sequence in which the posterior crest of the squamosal is progressively larger. This crest is very well developed in *Adocus*. Although not as elongate as in the Trionychia or *Nanhsiungchelys*, the condition could be considered to be derived relative to that of *Baptemys* and *Dermatemys*. *Claudius* and *Staurotypus* also have
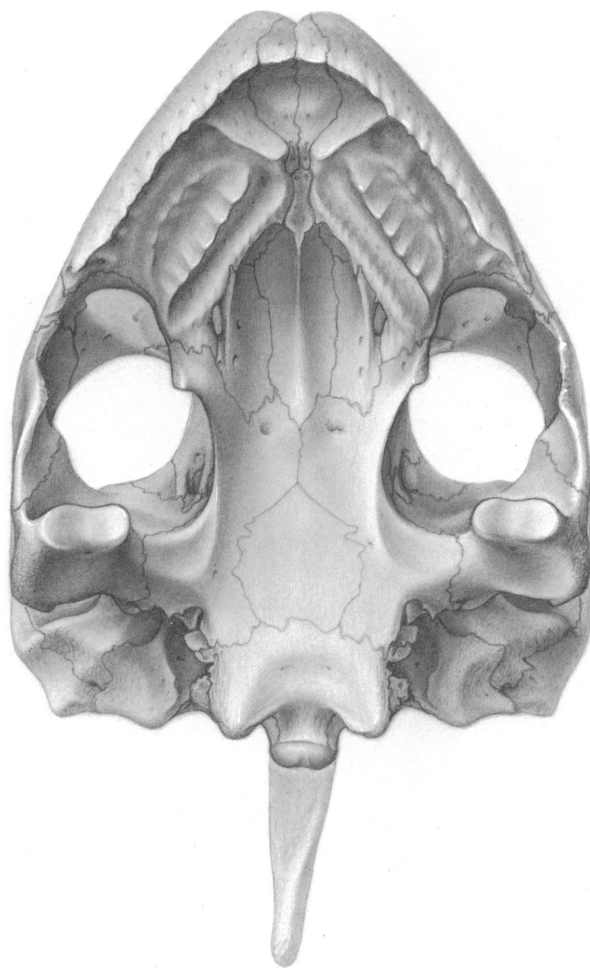
Fig. 7. Skull of *Dermatemys* in ventral view. Figure is based primarily on USNM 66666 with additions from USNM 66669.

somewhat elongate squamosals. The presence of such a crest is common in baenids, but the extent of it is greater in *Adocus* than in baenids.

The dermal roofing bones of *Adocus,* like those of *Dermatemys* and *Baptemys,* are unsculptured. The external surfaces of all of these elements are nearly smooth. Unlike those in *Dermatemys* and *Baptemys,* the skull roof of *Adocus* was clearly covered by discrete scales (fig. 4B). The presence of scales covering the dermal roofing elements is primitive for turtles. They are present in pleurodires, baenids, chelonioids, and in *Meiolania.* Elsewhere

among the Trionychoidea, scute sulci are present only in *Nanhsiungchelys.* All other fossil and living trionychoids lack scutes on the skull roof. Although the skull roof of *Adocus* and most trionychoids is unsculptured, there are two groups of trionychoids in which the skull roof is distinctly sculptured, the Carettochelyidae and *Nanhsiungchelys.* This is a derived condition.

PALATAL ELEMENTS: The premaxilla is preserved in both *Adocus* specimens. Laterally, the premaxilla meets the maxilla to form the triturating surfaces; medially, the premaxillae meet on the midline; and posteriorly, the
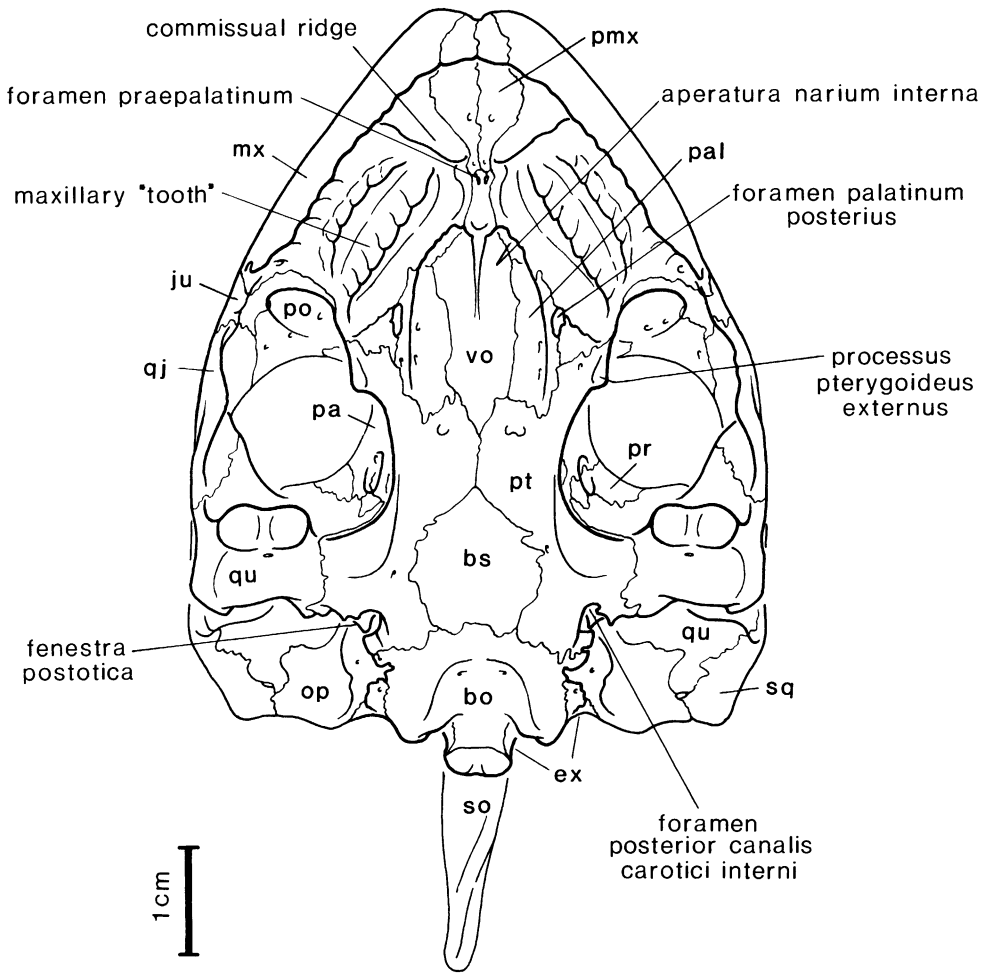
Fig. 7—*continued.* Key for figure 7. See figure 4 for abbreviations.

premaxilla meets the vomer. In *Dermatemys,* but not in *Adocus* or *Baptemys,* the maxillae meet dorsal to the premaxillae, preventing entry of the premaxillae into the narial opening. The premaxilla in anterior view is much higher in *Dermatemys* than in *Baptemys* or *Adocus.* In *Dermatemys* this dorsal extension forms an anterior wall for the ventral portion of the fossa nasalis that is absent in *Baptemys* and *Adocus.* Because of its wide occurrence in other turtles, the *Baptemys-Adocus* condition is hypothesized to be primitive.

The paired condition of the premaxillae of *Adocus, Baptemys,* and *Dermatemys* is typical of most turtles. Trionychoids and caret-

tochelyids are unique among the Trionychoidea and among cryptodires in having the premaxillae fused (Meylan, 1987).

The ventral portion of the premaxilla forms the anteriormost portion of the labial ridge and triturating surface. All three genera have a high and well-developed labial ridge with a slight concavity posterior to it on the triturating surface (figs. 5–7). The posterior contact of the premaxilla with the vomer is of the usual cryptodire pattern in *Adocus* and *Baptemys,* but in *Dermatemys* this contact is considerably narrowed transversely due to maxillary expansion. A sagittal view of the premaxilla in *Dermatemys* is provided in

Gaffney (1979, fig. 73) and shows the median concavity followed by a distinct thickening of the premaxilla (as well as the vomer). This thickening also occurs in *Baptemys* (AMNH 5967 and YPM 3754) in which it is not quite as well developed. This structure is only rudimentary in *Adocus* where the premaxilla in this region is relatively thin. This thickening is termed the commissural ridge and is discussed below. In *Adocus* there is no foramen intermaxillaris, an opening in the palate between the premaxillae and vomer found in carettochelyids, trionychids, and many specimens of staurotypine kinosternids.

The maxilla is preserved in both *Adocus* specimens. The contacts and general structure of the maxilla conform to the generalized pattern seen in most cryptodires that lack secondary palates. The maxilla may be divided into two plates: a dorsal-vertical one and a ventral-horizontal one. The dorsal-vertical plate is exposed on the lateral surface of the skull and articulates with the premaxilla anteriorly and the prefrontal dorsally. This dorsal process of the maxilla is much wider in *Dermatemys* than in *Adocus* and *Baptemys* (AMNH 5867) and is correlated with the relatively large choanal opening and large ventral area of the fossa nasalis in *Dermatemys*. One specimen of *Baptemys* (DMNH 511) has a broad dorsal process of the maxilla and is similar to *Dermatemys* in this respect.

The vomer is nearly complete but cracked in both specimens of *Adocus*. It has the generalized cryptodiran morphology as seen in *Chelydra*. It is a long element extending posteriorly from the premaxillae and maxillae, separating the palatines, to touch the pterygoid. In *Adocus* the ventral ridge of the vomer runs for nearly the entire length of the bone whereas in dermatemydids there is an anterior ridge only.

In having posterior contact to the pterygoids, the vomer of *Adocus* is like those of most other trionychoids. It is unlike the vomers of the Trionychia, which are quite reduced and fail to contact the pterygoids. Preliminary observation of *Nanhsiungchelys* suggests that it has a reduced vomer that may not reach the pterygoids.

The palate of *Adocus* is like those of most turtles in having the pterygoids in contact

anteromedially, separating the basisphenoid from the palatines. This condition occurs in all trionychoids except members of the Trionychia and possibly *Nanhsiungchelys*.

The palatine is preserved in both *Adocus* specimens. The anterolateral part of the bone forms part of the triturating surface and encloses a small foramen palatinum posterius. In *Baptemys* and *Dermatemys,* the palatine is less extensive and does not encroach onto the triturating surface. Anteromedially this element forms a complete roof to the apertura narium internum; it completely separates this structure from the fossa orbitalis. The palatine does not completely floor the apertura narium internum in all trionychoids. In *Nanhsiungchelys,* as in the Trionychia, the palatines are truncate anteriorly. Participation by the palatine in the triturating surface appears to be autapomorphic for *Adocus* as it does not occur to this extent in any other trionychoids (except in the secondary palate of some kinosternids). However, contributions of the palatine to the triturating surface are common in other turtle groups.

The two *Adocus* skulls have large dorsal processes of the palatines that form the anteroventral portion of the cavum cranii. This process forms part of the anterior margin of the lateral wall of the braincase, and is tallest just posterior to the margin of the foramen interorbitale. The processus inferior parietalis forms the rest of the cavum cranii wall. The dorsal process of the palatine in *Adocus* is best seen in CM 3428 but is also preserved on the right side of CCM 60-15. It is larger than in *Baptemys* or *Dermatemys* but smaller than in kinosternids or Trionychia. The process occurs in all known Trionychoidea and appears to be a synapomorphy for this group. A similar but less extensive dorsal spine also occurs in some broad-jawed batagurines and some *Pseudemys.* But these examples are here interpreted as homoplasy.

The triturating surfaces of *Adocus* are formed by the maxilla and premaxilla in the skull and the dentary in the mandible. *Adocus* has a high and sharp labial ridge that is marked, at least in CCM 60-15, by toothlike processes along the anterior portion of the maxilla. *Baptemys* also appears to have some undulation to the labial ridge and in *Der-*

matemys it is serrated, but neither has the distinct projections of *Adocus*. The maxillary surface of the triturating area has a posterior expansion in the region of the maxillary-palatine suture with a long lingual ridge. More anteriorly the lingual ridge rises, but the width of the surface of the maxillary is reduced. *Adocus* has a short, but well-developed, toothlike ridge or cusp in the midline of the posterior expanded area between the labial and lingual ridges. This ridge, here referred to as the maxillary tooth, is intermediate in height between the high labial ridge and the nearly absent lingual ridge and extends along half the length of the maxillary surface.

In *Baptemys* the maxillary tooth is crenulated but otherwise identical to that of *Adocus*. *Baptemys* differs from *Adocus* in having a transverse or commissural ridge just posterolateral to the premaxilla-maxilla suture, lying at right angles to the labial ridge. The commissural ridge is separated from the maxillary tooth by a trough but is nearly continuous with the lingual ridge. *Baptemys* also differs from *Adocus* in having a slight medial expansion of the triturating surface (presumably correlated with the commissural ridge). This is most evident in the increased contact between premaxilla and vomer. The anterior margin of the apertura narium interna in *Adocus* is distinctly embayed and the premaxilla has a very limited suture with the vomer. In *Baptemys* the embayment is reduced by the medial expansion of premaxilla and maxilla.

Dermatemys is apparently more derived than *Baptemys* or *Adocus* in having a division of the maxillary tooth so that two short ridges appear in this position. The groove separating the two maxillary ridges does not reach the level of the grooves delimiting these ridges from the labial and lingual ridges, respectively. This substantiates the notion that the two maxillary ridges of *Dermatemys* are the homolog of the single maxillary tooth in *Baptemys* and *Adocus*. *Dermatemys* also has an expanded anterior portion of the maxillary and premaxillary triturating surface, correlated with a commissural ridge that is nearly twice the length of that in *Baptemys*. In *Baptemys* the maxilla does not extend medially to meet the vomer, but in *Dermatemys* the

maxilla is in contact with the vomer due to this medial expansion of the anterior portion of the triturating surface. The commissural ridge of *Dermatemys* is high and straight, as opposed to the lower, cusplike commissural ridge of *Baptemys*.

The maxilla of *Adocus* meets only the jugal on the cheek. This appears to be the primitive condition for trionychoids. Contact between the maxilla and quadratojugal, as found in *Carettochelys* (but not anosteirines, FMNH PR 966; Gaffney, 1979: fig. 173) and kinosternids, is considered derived.

PALATOQUADRATE AND BRAINCASE: The quadrate is well preserved in both *Adocus* skulls, its general shape being quite similar to that of other eucryptodires. The incisura columella auris is nearly closed by a dorsal process extending upward just behind the stapes. In neither specimen, however, does the process meet bone above it, resulting in a comma-shaped opening. In *Dermatemys* and *Baptemys,* the incisura is more open; in kinosternids it is like that in *Adocus*; and in *Nanhsiungchelys* and the Trionychia it is completely closed. The right quadrate is preserved in a badly crushed skull of *Basilemys* (NMC 8890). It appears to have had a closed or nearly closed incisura columella auris with a strong postcolumellar ridge not unlike that of *Nanhsiungchelys*. The antrum postoticum of *Adocus* is developed to the extent seen in most eucryptodires and is very similar to that of *Dermatemys* and *Baptemys*. Among the Trionychoidea, the curved shape of the incisura columella auris is unique.

The processus trochlearis oticum of *Adocus* is unusually large and well developed, comparable in extent to that seen in the Trionychia. In *Adocus* the processus is formed laterally by the quadrate and more medially by the prootic, the usual cryptodiran condition. However, medial to the prootic the parietal sends a process laterally to form the medial third of the processus trochlearis oticum. The processus in *Adocus* is troughlike, concave dorsally, and protrudes into the adductor fossa to a greater extent than in dermatemydids, kinosternids, and other eucryptodires, except the Trionychia. *Carettochelys* is similar to *Adocus* in the shape and extent

of the processus and the distinct lateral parietal process forming part of the structure.

Contribution of the parietal to the processus trochlearis oticum is insignificant or, more typically, absent in most cryptodires. The large contribution made by the parietal in *Adocus*, about one-third of the total, is therefore of interest. Among other trionychoids, only the trionychids and carettochelyids have a similar parietal morphology. The kinosternids, *Staurotypus* and *Claudius*, are like *Dermatemys*, *Baptemys*, chelonioids, and chelydrids in having no parietal contribution at all. In the Kinosterninae and *Emarginachelys* there is minimal contribution of the parietal to the processus trochlearis oticum. The processus of *Nanhsiungchelys* remains unknown.

The opisthotic is complete in CCM 60-15 but only visible externally and through the fenestra postotica. In CM 3428 it is also visible through the cavum cranii but is not well preserved. The opisthotic of *Adocus* is similar to that in *Dermatemys*. In *Dermatemys* and *Baptemys*, the processus interfenestralis is visible ventrally and laterally to a greater extent than in *Adocus* and Trionychia due to the less extensive ossification of the pterygoid in this area. The fenestra postotica in *Adocus* is open laterally rather than closed as in nearly all other trionychoids, except members of the Trionychidae. *Baptemys* is another possible exception; in the only specimen preserving this area, YPM 3754, the fenestra is nearly closed on the right side but this may be the result of damage.

Despite the fact that the foramen nervi trigemini is preserved on both sides of both *Adocus* specimens, the contacts of the elements in the ethmoid region in *Adocus* are not clear. The region is similar in *Adocus*, *Baptemys*, and *Dermatemys*, with the prootic forming the posterodorsal margin, the parietal forming the anterodorsal margin, and the pterygoid forming the ventral margin of the foramen nervi trigemini. In *Adocus* the epipterygoid seems to form the anteroventral margin, whereas in *Dermatemys* (BMNH 1911.1.28.1, 2 skulls; UF 29168) the parietal sends a posteroventral process between the foramen and the epipterygoid. This process appears to be present on the left side of *Baptemys*, YPM 3754, but is not determinable

in other specimens. Some kinosternids examined also have this process (*Staurotypus*, BMNH 1879.1.7.5; *Claudius angustatus*, UF 57909, AUMP 231; and *Kinosternon scorpiodes*, UF 583917) but others do not (*Kinosternon herrerai*, UF 57916; *K. integrum*, UF 83-51-95).

The occipital bones are preserved in both *Adocus* specimens and are similar to those of *Dermatemys* and *Baptemys*. The crista supraoccipitalis lacks the horizontal portion seen in Trionychia. The basioccipital of *Adocus* differs from those of *Dermatemys*, *Baptemys*, and other trionychoids in having a basis tuberculi basalis. In all other trionychoids this structure is absent.

CANALIS CAROTICUS INTERNUS AND RELATED STRUCTURES: The systematic utility of the basicranial arteries in phylogenetic work with *Dermatemys* and *Baptemys* was expounded by McDowell (1961) who argued that the loss or reduction of the stapedial artery in *Dermatemys*, *Baptemys*, and kinosternids suggested common ancestry. Albrecht (1967, 1976) elaborated this idea and presented more detailed work on a broader array of taxa, including trionychids. Gaffney (1975) interpreted this information in the following way: the primitive chelonian arterial pattern is that seen in pleurodires and testudinoids. In these taxa the stapedial artery is large and well developed relative to the more medial branches of the carotid, the cerebral carotid, and the palatine artery. A derived condition exists within the Trionychoidea: the stapedial artery is reduced or absent and either the cerebral carotid artery (= the pseudopalatine of Albrecht) or the palatine artery is distinctly enlarged. The Kinosternidae and Dermatemydidae have this last pattern (fig. 8B, C) and it is a character supporting the monophyletic nature of this group.

In *Adocus* the foramen stapedio-temporale is large and well developed as in most turtles and is formed by the prootic and quadrate. Kinosternids usually have a minute but distinct foramen stapedio-temporale reflecting the presence of a minute stapedial artery (Albrecht, 1967: 92). But *Baptemys* and *Dermatemys*, as noted by McDowell (1961: 36), lack a foramen stapedio-temporale (as well as the canalis stapedio-temporalis) and a stapedial artery. Although *Baptemys* is extinct,
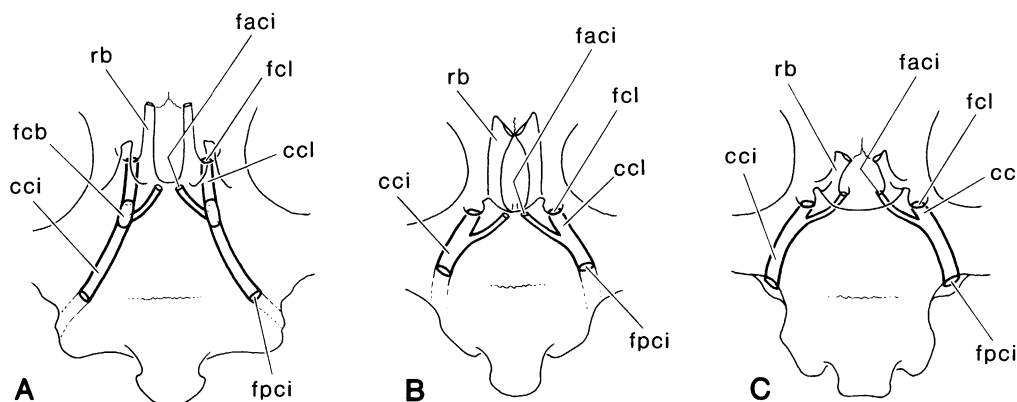
Fig. 8.   The internal carotid canals and foramina of selected trionychoid turtles. (**A**) *Adocus* sp. (based on CM 3428), (**B**) *Baptemys* sp. (based on DMNH 511), (**C**) *Dermatemys mawii* (based on USNM 66666). Abbreviations are as follows: cci, canalis caroticus internus; ccl, canalis caroticus lateralis; faci, foramen anterius canalis carotici interni; fcb, foramen caroticum basisphenoidale (= foramen caroticopharyngeale); fcl, foramen caroticum laterale; fpci, foramen posterius canalis carotici interni; rb, trabecula of basisphenoid.

we are confident that the stapedial artery was absent, but the condition of this artery cannot be so easily hypothesized for *Adocus*. A large foramen stapedio-temporale also occurs in trionychids which, nonetheless, have a reduced stapedial artery (Albrecht, 1967) so that the presence of a large foramen stapedio-temporale is consistent with both a large and a small stapedial artery.

The foramen posterius canalis carotici interni in *Adocus, Baptemys,* and *Dermatemys* is quite large, much larger than in plesiochelyids, for example. This may indicate that even in *Adocus,* the canalis caroticus internus bears the main arterial supply (as opposed to the stapedial artery). The foramen posterius canalis carotici interni in *Adocus,* as in *Baptemys* and members of the Trionychia, is formed entirely by the pterygoid (figs. 5, 6) and is slightly anterior to the posterior margin of the pterygoids. In contrast, *Dermatemys* and kinosternids have the foramen posterius canalis carotici interni at the posterior limits of the pterygoid (fig. 7). The position in *Baptemys* is not a particularly significant character contradiction, because the relative position of the foramen with regard to other structures appears to be the same in *Adocus, Baptemys,* and *Dermatemys.* The latter genus is characterized by less ossification in the fenestra postotica, resulting in the apparent difference in foramen position.

The canalis caroticus internus extends anteriorly within the pterygoid bone. In all the genera being considered here, as well as in most turtles, the prootic forms a portion of the roof of the canalis. In *Adocus* the foramen caroticum basisphenoidale lies in the floor of the canalis caroticus internus in the suture between basisphenoid and pterygoid, near the anterior end of the basisphenoid (fig. 5). This foramen has been enlarged somewhat during preparation, but some of the original edge is visible on the left side of CCM 60-15 and the left side of CM 3428. The foramen diameter was about ⅓ or ¼ the diameter of the canalis caroticus internus. The foramen occurs at the point of entry into the canalis of the foramen pro ramo and can be seen on the lateral margin of the canalis. A groove confluent with the foramen pro ramo nervi vidiani extends ventrally through the foramen onto the ventral surface of the skull, suggesting that this foramen in the floor of the canalis caroticus internus contained a branch of the palatine or vidian nerve. It is possible that this foramen is the foramen carotico-pharyngeale described by Albrecht (1967) in *Chrysemys* and *Sternotherus.* The foramen carotico-pharyngeale, however, is minute and formed only by the pterygoid. We have found what appears to be this foramen in *Baptemys, Dermatemys, Claudius, Anosteira* (or *Pseudanosteira*), and *Staurotypus,* as well as in many

other turtles. Albrecht described branches of the vidian nerve and the arteria carotico-pharyngealis as traversing the foramen (and canalis) carotico-pharyngeale.

With some misgivings, we tentatively homologize the foramen caroticum basisphenoidale in *Adocus* with the foramen carotico-pharyngeale described by Albrecht (1967). This is primarily because they both extend ventrally from the canalis caroticus internus to the ventral surface of the skull in the vicinity of the foramen pro ramo nervi vidiani. The differences are that the structure in *Adocus* is larger (possibly a primitive condition) and on the pterygoid-basisphenoid suture rather than within the pterygoid. The latter feature, however, is due to the fact that the canalis caroticus internus at the position in *Adocus* is formed in the basisphenoid-pterygoid suture. Plesiochelyids (Gaffney, 1976) also seem to have a foramen in this position; most of the specimens do have one, but at present it is difficult to determine whether or not this is the result of breakage in the thin floor of the canalis caroticus internus. The foramen posterius canalis carotici interni of baenids would appear to be at the position of the foramen caroticum basisphenoidale in *Adocus* because the foramen pro ramo nervi vidiani in baenids exits from the skull at the foramen posterius canalis carotici interni. Therefore, there is some basis for arguing that the presence of this foramen in *Adocus* is primitive for eucryptodires.

Just anterior to the foramen caroticum basisphenoidale in *Adocus,* the canalis caroticus internus divides to form the canalis caroticus lateralis. The more medial canal is still termed the canalis caroticus internus (fig. 8). This point of division is apparently the same in *Baptemys, Dermatemys,* and kinosternids.

The canalis caroticus lateralis in *Adocus* is about the same diameter as the more medial branch of the canalis caroticus internus that enters the basisphenoid (fig. 8A). This appears to be the primitive condition for turtles. It is present in pleurodires, chelydrids, primitive chelonioids, and testudinoids. In other trionychoids, the canalis caroticus lateralis may be distinctly smaller (in carettochelyids and trionychids) or distinctly larger (in *Dermatemys,* Kinosternidae) than the medial branch of the canalis caroticus internus. The presence of an enlarged canalis caroticus lateralis or an enlarged foramen anterior canalis carotici interni can both be considered derived.

Dermatemys and kinosternids have a canalis caroticus lateralis (and foramen caroticum laterale) that is at least twice the diameter of the canalis caroticus internus (fig. 8B, C). In *Baptemys* the canalis caroticus lateralis is visible only in part of the disarticulated basisphenoid in USNM 13437 and the foramen caroticum laterale is visible, although broken, only on the left side of DNHM 511. From the specimens, the size of the canalis caroticus lateralis and foramen caroticum laterale is at least as large as the foramen anterius canalis carotici interni and quite likely is distinctly larger, as in *Dermatemys* and kinosternids. In members of the Trionychia for which data are available, the foramen anterior canalis carotici interni is significantly larger than the foramen caroticum laterale.

In most turtles, the medial branch of the canalis caroticus internus goes through the basisphenoid and enters the cavum cranii at the foramen anterius canalis carotici interni. These foramina in *Adocus* are quite close together and posterior to the anterior edge of the dorsum sellae. In *Baptemys* and kinosternids, the foramina are also closer together, but are just under the anterior edge of the dorsum sellae. In *Dermatemys* the foramina are farther apart and slightly anterior to the anterior edge of the dorsum sellae. The dorsum sellae is low in all of these taxa and there is no sign of the condition seen in chelonioids in which a distinct area of the bone is developed between the dorsum sellae and the foramina anterius canalis carotici interni.

The rostrum basisphenoidale and sella turcica are similar in the taxa being dealt with here and comparable to that seen in Testudinoidea. *Adocus* has a short rostrum with each trabeculum having a sharp ridge (fig. 8A), whereas in *Baptemys* and kinosternids the trabeculae are long (fig. 8B), fully forming the sella turcica but with no ridges. The sella turcica of *Dermatemys,* however, has short trabeculae (fig. 8C). In general, the structure of the sella turcica, dorsum sellae, and foramen anterius canalis carotici interni agrees with the presumed primitive condition of eucryptodires.

The pterygoid of *Adocus* has a well-developed processus pterygoideus externus (fig. 5). It extends laterally well beyond the palate. The same condition occurs in *Baptemys, Dermatemys,* and *Emarginachelys.* In all other trionychoids this process is weakly developed or absent. The presence of this structure in most testudinoids, primitive chelonioids, chelydrids, plesiochelyids, and many other higher taxa suggests that its occurrence among trionychoids is plesiomorphic. The absence of this structure in certain trionychoid genera is considered derived.

At this point it may be useful to comment on the braincase of *Emarginachelys* because there are some errors in the literature. Whetstone (1978) described the only known skull as a chelydrid. Based on cranial and postcranial synapomorphies, however, we consider it to be a trionychoid (see discussion of monophyly of the Kinosternoidae). Whetstone (1978: 552) figured a restored dorsal view of the braincase but further preparation and examination of this area makes some of his restoration unlikely. The entire region is not well preserved and much is broken, as stated by Whetstone. The right side of the braincase is better preserved than the left. The right braincase wall, sulcus cavernosus, processus clinoideus, and foramen nervi trigemini are not seriously damaged. On the left side, however, the braincase wall has been broken by dorsoventral compression, producing a flange running below the foramen nervi trigemini. This flange is pushed onto the processus clinoideus of the left side. The actual position of the foramen cavernosum is not preserved on either side, contrary to Whetstone's statement (1978: 551) that its position is anterior and very unusual. His interpretation is based on the crushing and distortion of the left braincase wall and the postmortem contact of the processus clinoideus and the braincase wall. The dorsal surfaces of the basioccipital and basisphenoid are well preserved on the midline; and there is no evidence of a basis tuberculi basalis, as indicated in figure 12 of Whetstone (1978).

The dorsum sellae and sella turcica are preserved as described by Whetstone and there do appear to be trabecular fragments some distance anterior to the sella. There is no indication of the lateral margins of the sella turcica, and no sign of a small foramen caroticum laterale on either side of the rostrum basisphenoidale anteriorly as indicated by Whetstone (1978: fig. 12). The foramen caroticum laterale cannot be seen, probably as a result of postmortem damage, but the general relations of the braincase sidewall and processus clinoideus on the better preserved right side indicate enough room for a large foramen caroticum laterale opening ventrolaterally (and not visible dorsally) as in *Staurotypus,* or more posteriorly, as in *Baptemys.* Unfortunately, the sole specimen of *Emarginachelys* does not allow definite determination of the relative sizes of the canalis caroticus lateralis and canalis carotici interni, however, a large canalis caroticus lateralis is probable.

LOWER JAW

The lower jaws of *Adocus, Baptemys,* and *Dermatemys* are characterized by a distinctive "pocket" (here termed the dentary pocket) in the posterior portion of the dentary (figs. 9, 10). It is bounded by an anterolaterally directed ridge anteriorly and by the processus coronoideus posteriorly. The maxillary tooth fits into this pocket and together they form a distinctive triturating surface morphology. In *Baptemys* and *Dermatemys* the ridge forming the anterior margin of the dentary pocket forms a cusp where it meets the labial ridge of the dentary. In *Adocus* this point is marked only by a small cusp. The dentary pocket of *Dermatemys* has a low ridge running down its midline that fits into the trough dividing the maxillary ridges. The dentary triturating surface of *Dermatemys* is expanded anteriorly, matching the maxillary expansion, and the distinctive symphyseal pocket in *Dermatemys* is entirely absent in *Adocus* and *Baptemys. Dermatemys* has crenulations and cuspules on both the mandibular and maxillary triturating surfaces that are lacking in *Adocus* and appear only on the maxillary tooth of *Baptemys.*

Adocus and *Baptemys* have a relatively high and well-developed coronoid process (figs. 9A, 10A), whereas *Dermatemys* has a very low one (fig. 10B), a condition probably autapomorphic for *Dermatemys.* However, the
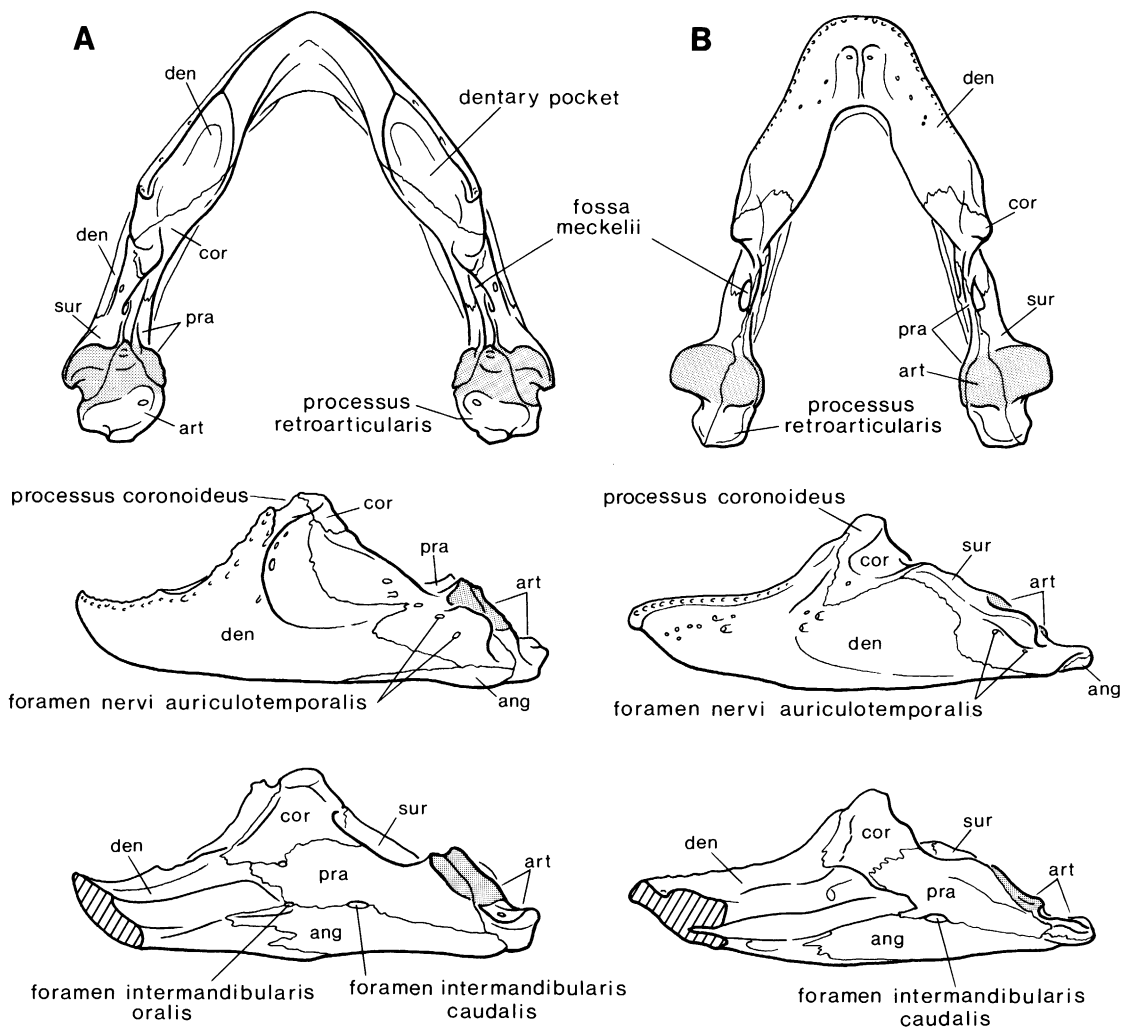
Fig. 9. Lower jaws of (A) *Adocus* sp. (CCM 60-15) and (B) *Amyda cartilaginea* (RH 129) in dorsal (top), lateral (middle), and medial (bottom) views. The area articularis mandibularis is shaded; the section through the symphysis (medial view) is hatched. Abbreviations are as follows: ang, angular; art, articular; cor, coronoid; den, dentary; pra, prearticular; sur, surangular.

coronoid of *Adocus* reaches its greatest height in the middle of the lower jaw. This is unlike the condition in *Baptemys* and *Dermatemys* in which the processus coronoideus is more posteriorly located. The condition in *Adocus* is quite similar to that in trionychids (fig. 9B) and carettochelyids (fig. 174 in Gaffney, 1979). A tall processus coronoideus, located at the middle of the lower jaw, does not occur in dermatemydids, kinosternids, chelydrids, chelonioids, or testudinoids.

Posterior to the processus coronoideus is

the fossa meckelii which is particularly small in *Baptemys,* in contrast to the more normal proportions in *Adocus* and *Dermatemys.* The whole postcoronoid portion of the jaw in *Baptemys* is shortened relative to that in *Adocus* and *Dermatemys,* the fossa meckelii is small, and the area articularis mandibularis tilts posteriorly so that it faces more posteriorly than vertically.

A retroarticular process that is about half the length of the area articularis mandibularis extends posteriorly from the lower jaw in both
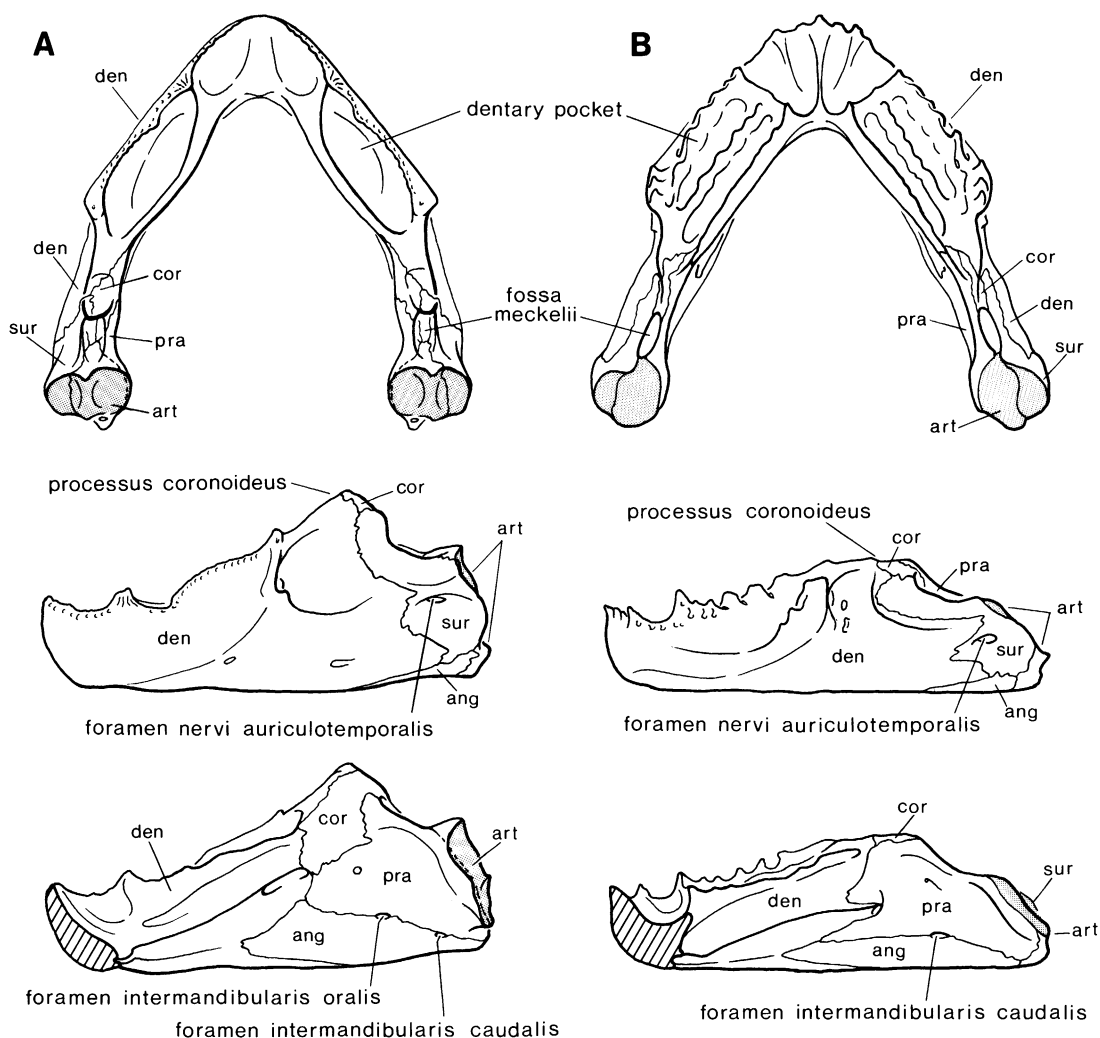
Fig. 10.   Lower jaws of (**A**) *Baptemys* sp. (YPM 3754) and (**B**) *Dermatemys mawii* (USNM 66669) in dorsal (top), lateral (middle), and medial (bottom) views. The area articularis mandibularis is shaded; the section through the symphysis (medial view) is hatched. See figure 9 for abbreviations.

Adocus specimens. It is composed entirely of the articular (fig. 9A). In two specimens of *Baptemys* (DMNH 511 and YPM 3754), the articular extends ventrally from the area articularis mandibularis but does not form a retroarticular process. The same is true of lower jaws of *Dermatemys*. Among other turtles, only members of the Trionychia (fig. 9B) and *Eubaena* (Gaffney, 1982) have retroarticular processes as well developed as those of *Adocus*.

The area articularis mandibularis of *Adocus* has a large contribution by the surangular.

This is typical for members of the Trionychia in which the surangular comprises more than half of this area (Meylan, 1987). In most other turtles, except for some chelonioids, the surangular makes up little or none of the area articularis mandibularis.

In both *Adocus* specimens the foramen nervi auriculotemporalis is divided up into several small foramina. In *Dermatemys* and *Baptemys,* the foramen is a single large lateral opening. However, this morphology is highly variable within higher taxa [both morphologies are present in some species of the Tri-

onychidae (Meylan, 1987)] and may not be of systematic value.

The presence of the maxillary tooth/dentary pocket in *Adocus, Baptemys, Dermatemys*, and also *Emarginachelys* is significant because we hypothesize this structure as synapomorphic for all Trionychoidea, even though it is absent in Trionychia and Kinosternidae. Based on other characters (see Gaffney and Meylan, 1988, and fig. 22), we propose *Adocus* as the sister taxon to the Trionychia, and *Baptemys* plus *Dermatemys* (the Dermatemydidae) as the sister-group to the Kinosternidae. The maxillary tooth/dentary pocket would then have to be derived independently in both groups or be a common feature. Because of the very close similarity between the triturating surfaces in *Adocus* and *Baptemys*, we prefer the interpretation of this structure as a common feature of all trionychoids that is lost independently in Trionychia and Kinosternidae.

CARAPACE

The shell of the Carter County Museum *Adocus* specimen (CCM 60-15) is nearly complete (fig. 11). The carapace lacks only the seventh and eighth costal bones (the term pleural is reserved for scales), the suprapygal(s), and the peripherals (the term marginal is reserved for scales) posterior to number 7 on the right and posterior to number 9 on the left. The neural series is complete through neural 6. The plastron is missing only the most posterolateral portions of the right xiphiplastron.

CARAPACE FORM: The overall shape of the carapace appears to be relatively undistorted. It is fractured across most of its surface but is not badly distorted although somewhat flattened anteriorly. It forms a low, smooth arc in cross section and lacks midline or lateral keels. If the carapace were complete, it would undoubtedly be considerably longer than wide. The entire surface is finely sculptured with a very regular arrangement of minute tubercles lying close enough together that the pattern could also be described as rows of small depressions.

The carapace of CCM 60-15 is representative of a primitive eucryptodiran in its basic structure. Although it shows several derived

features that are important in determining the relationships of *Adocus*, its general shape is unmodified. It is low and wide and without keels. Among trionychoids, most carettochelyids, *Zangerlia*, and *Baptemys* have a mid-dorsal keel that is best developed posteriorly. In anosteirine carettochelyids, this midline crest is developed into at least one dorsal spine. *Baptemys tricarinata*, all *Hoplochelys*, *Staurotypus*, *Xenochelys*, *Agomphus alabamensis*, and some kinosternines have three well-developed keels. Other members of the genera *Baptemys* (e.g., *B. wyomingensis*, AMNH 5967) and *Kinosternon* retain some evidence of all three keels but these may be lost with age. It is possible that tricarination has appeared once in the Kinosternoidae as proposed by Hutchison and Bramble (1981) and has been lost repeatedly or that it has appeared on several occasions independently.

The sculpture pattern of the CCM 60-15 is typical for the genus. All *Adocus*—as well as *Basilemys, Zangerlia, Nanhsiungchelys, Peltochelys*, carettochelyids, and trionychids—have some type of wave-form or punctate sculpturing. In *Basilemys* and *Zangerlia*, it is so well developed that it is best described as "pock-mark" sculpturing (Mlynarski, 1976). In the Trionychinae, wave-form, rather than punctate, sculpture predominates.

NUCHAL: The nuchal bone is wider than long and is approximately pentagonal. It appears to have had a nuchal scale but the anterior margin of this element is badly broken and the existence of this structure is uncertain. Costiform processes do not appear to be present and ventral processes of the nuchal are absent.

The presence of a cervical scale on the nuchal bone of turtles is the primitive condition. It is present in all trionychoids that retain their scales except for the genus *Shachemys* Kuznetsov (1976) which was considered by Nessov (1977) to be closely related to *Adocus*. Paired ventral processes of the nuchal occur only within the Trionychoidea. They are well known in the Carettochelyidae and also occur in the extinct genus *Peltochelys*.

NEURALS: Neural bones 1 through 7 form a continuous row in CCM 60-15 (fig. 11A). Neural 1 is hexagonal with the short sides facing posteriorly and contacting the second
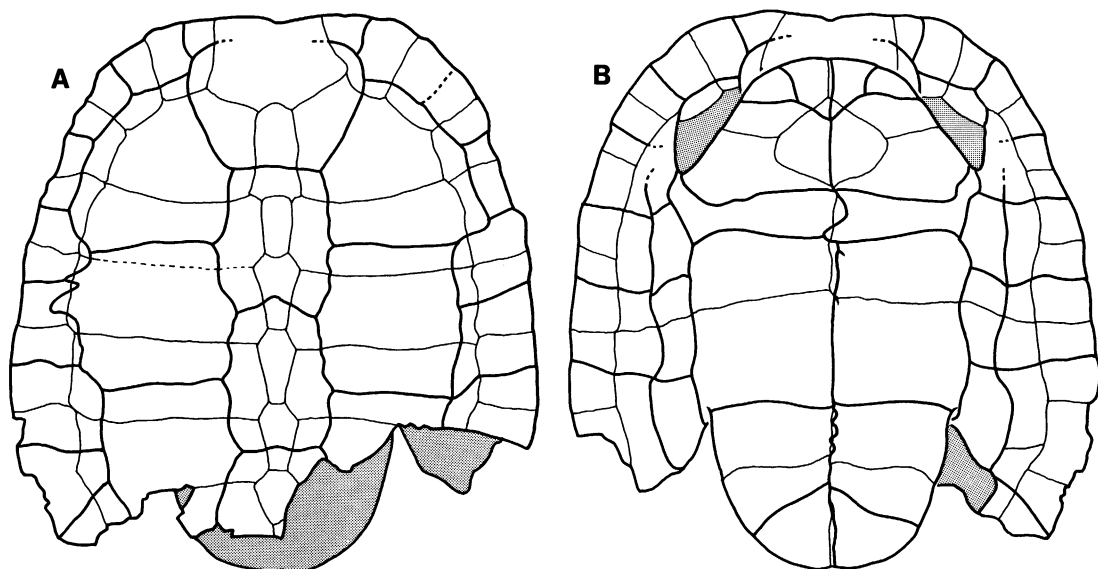
Fig. 11. Shell of *Adocus* sp. (CCM 60-15) in (**A**) dorsal and (**B**) ventral views. Heavy lines indicate scute sulci; light lines indicate bone sutures.

costal bones. Neural 2 is small and four sided; it contacts only neurals 1 and 3 and the second costals. Neurals 3 through 5 are hexagonal with short sides anterior (contacting the previous pair of costal bones). Neural 6 is similar but has a diagonal suture with the seventh neural. The shape of the seventh neural and the presence of additional neurals in this specimen remain unknown.

The neural formula found in the CCM *Adocus* (6 4 6 6 6 6 ?) is uncommon among eucryptodires. It occurs in every *Adocus* specimen for which a neural series is known. This neural formula also occurs in the trionychoid genera *Basilemys* (Langston, 1956) and *Zangerlia* (Mlynarski, 1972), a series of London Clay cheloniids (Owen and Bell, 1849), and a Jurassic pleurodire, *Platychelys* (Bräm, 1965). In the trionychoids *Basilemys* and *Zangerlia* the neural series is not divided posteriorly by costal bones meeting on the midline, as it is in *Adocus*.

The most common neural formula for casichelydians is 4 6 6 6 6 6. A survey of neural patterns in Hay (1908a) and Mlynarski (1976) reveals this pattern in Pleurodires (*Pelusios, Phrynops, Podocnemis, Stereogenys, Taphrosphys*), pleurosternids (*Glyptops*), baenids (*Baena, Boremys, Chisternon, Neurankylus, Plesiobaena*), chelydrids (*Chelydropsis*), nu-

merous chelonioids (*Allopleuron, Argillochelys, Caretta, Chelonia, Desmatochelys, Erquelinnesia, Eurysternum, Glarichelys, Lophochelys, Osteopygis, Porthochelys, Thinochelys,* and *Toxochelys*), plesiochelyids (*Plesiochelys, Eurysternum,* and *Thalassemys*), some trionychoids (*Dermatemys, Baptemys, Agomphus,* and *Anosteira*), and many testudinoids (*Chinemys, Cuora, Emys, Echmatemys, Geomyda, Kachuga, Mauremys, Ocadia, Pseudemys, Sakya, Stylemys,* and *Terrapene*). This neural formula has also been shown for *Proganochelys* based on the Jaekel (1918) reconstruction, but recent work by Gaffney (in prep.) can only confirm that neurals 4 to 7 had contact to anterior costal bones (short sides anterior).

The common occurrence of a 4 6 6 6 6 6 6 neural formula in all possible outgroups to the Trionychoidea suggests that such a neural formula is primitive for trionychoids and in fact may be primitive for all turtles. Alteration of this condition has occurred numerous times. At least five independent occurrences can be hypothesized in the Trionychoidea. However, these modifications have usually resulted in differing and unique new neural patterns, and, as in the case of a 6 4 6 6 6 6 formula in *Adocus, Basilemys,* and *Zangerlia,* are evidence of shared common ancestry.
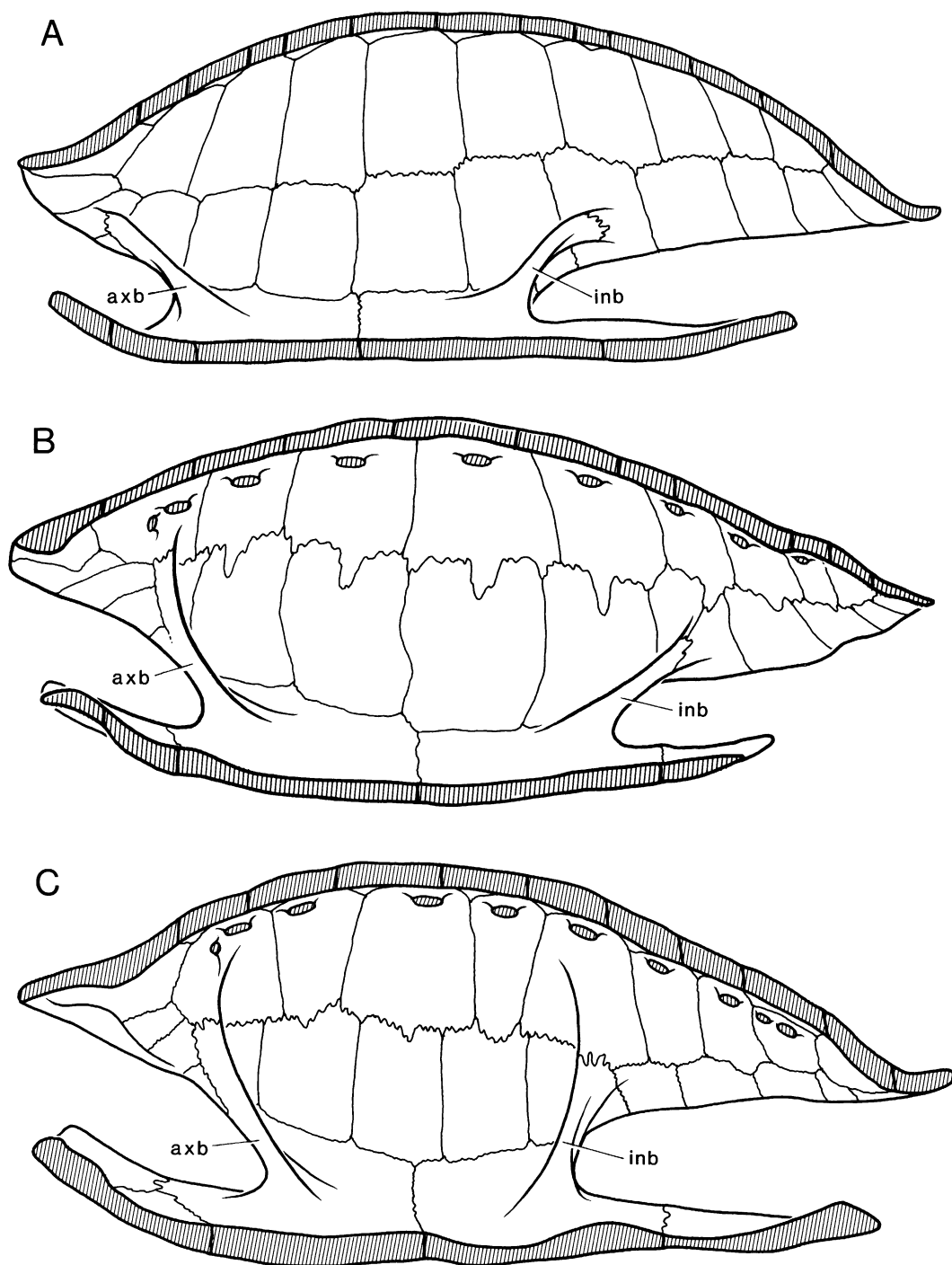
A

axb

inb

B

axb

inb

C

axb

inb

Fig. 12.   Diagrammatic medial cross sections of the shells of selected chelomacryptodiran turtles. (A) *Adocus* sp. (a composite reconstruction based on AMNH 1204 for external shell form and CCM 60-15, USNM 8613, and AMNH 22600 for internal contacts), (B) *Dermatemys mawii*, and (C) *Pseudemys floridana*. The ribheads have not been included in *Adocus*.

Among trionychoids the primitive neural configuration is widespread. It occurs in *Baptemys, Dermatemys, Emarginachelys, Agomphus, Hoplochelys, Kizylkumemys, Anosteira,* some *Claudius,* some *Staurotypus,* and some *Carettochelys.* Deviation from this primitive pattern among trionychoids includes the development of numerous posterior-facing six-sided neurals in trionychids and kinosternids. It also includes the development of at least one eight-sided neural, probably number 2, in *Nanhsiungchelys,* and sometimes number 2, but almost always number 7, in *Staurotypus. Peltochelys* has a unique 4 6 4-4 6 6 formula. The advanced anosteirine, *Pseudanosteira,* has a 6 4-4 8 4 6 6 formula and among specimens of *Carettochelys insculpta* there are a variety of neural arrangements including several in which numerous anterior costal bones meet on the midline.

Primitively, the neural series in turtles is complete between the nuchal and suprapygals. *Adocus* is like several other trionychoids in having posterior costal bones that meet on the midline, interrupting the neural series. In some species of *Adocus* there are no neurals in evidence posterior to number 6 (*A. bossi, A. hesperius*) or posterior to number 7 (KU unnumbered). In others there is what is usually identified as an isolated neural posteriorly (*A. kirtlandius, A. punctatus*). Costal bones meet on the midline posteriorly in all carettochelyids, all trionychids, *Dermatemys,* and all kinosternids except most *Staurotypus triporcatus* (UF uncat., JI 1053, 83-JI-201). Based on new material from the New Jersey State Musem (NJSM 13753; fig. 13), *Agomphus* from the Cretaceous of New Jersey appears to have posterior costal bones completely divided by neurals (contra Hay, 1908a; Mlynarski, 1976). *Basilemys nobilis* Hay has been reconstructed with this condition, but the critical area is represented by dashed lines, suggesting that it is hypothetical. *Basilemys* is therefore considered to possess the primitive condition as indicated by the best preserved specimen, *B. sinuosa* Riggs (FMNH P12008).

COSTALS: Costal bones 1 through 4 are preserved on both sides of CCM 60-15. Number 5 is complete on the left but only the proximal part is present on the right. Proximal and
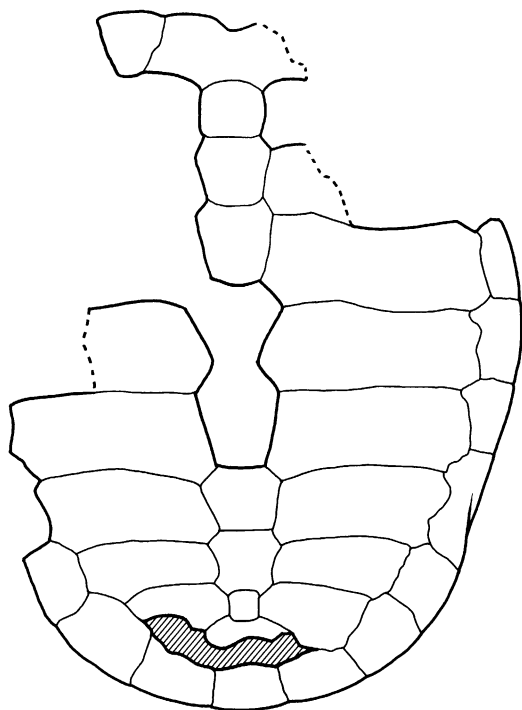

Fig. 13. Partial shell of *Agomphus* (NJSM 13753). Hatched area indicates missing bones; dashed lines mark the limits of broken elements. Scute sulci are not visible on this specimen but scutes are present in *Agomphus.*

distal parts of costal 6 are present on the left. All preserved costal bones are subequal in length except the first which is nearly twice as long laterally as the others. Since the plastral buttresses do not reach the costal bones in *Adocus* (fig. 12A), there is no lateral morphology worthy of mention. As in all turtles the first costal receives thoracic ribs 1 and 2.

PERIPHERALS: The peripheral bones are well sutured to the costal bones. Posteriorly, the series is incomplete, and those peripherals that are preserved are lacking their distal margins. In the majority of turtles, peripheral bones are present and are sutured to the costals. This is the case in *Adocus* and most other trionychoids. Peripherals are absent in most members of the Trionychidae. Within this family, only the genus *Lissemys* retains them. In this taxon they are completely free of the costals (see Meylan, 1987, for a discussion of the homology of the peripheral bones of *Lissemys* to those of other turtles). Peripheral
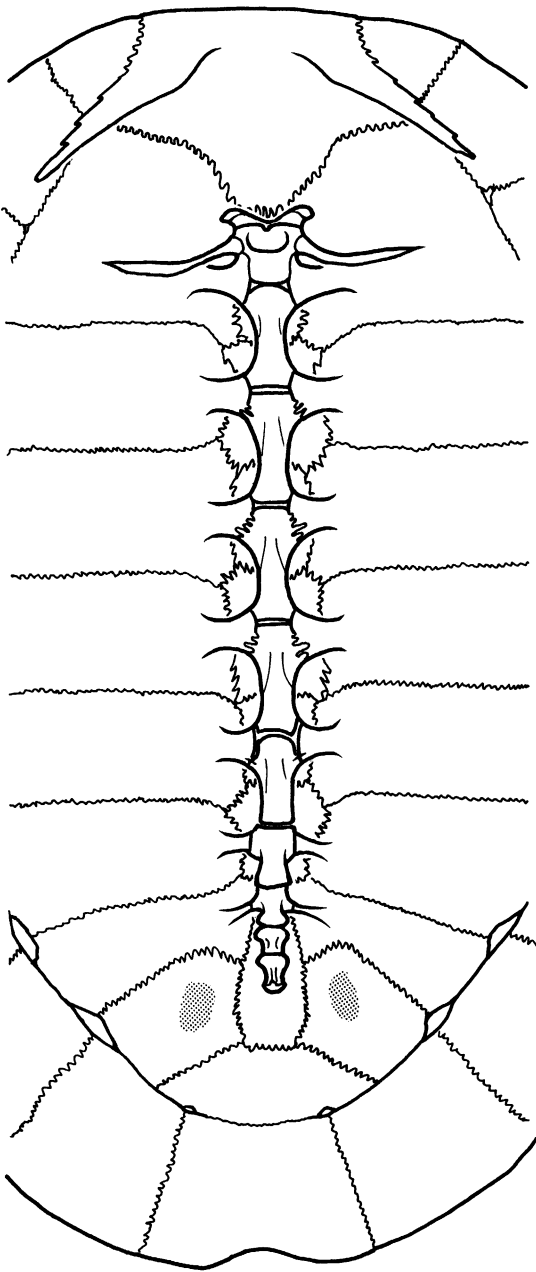
Fig. 14. Internal view of the carapace of *Staurotypus triporcatus* (83-JI-201) showing the free 9th and 10th thoracic vertebrae.

bones appear to be free of, or very weakly connected to, the costals in all carettochelyids. This is certain for the living genus *Carettochelys*. However, the first peripheral may be sutured in *Anosteira* from the Bridger For-

mation (AMNH 5983). The weakness or absence of costoperipheral sutures may be responsible for the frequent absence of peripheral bones from fossil carapaces of carettochelyid genera that almost certainly had them (Dollo, 1884; Hummel, 1929). Outside the Trionychoidea, absence of costoperipheral sutures in adults may occur in chelydrids and is common in chelonioids. Costoperipheral sutures are present in *Proganochelys,* pleurodires, pleurosternids, baenids, and *Meiolania* and thus seem likely to be primitive for the Eucryptodira.

The exact number of peripherals in the CCM *Adocus* specimen is not known. Other complete specimens representing this genus have the primitive number for casichelydians, 11 on each side. Portions of eight are preserved on the left side of CCM 60-15 and, as in other specimens of *Adocus,* number 8 is in contact with costal bone 5. Nothing suggests that peripherals 9, 10, and 11 were absent. However, certain other trionychoids do not retain the primitive number of 11 peripherals. All genera of the Kinosternidae (*Claudius, Kinosternon, Staurotypus,* and *Xenochelys*), the Carettochelyidae (*Allaeochelys, Anosteira, Carettochelys, Kizylumemys,* and *Pseudanosteira*), and the genus *Peltochelys* have 10 peripheral bones on each side. All trionychids except for the genus *Lissemys* lack peripherals altogether. *Lissemys* has a variable number but never more than nine on each side. The remaining trionychoids under consideration here have the primitive number, 11 peripheral bones per side (the condition in *Nanhsiungchelys* is unknown).

Other described specimens of *Adocus* (types of *A. beatus* and *A. lacer*) have the anterior peripheral bones very finely recurved (Hay, 1908a; White, 1972). The condition of this character is unknown in the Carter County Museum specimen due to the incomplete nature of the anterior peripherals.

SUPRAPYGALS: The number of suprapygals in the CCM *Adocus* is unknown. All figured specimens of *Adocus,* including *A. bossi, A. hesperius, A. kirtlandius,* and *A. punctatus* (= *beatus*), as well as all material of *Adocus* examined during this study, have at least one large suprapygal, and it is always in contact with the pygal. In some specimens, this ele-

ment is isolated anteriorly by the eighth costals meeting on the midline. But in others (including types of *A. punctatus* Marsh and *A. kirtlandius* Gilmore), a smaller midline element meets this large suprapygal. In the past this small midline element has been considered a neural. But based on its position relative to the site of articulation of the pelvic girdle to the shell, where the thoracic vertebrae posterior to number 10 are free of the shell, this element would not have had a neural arch fused to it. Lacking this definitive character of a neural, this element must be considered a suprapygal. Therefore we consider those *Adocus* with a small midline element in contact with a large suprapygal to have two suprapygals. A similar argument can be made for the same small element in *Dermatemys*.

Elsewhere among the Trionychoidea, a single suprapygal is present in carettochelyids and kinosternids. Two suprapygals are present in *Basilemys* (may have two or three) (Estes et al., 1969), *Zangerlia* (Mlynarski, 1972), *Peltochelys* (Meylan, 1988), *Agomphus* (fig. 13), *Baptemys* and *Hoplochelys* (Hay, 1908a), and rarely in *Dermatemys*. The absence of suprapygal elements is one of many unique features of the Trionychidae.

CARAPACIAL SCUTES: The carapace of the CCM *Adocus* is incomplete but there is no evidence that anything other than 5 vertebrals, 4 pairs of pleurals, and 12 pairs of marginal scutes were present. The anterior part of the nuchal bone is badly damaged and the presence of a cervical scute could not be determined. The first vertebral is very wide; its lateral edges do not touch the nuchal bone. The remaining vertebrals are quite narrow, about 1.5 times longer than wide. The first pleural scute is also the broadest, reaching well onto the peripheral bones. The second pleural makes some contact with the peripherals on the left side only, the remaining pleural scutes do not contact the peripheral bones.

The relationship of the peripheral bones to the marginal scutes changes along the length of the shell (see fig. 11A). Marginal scutes 1 through 4 lie entirely on the peripheral elements. The fifth marginals lie entirely on the fourth peripheral anteriorly, but posteriorly they extend toward the midline crossing the costoperipheral suture onto the second cos-

tal. On the right side the sulcus formed by marginal scutes 6 and 7, at their junction with pleural scutes 2 and 3, lies entirely on the costal bones. On the left side the common sulcus of marginals 5 and 6 and pleurals 1 and 2 is sinuous, crossing the costoperipheral suture a total of five times. Marginal scutes 7 through 9 have their medial sutures entirely restricted to the costals. It is likely that the most posterior marginal-pleural sulci remained entirely on the costal bones, as in other *Adocus* specimens (see pl. 1 in Wieland, 1904; fig. 296 in Hay, 1908a; and figs. 7, 9, and 11 in Gilmore, 1919).

The number of carapacial scutes on the CCM *Adocus* specimen is considered to be the primitive number as far as it can be discerned. Primitively, the five vertebral scutes of turtles were quite wide (Zangerl, 1969), and approximately equal in width. The narrowed vertebrals 2 through 5 in *Adocus* are derived relative to the primitive condition, but the level of generality of this derived condition is difficult to determine.

The unique relationship of the marginal scutes to the costoperipheral suture line in the CCM *Adocus* is consistent with the condition described in the type of Marsh's *Adocus punctatus* (Hay, 1908a) as well as *A. bossi*, *A. kirtlandius*, and *A. hesperius* (Gilmore, 1919). Although in some other turtles (*Pleurosternon*) the pleuromarginal sulcus is located on the costal bones, in no turtles known to us does this sulcus move so abruptly and completely from being entirely on the peripheral bones to entirely on the costals, as in the case of *Adocus*. This configuration of the marginal scutes appears to be an autapomorphy for the genus.

INTERNAL SHELL MORPHOLOGY: The interior surface of the carapace of CCM 60-15 is well preserved and has most of the thoracic vertebral centra in place. Ribheads of most costals are preserved and are narrow and moderately developed. Plastral buttresses apparently do not rise onto the first costal bone. No suture is visible for such a structure on the internal surface of this costal. Only parts of the fifth and sixth costal bones are preserved, and therefore, we cannot be sure if there were sutures on the visceral surfaces of these elements to receive an inguinal buttress. But based on other specimens of *Adocus*, es-

pecially AMNH 22600, USNM 8613, and USNM 8593, we have reconstructed the shell with both axillary and inguinal buttresses failing to reach the costal bones (fig. 12A).

Cope's name, *Adocus,* meaning "without rafters," refers to the extreme weakness of the ribheads in the type species *A. beatus.* The ribheads in CCM 60-15 are very well preserved and are moderately developed. There is a possibility that the condition of the ribheads in the type of *A. beatus* is due to postdepositional wear. Moderately to weakly developed ribheads which are not firmly sutured to the adjacent vertebral centra seem to be the common condition for eucryptodires. Although the ribheads of *Adocus* may be slightly reduced relative to those of most trionychoids, a more remarkable condition is found in the Trionychidae and Carettochelyidae (Meylan, 1987). In members of these two families, the ribheads are greatly enlarged and strongly sutured to the vertebral centra.

Description of the condition of the 10th body vertebra in *Adocus* cannot be based on CCM 60-15. This portion of the carapace is missing. In his redescription of *Adocus punctatus,* Wieland (1904) marked a location on his Plate 1 where the "rib of tenth dorsal vertebra unites suturely with eighth pleural [= costal], *or else* point of iliac support." His commitment to a complete transverse process on the 10th body vertebra seems equivocal. However, Baur (1891a) stated that transverse processes of the 10th body vertebra do reach the eighth costal. The members of the family Kinosternidae are unique among turtles in having both the 9th and 10th thoracic ribs failing to reach the carapace (Meylan, 1987: fig. 14).

The first body vertebra of the CCM *Adocus* is procoelous with a wide cotyle (about three times wider than tall). The articular areas of the prezygapophyses are restricted to their dorsal surface. They are wide and approach each other medially where they are divided by a large U-shaped emargination of the neural arch. Posterior to this emargination is a broad dorsal neural process which appears to be provided with sutures for firm anchorage to the overlying carapacial element (probably the first neural). The first rib is slightly separated from the first vertebra on the right side, but in life it would have sutured to the

centrum across a broad surface just posterior to the cotyle. The first rib becomes quite narrow laterally. It appears to have articulated with the rib of the second vertebra on the first costal bone.

PLASTRON

PLASTRAL BONES: The plastron of CCM 60-15 is broad, well ossified, and akinetic (fig. 11B). Its finely sculptured appearance is due to numerous closely spaced tubercles. The bridges are quite long (almost exactly one-half total plastron length), and the anal notch is absent. The plastron consists of the typical nine elements with the standard contacts found in nearly all eucryptodires (mesoplastra are absent). The epiplastra share a long common suture on the midline. They contact the entoplastron posteromedially and the hyoplastra posteriorly. The entoplastron is large and lies between the paired epiplastra and paired hyoplastra. The hyoplastra extend posteriorly to meet the hypoplastra. Laterally they contact peripheral bones 2, 3, 4, and 5. The hyo-hypoplastral suture lines up laterally with the suture between the fifth and sixth peripherals. The hypoplastra extend posteriorly to meet the paired xiphiplastra. Laterally the hypoplastra contact peripherals 6, 7, and 8. The hyoplastra and hypoplastra appear to have been well sutured to the carapace. Axillary buttresses extend anteriorly, nearly to the level of the anterior end of the entoplastron. Inguinal buttresses extend posteriorly beyond the level of the hypo-xiphiplastral suture. Neither axillary nor inguinal buttresses are markedly produced dorsally. It is unlikely that they reached dorsally to contact the interior surface of the costal bones (see descriptions of costals above and Hay, 1908a: 238).

The xiphiplastra have ridges that lie across the center of their dorsal surface anteromedially. These would have contacted the pectinial processes of the pubic bones. The internal surface of the anterior plastral lobe also shows some relief. The epiplastra are quite thickened laterally, as is the central portion of the entoplastron. A median ridge appears on the midline of the entoplastron with depressions lateral to it on either side. These depressions are probably the insertion site for

the acromial ligament which fixes the acromial process of the scapula to the plastron.

The plastra of nearly all other trionychoids consist of the same nine elements found in *Adocus*. The general shapes and contacts of the bones of the *Adocus* plastron are primitive for turtles and nearly uniform among trionychoids. Only in members of the family Trionychidae are the epiplastra reduced to an I- or J-shaped deep dermal element which may or may not be covered by a superficial dermal callosity. Neither the callosity nor the deeper element in trionychids is sutured to any other elements. The epiplastra of the CCM *Adocus*, other examples of the genus, and other trionychoids in general are not large. Those of *Emarginachelys, Claudius,* and kinosternines are much longer than those of other trionychoids. In *Emarginachelys* and *Claudius*, these elements extend laterally to the entoplastron, nearly to the bridge. In kinosternines the entoplastron is absent and the epiplastra make up the entire anterior plastral lobe.

The epiplastra of *Adocus* and most trionychoids are not thickened or elaborated on the dorsal surface. Only *Basilemys* and *Zangerlia* have thickened epiplastra analogous to the condition in testudinids.

The entoplastron in the majority of trionychoids is similar in shape to that of *Adocus*. However, in the Trionychidae it is so different that Williams and McDowell (1952) questioned the homology of this unpaired element in the anterior lobe of the trionychid plastron. Bramble and Carr (MS) have shown that it is in fact the entoplastron. In trionychids this element consists of a deep V-shaped or boomerang-shaped element with the free ends oriented posteriorly. In about half of the living trionychid species, a circular superficial dermal callosity is centered on the anteriormost part of the entoplastron. This callosity and the underlying element never suture to other plastral elements in living forms. However, in one fossil form the entoplastral callosity is tightly sutured to those of the hyoplastra (Hutchison, personal commun.).

The entoplastron of other trionychoids is a simpler single ossification that is usually round or oval. In *Emarginachelys* it is anteroposteriorly elongate. As discussed above, this element is absent in kinosternines. Where

present in other trionychoid taxa with anterior-lobe kinesis, carettochelyids, and staurotypines, it forms an elongate triangle with the apex anterior.

Hyo- and hypoplastra are quite constant in general shape and contacts among trionychoids. They always form the majority of the plastron although in many cases (trionychines, anosteirines, *Emarginachelys, Hoplochelys,* and kinosternids) these elements are somewhat reduced. They are sutured to one another in all trionychoids and in some trionychids they are fused. The hyo- and hypoplastra are usually firmly sutured to the carapace, as is the case in the CCM and all other *Adocus*, but in certain taxa these sutures are absent and only a ligamentous connection exists. This is the case for all trionychids and carettochelyids, as well as *Emarginachelys* and *Claudius*.

The plastral buttresses fail to reach the costal bones in all trionychoids (fig. 12A) except *Baptemys* (AMNH 1078, 1103, 5934) and *Dermatemys*. In these two genera the very long axillary buttresses barely reach the first costal (fig. 12B). The inguinal buttresses do not reach the costals in these genera (contra Hay, 1908a). Plastral buttresses extend from the hyo- and hypoplastra to the costal bones of pleurodires, baenids, and testudinoids (fig. 12C).

The xiphiplastra of other *Adocus* specimens and most trionychoids are like those of CCM 60-15, being broadly rounded posteriorly and lacking an anal notch. Only in *Dermatemys, Xenochelys,* and some *Kinosternon* is an anal notch present. Several genera including all of the Anosteirinae, some *Baptemys, Hoplochelys, Emarginachelys,* and the staurotypines have elongate xiphiplastra that are narrow and come to a point posteriorly. The ridges noted on the dorsal surface of the xiphiplastra in CCM 60-15 have also been noted in other *Adocus* including *A. agilis, A. lacer, A. syntheticus,* and *A. bossi,* as well as *Basilemys sinuosa* and *B. variolosa.* They are also present in nontrionychoids such as *Pleurosternon* and *Plesiochelys,* and are probably primitive for Cryptodira.

In all trionychoids except for the Trionychidae, all plastral elements are sutured in a normal pattern. Sutures are kinetic in certain of these taxa. In trionychids the anterior lobe

is greatly reduced, and the plastral elements do not normally suture on the midline (they do so regularly in *Plastomenus* and rarely in *Apalone* and members of the Cyclanorbinae). The epiplastra never suture to the entoplastron in trionychids. In only one highly derived trionychid does the entoplastron suture to the hyoplastra (Hutchison, in prep.). Contact between the hyo- and xiphiplastra is minimal in members of this family. The absence of sutures between so many of the elements of the plastron in trionychids allows longitudinal kinesis along the midline and transverse kinesis along the anterior edge of the hyoplastra (Bramble and Carr, MS).

Anterior-lobe kinesis also occurs along the anterior edge of the hyoplastra in living kinosternids (except *Claudius*). As is the case in trionychids, the hyoplastra are more or less immobile relative to the carapace, and the entoplastron (if present) and epiplastra move anterior to them. Anterior-plastral-lobe kinesis in the testudinoids (except *Pyxis*) and *Pelusios* occurs along the posterior edge of the hyoplastra. In *Claudius*, plastral kinesis occurs at the bridge (Bramble et al., 1984).

In most members of the genus *Kinosternon*, the posterior plastral lobe is also kinetic. In these forms mobility occurs along a transverse suture between the hypo- and xiphiplastra.

Unlike the plastron of *Adocus*, the plastra of some trionychoid genera do not join the carapace by a strong bony suture. This is the condition in members of the Trionychia and in *Emarginachelys* (fide Whetstone, 1978) and *Claudius*.

PLASTRAL SCALES: CCM 60-15 has seven pairs of plastral scales (fig. 11B). Set number 1, the gulars, are restricted largely to the epiplastra but do extend across the anterior quarter of the entoplastron. Lateral to the gulars, set 2, the extragulars, are restricted entirely to the epiplastra. They are separated from each other by the gulars and from the entoplastron by contact of set 3, the humerals, and set 1, the gulars, on the epiplastra.

The humeral scales extend from the posterior half of the epiplastra across the entoplastron and onto the anterior third of the hyoplastra. Their medial contact is restricted entirely to the entoplastron and they exclude the set 4 scales, the pectorals, from that ele-

ment. Posteriorly and laterally, they contact only the pectorals; they do not contact any inframarginals.

The pectoral scales (set 4) are narrow. They are slightly wider medially than laterally and are restricted entirely to the hyoplastra. The right pectoral extends broadly across the midline onto the left hyoplastron. The left pectoral also overlaps the midline onto the right hyoplastron but to a lesser extent. Laterally each pectoral contacts the two anteriormost of four inframarginals and extends anteriorly into the axillary notch. The pectorals reach the entoplastron but do not overlap it.

The abdominals (set 5) are the largest of the plastral scales. They cover the posterior third of the hyoplastra and the anterior two-thirds of the hypoplastra, thus crossing the hyo-hypoplastral suture. Laterally they contact the second, third, and fourth inframarginals. They reach the inguinal notches posteriorly and therefore prevent contact of the femorals (set 6) and the inframarginals.

The femoral scales cover the posterior third of the hypoplastra and the anterior half of the xiphiplastra. They extend across the hypo-xiphiplastral suture. Anteriorly, they contact only the abdominals and posteriorly, they contact only the anals (set 7).

The anal scales, set 7, are restricted to the xiphiplastra. The femoro-anal sulcus makes about a 60° angle to the midline. The cast from which these descriptions are being made is not complete enough to allow a description of anal overlap onto the dorsal surface of the xiphiplastra; similarly, descriptions of the femoral, humeral, extragular, and gular scales on the dorsal surface of the plastron are lacking. The midline sulcus of the plastron, though not highly sinuous, does not follow the midline sutures very closely. The gular scales are offset to the left. Both pectorals extend onto the opposite hyoplastron, the right pectoral remarkably so. The interabdominal seam lies on the left hyoplastron but then crosses over to the right hypoplastron. Both interfemoral and interanal sulci remain close to the midline suture but undulate slightly over their entire length. Among trionychoids, *Agomphus*, *Basilemys*, and *Peltochelys* are like *Adocus* in having a sinuous midline sulcus. Outside of the Trionychoidea this unusual

feature is also present in some baenids and some *Compsemys.* It is, therefore, considered to be derived within the Trionychoidea.

All other specimens of *Adocus* for which the plastron is known have seven pairs of plastral scales, as do all known *Basilemys* and *Peltochelys. Mongolemys* has six pairs of plastral scales due to the absence of the extragulars (set 2). This genus was originally described as a dermatemydid (Khosatzky and Mlynarski, 1971) and has been used as a model for the ancestral condition of the plastron in the dermatemydid-kinosternid clade (Hutchison and Bramble, 1981). However, examination of a well-prepared skull of *Mongolemys* suggests to us that this genus is not a trionychoid but a testudinoid. Scale set 2 is also missing in *Nanhsiungchelys* but the posterior portion of the plastron is unknown; therefore a complete account of the plastral scales of this genus cannot be given.

The members of the Kinosternidae and *Dermatemys* have six pairs of plastral scales, but Hutchison and Bramble (1981) argued that these scales are not homologous to pairs 1, 3, 4, 5, 6, and 7 found in *Mongolemys.* They suggested that a new pair, intergulars (set 8), has been added to a condition seen in *Baptemys* (sister-group to *Dermatemys* based on shared absence of foramen stapedio-temporale) in which scale set 4, the pectorals, has apparently been lost. Following the model of Hutchison and Bramble (1981), scale sets 2 and 4 are apparently also absent from *Emarginachelys, Agomphus, Hoplochelys,* and the Kinosternidae. In *Hoplochelys,* the abdominals, scale set 5, do not meet on the midline, so only sets 1, 2, 3, 6, and 7 do meet. In the Kinosterninae a pair of scales analogous, but not homologous, to the intergulars of *Dermatemys* has been added and scale set 3 has been divided by a hinge-line to give a total of six pairs of plastral scales. The staurotypines, *Staurotypus* and *Claudius,* are the trionychoids with the fewest scales on the plastron. They have only four pairs, pairs 1, 3, and 5 being completely absent.

In addition to reduction in number, some trionychoids lose plastral scales altogether. This is the case in the Trionychidae and Carettochelyidae. Scale set 1, the gulars, is present in all scaled trionychoids. As in *Adocus*

they are largely confined to the epiplastra and barely overlap onto the entoplastron in *Basilemys, Nanhsiungchelys, Peltochelys,* and *Xenochelys.* One-half or more of the entoplastron is covered by set 1 scales in *Baptemys, Dermatemys, Emarginachelys, Hoplochelys, Staurotypus,* and *Claudius*; a smaller portion (about one-third) is covered in *Agomphus.*

Set 1 scales are normally paired as is seen in CCM 60-15 and most other *Adocus* specimens. However, fusion of set 1 scales occurs among trionychoids in some *Adocus* (*A. kirtlandius*), *Basilemys* (the type of *B. nobilis* Hay and NMC 376), and in *Nanhsiungchelys* (*Zangerlia* unknown).

As mentioned above, set 2 scales are present only in *Peltochelys, Zangerlia, Basilemys,* and *Adocus* among the Trionychoidea. In all of these taxa, except some *Basilemys,* this pair of scales is isolated on the epiplastron by contact between the gular (set 1) and humeral (set 3) scales as described in the CCM specimen. Some *Basilemys* also show this condition (*B. variolosa, B. nobilis*; see Langston, 1956), but others have the set 2 scale elongate posteriorly, meeting on the midline and thus isolating set 1 from set 3 scales.

Set 3 scales are persistent in trionychoids. They are one of the pairs that remains even in the most reduced scale pattern of *Hoplochelys* and the Staurotypinae. In all cases, as in CCM 60-15, they are restricted largely to the hyoplastra although they always cover part of the entoplastron. In *Baptemys* they reach the posterior edge of the epiplastra. When set 4 scales are absent as in *Baptemys, Dermatemys, Agomphus, Hoplochelys,* and kinosternids, set 3 scales contact the inframarginals laterally.

When present, set 4 scales, the pectorals, lie between the humerals (set 3) and abdominals (set 5). They always isolate the scales of the anterior plastral lobe from the inframarginals as in CCM 60-15. As in that specimen, these scales lie entirely or nearly entirely on the hyoplastra. In nontrionychoids with pectorals these scales are typically well posterior to the entoplastron. The close approach of the pectoral scales to the entoplastron due to their medial expansion (as in CCM 60-15) can be considered a derived feature. In some *Adocus* (*A. lacer, A. syntheticus, A. annexus*)

TABLE 2

Characters and Character States Used in the Analysis of Relationships Among the Members of the Trionychoidea

(The primitive condition for the Chelomacryptodira, based on outgroup considerations, is given as state 0. The states of those multistate characters marked with an asterisk are not considered to form a transformation series and were run unordered in the phylogenetic analyses.)

1. Foramen stapedio-temporale
   - 0) large
   - 1) small
   - 2) absent
2. Size of foramen caroticum laterale (FCL) relative to size of foramen anterius canalis carotici interni (FACCI)*
   - 0) FCL = FACCI
   - 1) FACCI > FCL
   - 2) FCL > FACCI
3. Foramen posterius canalis carotici interni completely surrounded by pterygoid
   - 0) no
   - 1) yes
4. Basis tuberculi basalis
   - 0) present
   - 1) absent
5. Maxillary "tooth"
   - 0) absent
   - 1) present
6. Commissural ridge
   - 0) absent
   - 1) present
7. Premaxillae fused
   - 0) no
   - 1) yes
8. Foramen intermaxillaris
   - 0) absent
   - 1) present
9. Vomer reduced
   - 0) no
   - 1) yes
10. Palatines truncated anteriorly
    - 0) no
    - 1) yes
11. External process of pterygoid
    - 0) present
    - 1) absent
12. Basisphenoid-palatine contact
    - 0) absent
    - 1) present
13. Incisura columellae auris closed
    - 0) no
    - 1) yes
14. Scutes sulci of skull roofing bones
    - 0) present
    - 1) absent
15. Skull roofing bones sculptured
    - 0) no
    - 1) yes
16. Frontal bones enter orbit
    - 0) yes
    - 1) no
17. Maxilla contacts quadratojugal
    - 0) no
    - 1) yes
18. Retroarticular process
    - 0) absent
    - 1) present
19. Three keels on carapace
    - 0) no
    - 1) yes
20. Neural formula 6 > 4 < 6 < 6 < 6 < 6
    - 0) no
    - 1) yes
21. Costal bones meet on the midline
    - 0) no
    - 1) yes

TABLE 2—(Continued)

22. Number of peripheral bones*
    - 0) 11 per side
    - 1) 10 per side
    - 2) 9 or fewer per side
23. Transverse processes of thoracic vertebra 9 sutured to overlying costal
    - 0) yes
    - 1) no
24. Axillary buttress of hyoplastron reaches overlying costal bones
    - 0) no
    - 1) yes
25. Rib ends strongly articulated to vertebral centra
    - 0) no
    - 1) yes
26. Ventral process of eighth cervical vertebra*
    - 0) single
    - 1) double
    - 2) absent
27. Number of suprapygals
    - 0) two
    - 1) one
    - 2) none
28. Plastral kinesis present along anterior edge of hyoplastra
    - 0) no
    - 1) yes
29. Plastron strongly sutured to carapace at bridge
    - 0) yes
    - 1) no
30. Midline plastral scute sulcus sinuous
    - 0) no
    - 1) yes
31. Extragular scales (set 2)
    - 0) present
    - 1) absent
32. Pectoral scales (set 4)
    - 0) present
    - 1) absent
33. Pectoral scales reach entoplastron
    - 0) no
    - 1) yes
34. Scale set 5 (abdominals)
    - 0) meet medially
    - 1) displaced laterally
    - 2) absent
35. Number of inframarginal scales
    - 0) 5/5 to 4/4 within one genus
    - 1) 4/4 to 3/3 within one genus
    - 2) 3/3 to 2/2 within one genus
36. Notch present in ilium just posterior to acetabulum
    - 0) no
    - 1) yes
37. Thelial process
    - 0) absent
    - 1) present
38. Biconvex cervical
    - 0) is number 4
    - 1) is number 3
    - 2) is number 2
39. All intercervical articulations opisthocoelous
    - 0) no
    - 1) yes
40. Phalangeal formula*
    - 0) 2-3-3-3-3
    - 1) 2-2-2-2-2
    - 2) shows hyperphylangy
41. Paired ventral processes of the nuchal
    - 0) absent
    - 1) present

TABLE 2—(*Continued*)

42. Cheek emargination reaches level of orbit	0) yes 1) no
43. Coronoid tall and located near middle of mandible	0) no 1) yes
44. Parietal contribution to processus trochlearis oticum	0) little or none 1) large
45. Costoperipheral sutures	0) present 1) absent
46. Shell scales*	0) present 1) absent from plastron 2) absent from plastron and carapace
47. Marginal scales reach costal bones	0) no 1) posteriorly only 2) posteriorly and laterally
48. Antrum postoticum reduced	0) no 1) yes

and in *Basilemys* and *Nanhsiungchelys,* the pectorals extend across as much as half of the entoplastron. In those *Adocus* in which the pectorals do not extend onto the entoplastron, they are always quite close to its posterior edge (*A. agilis, A. kirtlandius, A. bossi,* CCM 60-15). There is also variation in the contacts between the pectorals and inframarginals (these will be discussed below under variation of inframarginals). Set 4 scales are absent in the scaled plastra of *Emarginachelys, Dermatemys, Baptemys, Agomphus, Hoplochelys, Staurotypus, Claudius,* and *Kinosternon* (Hutchison and Bramble, 1981). They are also absent from the unscaled plastra of *Anosteira, Carettochelys,* and all trionychids.

Set 5 scales (the abdominals) always cover the hyo-hypoplastral suture when they are present. Following the work of Hutchison and Bramble (1981), it is proposed that set 5 scales are completely absent from the Kinosternidae. In *Hoplochelys,* set 5 scales are displaced laterally onto the bridges and do not meet on the midline. This pair of scales, if present, separates the scales of the posterior plastral lobe from the inframarginals except in *Basilemys* and *Zangerlia* (Langston, 1956; Mlynarski, 1972) and *Dermatemys* (Mlynarski 1976; BMNH 1911.1.28.1) in which the femorals extend forward sufficiently to contact

the posterior portion of the inframarginal series.

Scale sets 6 and 7, the femorals and anals, are present in all scaled trionychoids. The femorals normally cover the hyo-xiphiplastral suture and the anals are usually restricted to the xiphiplastra. In *Hoplochelys* and staurotypines, set 6 approaches or reaches the hyo-hypoplastral suture. In one species of *Hoplochelys* (*H. elongata* Gilmore), the anal scales overlie the hypo-xiphiplastral suture. In kinosternines with a mobile posterior plastral lobe the anterior edge of scale set 6 lines up with the hypo-xiphiplastral suture.

INFRAMARGINAL SCALES: There are four inframarginals on each side of CCM 60-15 (fig. 11B). They are approximately equal in size, the first being only slightly narrower than the remaining three. The first inframarginal, the axillary, lies entirely on the hyoplastron. It contacts at least the fourth and possibly the third right marginal scales laterally, the second inframarginal posteriorly, and the pectoral medially. The fourth inframarginal, the inguinal, lies completely on the hypoplastron. It contacts the abdominal medially, the third inframarginal anteriorly, and the seventh and possibly the eighth marginals laterally. The second and third inframarginals lie between the fifth and sixth marginals laterally and the pectorals and abdominals medially. The second lies entirely on the hyoplastron; the third crosses the hyo-hypoplastral suture.

The number of inframarginal scales varies among the taxa of the Trionychoidea but also varies within genera assigned to this superfamily (table 2). Based on the presence of complete inframarginal series (four scales per side) in pleurosternids, plesiochelyids, baenids, chelonioids, and some trionychoids, a low number of inframarginals can be considered derived within the Trionychoidea. The problem is recognizing states in the character, given the known variability. *Adocus* has four scales per side with only one exception. *Dermatemys* has either four or five per side. *Baptemys* has three or four, *Hoplochelys* has three per side, *Agomphus* has two or three, and all kinosternids only two per side. Taxa are considered to have the primitive condition if most individuals had at least one side with four inframarginals. Those with three or fewer per
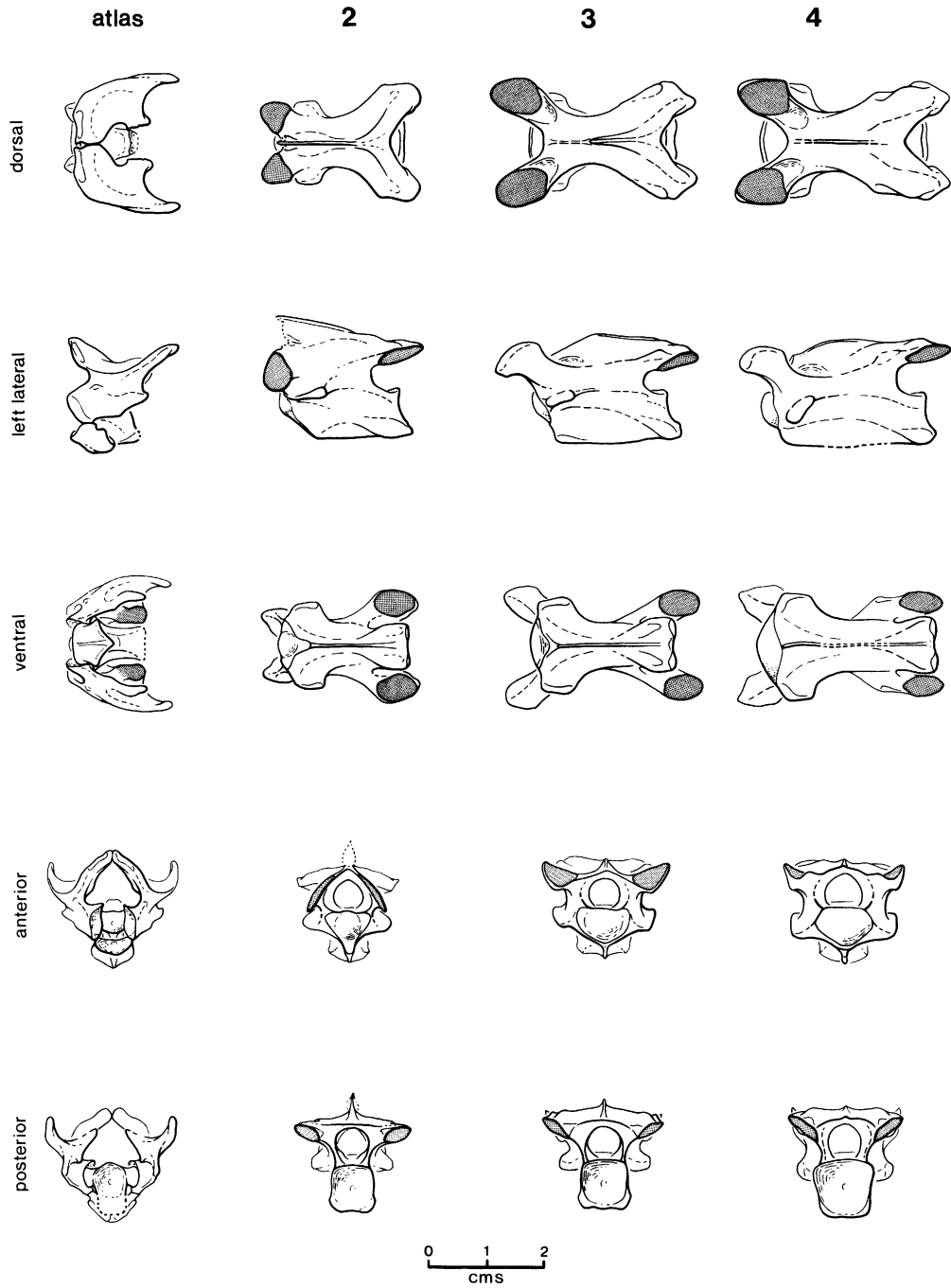
Fig. 15. The cervical vertebrae of *Adocus* sp. (CCM 60-15). Vertebrae are arranged from anterior (atlas) on the left to posterior (cervical 8) on the right.

side are considered derived; those with two per side are further derived. Those taxa that lack any shell scales were scored separately.

Ideally this character would be treated as partially ordered in numerical analysis.
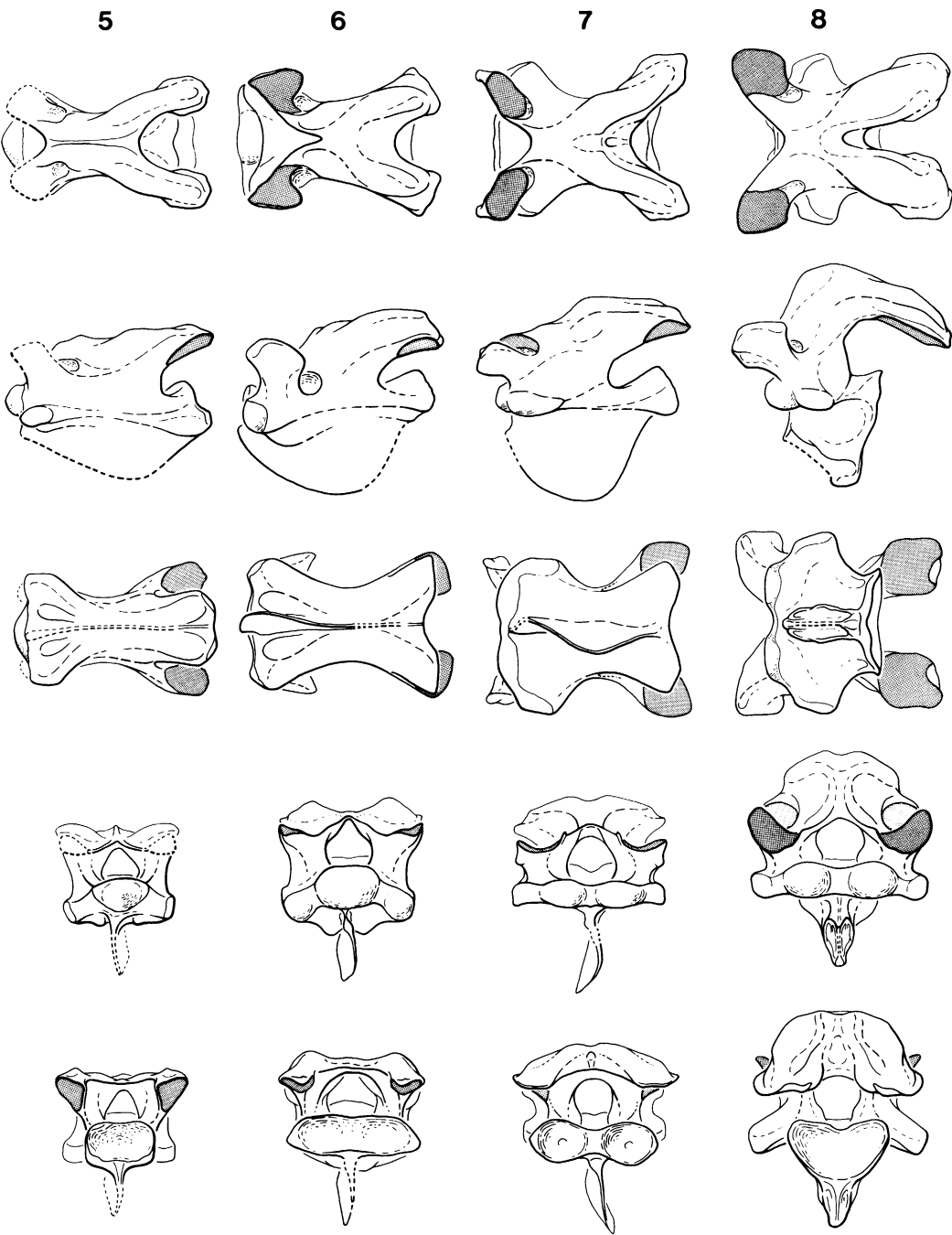
In most trionychoids the inframarginals

Fig. 15—*continued.*

completely separate the plastral and carapacial scales. This condition appears to be primitive for turtles. Division of the inframarginal series by contact of plastral and carapacial scales appears to occur when the number of inframarginals is reduced. Within the trionychoid genera treated here, it occurs in all *Basilemys* and in some *Kinosternon.* Else-

TABLE 3
The Number of Inframarginals in Members of the Trionychoidea
(All kinosternids have two inframarginals and they are not included in this table)

Taxon	Number of inframarginals (left/right)					
	5/5	5/4	4/4	4/3	3/3	2/2
Adocus			CCM 60-15 AMNH 6712 USNM 6539 USNM 8593		USNM 8577	
Agomphus					ANSP 15359 AMNH 1478	YPM 671 YPM 774
Baptemys			AMNH 6004	USNM 13437 USNM 13438 MCZ Seton, 1951	UCMP 45477 AMNH 6109 AMNH 5967 AMNH 5934 YPM 3754	
Basilemys						FMNM 11084
Dermatemys	UNAM 2612 UNAM 2480	UNAM 2613 UNAM 2483	UNAM 2479 UNAM 51072			
Emarginachelys					KU 23488	
Hoplochelys					USNM 8646 USNM 6549 USNM 8525 USNM 8553	
Peltochelys					IRSNB 1536	

where it occurs in all Pleurodira except *Proterochersus* and in all Testudinoidea.

THE CERVICAL VERTEBRAE

The cervical series of CCM 60-15 is complete (fig. 15). The first thoracic vertebra is preserved in place within the carapace. The anterior cervicals are lightly built, long, and narrow. The more posterior ones are broad and robust. Centra 2 through 5 are at least twice as long as they are wide; 6 and 7 are somewhat wider; 8 is as wide as long. These centra are remarkable in that all are opisthocoelous. Centra 1 through 5 have single concave posterior articular surfaces; in 6 and 7 these surfaces are doubled, and number 8 is single. Centra 1 through 6 have single, convex, anterior articular surfaces; numbers 7 and 8 have clearly developed double anterior articular surfaces. Centra 2 through 5 are rectangular in ventral view with well-developed and anteriorly placed parapophyses; centra 6 and 7 are hourglass-shaped, and 8 is square with large parapophyses. Ventral keels are present on centra 2 through 8. They are thin

and only weakly projecting on centra 2 through 4, but they are very broad on centra 6 and 7. The keel is missing on centrum 5 but appears to have been moderately developed. The keel on the eighth cervical differs from the others in having small accessory keels lying on either side.

The neural arches are typical of eucryptodiran turtles having widely separated pre- and postzygapophyses. The postzygapophyses become more robust posteriorly and are quite thick on vertebrae 6, 7, and 8. The two most angular contacts between successive pairs of zygapophyses are those between vertebrae 5 and 6, and 7 and 8.

The paired atlantal neural arches meet on the midline but are neither sutured nor fused. They articulate posterolaterally with the prezygapophyses of the second cervical (the axis). Beyond this articulation extends a narrow, free process that reaches a point about halfway across the axis. Anteromedially the atlantal neural arches contact the first vertebral centrum; anteroventrally they contact the atlantal intercentrum. Together with the atlantal intercentrum the two neural arches form

the atlantal ring, which articulates with the occipital condyle. The atlantal intercentrum is braced posteriorly by a thick ventrally directed portion of the first vertebral centrum.

Opisthocoely of the cervical series of *Adocus* is a remarkable feature. Complete cervical opisthocoely has been reported elsewhere among turtles only in the Trionychidae and Carettochelyidae. New evidence shows that *Basilemys*, like *Adocus* and the Trionychia, has opisthocoelous posterior vertebrae. Two different specimens of *Basilemys* (AMNH 5448 and NMC 8890) each include a single cervical vertebra. In both cases it appears to be number 6. This element has a broad, opisthocoelous centrum in both examples, which can be seen to be double in NMC 8890 (fig. 16A, B). The anterior articular surface is a large, convex structure in both specimens. The prezygapophyseal facets are inclined at a high angle to the centrum as they are in the sixth centrum of *Adocus*.

In all other trionychoids for which the cervical series is known, one to three anterior vertebrae are opisthocoelous. These are followed by a single biconvex cervical; the remainder of the cervicals are procoelous. The fourth cervical is biconvex in the single available cervical column of *Emarginachelys* (KU 23488). In *Baptemys* (USNM 13437) and nearly all kinosternids (Williams, 1950), the third cervical is biconvex, with all more posterior cervicals being procoelous (fig. 16). In *Dermatemys* the second cervical is biconvex.

Among cryptodirans with formed cervical centra (the Centrocryptodira of Gaffney and Meylan, 1988), typically the fourth cervical is biconvex. Of those eucryptodires examined by Williams (1950), 115 of 117 chelydrids (98.3%), 647 of 694 emydids (93.2%), 70 of 72 cheloniids (97.7%), and 136 of 358 of testudinids (40.0%) have a biconvex fourth cervical. The occurrence of this feature in *Meiolania* and its broad distribution throughout the Centrocryptodira lead Gaffney (1985a) to propose that it is the generalized condition for this group. The distribution of this feature in a complete phylogeny of turtles (Gaffney and Meylan, 1988) is in agreement with this hypothesis.

In most turtles, as in *Adocus,* the ventral process of the eighth cervical is not a paired structure. In certain other taxa (e.g., *Trachemys scripta,* AMNH 11961; fig. 19 in Meylan, 1987), this process is accompanied by accessory ridges on either side, but only in certain trionychoids is this structure paired. As shown in Meylan (1987: fig. 19), the ventral process of the eighth cervical is paired in kinosternids and carettochelyids.

PECTORAL GIRDLE AND FORELIMB

The coracoid of *Adocus* (CCM 60-15) is very long and narrow (fig. 17). It is substantially longer than the acromion process of the scapula and only slightly shorter than the body of the scapula.

The coracoids of most aquatic turtles are long and narrow, as they are in all of the trionychoids examined during this study. Those of trionychids are curved, those of *Basilemys* are distally expanded and very long (NMC 8890, AMNH 5448), and those of kinosternids are only very weakly sutured to the scapula. No feature of the coracoid was distributed in such a manner that it might be useful in suggesting relationships among the taxa of interest here.

The right humerus of CCM 60-15 is preserved in nearly perfect condition (fig. 18). The caput humerus is large and is located at the end of a short neck that extends from the shaft of the humerus at an angle of about 90°. It has a weakly developed groove in its anterior edge. The main axis of the articular surface of the caput humerus lies at a slight angle to the main axis of the shaft. The medial process of the humerus is about three times larger than the lateral process; between them is a well-developed intertubercular fossa. The medial process extends posteriorly from the shaft at an angle of nearly 40°, and extends as far medially as does the caput humeri. The lateral process diverges anteriorly from the shaft at an angle of about 10°. It does not extend medially to the level of the medial process or caput humeri. The two distal trochanters, the capitellum and trochlea, are approximately equal in size and do not completely cover the distal end of the element. The ectepicondylar foramen is closed.

The humerus of *Adocus* is essentially identical to that of *Baptemys* (USNM 13437), *Staurotypus,* and *Dermatemys.* The humerus of *Basilemys* (CM 8890) is similar but the lesser trochanter curves posteriorly, further enclosing the intertubercular fossa. It also has
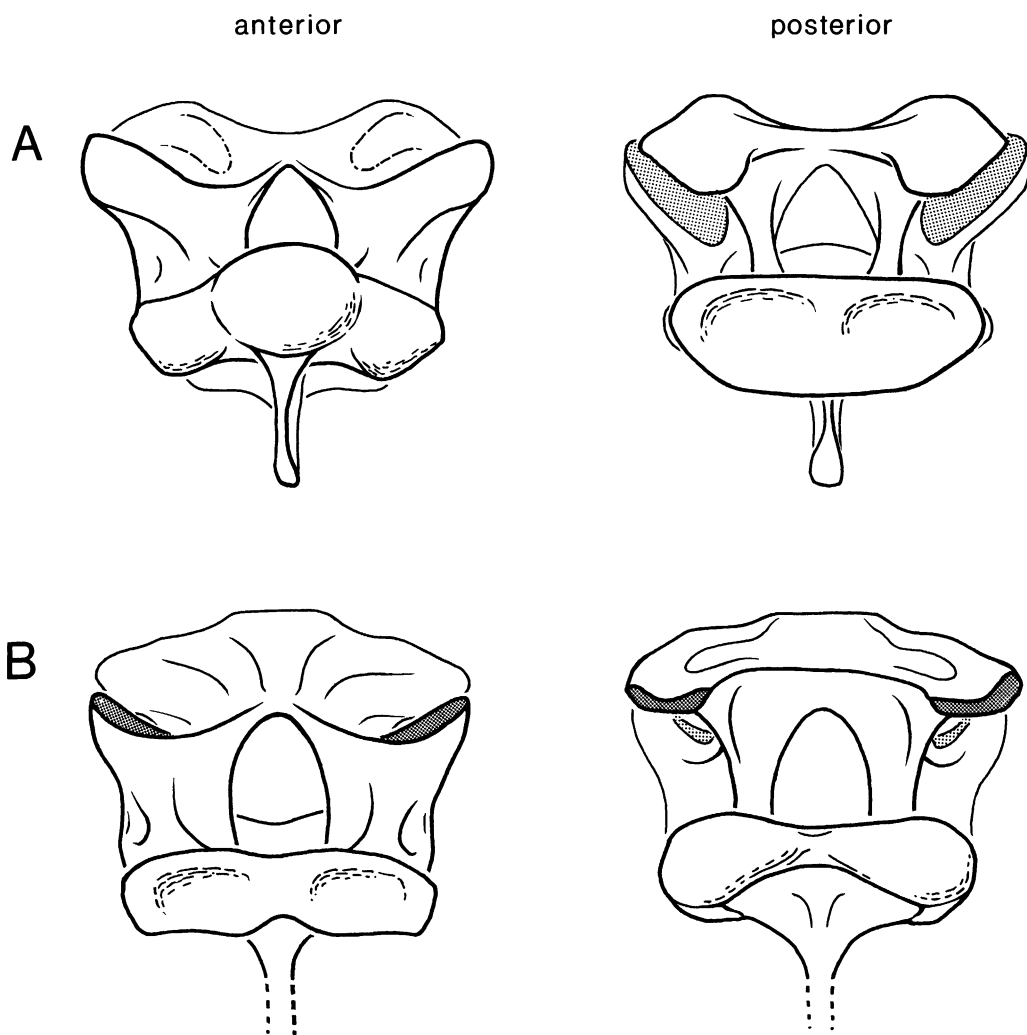
anterior   posterior

A

B

Fig. 16.   Posterior cervical vertebrae of selected trionychoid turtles. **A,** Anterior and posterior views of the sixth cervical of *Basilemys* sp. (NMC 8890 with reference to AMNH 5548). **B,** Anterior and posterior views of the seventh cervical of *Baptemys* sp. (USNM 13437).

large distal trochanters that cover the entire distal portions of the element and the main axis of the caput humeri lies at a higher angle to the shaft. The lateral process in trionychids is larger than in other trionychoids. In carettochelyids it is smaller and displaced distally on the humeral shaft. The similarity of the humeri among trionychoids (except for autapomorphies in *Basilemys,* carettochelyids, and trionychids) restricts their utility in the cladistic analysis. No characters were developed using humeral morphology.

Both the right and left forelimbs of CCM 60-15 are well preserved (figs. 2, 19). Both radius and ulna are complete and appear to lie close to their correct natural position with respect to the manus. They are about equal in length and both are distally expanded. The ulna is broader throughout its length than the radius.

The contacts between the radius and ulna and the carpus are best preserved in the right foot. It appears that the radius contacted the intermedium and a medial centrale and is only slightly separated from the first carpal. The ulna is separated from the radius by the intermedium. It contacts only the intermedium and the ulnare.

The carpus is composed of four rows of elements: the intermedium; the medial and lateral centrale and ulnare; five subequal-size carpals; and five metacarpals. The medial centrale appears to have a partially fused radiale medially. There is no evidence of a pisiform. The phalanges are 2-3-3-3-3, with claws present on all five digits.

The manus of *Adocus* is much like those of living casichelydians. It has a primitive number of carpals and phalanges, and retains evidence of a radiale. The absence of a pisiform is ascribed to loss during preservation.

Elsewhere among the Trionychoidea, derived manus and pes morphology is found in carettochelyids and trionychids. Both have a reduced number of clawed digits; the latter also exhibit hyperphylangy (Meylan, 1977). In *Basilemys* there is a reduced number of phalanges in the pes (2-2-2-2-1 based on AMNH 5448). A reduction in the number of phalanges also appears to exist in *Nanhsiungchelys*, but this needs verification.

PELVIC GIRDLE

Part of the pelvic girdle of CCM 60-15 is preserved in a block of matrix with the head of the right femur and a series of caudal vertebrae. However, enough of it is exposed or free from the block that the entire structure can be described and reconstructed (fig. 20). The pubes make up one-third of the acetabulum. They are broad and long, extending anteriorly well beyond the pectineal processes. There is broad interpubic contact and the pectineal processes are elongate. These elements project into the thyroid fenestra at the midline but do not contact the ischia. Instead they lie dorsal and anterior to the ischia, which results in an undivided thyroid fenestra. The ischia make up the posteroventral third of the acetabulum. They have extremely well-developed metischial processes as well as anterior projections that extend halfway across the thyroid fenestra. The ilia form the dorsal third of the acetabulum from which they extend posterodorsally and somewhat medially. They are not curved but have weakly defined thelial processes that are best seen in lateral view.

The pelvis of *Adocus* is primitive in general appearance. The open thyroid fenestra, large metischial processes, dorsomedially directed
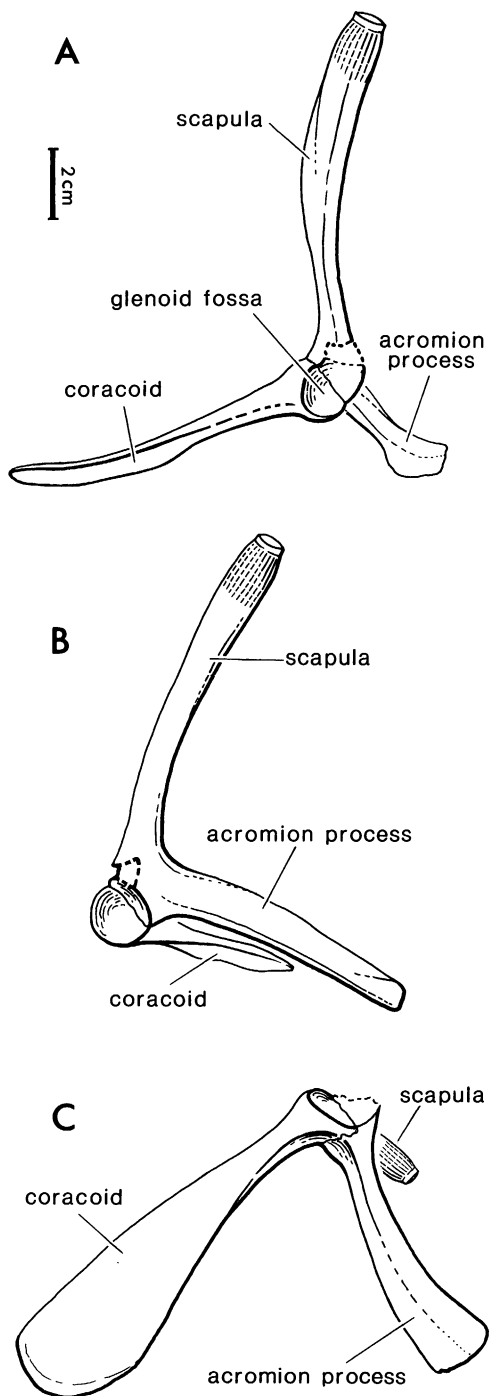

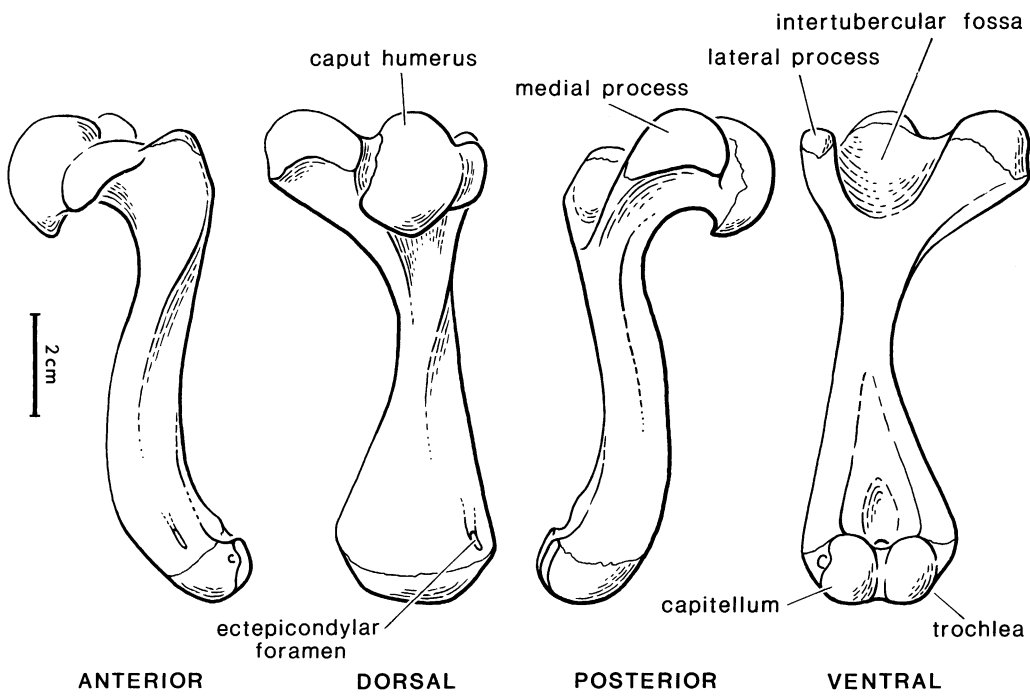Fig. 17. The right pectoral girdle of *Adocus* (CCM 60-15) in (**A**) lateral, (**B**) anterior, and (**C**) ventral views.

caput humerus

intertubercular fossa

lateral process

medial process

ectepicondylar
foramen

capitellum

trochlea

ANTERIOR   DORSAL   POSTERIOR   VENTRAL

Fig. 18.   The right humerus of *Adocus* sp. (CCM 60-15).

A

2 cm

B

right
ulna

right
radius

left
radius

left
ulna

ulnare

medial
centrale

lateral
centrale

intermedium

distal
carpals
(1-5)

phalanges

V   I

I   V

IV

II

II

IV

III

III
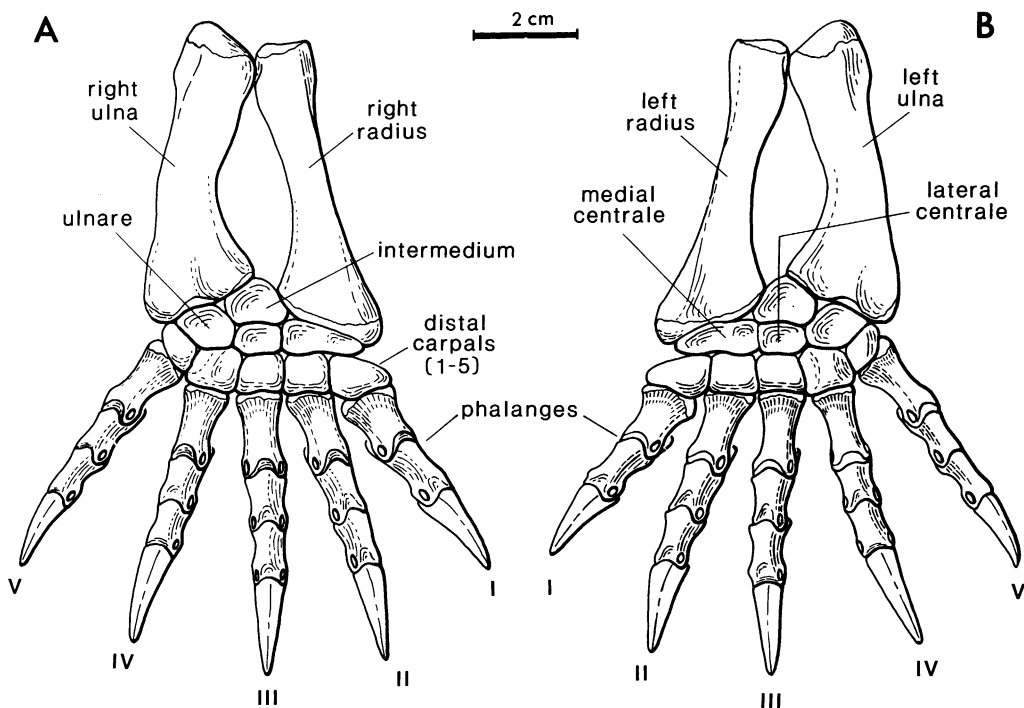
Fig. 19.   The right (A) and left (B) manus of *Adocus* (CCM 60-15) in dorsal view.
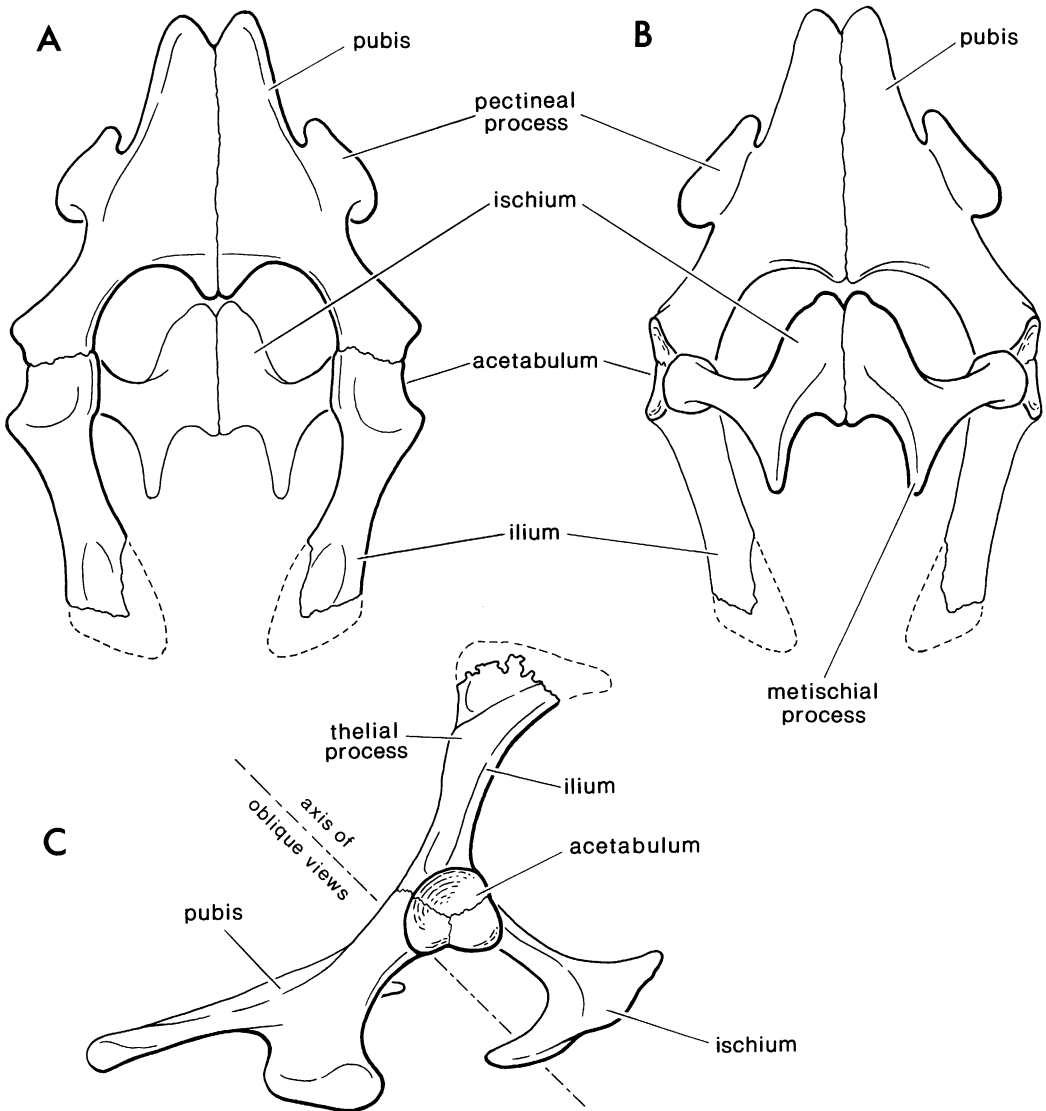
Fig. 20. The pelvic girdle of *Adocus* sp. (CCM 60-15) in (A) dorsal, (B) ventral, and (C) lateral views.

and dorsally expanded ilia, and unexpanded pectineal processes appear to be primitive for eucryptodirans (fig. 21; Baur, 1891a). The presence of the thelial process is of interest. This structure is well developed only in kinosternids (fig. 21B), carettochelyids (fig. 21D), and *Baptemys* (fig. 342 in Hay, 1908a; UCMP 45477, AMNH 5934). It is weakly developed in *Adocus, Emarginachelys* (Whetstone, 1978), and *Lissemys* (Meylan, 1987). Its distribution is best explained as a synapomorphy for the Trionychoidea, with independent

losses in the Trionychidae and *Dermatemys*. The ilial notch, known to occur in kinosternids, is absent from the ilium of *Adocus*. This structure is present in *Baptemys* (USNM 13437).

DISCUSSION:
MONOPHYLY OF THE TRIONYCHOIDEA
(Fig. 22, Node 1)

The current study indicates that the Trionychoidea of Gaffney (1975, 1984) is a
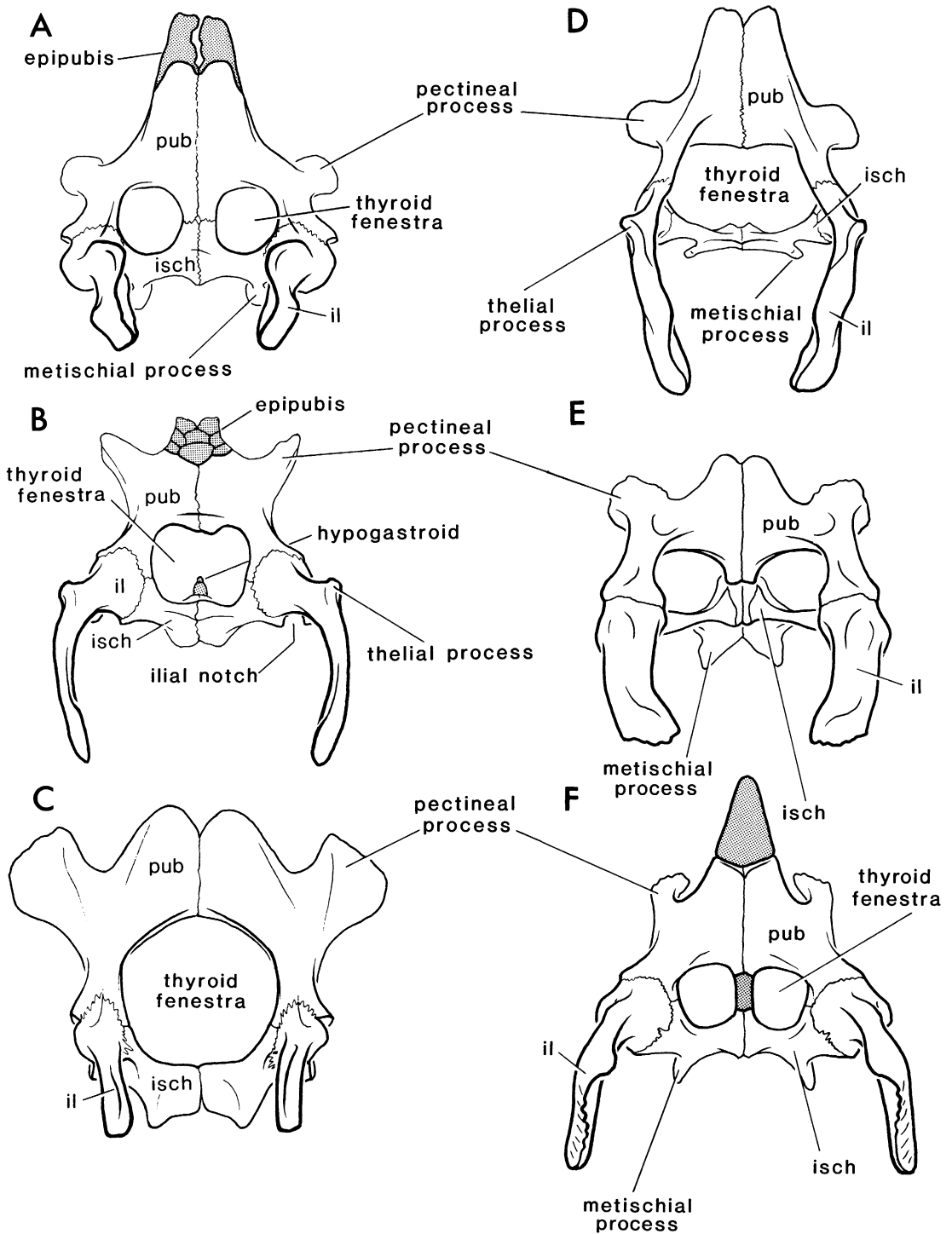
Fig. 21.   Dorsal views of the pelvis of six eucryptodiran turtles. **A,** *Pseudemys nelsoni* (AMNH 129736); **B,** *Staurotypus triporcatus* (UF 13482); **C,** *Apalone ferox* (AMNH 129737); **D,** *Carettochelys insculpta* (AMNH 84212); **E,** *Basilemys* sp. (NMC 8890); **F,** *Macroclemys temmincki* (AMNH 58251). Abbreviations: il, ilium; isch, ischium; pub, pubis. Stippled areas represent calcified cartilage.

monophyletic group that can be considered to include the extinct genera *Adocus, Basilemys, Nanhsiungchelys, Peltochelys, Emarginachelys, Baptemys, Hoplochelys,* and *Xenochelys.* This superfamily is diagnosed on the basis of a combination of characters used by Gaffney (1975, 1984), Meylan (1987), and Gaffney and Meylan (1988). The inclusion of data from the fossil record requires a reexamination of the diagnostic features of the Trionychoidea as summarized for living taxa by Meylan (1987: table 19).

The features which led Gaffney (1975, 1984) to suggest the existence of this natural group, the enlarged internal carotid canal and apparent reduction of stapedial circulation, remain of greatest importance (Gaffney, 1979; Albrecht, 1967, 1976; McDowell, 1961). Surveys of new material indicate that significant participation by the palatine in the braincase is also diagnostic (Gaffney, 1979; Meylan, 1987). This feature occurs elsewhere sporadically in species of the Deirochelyinae (sensu Gaffney and Meylan, 1988), in the genera *Graptemys* and *Pseudemys* (Meylan, personal observ.), and in certain batagurines (e.g., *Batagur*; Gaffney, 1979).

Transverse processes do not reach the costal bones in any trionychoids for which the 10th vertebra is well known. The only possible exception is *Adocus.* Baur (1891a) summarized his observations on the contacts of the ribs of the 10th vertebra among the Testudines and indicated that those of the Adocidae are present and sutured to the eighth costal bone. His observations were based on Marsh's *Adocus punctatus* which he reconstructed (Baur, 1891b). However, Wieland (1904) thoroughly described the same specimen, and in an accompanying figure indicated the point at which "[the] rib of tenth dorsal vertebra unites suturally with the 8th costal, *or else* point of iliac support." Wieland's observations, combined with our experience with material preserved in New Jersey Greensands, suggest that Baur's description may have been hypothetical, based on observed scars and breaks. We have not found decisive material and must consider this feature unknown for *Adocus.*

The possession of a thelial process of the ilium appears to be a derived feature of the Trionychoidea. This character has a limited distribution among the living members of the superfamily, occurring only in the Kinosternidae, *Carettochelys,* and *Lissemys* and has been used as evidence for monophyly of the Kinosternidae plus Trionychia (Meylan, 1987). However, the observation that this structure is present in *Emarginachelys, Baptemys,* and *Adocus* suggests that its presence is primitive for the superfamily and lost in the common ancestor of *Basilemys* and *Nanhsiungchelys,* in *Dermatemys,* and within the Trionychidae. Thelial processlike structures occur elsewhere only in testudinoids with kinetic plastra (*Cuora, Terrapene, Pyxidea, Kinixys*). In these taxa they appear to mark the anterior limit of a broad blade for insertion of an expanded m. testoiliacus (Bramble, 1974). They are not homologous to the thelial process in trionychoids.

The presence of a maxillary tooth is rare among living trionychoids, occurring only in *Dermatemys.* But it is known to occur in the extinct genera *Adocus, Baptemys,* and *Emarginachelys.* Cladistic analysis of about 50 morphological characters suggests that these four taxa are basal in the trionychoid clade and that the presence of a maxillary tooth is primitive for, and diagnostic of, the Trionychoidea. The maxillary tooth is lost twice within the Trionychoidea.

The presence of a caudifibularis muscle is unique to *Dermatemys,* kinosternids, and trionychids (Zug, 1971). Although unknown for *Carettochelys* and the fossil taxa considered in the current study, it is used as evidence for the monophyly of the Trionychoidea here and elsewhere (Gaffney and Meylan, 1988).

The addition of new data, especially on fossil forms, suggests that several characters used by Meylan (1987) to support monophyly of the Trionychoidea no longer apply. The distribution of plastral buttresses that reach overlying costal bones among the Cryptodira has been reconsidered (Gaffney and Meylan, 1988). The absence of enlarged plastral buttresses in all trionychoids other than *Dermatemys* and *Baptemys* can best be attributed to retention of the primitive condition for the Eucryptodira. The appearance of axillary buttresses that reach anterior costals in *Baptemys* and *Dermatemys* is a synapomorphy for a restricted Dermatemydidae. The
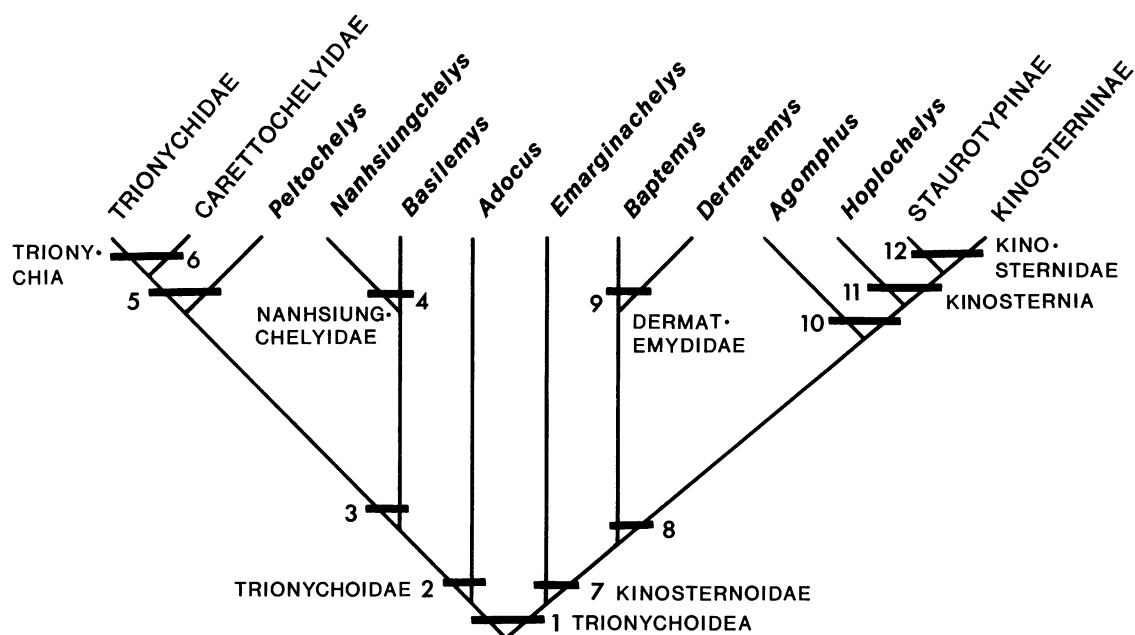
Fig. 22. A cladogram for the Trionychoidea. Characters supporting monophyly at indicated nodes are as follows:

Node 1: Trionychoidea
1) decrease of stapedial circulation and increase of carotid circulation
2) significant contribution to braincase made by palatine
3) 10th body vertebra free from costals
5) loss of basis tuberculi basalis (present in *Adocus*)
6) anal notch absent (may be primitive condition for polycryptodira)
7) maxillary "tooth" present (lost at nodes 6 or 7 and 10)
8) thelial process present
9) presence of a caudifibularis muscle (Zug, 1971)

Node 2: Trionychoidae
1) articulations between cervical vertebrae opisthocoelous
2) foramen posterior canalis carotici interni very ventral, completely enclosed by pterygoids (occurs also in *Baptemys*)
3) large portion of processus trochlearis oticum made up by parietal
4) coronoid process tall and located in middle of jaw ramus
5) well-developed retroarticular process
6) sinuous midline plastral sulcus (occurs also in *Agomphus*)

Node 3: *Nanhsiungchelys, Peltochelys,* and the Trionychia (skull characters not known for *Peltochelys*)
1) vomer reduced
2) palatines truncated anteriorly allowing large area of communication between the apertura narium internum and the fossa nasalis
3) no processus externus of pterygoid
4) incisura collumella auris closed
5) cheek emargination absent
6) top of skull sculptured (lost in Trionychidae, present in *Basilemys*)
7) basisphenoid contacts palatines and divides pterygoids

Node 4: Nanhsiungchelyidae
1) reduced number of phalanges
2) thelial process absent

Node 5: *Peltochelys,* Carettochelyidae, and Trionychidae

1) 10 or fewer peripheral bones
2) ventral processes of the nuchal

Node 6: Trionychia (Trionychidae and Carettochelyidae)
1) peripherals not sutured to costals
2) ribheads strongly sutured to vertebral centra
3) premaxillae fused
4) radius and ulna in contact adjacent to manus
5) number of clawed digits three or fewer
6) coracoid longest of three pectoral processes
7) carapace not sutured to plastron

Node 7: Kinosternoidae
1) scale set 2 (extragulars) lost from plastron (Hutchison and Bramble, 1981)
2) scale set 4 (pectorals) lost from plastron (Hutchison and Bramble, 1981)
3) no scales on skull roof (occurs also at node 11)

Node 8: Dermatemydidae, *Agomphus, Hoplochelys,* and Kinosternidae
1) foramen caroticum laterale larger than foramen anterior canalis carotici interni
2) biconvex cervical is number 3 or 2
3) foramen stapedio-temporalis reduced or closed

Node 9: Dermatemydidae (restricted to the genera *Baptemys* and *Dermatemys*)
1) commissural ridge on triturating surface
2) foramen stapedio-temporalis closed
3) axillary buttresses reach costal bones

Node 10: *Agomphus, Hoplochelys,* and Kinosternidae
1) no more than three inframarginal scales present on each bridge (occurs also in *Basilemys*)

Node 11: *Hoplochelys* and Kinosternidae
35) reduction of scale set 5, abdominals (Hutchison and Bramble, 1981)
19) tricarinate carapace

Node 12: Kinosternidae
 1) 10 peripheral bones on each side of carapace
 2) no ribs connecting ninth and tenth body vertebra to eighth costal
 3) anterior lobe kineses that includes entoplastron (when it is present)
 4) frontal not reaching orbit
 5) maxilla contacting quadratojugal
 6) ilio-ischial notch in acetabulum (occurs also in *Baptemys*)
 7) only two inframarginals (occurs also in *Basilemys*)
 8) stridulating organs present in males (lost in *Kinosternon scorpioides* group)
 9) scale set 5 (abdominals) absent
10) incised anterior musk ducts

contact of all four buttresses to overlying costal bones is a synapomorphy for the Testudinoidea (Hirayama, 1985; Gaffney and Meylan, 1988).

Cheek emargination is well developed in *Adocus* (fig. 4A), *Emarginachelys,* and *Baptemys*. This distribution eliminates reduced cheek emargination as a synapomorphy for the Trionychoidea (Meylan, 1987). Such reduction appears to occur at least three times within the superfamily and is thus no longer considered a synapomorphy for the super-

family. Similarly, a basis tuberculi basalis is present in *Adocus,* suggesting that the absence of this structure is not a synapomorphy of the superfamily. Also, the quadrate appears to make up a large portion of the processus trochlearis oticum in *Emarginachelys,* suggesting that small quadrate contribution to the processus trochlearis oticum is not a synapomorphy of the Trionychoidea.

Nessov (1977) acknowledged monophyly of the family Adocidae but placed it within the Testudinoidea. He supported this posi-

tion by suggesting that the members of this taxon do not have a reduced foramen stapedio-temporale typical of the Dermatemydidae (which he implies is the sister-group of the Testudinoidea). However, as the condition of the foramen stapedio-temporale of *Adocus* is primitive for turtles, it does not support Nessov's hypothesis. Other derived features of *Adocus* discussed above suggest that it belongs within the Trionychoidea (sensu Gaffney 1975, 1984), which is the sister-group to the Testudinoidea.

This study confirms monophyly of the Trionychoidea and presents the first opportunity to fully explore the relationships of living and extinct members of the group down to genus (fig. 22).

The relationships among members of the superfamily Trionychoidea are best reflected by the recognition of two large monophyletic groups, each containing several families of turtles (fig. 22). The rank of epifamily is used here to acknowledge this level of relationship as suggested by Bour and Dubois (1985, 1986). The names Trionychoidae (Fitzinger, 1826; as Trionychoidea) and Kinosternoidae (Agassiz, 1857; as Kinosternidae) have already been employed (Gaffney and Meylan, 1988).

The Trionychoidae are considered to include the monophyletic families Adocidae Cope, 1870 (not including *Basilemys*; contra Gaffney and Meylan, 1988), Nanhsiungchelyidae (Yeh, 1966, including *Basilemys*), Carettochelyidae Boulenger, 1887, and Trionychidae Fitzinger, 1826, as well as the genus *Peltochelys*. The Kinosternoidae are considered to include the Dermatemydidae Gray, 1870, the Kinosternidae Agassiz, 1857 (including *Xenochelys*), and the genera *Emarginachelys, Agomphus,* and *Hoplochelys.* The relationships within and among these taxa are discussed below.

An important taxonomic result of this work is the proposed restriction of the family Dermatemydidae Gray, 1870. Our results suggest that the taxa assembled under this name by most authors (e.g., Hay, 1908a; Mlynarski, 1976) form a paraphyletic group. We have reduced the included genera in order to: (1) form a monophyletic group; and (2) exclude members of the Kinosternidae (Agassiz, 1857), which would have priority over, and

thus terminate use of, the family group name Dermatemydidae. These criteria limit the included genera to *Dermatemys* and *Baptemys.* The priority of the Kinosternidae (Agassiz, 1857) over Dermatemydidae (Gray, 1870) reduces the role of this previously broadly applied name.

MONOPHYLY OF THE TRIONYCHOIDAE
(Fig. 22, Node 2)

Six morphological features are important in establishing the monophyly of the Trionychoidae. Five of these are established for *Adocus* for the first time in this paper.

In all members of the epifamily Trionychoidae in which cervical central articulations are known, all articulations between cervicals are opisthocoelous. Based on CCM 60-15, *Adocus,* like carettochelyids and trionychids, can be shown to be completely opisthocoelous (fig. 15). Two cervical vertebrae of *Basilemys,* one from each of two different specimens (AMNH 5448 and NMC 8890) suggest that it, too, has opisthocoelous vertebrae in the posterior part of the cervical series (fig. 16A, B). The only turtles with opisthocoelous posterior cervicals are those in which the entire column is opisthocoelous (Williams, 1950). Opisthocoely of the cervicals in this epifamily is unique for the Testudines. Although the cervical series of *Nanhsiungchelys* is known, the degree of preparation of the material does not allow reconstruction of the cervical central articulations. The cervicals of *Peltochelys* are unknown.

A feature of the internal carotid circulation used by Meylan (1987) as evidence for monophyly of the Trionychia (Carettochelyidae plus Trionychidae) is also present in *Adocus.* Like members of the Trionychia, *Adocus* has the foramen posterius canalis carotici interni completely surrounded by the pterygoid (fig. 5). This condition also occurs in *Baptemys* (fig. 6), but the available data suggest that it is independently derived. The exact position of the foramen posterius canalis carotici interni in *Nanhsiungchelys* should be determinable from further study of the type skull.

As pointed out by Gaffney (1979: 115), the processus trochlearis oticum of trionychids is distinct in being made up in large part by the

descending process of the parietal. The current study reveals that the same is true of carettochelyids (Gaffney, 1979: figs. 173–175) and *Adocus* (figs. 4, 5). This region of the skull appears to be the same in *Nanhsiungchelys* but it is unknown in *Basilemys*.

Two characters of the lower jaw used previously to support monophyly of the Carettochelyidae plus Trionychidae (Meylan, 1987) are also present in *Adocus* and thus support monophyly of the Trionychoidae. In this taxon the coronoid process is quite tall and is located in the middle of the mandible rather than in the posterior half (figs. 9, 10). The known members of the taxon also possess a well-defined retroarticular process of the mandible.

Adocus, Basilemys, and *Peltochelys* are unlike other scaled trionychoids, other than *Agomphus,* in having a sinuous midline plastral sulcus, presumably a derived condition within the Eucryptodira. Only the anterior half of the plastron of *Nanhsiungchelys* is known and the midline plastral sulcus is not discernible from available figures and photographs.

There have been previous hypotheses of relationship of *Adocus, Basilemys,* and *Nanhsiungchelys* (Chkhikvadze, 1975), and a distinction drawn between the Adocidae and Dermatemydidae (sensu lato) (Nessov, 1977). However, the arrangement employed in Gaffney and Meylan (1988), and modified slightly in the present paper, is novel. Available data suggest that the Adocidae (*Adocus* and related Asiatic genera) is the sister-group to the Nanhsiungchelyidae, *Peltochelys,* and the Trionychia; and that the Nanhsiungchelyidae is the sister-group of *Peltochelys* and the Trionychia. Elsewhere, one of us (Meylan, 1988) has argued that *Peltochelys* can be considered the sister-group of a monophyletic Trionychia.

MONOPHYLY OF THE ADOCIDAE

The concept of the Adocidae in this paper differs from that used in Gaffney and Meylan (1988) in the exclusion of the genus *Basilemys.* The family can be diagnosed by the presence of marginal scales that extend well up onto the costal bones beginning in the vicinity of peripheral 4 (fig. 11A, and all other

dorsal views of the carapace; see Wieland, 1904; Hay, 1908a; Gilmore, 1919). The results of the present study suggest that the distribution of the character used previously to place *Basilemys* in the Adocidae, the unusual 6 4 6 6 6 6 neural pattern (Gaffney and Meylan, 1988), is most parsimoniously explained as two independent occurrences. However, improved knowledge of the cranial morphology of *Basilemys* and *Nanhsiungchelys* is required to refute or corroborate the current hypothesis.

Nessov (1977) revived the name Adocidae and considered this family to include *Adocus, Zygoramma,* and *Alamosemys* as members of the subfamily Adocinae, and *Shachemys* and *Ferganemys* as members of the subfamily Shachemydinae. As the current analysis suggests, he, too, considered *Basilemys* to belong to the Nanhsiungchelyidae of Yeh (Nessov, 1986).

Zygoramma Cope, 1870, was differentiated from *Adocus* by its describer by differences in buttress construction. However, it is identical to *Adocus* in having buttresses restricted to the peripheral bones. It does not deserve generic recognition and is placed in synonymy with *Adocus.*

Alamosemys Hay, 1908a, was differentiated from *Adocus* in having the marginal scales wholly excluded from the costal bones. Reexamination of the type (AMNH 1204) reveals that the carapacial sutures cannot be seen in this badly eroded shell. It has been impossible to substantiate the diagnostic feature of the genus, and it is considered a synonym of *Adocus* following Gilmore (1919).

Evidence can be taken from Khosatzky and Nessov (1977) and Nessov (1977, 1986) that *Ferganemys* is an adocid, differentiated from *Adocus* by its less expanded marginal scales (fewer reach the costal bones than in *Adocus*) and the extra pair of scales in the axillary region of the plastron. This genus, described from the Albian of Kirgizia, USSR, is known from shell and skull material (see fig. 8 in Nessov, 1986). *Ferganemys* retains primitive eucryptodiran shell features including a complete set of plastral scales, complete inframarginal series, no mesoplastra, plastral buttresses restricted to peripheral bones, and a raised area for pubic contact on the dorsal surface of xiphiplastra. It also exhibits two

derived shell features that are also found in *Basilemys* and *Adocus,* the 6 4 6 6 6 6 neural pattern, and medially expanded pectoral scales. *Ferganemys* shares with *Adocus* the presence of a large posterior suprapygal bone and marginal scales that extend dorsally beyond the peripheral bones. The latter feature occurs only posteriorly in *Ferganemys* and not posteriorly and laterally, as in *Adocus.*

The skull of *Ferganemys* described by Nessov (1977) supplies additional evidence that this genus should be referred to the Adocidae. The description of the foramen posterius canalis carotici interni as similar in size to the foramen stapedio-temporale suggests that *Ferganemys* is a trionychoid. Nessov described the processus trochlearis oticum as large but with the prootic narrow (see also Khosatzky and Nessov, 1977). This description implies that the parietal contribution must be large, as indicated by figures 1 and 2 in Nessov (1977). This feature is employed here as a character of the Trionychoidae. *Ferganemys* is also like *Adocus* in retaining primitive features such as the basis tuberculi basilis, a large foramen stapedio-temporale, and small foramen caroticum laterale.

Shachemys is more problematical than *Ferganemys. Shachemys* Kuznetsov, 1976, was originally based on a series of isolated elements of a carapace and plastron from the Upper Cretaceous of Kazakhstan. This genus was further described and figured by Nessov (1986). It is like *Adocus* in having fine punctate sculpturing, but this sculpturing apparently differs in detail from that of *Adocus* and *Ferganemys.* Like *Adocus* and *Basilemys,* it has medially expanded pectoral scutes, and like *Adocus* and *Ferganemys,* it has an enlarged posterior suprapygal. *Shachemys* and *Ferganemys* also have the posterior marginal scutes extending dorsally beyond the peripheral elements. However, *Shachemys* exhibits a series of features that are not known to occur elsewhere in the Adocidae. It lacks a cervical scale and inframarginal scales, as well as neural bones. Also the epiplastra are apparently hinged transversely across the anterior lobe of the plastron. If *Shachemys* is considered an adocid, these features must all be treated as autapomorphies. An absence of inframarginals and the presence of mobile epiplastra also occur in *Mongolemys,* which

we consider to be a testudinoid. The possibility that *Shachemys* could be either a trionychoid or testudinoid suggests that it should be referred to Eucryptodira, incertae sedis, until it is better known.

Hay (1908a) characterized *Adocus* as "the least modified of the Dermatemydidae." Since his concept of the Dermatemydidae (inclusive of *Adocus, Basilemys, Dermatemys, Baptemys, Hoplochelys,* and *Anosteira*) is equivalent to our use of Trionychoidea, we are in general agreement with this statement, especially applied to shell morphology. However, derived features of the skull, lower jaw, and neck indicate that *Adocus* is more transformed than previously recognized and is a member of the Trionychoidae.

MONOPHYLY OF THE
NANHSIUNGCHELYIDAE, *PELTOCHELYS,*
AND THE TRIONYCHIA
(Fig. 22, Node 3)

Monophyly of the sister-group to the Adocidae is supported by characters of skull morphology. However, the skulls of *Basilemys* and *Peltochelys* remain unknown. *Basilemys* is included in this clade because it shares derived features of the shell, pelvis, and feet with *Nanhsiungchelys. Peltochelys* is included because it shares derived shell features of the Trionychoidea and Trionychia. The numerical method employed here (PAUP 2.4; Swofford, 1984) assumes that these and all missing values should take the most parsimonious condition based on known character states.

The important skull features at this level are those shared by *Nanhsiungchelys,* members of the Carettochelyidae, and members of the Trionychidae. In these taxa the vomer is reduced. It does not reach the palatine-pterygoid suture as in *Adocus* and nearly all other cryptodires. The anterior palate of these taxa is further derived in having the palatines truncated anteriorly, allowing a large area of communication between the fossa orbitalis and the apertura narium interna, and in having the processus pterygoideus externus nearly absent. The former feature also occurs in some chelonioids that lack a secondary palate (*Dermochelys*); the latter occurs also in some kinosternids and some *Dermatemys,* and

outside of the Trionychoidea in some cheloniids and testudinoids (Meylan, 1987). The quadrate in *Nanhsiungchelys* and members of the Trionychia completely encloses the stapes. This closure of the incisura columellae auris is unique within the Trionychoidea. It occurs outside the superfamily in meiolaniids, chelydroids, and testudinids (Gaffney, 1979; Meylan, 1987). This closure is one of the few features visible on the crushed skull of *Basilemys* (NMC 8890). In this specimen the incisura columellae auris is closed; unfortunately, it cannot be determined with certainty that this is not due to crushing.

In its general form, the skull of *Nanhsiungchelys* is like that of carettochelyids and trionychids in having significantly reduced cheek emargination. Reduction of cheek emargination occurs also within the Kinosternoidae in *Dermatemys* and in the Kinosternidae. *Nanhsiungchelys* is also like *Carettochelys* in having a sculptured skull roof. In these taxa the texture of the skull roof sculpture approaches that of the shell. Sculpture of this type is absent in other trionychoids including members of the Trionychidae.

Although Gaffney (1979) considered *Nanhsiungchelys* to be Cryptodira incertae sedis, several authors have anticipated the results of the current study by suggesting a relationship between this genus and other members of the Trionychoidea (Nessov and Julinen, 1977; Hirayama, personal commun., 1986).

MONOPHYLY OF THE NANHSIUNGCHELYIDAE
(Fig. 22, Node 4)

Our data suggest that *Nanhsiungchelys* and *Basilemys* form a monophyletic group that is the sister-group to *Peltochelys* and the Trionychia. This clade is best termed the Nanhsiungchelyidae and probably includes the genus *Zangerlia* Mlynarski (1972).

Two features are suggested to support monophyly of this family: a reduced number of phalanges and no thelial process. The presence of a thelial process is considered to be primitive for the Trionychoidea. The feet of *Basilemys* are best known from AMNH 5448 from the Belly River Formation. Both hind feet are preserved and are nearly completely

articulated. They indicate a phalangeal formula of 2-2-2-2-1 for this genus. The foot of *Nanhsiungchelys* was described as having short, broad phalanges (Yeh, 1966) and being testudinid-like. It appears to have shortened digits, but further preparation of the type is necessary to verify this.

Nanhsiungchelys and *Basilemys* are also similar in having "pock-mark" sculpturing (Mlynarski, 1972), and in the form of their anterior plastral lobe. In both genera this lobe is a short triangle rounded anteriorly with a tendency to fuse the intergular sulcus (set 1 scales) (type of *B. nobilis,* USNM 11084, and *Nanhsiungchelys*) and to have the extragulars (set 2) greatly reduced (type of *B. variolosa,* type of *B. nobilis,* USNM 11084) or absent (Yeh, 1966; Langston, 1956).

Zangerlia was described from the Upper Cretaceous Upper Nemegt Beds of Mongolia and is reported to be similar to *Basilemys* in having "pock-mark" sculpturing, a 6 4 6 6 6 neural formula, reduction in the phalangeal formula, and contact between plastral and marginal scutes (as in *Basilemys*; see Langston, 1956). Unlike *Basilemys,* it retains a full set of four inframarginals (primitive) and has a midline keel (derived). Sukhanov and Narmandakh (1974) suggested synonymizing this genus with *Basilemys.* However, the derived shell feature which best defines *Basilemys,* the absence of an inframarginal series, does not occur in *Zangerlia,* and thus it is not desirable to add *Zangerlia* to this genus. *Zangerlia* can be recognized by its middorsal keel, but the data are insufficient to allow determination of its relationships to *Nanhsiungchelys* and *Basilemys.*

Mlynarski (1976) included the genera *Basilemys, Zangerlia, Tretosternon* (including the synonyms *Peltochelys* and *Helochelydra*), and *Peishanemys* in his Adocinae. The data available to us suggest that *Basilemys* and *Zangerlia* share a common ancestor with *Nanhsiungchelys,* not shared by *Adocus* or any other trionychoids; they are better placed in the Nanhsiungchelyidae. Meylan (1988) has shown that *Peltochelys* is not a synonym of *Tretosternon* but rather a trionychoid and is best treated as the sister-group of the Trionychia. *Tretosternon* (including its synonym *Helochelydra*) is best placed in the Pleurosternidae (Meylan, 1988). *Peishanemys* has

been placed in the Testudinoidea by Chkhik-vadze (1975) and Nessov (1981) and we know of no characters that support its inclusion in the Trionychoidea.

MONOPHYLY OF *PELTOCHELYS* AND THE TRIONYCHIA
(Fig. 22, Node 5)

Our numerical analysis of data for the Trionychoidea suggests a number of plausible hypotheses for the placement of *Peltochelys* among the Trionychoidea. Although these hypotheses are equally parsimonious, one of us (Meylan, 1988) has argued that the genus be considered the sister-group to the Trionychia. In the arrangements that place *Peltochelys* closer to the base of the cladogram, it is excluded from placement as sister taxon to the Trionychia because it lacks certain relatively insignificant derived characters. Instead it retains such trivial primitive characters as costal bones not meeting on the midline, pectoral scutes not reaching the entoplastron, and possession of two suprapygals. An equally parsimonious hypothesis, in which homoplasy in the derived features of *Peltochelys* is minimized, places *Peltochelys* as the sister taxon to the Trionychia. Characters supporting this relationship include the presence of a sinuous midline plastral sulcus, the reduction of the number of peripheral elements to 10 per side (or fewer in the Trionychidae), and the presence of ventral processes of the nuchal (Meylan, 1988). Reduction in the number of peripherals occurs elsewhere only in the Kinosternidae but the presence of a meandering midline plastral sulcus suggests the Trionychoidae rather than the Kinosternoidae.

The relationship of *Peltochelys* to the Trionychia was proposed by Hummel (1929: 428) who figures it as the common ancestor of the Trionychia and Chelydroidea. However, Lydekker's (1889) synonymy of *Peltochelys* with *Tretosternon* has resulted in some confusion, with both genera being considered members of the Dermatemydidae (in the broad sense) (Mlynarski, 1976). But *Peltochelys* is easily distinguished from *Tretosternon* which has large, medially meeting mesoplastra (Meylan, 1988) and the former has been placed among the Carettochelyidae (Ji-menez-Fuentes, 1971; Broin, 1976) and Nanhsiungchelyidae (Nessov and Julinen, 1977).

MONOPHYLY OF THE TRIONYCHIA
(Fig. 22, Node 6)

Monophyly of the Trionychia is one of the best corroborated hypotheses of turtle phylogeny. Meylan (1987) listed 17 morphological features that support the recognition of the Trionychia among living taxa. Inclusion of fossils in the hypothesis of relationship among the members of the Trionychoidea suggests that about one-half of these characters have a greater level of generality than if only living taxa are examined. Nonetheless, we know of no other competing hypothesis of sister-group relationship for the families Carettochelyidae and Trionychidae. Non-morphological data including karyology (Bickham and Carr, 1983; Bickham et al., 1983) and serology (Frair, 1985) also support monophyly of the Trionychia. The relationships among the genera of the Trionychia are discussed by Meylan (1985, 1987, 1988) and are not elaborated on in the present study.

MONOPHYLY OF THE KINOSTERNOIDAE
(Fig. 22, Node 7)

Hutchison and Bramble (1981) examined the relationships among the group of trionychoids that we have termed the Kinosternoidae (Gaffney and Meylan, 1988). To those taxa included in this clade (labeled as Dermatemydinae plus Kinosternidae in their figure 4), we would add the genus *Emarginachelys*. Although this genus was originally referred to the Chelydridae, it exhibits six of the eight characters that diagnose the Kinosternoidae as listed by Hutchison and Bramble (1981) including: absence of scale set 2, absence of scale set 4, reduced width of posterior lobe of the plastron, reduced number of inframarginals (secondarily increased in *Dermatemys*), inguinal scale overlapping hyo-hypoplastral suture, and absence of pedicellate sculpturing.

The numerical analysis of data for the current study has not included considerations of the width of the posterior plastral lobe, position of the inguinal scale, or presence/ab-

sence of pedicellate sculpturing. Variation in the shape of the posterior plastral lobe among the genera considered in this study is difficult to divide into discrete morphologies. The position of the inguinal scale over the hyo-hypoplastral suture occurs in all trionychoid taxa with three or fewer inframarginals, apparently making these features redundant. Characters of sculpture are difficult to homologize and have been ignored. Furthermore, the absence of sculpturing in the Kinosternoidae may best be explained as retention of the primitive condition for turtles.

The characters most important for supporting monophyly of the Kinosternoidea, including *Emarginachelys,* are those most thoroughly discussed by Hutchison and Bramble (1981): the loss of certain scales of the plastron. Unlike all of the other scaled members of the Trionychoidae, all chelonioids, and all nonpolycryptodiran cryptodires, the kinosternoids do not have a complete set of seven pairs of plastral scales. *Emarginachelys* was figured with four pairs of plastral scales but, based on further preparation of the type and a referred posterior plastral lobe in the UCMP collection, it can now be shown to have five pairs (J. H. Hutchison, personal commun.). Based on the positions of the figured scales and the postulates of Hutchison and Bramble (1981) concerning scale loss, the five pairs are considered to be scale sets 1, 3, 5, 6, and 7, or gulars, humerals, abdominals, femorals, and anals. All other kinosternoids also lack sets 2 and 4, and these characters support monophyly of the epifamily.

Another derived feature found in all members of the Kinosternoidae is the absence of scale sulci on the skull roof. These sulci are present primitively in the Trionychoidea.

Emarginachelys was originally described as a chelydrid (Whetstone, 1978). However, a reexamination of this taxon suggests that it should be placed among the Trionychoidea. Whetstone (1978) listed five characters which he considered to support monophyly of the Chelydridae, including *Emarginachelys*: (1) cruciform plastron, (2) long costiform processes, (3) ligamentous attachment of the plastron to carapace, (4) an elongate jugal, and (5) pectineal processes of pelvis nondivergent. All five of these characters are of

questionable value because they may represent primitive conditions.

Following Gaffney and Meylan (1988), cruciform plastra are primitive for chelydrids and chelonioids and thus may be considered primitive for the Polycryptodira. Large costiform processes appear sporadically among cryptodires, in chelydrids, in modified form in dermochelyids and trionychids, and in *Dermatemys.* Their apparent absence in many fossil taxa may only reflect the fact that they are completely hidden in articulated shells as is the case in *Dermatemys.* Large costiform processes are present in hatchlings and juveniles of many cryptodires and their differential retention in adults appears to be highly variable. A nonsutural contact at the bridge occurs both in chelydrids and chelonioids and could be considered primitive for all polycryptodirans. Similarly, a large jugal with surrounding contacts like those of *Emarginachelys* is widespread among eucryptodires and must be considered primitive. The pectineal processes of *Emarginachelys* and chelydrids (fig. 21F) are like those of *Adocus* (fig. 20A, B), *Basilemys* (fig. 21E), and plesiochelyids (Bräm, 1965) in being anteriorly directed. The distribution of this feature, like those listed above, suggests that it may be the generalized condition and thus weakens Whetstone's argument for the monophyly of the Chelydridae inclusive of *Emarginachelys.*

Three characters argued by Gaffney (1975) to support monophyly of the Chelydridae do not occur in *Emarginachelys.* All members of the family except *Chelydropsis* have some degree of hooking of the premaxillae, all have the frontals excluded from the orbits, and all have the incisura columellae auris enclosed around the stapes. It might be argued, however, that these are all features of those members of the Chelydridae that are the sistergroup to *Emarginachelys* (as in fig. 21 in Whetstone, 1978). Therefore, it is the presence of derived features of the Chelomacryptodira, and specifically the Trionychoidea, in *Emarginachelys* that suggest that this genus should not be placed among the Chelydridae.

The monophyly of the Chelomacryptodira (Trionychoidea plus Testudinoidea) is supported by a single character, the absence of postorbital-squamosal contact. This feature is quite apparent in *Emarginachelys* (figs. 7

and 8 in Whetstone, 1978). Furthermore, *Emarginachelys* has a maxillary tooth, a feature primitively diagnostic of the Trionychoidea. It has a 10th thoracic vertebra with transverse processes that are free of the overlying costal bones (among chelydrids this occurs only in some *Chelydra*). *Emarginachelys* also has a thelial process and lacks a basis tuberculi basalis, both of which are considered here to be features of the Trionychoidea. Participation by the palatine in the braincase cannot be determined from the type skull.

The position of *Emarginachelys* among the Kinosternoidea has been considered as part of our numerical cladistic analysis. The most parsimonious solution suggests that *Emarginachelys* be considered the sister taxon to the remainder of the Kinosternoidae. This is supported by characters of the cervical vertebrae and cranial circulation. Monophyly of the Dermatemydidae and Kinosternia, exclusive of *Emarginachelys,* is supported by the presence of a biconvex cervical number 2 or 3, a reduced or absent foramen stapediotemporale, and a foramen caroticum laterale significantly larger than the foramen anterius canalis carotici interni. We can be certain that *Emarginachelys* has the primitive condition for at least two of these features: the fourth cervical is biconvex and the foramen stapedio-temporale is large.

MONOPHYLY OF THE DERMATEMYDIDAE,
AGOMPHUS, AND KINOSTERNIA
(Fig. 22, Node 8)

Monophyly of the restricted Dermatemydidae (Gaffney and Meylan, 1988), *Agomphus,* and the Kinosternia (*Hoplochelys* and the Kinosternidae) is supported unequivocally by three characters. Unfortunately, the condition of these characters is not known for *Agomphus* or *Hoplochelys.* In dermatemydids and kinosternids, the second or the third cervical vertebra is biconvex (Williams, 1950; current study). Primitively, the fourth cervical is biconvex in cryptodires. In dermatemydids and kinosternids, the cranial arteries differ significantly from those of most cryptodires. The foramen caroticum laterale and the foramen anterius canalis carotici in-

terni are not equal in size, the former being significantly larger than the latter. This condition occurs elsewhere in the Euchelonioidea (Gaffney and Meylan, 1988). Dermatemydids and kinosternids also show reduction (kinosternids) or closure (dermatemydids) of the foramen stapedio-temporale. This type of reduction is not known to occur among other turtles.

Two other characters might support monophyly of the Dermatemydidae and Kinosternia. With the exception of *Dermatemys,* all members of this group (for which a pelvis is known) have an ilial notch (see fig. 21B) and all except *Baptemys* lack cheek emargination. Both of these features could, with equal parsimony, have occurred once within the Dermatemydidae and once in the Kinosternia, which eliminates their support for the arrangement preferred here.

The skull, neck, and pelvis of *Hoplochelys* and *Agomphus* remain unknown. The inclusion of these two genera in this study relies on features that they share with the Kinosternidae. These features are discussed below.

MONOPHYLY OF THE DERMATEMYDIDAE
(Fig. 22, Node 9)

Three characters provide strong corroboration for a monophyletic Dermatemydidae. If this family is restricted to the genera *Dermatemys* and *Baptemys,* it is diagnosed by the presence of axillary buttresses that reach the overlying costal bones (fig. 12B), the presence of commissural ridges on the maxillary triturating surfaces (figs. 6, 7), and the absence of a foramen stapedio-temporale.

Plastral buttresses that extend to the costals are not found in chelydrids, chelonioids, or elsewhere among the Trionychoidea. When they do occur elsewhere among the Polycryptodira (in the Testudinoidea), both the axillary and inguinal pairs reach the overlying costal bones (except in some kinetic forms). The presence of a commissural ridge and complete closure of the foramen stapedio-temporale may be unique to the Dermatemydidae. However, certain species of the genus *Kinosternon* have the foramen stapedio-temporale reduced to the point that it is

barely visible (e.g., *Kinosternon herrerai,* UF 57916).

MONOPHYLY OF *AGOMPHUS* AND THE KINOSTERNIA
(Fig. 22, Node 10)

Elsewhere we have termed the sister-group to the Dermatemydidae as the Kinosternia (Gaffney and Meylan, 1988). This taxon, of unspecified rank, was proposed to recognize the special relationship of *Hoplochelys* to the Kinosternidae. Examination of the genus *Agomphus* suggests that it, too, may be part of the clade that is the sister-group to the Dermatemydidae. However, in order to maintain nomenclatural stability, we will continue to restrict the name Kinosternia to those taxa it originally included rather than modify its definition to include *Agomphus.* The limited data for *Agomphus* suggest that it is the sister-group to the Kinosternia.

Agomphus is a shell taxon and can be placed among the Kinosternoidae only because it has a reduced number of plastral scales (five pairs; Hutchison and Bramble, 1981). It was considered the sister-group to the Dermatemydidae plus Kinosternia (*Hoplochelys* and the Kinosternidae) (Hutchison and Bramble, 1981: fig. 4). The monophyly of the latter set of taxa was supported by the presence of tricarination, costiform processes that span peripheral 1, and a reduced bridge, all of which are lacking in *Agomphus.* However, each of these characters is subject to an alternative interpretation. Tricarination is absent in most species of *Baptemys* and in *Dermatemys* and is actually more parsimoniously explained by independent occurrences within *Baptemys* and the Kinosternia rather than an appearance early in the Kinosternoidae with independent loss within *Baptemys* and in *Dermatemys.* Short costiform processes (in *Baptemys*) and a long bridge (in *Dermatemys*) are both found within the Dermatemydidae. Thus, these characters could be used as evidence of the monophyletic Dermatemydidae plus Kinosternia only by assuming that a reversal has occurred in each character within the Dermatemydidae. They could otherwise be viewed as occurring independently within dermatemydids and in all Kinosternia.

Given the ambiguity in the characters mentioned above, we are forced to rely on the number of inframarginals, an admittedly weak character, for our decision to propose that *Agomphus* be considered the sister taxon to the Kinosternia. Inspection of table 2 will reveal that *Agomphus* is like *Hoplochelys* and kinosternids in never having more than three inframarginals per side; in fact, some specimens have only two. Some *Baptemys* also have only three inframarginals per side, but most have four on at least one side. *Dermatemys* specimens have four or five per side.

The variability of this character makes it less than ideal. However, it is used here to provisionally determine the phylogenetic position of *Agomphus.* Node 10 in figure 22 is supported by a single character: never more than three inframarginals present. Only the availability of additional data will allow us to retest the phylogenetic position of *Agomphus* among the Trionychoidea. The absence of an enlarged axillary buttress suggests that *Agomphus* does not belong within the dermatemydids as defined here. However, it might be the sister-group to the Dermatemydidae, the sister-group to the Dermatemydidae plus *Hoplochelys* and the Kinosternidae (as suggested by Hutchison and Bramble, 1981), or perhaps it lies even closer to the genus *Emarginachelys.*

MONOPHYLY OF THE KINOSTERNIA
(Fig. 22, Node 11)

The Kinosternia was originally diagnosed by the reduction or loss of scale set 5, the abdominals (Hutchison and Bramble, 1981), and by the presence of tricarination (considered to occur independently within *Baptemys*) (Gaffney and Meylan, 1988). Hutchison and Bramble (1981) also list megacephaly as evidence for this clade but the skull of *Hoplochelys* is unknown.

The monophyly of this taxon is best supported by the reduction and loss of scale set 5, a character whose use depends on the assignment of plastral scale homologies provided by Hutchison and Bramble (1981). We can find no characters that conflict directly with the evolutionary scenario for plastral scales proposed by these authors and several characters are consistent with it (reduction in

inframarginals, reduction in peripherals). However, the discovery of a skull of *Hoplochelys* would provide the best test for the currently favored arrangement.

MONOPHYLY OF THE KINOSTERNIDAE
(Fig. 22, Node 12)

Monophyly of the Kinosternidae is supported by a series of shell, cranial, and non-shell postcranial characters. However, since the skulls of *Agomphus* and *Hoplochelys* are as yet unknown, it is conceivable that the distribution of certain characters used here is actually greater than described. Shell characters diagnosing the Kinosternidae include the presence of only 10 pairs of peripheral bones (considered to occur independently in *Peltochelys* and the carettochelyids), abdominal scales absent, incised anterior musk duct, one suprapygal (occurs independently in Trionychia), plastral kinesis (occurs independently in the Trionychia), and never more than two inframarginals present (occurs also in *Basilemys*). Kinosternids also lack complete connections of the ribs of the ninth and tenth body vertebrae to the eighth costal (fig. 14). The presence of two articular surfaces on the eighth costal in one of the best preserved specimens of *Hoplochelys* (USNM 8527) indicates that at least the ninth vertebra was connected to the eighth costal in this genus. The second articular surface may have served as the site of contact of the tenth body vertebra, the ilium, or both. Characters that can at present be used to diagnose the Kinosternidae but are not known for *Hoplochelys* or *Agomphus* include: frontal excluded from orbit, maxilla in contact with the quadratojugal (occurs also in *Carettochelys*), absence of a maxillary tooth, reduction of the external process of the pterygoid, and the presence of a pair of ventral processes of the eighth cervical (the last three characters occur independently in the Trionychia).

The morphological data provide abundant evidence that Staurotypinae is not closely related to Testudinoidea, as suggested by Bickham and Carr (1983). The single character supporting their arrangement, a group B macrosome to which a supposedly homologous microsome has fused, is called into question. The conflict in the data could be resolved by:

(1) considering the microsomes fused to the same group B macrosome to be nonhomologous (see King, 1985); (2) considering the microsomes homologous but the fusion to the same macrosome homoplasious; or (3) considering the numerous morphological characters cited here to all be homoplasious. For the present, the first alternative for resolving this character conflict seems most appropriate.

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