

Chapter 18

A New Species of *Bairdemys* (Pelomedusoides: Podocnemididae) from the Oligocene (Early Chattian) Chandler Bridge Formation of South Carolina, USA, and Its Paleobiogeographic Implications for the Genus

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Abstract A new species of podocnemidid pleurodire turtle, *Bairdemys healeyorum*, is described from the upper Oligocene Chandler Bridge Formation of South Carolina, USA, on the basis of a nearly complete shell found with associated skull fragments, lower jaw, girdle elements, and limb elements. This is the first record of an Oligocene pleurodire turtle from North America. The shell and lower jaw are unique in detail but similar in overall morphology to equivalent parts of *Bairdemys venezuelensis* and *B. sanchezi*. The plastron of this new species also shares many features with the previously described Maryland Miocene species of podocnemidid, “*Taphrosphys*” *miocenica*, so the Miocene taxon is here referred to *Bairdemys*. In the Oligocene and Miocene, North and South America were separated by broad expanses of salt water, so *Bairdemys* probably was salt-water tolerant and reached North America by “island hopping” from South America across the Caribbean Sea.

Keywords Calvert Formation • Pungo River Formation • Shell • Skull • Venezuela

Introduction

A largely complete shell and other skeletal elements of a side-neck turtle were discovered in 1989 by Craig and Alice Healey, two experienced museum volunteers, during

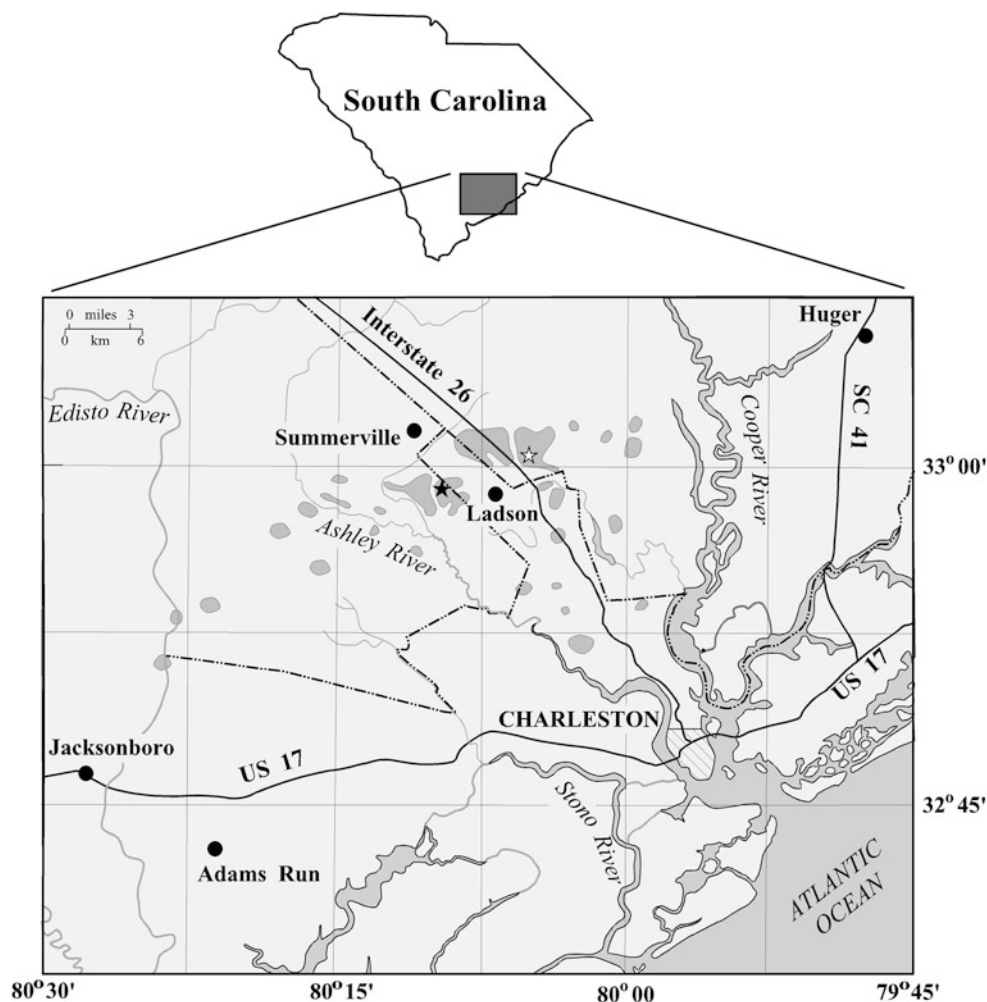
development of the Crowfield Plantation neighborhood near Ladson in Dorchester County, South Carolina, northwest of the city of Charleston (Fig. 18.1). The specimen was recovered from the upper Oligocene (lower Chattian) Chandler Bridge Formation (Fig. 18.2). The Chandler Bridge Formation, although typically only 2–4 feet thick, is widespread in the Ladson-Summerville region. It long went unrecognized for lack of outcrops, but major suburban expansion along the Interstate 26 corridor from Charleston northwest through Ladson and Summerville, South Carolina created many new excavations throughout that area, especially in the 1970s and 1980s. It was during this building boom that the Chandler Bridge Formation was recognized as a new and paleontologically important stratigraphic unit (Sanders et al. 1982). Based primarily on its cetacean fauna, the Chandler Bridge Formation can be assigned to the early part of the late Oligocene (early Chattian), which places its age at about 27–28 Ma.

The Chandler Bridge Formation was deposited in a coastal marine setting, with estuarine, lagoonal, beach, and shallow marine environments being represented (Sanders et al. 1982; Weems and Sanders 1986; Katuna et al. 1997; Cicimurri and Knight 2009). There apparently was little fluvial input into this depositional environment (*contra* Katuna et al. 1997) because the preserved vertebrate fauna overwhelmingly consists of marine sharks and rays (Cicimurri and Knight 2009), marine bony fishes (e.g., Fierstine and Weems 2009), cetaceans, dugongs, sea turtles, and sea birds (Sanders 1980). Other animal remains are encountered only rarely, such as land birds, land mammals, and salt-water tolerant crocodylians (Erickson and Sawyer 1996). Equally rare are the remains of gopher tortoises (one specimen; Franz and Franz 2004), soft-shelled turtles (one specimen; ChM PV4882, unpublished), and the side-neck turtle described here (two specimens). No remains have been found that are referable to typical freshwater fish (such as sturgeons, gars, ictalurid catfishes, etc.), amphibians, most kinds of freshwater turtles (emydids, kinosternids, chelydrids), alligators, or aquatic freshwater mammals.

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Fig. 18.1 Map of the Charleston region in the southeastern part of South Carolina, USA, showing the distribution of the Chandler Bridge Formation (shaded in *medium gray*), and the locations where the holotype (*white star*) and referred specimen (*black star*) of *Bairdemys healeyorum* were found. City of Charleston shown by *diagonal hachure*. Geology adapted from Weems and Lewis (2002)



Systematic Paleontology

Order Testudines Linnaeus 1758
 Suborder Pleurodira Cope 1864
 Hyperfamily Pelomedusoides Cope 1868a
 Family Podocnemididae Cope 1868b
 “*Shweboemys* Group” sensu Meylan 1996
Bairdemys Gaffney and Wood 2002

Type species: *Bairdemys hartsteini* Gaffney and Wood 2002

Referred species: *Bairdemys venezuelensis* (Wood and Díaz de Gamero 1971), *Bairdemys hartsteini* Gaffney and Wood 2002, *Bairdemys sanchezi* Gaffney et al. 2008, *Bairdemys winklerae* Gaffney et al. 2008, *Bairdemys miocenica* (Collins and Lynn 1936; new combination), *Bairdemys healeyorum*, sp. nov. (this study).

Occurrence: Oligocene of South Carolina; Miocene of Venezuela, Puerto Rico, and the United States (Maryland and North Carolina).

Revised diagnosis (expanded from Gaffney and Wood 2002): A “*Shweboemys* Group” Pelomedusoides turtle (sensu Meylan 1996) known from skull, jaw, shell, and some girdle and limb elements; secondary palate shorter than in all “*Shweboemys* Group” except “*Shweboemys*” *gaffneyi* (per Gaffney and Wood 2002); medial edges of palatal cleft curved as in “*Shweboemys*” *gaffneyi*; ventral convexity on triturating surface larger than in all other “*Shweboemys* Group”; eustachian tube separated by bone from rest of *fenestra postotica* in contrast to all other known Podocnemididae; *antrum postoticum* extremely small and slit-like in contrast to all other “*Shweboemys* Group”; frontal and prefrontal strongly convex on dorsal surface in contrast to all other “*Shweboemys* Group”; basisphenoid separated from palatines by medially meeting pterygoids as in “*Shweboemys*” *antiqua* (per Gaffney and Wood 2002) and *S. pilgrimi*; basioccipital longer than in *Shweboemys pilgrimi*; jugal-ptyergoid contact prevents palatine-parietal contact. Intergular, gular, and humeral scutes greatly reduced and restricted to the far anterior plastron, pectoral

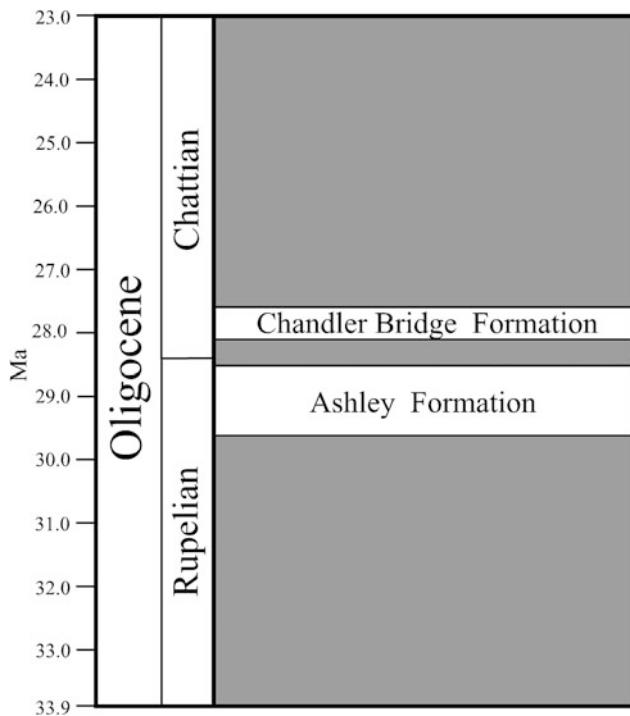


Fig. 18.2 Chart showing the position and age of the Chandler Bridge Formation within the Oligocene stratigraphic column of the Charleston region in the southeastern part of South Carolina, USA (after Weems et al. 2006). Most of the fossil vertebrate material in this area has come from the Chandler Bridge Formation (deposited in near-shore to lagoonal environments) and the Ashley Formation (deposited in a mid-shelf environment)

scutes compensatorially greatly expanded forward. Caput of humerus strongly elongated into an elliptical shape, its long axis close to parallel with the humerus shaft.

Bairdemys healeyorum sp. nov.

(Figs. 18.3, 18.4, 18.5, 18.6, 18.7, 18.8, 18.9, 18.10, 18.11, 18.12)

Holotype: South Carolina State Museum specimen SC 90.16, a largely complete skeleton, but lacking most of the skull and the distal limbs (Figs. 18.3a–d, 18.4, 18.6, 18.9, 18.10).

Holotype unit, locality, and age: Chandler Bridge Formation; northeastern shore of Crowfield Lake (now submerged), northeast of Ladson, Dorchester County, South Carolina, USA (Fig. 18.1); late Oligocene, early Chattian (Fig. 18.2).

Referred specimen: Charleston Museum specimen ChM PV4794, a partial anterior carapace from Bed 2 of the Chandler Bridge Formation. Found by Albert E. Sanders and Peter S. Coleman, 07 July 1979, north side of Ladson Road (County Road 230) about 0.12 mile (0.2 km) east of Chandler Bridge Creek, Dorchester County, South Carolina, USA.

Diagnosis: A species of *Bairdemys* differing from *Bairdemys hartsteini* and *Bairdemys sanchezi* in its relatively narrower lower jaw, from *Bairdemys venezuelensis* and *Bairdemys sanchezi* in the absence of a raised ridge along the midline of the fused dentaries, from *Bairdemys winklerae* in its relatively narrow quadrate articular surfaces and in the short length of the quadrate shaft above the articular surface which produces a very stocky appearance in lateral view, and from *Bairdemys miocenica* in its relatively wider and shorter anterior plastral lobe, relatively wider nuchal, and less robust humeral shaft.

Description

Skull: Fragments of a right maxilla and both quadrates were found, which suggest that the skull was preserved with the rest of the skeleton but was destroyed at the time the specimen was unearthed. The preserved piece of the right maxilla is very imperfect (Fig. 18.3b) but clearly lay below the posterior margin of the orbit and had a palatal shelf component that formed the edge of a secondary palate. The depth of this bone is less than found in *Bairdemys hartsteini*, *B. venezuelensis*, or in *B. sanchezi*, but is similar to the rearmost portion of the maxilla of *B. winklerae*. This suggests that the maxilla extended well up along the lower posterior edge of the orbit as in *B. winklerae*, presumably reducing the degree of contribution of the jugal to the orbital rim. Only the distal ends of the quadrates are preserved; the left is more complete than the right (Fig. 18.3c, d). The articular surface is relatively narrow side-to-side as in *B. hartsteini*. Also as in *B. hartsteini*, the length of the quadrate shaft above its articular surface is relatively short and therefore stouter in lateral appearance than in *B. venezuelensis*, *B. winklerae*, or *B. sanchezi*.

Lower jaw: The lower jaw is nearly complete (Fig. 18.4a) and shows an extensive fusion and rearward expansion of the triturating portion of the dentaries, which is typical of turtles that have a matching secondary palate on the roof of the mouth. This particular lower jaw morphology is very similar to the jaw morphology of *Bairdemys venezuelensis* and *B. sanchezi*, and all three species represent an intermediate stage in what appears to be a morphocline between the less specialized lower jaw of podocnemidids such as *?Roxochelys* and the highly specialized jaw of shweboemines such as *Stereogenys* (Fig. 18.5). The bothremydid *Bothremys cooki* also has an expanded secondary palate and triturating surface on the lower jaws (Fig. 18.5), but its lower jaw specializations (including a very high and broad lingual ridge and rising labial ridges that form large, deep, cone-shaped pits) are quite

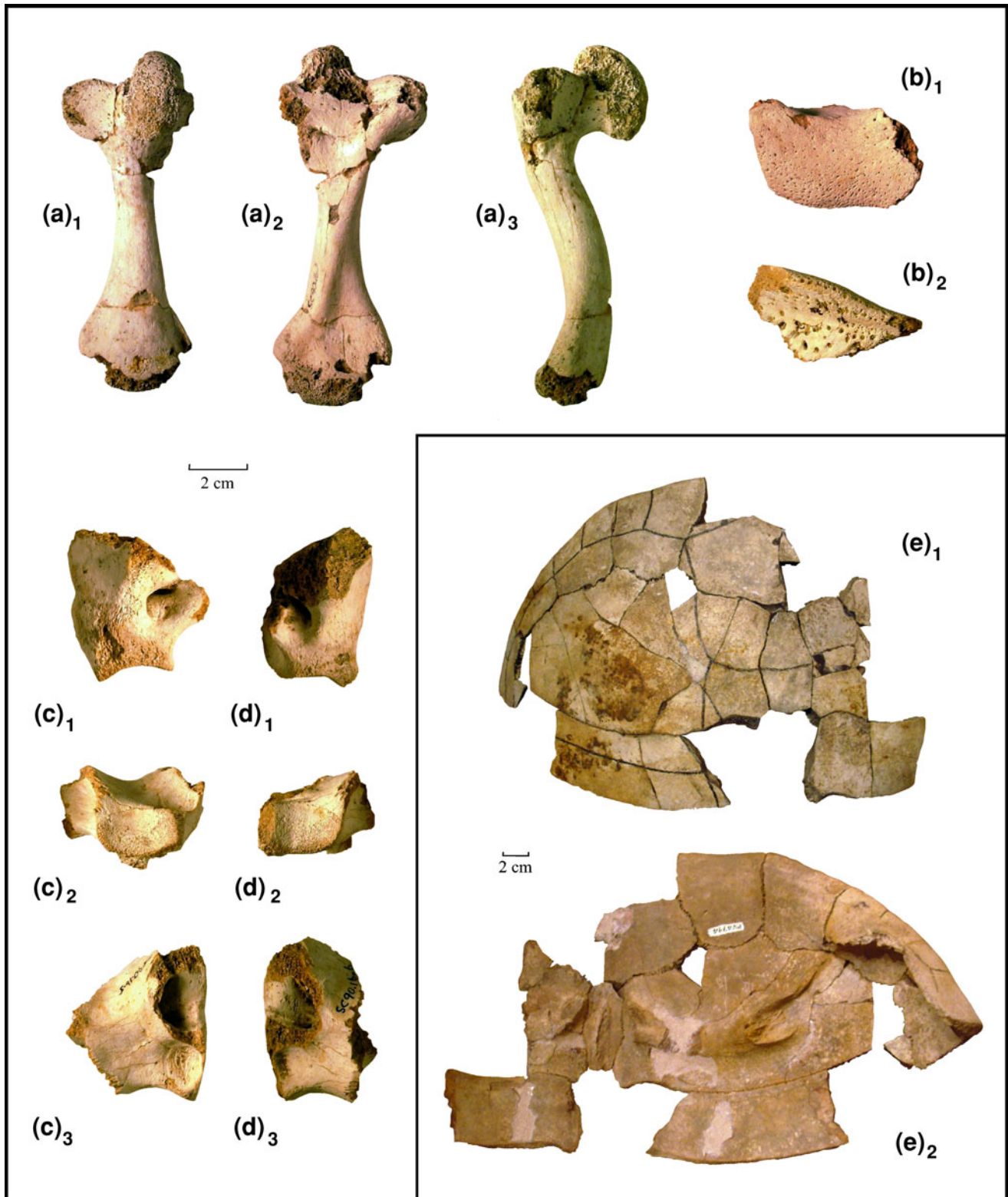


Fig. 18.3 Skeletal elements of *Bairdemys healeyorum*, from the Chandler Bridge Formation (late Oligocene), South Carolina, USA. **a**₁–**d**₃ Non-shell elements from holotype skeleton (SC 90.16): **a** humerus in **a**₁ internal, **a**₂ antero-lateral, and **a**₃ posterolateral views; **b** right maxilla in **b**₁ external and **b**₂ ventral views, both with anterior

end to right; **c** left quadrate in **c**₁ posterior, **c**₂ ventral, and **c**₃ anterior views; **d** right quadrate in **d**₁ posterior, **d**₂ ventral, and **d**₃ anterior views. **e** Anterior portion of referred carapace (ChM PV4794) in **e**₁ external and **e**₂ visceral views

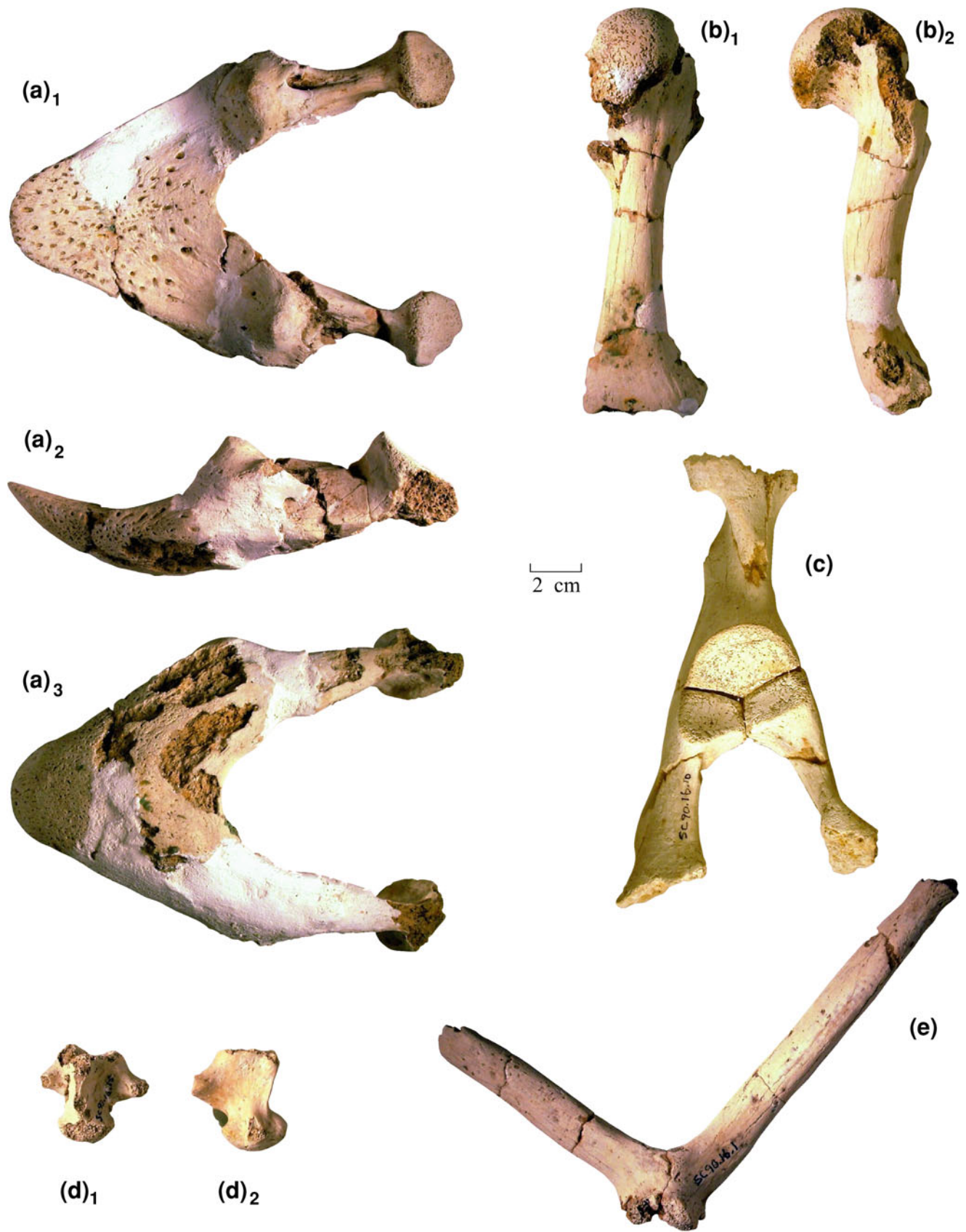


Fig. 18.4 Skeletal elements of *Bairdemys healeyorum*, part of holotype skeleton (SC 90.16), from the Chandler Bridge Formation (late Oligocene), South Carolina, USA. a Fused lower jaws in (a₁) occlusal (internal), a₂ left lateral, and a₃ ventral views. b

dorsal b₁ and posterior b₂ views. c Left pelvic girdle in external view. d Cervical vertebrae: eighth cervical d₁ in ventral view and sixth(?) cervical d₂ in lateral view, both with anterior end towards top of figure. e Right scapula in posterior view

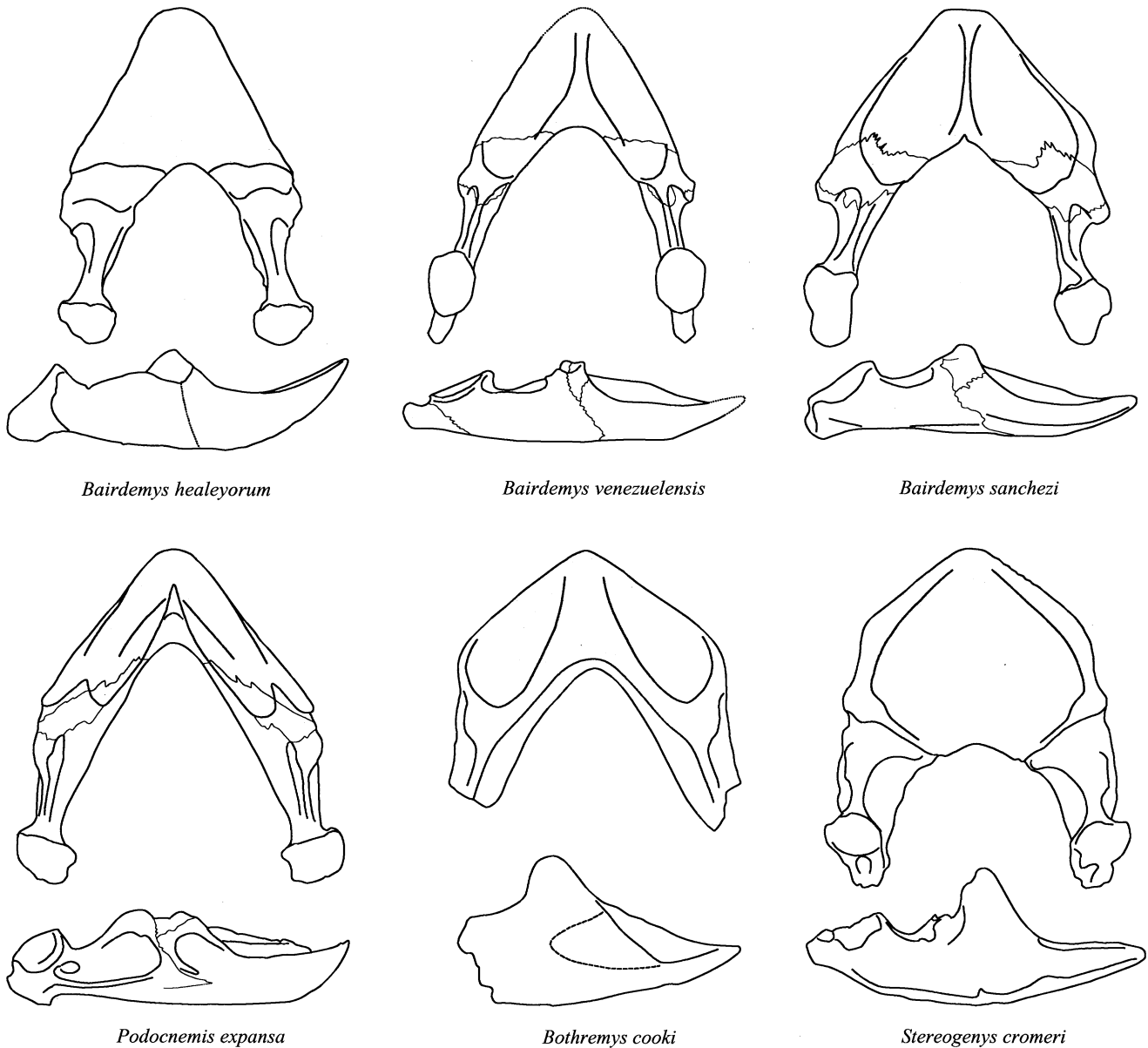


Fig. 18.5 Comparison of lower jaws in different species of *Bairdemys* and other podocnemidid turtles. For each species, jaws are shown in occlusal (top) and right lateral (bottom) views. *Bairdemys healeyorum* based on material reported here; *Bairdemys venezuelensis* from

Sánchez-Villagra and Winkler (2006); *Bairdemys sanchezi* from Gaffney et al. (2008); *Podocnemis expansa* from Hay (1908); *Bothremys cooki* from Gaffney et al. (2006); and *Stereogenys cromeri* from Andrews (1906)

different from the specializations found in members of the “*Shweboemys* group.” It is difficult to envision how the *Bothremys* pattern could have evolved into the “*Shweboemys* group” pattern, so almost certainly these two lineages independently evolved analogous feeding mechanisms and are not intimately related. The anterior angle formed by the jaw of *B. healeyorum* is somewhat more acute than the angle of *B. venezuelensis* and *B. sanchezi*, and *B. healeyorum* also has a shallower posterior emargination at the back of the triturating surface. Additionally, *B. healeyorum* has only a very low and very broad medial swelling along the midline of the

triturating surface, and the depressions to either side of it are extremely shallow and restricted to the posterior parts of the triturating surface. The triturating surface extends backward onto the coronoids as far as the base of the pronounced and rounded coronoid processes. The jaw ramus formed by the prearticular and surangular is short and stout, comparable to *B. venezuelensis* and *B. sanchezi* but much less stout than in *Stereogenys cromeri*. The joint surface on the articular is relatively short anteroposteriorly, oval-shaped, and directed more obliquely rearward than the joint surface in *B. venezuelensis* and *B. sanchezi*.



Fig. 18.6 External (dorsal) view of carapace of *Bairdemys healeyorum*, part of holotype skeleton (SC 90.16), from the Chandler Bridge Formation (late Oligocene), South Carolina, USA

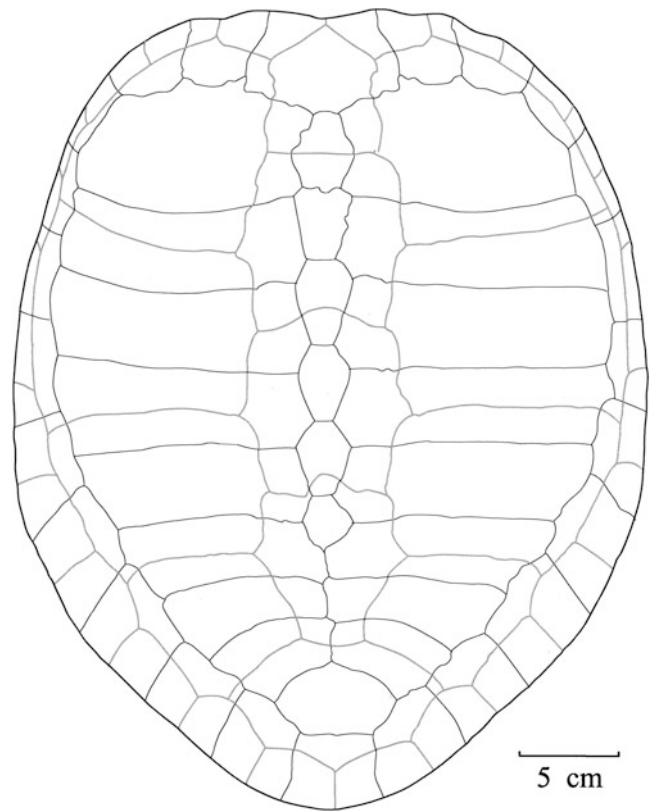


Fig. 18.7 Reconstruction of carapace of *Bairdemys healeyorum* in external (dorsal) view, based on the holotype (SC 90.16) and referred (ChM PV4794) specimens

Vertebrae: The centra and parts of the transverse processes of two procoelous cervical vertebrae are preserved. One, by comparison with the cervicals of *Podocnemis*, is probably the sixth. It is rather elongate and has a ventral keel at the anterior end of the centrum that tapers away posteriorly (Fig. 18.4d₂). In posterior view, its posterior convex articular surface is rather heart-shaped in outline. The other vertebra, with a broken but obviously pronounced and basally elongated ventral keel, is almost certainly the eighth (Fig. 18.4d₁). Its posterior convex articular surface is broadly U-shaped and much shallower dorsoventrally than the posterior articular surface on the sixth(?) cervical vertebra.

Carapace: The fourth left costal, most of the first right costal, the first, second, and third right peripherals, and about half of the nuchal were not found. Otherwise the carapace is essentially complete (Fig. 18.6) and allows a complete restoration of its appearance in life (Fig. 18.7). The carapace as preserved is slightly too wide to attach snugly to the plastron ventrally, indicating that it became somewhat flattened and spread during burial. This flattening has been taken into account in the restoration of the shell in dorsal and ventral views. The sulcal grooves are easily seen on most parts of the carapace, allowing accurate placement of the dorsal scute boundaries.

For the most part, the carapace is that of a typical generalized podocnemidid turtle like *Bauruemys* and ?*Roxochelys*, and it also shows much similarity to the shell of bothremydids like *Foxemys* (Fig. 18.8). The scute pattern, however, is unusual in that the first vertebral scute extends far forward, almost but not quite separating the anteriormost marginal scutes. This condition approaches that found in *Shweboemys pisdurensis* (Fig. 18.8), in which the anterior vertebral scute extends fully to the front of the shell and completely separates the anteriormost marginal scutes (Jain 1986). There is no indication that a cervical scute was present.

One slight tendency toward skeletal specialization in *Bairdemys healeyorum* is that only the six anteriormost neurals are present; the seventh and eighth are not developed. This represents an early stage in an evolutionary trend in this genus that culminated in *B. venezuelensis* (Fig. 18.8), in which all neurals are lost from the carapace and the costals all meet each other directly along the midline of the shell (Wood and Díaz de Gamero 1971). The nuchal is large and wider than long. On the ventral side of the carapace (Fig. 18.9), the sutural scar for attachment of the anterior plastral buttress extends far medially toward the midline along the first costal to about the middle of that element. In

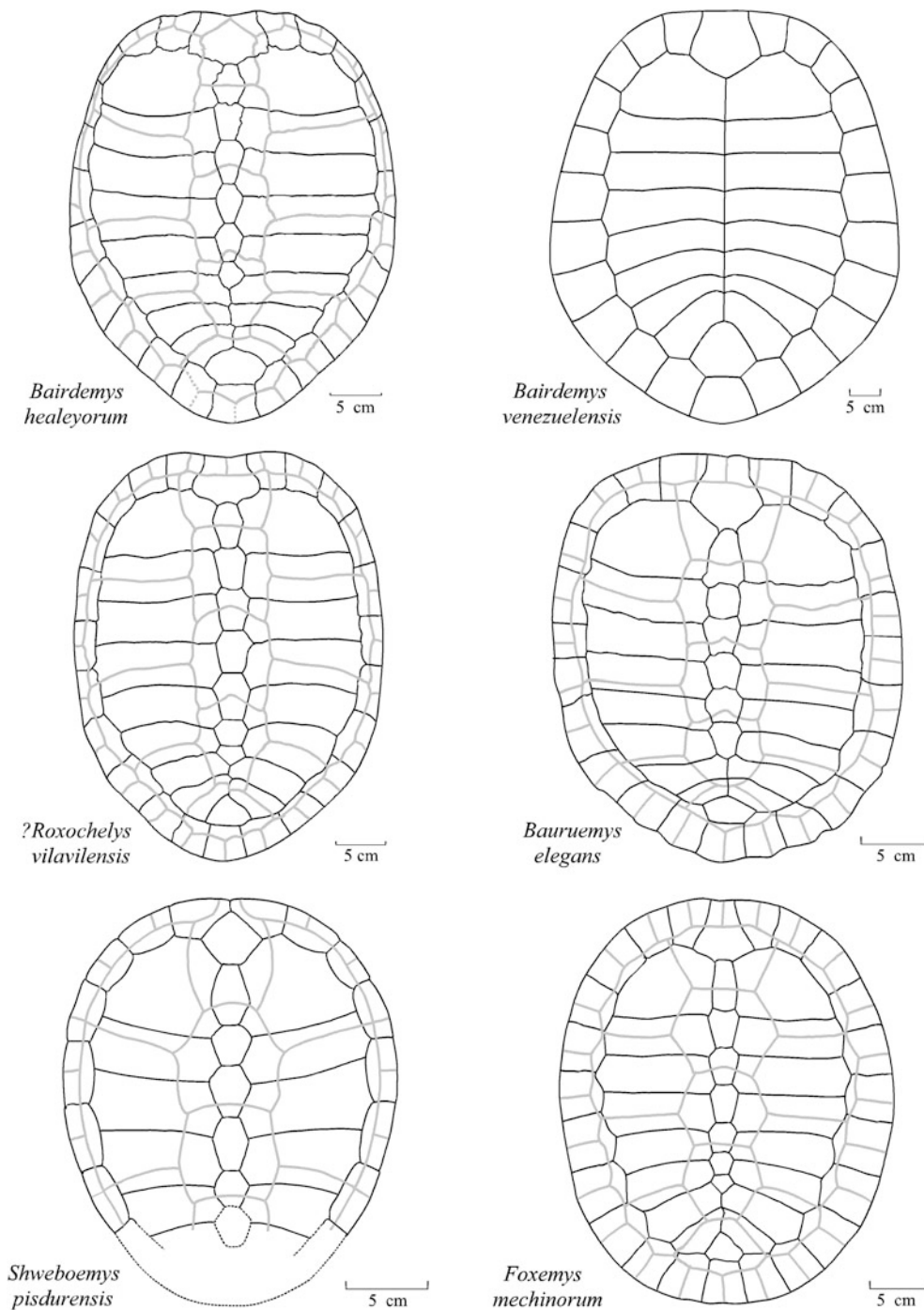


Fig. 18.8 Comparison of carapaces in *Bairdemys* and other podocnemid turtles, all in external (dorsal) view. *Bairdemys healeyorum* based on material reported here; *Bairdemys venezuelensis* from Wood and

Díaz de Gamero (1971); *?Roxochelys vilavilensis* from de Broin (1971); *Bauruemys elegans* from Suarez (1969); *Shweboemys pisdurensis* from Jain (1986); and *Foxemys mechinorum* from Tong et al. (1998)

contrast, the posterior plastral buttress is less strongly developed, extending medially along the fifth costal for only about a fourth of its length. The sutural scar for attachment of the distal end of the ilium to the carapace is located on the posterior part of the seventh costal and on the anterior

part of the eighth costal, about one-fourth of their lengths from the midline.

The partial anterior carapace in the Charleston Museum collection (CM-PV4794) mostly represents the part of the carapace not present in the type specimen (Fig. 18.3e).



Fig. 18.9 Visceral (ventral or internal) view of carapace of *Bairdemys healeyorum*, part of holotype skeleton (SC 90.16), from the Chandler Bridge Formation (late Oligocene), South Carolina, USA

It represents a somewhat smaller individual, however, and was recovered from a different locality, so it clearly is not a part of the individual represented by the type specimen. Its surface is somewhat better preserved than that of the type, and shows a faintly developed nodular surface texture that is largely worn away on the type.

Plastron: The plastron is virtually complete except for some distal parts of the plastral bridges that were broken away (Fig. 18.10); its ventral surface is poorly preserved. In most areas the sulcal grooves are readily discernable, and this allows an essentially complete restoration of the plastron in ventral view (Fig. 18.11). The mesoplastra are subround in shape, relatively small, and located far from the midline. The plastron is broadly attached to the carapace by a plastral bridge that extends from the front edge of the fourth peripheral to as far back as the anterior portion of the eighth peripheral. The ratios of the anterior lobe, plastral bridge, and posterior lobe are roughly 1:2:2. The midline of the plastron is sutured along its entire length. The xiphiplastra are wide, flattened, elongated, and rounded at their posterior ends with a fairly large and rounded anal notch between them. The sutural scars where the ischium and pubis attach to the plastron are both on the xiphiplastra; the anterior ischial suture being about twice as large as the posterior pubic suture.

The abdominal, femoral, and anal scutes on the central and posterior part of the plastron are unexceptional, but the anterior scutes are much reduced and compressed toward



Fig. 18.10 External (ventral) view of plastron of *Bairdemys healeyorum*, part of holotype skeleton (SC 90.16), from the Chandler Bridge Formation (late Oligocene), South Carolina, USA

the anterior midline region. The intergular scute is pentagonal in shape, largely confined to the anterior border region of the epiplastra, and extends backward onto the entoplastron only slightly. The gulars likewise are greatly reduced to small, triangular-shaped scales that occupy less than half the anteroposterior length of the epiplastra. The humeral scutes also are much compressed anteroposteriorly, mostly occupying the central region of the epiplastra, the anterior one-third of the entoplastron, and extending back barely onto the anteriormost edges of the hyoplastra. This forward compression of the anterior scutes is balanced by a pronounced forward expansion of the pectoral scutes, which occupy most of the anterior half of the hyoplastra, the rear two-thirds of the entoplastron, and the posterior portions of the epiplastra. This combination of traits is a distinctive feature of *Bairdemys* (Fig. 18.12). *?Roxochelys*, *Dacquemys* and some bothremydids show a strong tendency in this direction, but no other pleurodire is known to have taken this trend to such an extreme. *Stereogenys* and *Shweboemys* do not show any pronounced forward compression of the intergular and gular scutes, but they do show a comparably strong forward expansion of the pectoral scutes that is made possible because the humeral scutes are very greatly

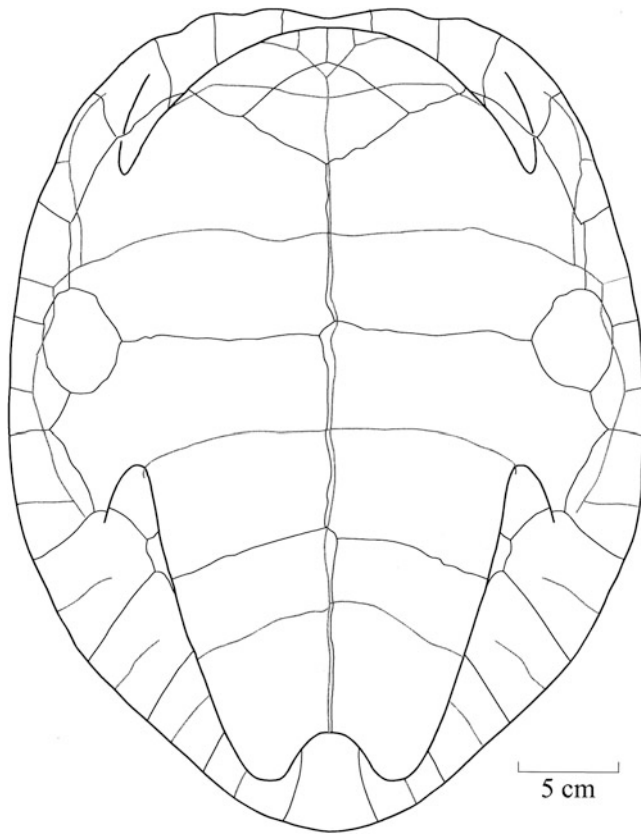


Fig. 18.11 Reconstruction of plastron of *Bairdemys healeyorum* in external (ventral) view, based on the holotype (SC 90.16)

reduced, so much so that they become separated along the midline by the intergular scutes (Fig. 18.12). This unusual condition is found elsewhere among podocnemidoid turtles only in the Taphrosphyini.

Pectoral girdle: Most of the right scapula was recovered, but the distal ends of its long and slender dorsal and acromial processes were broken away (Fig. 18.4e). The dorsal process is fairly rounded distally in cross-section, but the shorter acromial process is distinctly flattened and slightly curved into a C-shape toward its internal side. These processes form an angle of about 100° . Neither coracoid was recovered.

Front limb: The only part of the front limb recovered was the right humerus. Its distal end is somewhat eroded, but otherwise it is fairly complete and provides a good idea of its appearance. The distal end of the humerus is distinctly down-turned. The entepicondyle and ectepicondyle are inconspicuously developed, but the ectepicondylar groove is deep and well developed along the external margin. At its proximal end, the lateral and medial processes are connected to the head of the humerus by relatively thin but rounded bony bridges. The head of the humerus (humeral caput) is elongated into a flattened ellipse with its long axis nearly parallel to the axis of the humeral shaft (Fig. 18.3a). Extreme

elongation of the caput serves to channel most movement on the caput into the plane of the long axis, which in this case would have resulted in an up and down rowing motion. Turtles adapted to walking or to a wide range of motions in the forelimbs while swimming tend to have a rounded humeral caput (e.g., *Chelydra*, *Terrapene*, *Actinemys*, *Chrysemys*, *Gopherus*, *Testudo*, and some trionychid turtles) (Hay 1908, Fig. 595; Olsen 1968), whereas turtles with an elongated humeral caput generally show strong aquatic adaptation and a tendency to use the forelimbs as rowing organs (e.g., *Kinosternon*, *Pseudemys*, and some trionychids) (Hay 1908, Fig. 661, pl. 3; Olsen 1968). The marine cheloniid sea turtles, all of which are highly specialized for rowing, also show pronounced elongation of the caput (e.g., *Lepidochelys*; Hay 1908, pl. 2). Therefore, the extreme elongation of the humeral caput in *B. healeyorum* almost certainly was a specialization for swimming or even for rowing and not for walking.

Pelvic girdle: Both the left and right sides of the pelvic girdle were recovered (Fig. 18.4c). The ischium and pubis were sutured at their distal ends to the plastron, and the distal end of the ilium was similarly sutured along a broad attachment surface to the carapace. All three bones contribute to the acetabulum, with the ischium and pubis each contributing about one-fifth of its area and the ilium about three-fifths.

Hind limb: The only part of the hind limb recovered was the left femur (Fig. 18.4b), which is damaged and thus provides only limited information about this bone. However, enough is preserved to show that it is distinctly larger than the humerus, as is typical for freshwater turtles. The caput is partly eroded away; it is somewhat elongated, but not so elongated as the head of the humerus. Relative to the base of the trochanter major, the base of the trochanter minor diverges from the shaft much farther down and at a greater angle. The overall proportions of the proximal femur are rather reminiscent of the proportions of the femora of soft-shelled turtles, suggesting strong aquatic specialization. The femur is strongly down-turned at its distal end.

Bairdemys miocenica (Collins and Lynn 1936) new combination

Synonymy: *Taphrosphys miocenica*, (Collins and Lynn 1936).

Holotype: United States National Museum specimen USNM 13784, anterior plastron (epiplastra, entoplastron, and hyoplastra) of a single individual.

Holotype locality, unit, and age: One-quarter mile (0.4 km) south of Camp Roosevelt along the Calvert Cliffs, Calvert County, Maryland, USA; “Zone 10” of Shattuck (1904), Calvert Formation; early middle Miocene (early Langhian, ca. 15–16 Ma; Weems and Edwards 2007).

Referred material: Nuchal and humerus described and figured in Zug (2001).

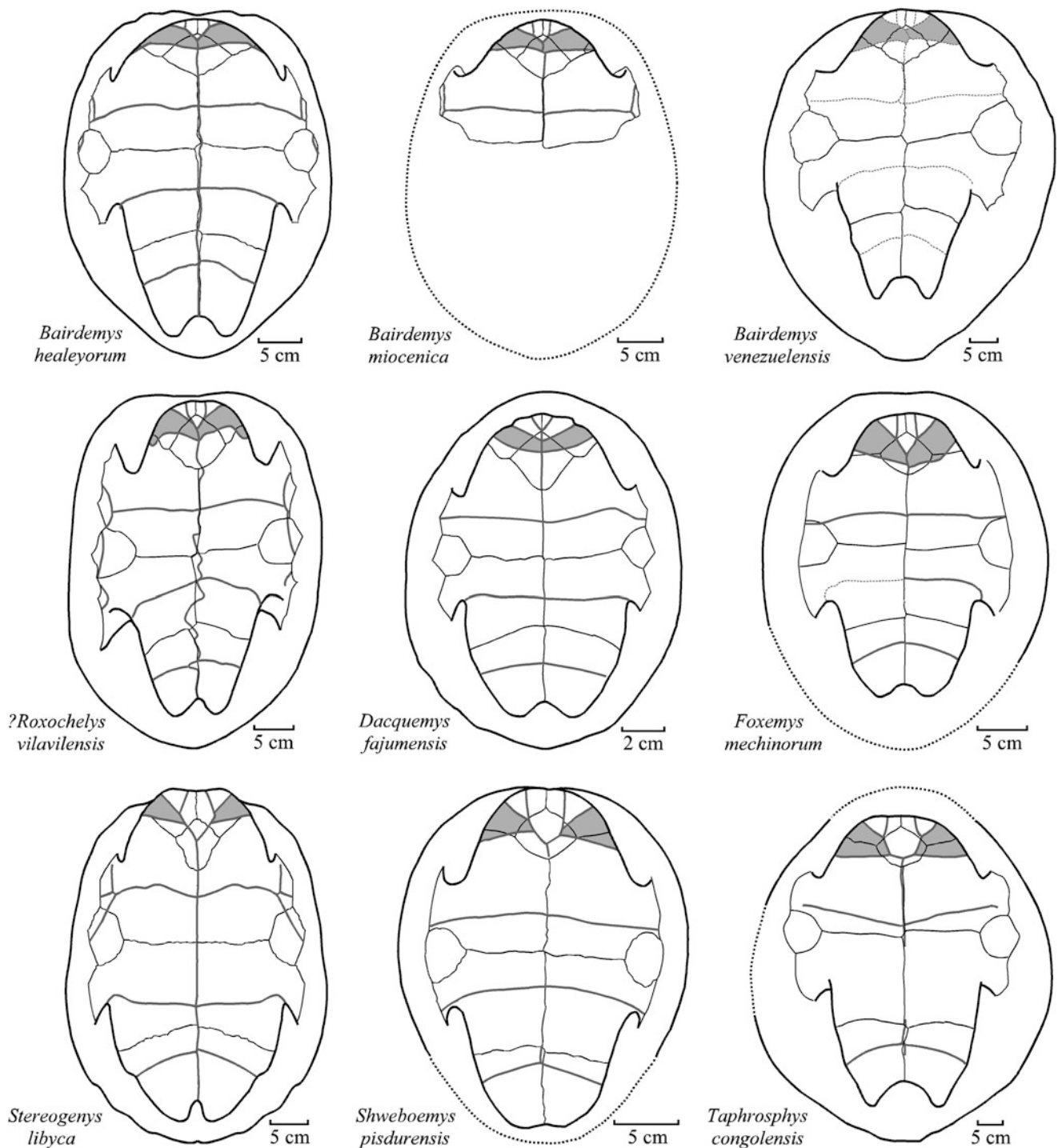


Fig. 18.12 Comparison of the plastron in different species of *Bairdemys* and other podocnemidid turtles, all in external (ventral) view. *Bairdemys healeyorum* based on material reported here; *Bairdemys miocenica* from Collins and Lynn (1936); *Bairdemys venezuelensis* from Gaffney et al. (2006); *?Roxochelys vilavilensis*

from de Broin (1971); *Dacquemys fajumensis* from Andrews (1906); *Foxemys mechinorum* from Tong et al. (1998) *Stereogenys libyca* from Andrews (1906); *Shweboemys pisdurensis* from Jain (1986); and *Taphrosphys congolensis* from Gaffney et al. (2006)

Diagnosis: Anterior lobe of plastron short, broad and rounded with well developed but rather thin axillary buttresses, maximum length of hyoplastron about equal to its

breadth, mesoplastral contact with hyoplastron indicates that mesoplastra were relatively small, located far from the midline, and rather polygonal in shape. Intergular scute

small, pentagonal, mostly located on the epiplastra and only slightly projecting backward onto the entoplastron; gular scutes small, triangular, and located far forward and entirely on only a small part of the epiplastra; humeral scutes also relatively small and forwardly located, meeting along the midline beneath the intergular; pectoral scutes large, covering the anterior two-thirds of the hyoplastra, the posterior two-thirds of the entoplastron, and extending forward onto the posterior part of the epiplastra. Nuchal much wider at rear than at front, being anteriorly constricted by encroachment of the first peripherals; cervical scute not present. Caput of humerus elongated roughly along the axis of the humeral shaft, which is rather thick and stout.

Remarks: The proportions of the gular and intergular scutes on the anterior plastron of *Bairdemys miocenica* are quite similar to, though not exactly identical with, the proportions of the gulars and intergular of *Bairdemys healeyorum* (Fig. 18.12). This strongly suggests that the anterior pleurodire plastron from the Calvert Formation of Maryland, described by Collins and Lynn (1936) as “*Taphrosphys*” *miocenica*, was derived from the Oligocene species *Bairdemys healeyorum* and should be referred to that genus.

Since the discovery and description of this species, no new material has been forthcoming from the Calvert Cliffs of Maryland. However, pleurodire carapace and plastron fragments have been collected in the Lee Creek Mine near Aurora, North Carolina from the Pungo River Formation (Zug 2001); this unit is age-equivalent to much of the Calvert Formation. As the North Carolina material is from at or near the same stratigraphic horizon as the type plastron from Maryland, in all likelihood it pertains to *Bairdemys miocenica* and helps to better characterize this species. Notable is the nuchal element (Zug 2001) which shows that *B. miocenica* did not have a cervical scute and therefore can be firmly placed among the pelomedusoid pleurodires (Gaffney and Meylan 1988). Also, although the relationship of the posterior border of the nuchal with the first neural and first costals is very similar to that seen in *B. healeyorum*, the anterior constriction of the nuchal between the first peripherals clearly shows that the nuchal of *B. miocenica* is not specifically referable to *B. healeyorum*. The humerus is close to that of *B. healeyorum* and like it has a very elongate caput (Zug 2001), but it differs in that the shaft is relatively thicker and stouter in its construction.

Discussion

Only the femur and humerus of *Bairdemys healeyorum* are known, so the more distal parts of the limbs cannot be evaluated. These two proximal limb elements, however,

strongly suggest that *Bairdemys* had legs that were specialized for aquatic locomotion. Because the head of the humerus was elongated into an extreme ellipse with its long axis nearly parallel to the shaft as in cheloniid sea turtles, this bone obviously was designed to accommodate motion almost exclusively in a vertical plane. This implies that the forelimb functionally was a flipper. The strong similarities between the proximal end of the femur of *Bairdemys* and the proximal femora of trionychid soft-shelled turtles also suggest strong aquatic adaptation in the rear limbs. Indeed, this combination of front and rear limb traits is strikingly similar to the combination of limb functions found in the living pig-nosed turtle, *Carettochelys insculptata*, which lives in rivers, lagoons, and estuaries of southern New Guinea and northern Australia. Interestingly, *Carettochelys* also is found occasionally in brackish water (Georges and Rose 1993; Visser and Zwartepoorte 2005).

No occurrences of Eocene pleurodire turtles have been reported from anywhere in North America, and this strongly suggests that the last of the North American bothremydids (*Taphrosphys* and *Bothremys*?) survived through the Paleocene in southeastern North America (Hutchison and Weems 1998; Gaffney et al. 2006) but then died out by the end of that epoch. The distinctive lower jaw and anterior plastron of *Bairdemys* bear little similarity to any of the better known members of the family Bothremydidae (i.e., *Bothremys*, *Chedighaii*, *Taphrosphys*) (Gaffney et al. 2006, 2009), and this greatly weakens any argument that *Bairdemys* might have evolved from some unknown North American bothremydid ancestor. Similarly, although some bothremydids survived in the northern African region until the Miocene (Roger et al. 1994), derivation is equally unlikely from any of the late surviving Old World members of this group.

The greatest plastral similarity to *Bairdemys* is found among podocnemidid turtles, such as the South American podocnemidine *?Roxochelys vilavilensis* (de Broin 1971) and the African erymnochelyine *Dacquemys fajumensis* (Andrews 1906) (Fig. 18.12). Although *Bairdemys* shares distinctive derived cranial characteristics with *Stereogenys* and *Shweboemys* (Gaffney and Wood 2002), in its plastron *Bairdemys* is more similar to other podocnemid turtles in that its humeral scutes meet along the midline and are not separated by the intergular (Fig. 18.12). This trait, along with the less strongly expanded secondary palate and less robust lower jaw found in *Bairdemys*, indicates that the *Bairdemys* lineage diverged from the *Shweboemys*-*Stereogenys* lineage well before the mutual ancestor of the latter two genera developed the distinctive plastral scute arrangement present in both of them. The oldest well documented member of the *Shweboemys*-*Stereogenys* lineage is *Shweboemys pisdurensis* from the Maastrichtian of India (Jain 1986), so the *Bairdemys* lineage therefore must have



Fig. 18.13 Oligocene (circle) and Miocene (triangle) occurrences of *Bairdemys* shown on an Oligocene paleogeographic map of the Caribbean and adjacent regions. Along the Atlantic seaboard of North America, shallow seas in the middle Miocene transgressed westward across the modern landscape about 50 miles (80 km) farther inland than they did in the late Oligocene. From south to north, localities are in present day Venezuela, Puerto Rico, South Carolina, North Carolina, and Maryland. Paleogeographic land–sea relationships are adapted from Global Paleogeographic Views of Earth History—Late Precambrian to Recent <http://jan.ucc.nau.edu/~rcb7/35moll.jpg>. The

anatomical similarities between the *Bairdemys* lineage and the Afro-Asian *Shweboemys-Stereogenys* lineage strongly suggest that all of these genera were derived from ancestors that originated in Africa and/or India. There is little chance that the ancestors of the *Bairdemys* lineage crossed the Atlantic directly from Africa to North America, because the strongly clockwise current pattern in the North Atlantic (green arrows) would have precluded dispersal in that direction. It is far more likely that the *Bairdemys* ancestors crossed the Atlantic Ocean from Africa to South America and then “island hopped” from South America to North America

split from the *Shweboemys-Stereogenys* lineage well before the end of the Cretaceous.

Bairdemys healeyorum from the upper Oligocene Chandler Bridge Formation is the oldest known species within the *Bairdemys* lineage. This is not what would have been anticipated, because the anatomical similarities between the *Bairdemys* lineage and the Afro-Asian *Shweboemys-Stereogenys* lineage, as well as mutual similarities with the Old World Erymnochelyinae, indicate that all of these genera were derived from a common ancestor that lived in Africa and/or southern Asia (de Lapparent de Broin 2000). Thus, given the Late Cretaceous and Paleogene paleogeography of the Atlantic basin, the ancestor of the *Bairdemys* lineage must have come to the Americas either by making a daunting “sweepstakes” crossing of the Atlantic Ocean directly from Africa to North America in Oligocene time or else by making an Oligocene or earlier crossing of the Atlantic from Africa to South America, followed by an “island-hopping” crossing of the Caribbean from South America to North America. The sweepstakes

model seems very unlikely because the North Atlantic is dominated by a strong clockwise current flow, induced by the Coriolis effect, that would have been present even well before the Oligocene (Fig. 18.13). Therefore, any direct “sweepstakes” crossing of the Atlantic from Africa (or Europe) to North America in the Oligocene would have had to occur against a strong prevailing oceanic current going in the opposite direction. In contrast, a crossing from Africa to South America not only would have been much shorter, it also would have been made easier by going with the direction of the prevailing current. Thus, even though there is no fossil evidence so far to support a dispersal route first from Africa to South America, and then from South America to North America, this by far seems the more plausible possibility.

Once established in the southeastern United States, colonization by *Bairdemys* apparently was successful for about 17 million years, from the late Oligocene through the middle Miocene. Probably Neogene climatic deterioration in the southeastern United States, which began in earnest at

the beginning of the late Miocene, heralded the demise of these tropically adapted turtles in North America. In tropical Venezuela, however, *Bairdemys* continued to thrive throughout most or all of the late Miocene (Gaffney et al. 2008), and the related genus *Shweboemys* even survived in tropical Burma until the Pliocene or Pleistocene (Jain 1986).

Modern side-neck turtles primarily occupy fresh water habitats, but prolonged tolerance of salt water has been documented in at least some chelids (e.g., *Hydromedusa*, *Pelusios*, *Chelodina*; Frazier 1986). Salt-water tolerance has been suggested for the extinct podocnemidid *Stupendemys* (Wood 1976) and for a number of species within three clades of the Pelomedusoides (Bothremydini, Taphrosphyriini, and the *Shweboemys* Group) (Meylan et al. 2009). The scarcity of remains of *Bothremys* in the shallow marine to estuarine strata of Maryland, North Carolina, and South Carolina, and its absence so far in deposits of the same age in Virginia, strongly suggests that the preferred habitat of this turtle was fresh water. Even so, such a preference in habitat by no means precluded a tolerance to prolonged immersion in salt-water and the potential for wide dispersal that this trait would have presented. A strong tolerance for salt water, coupled with its exceptional specialization for swimming, may well explain how *Bairdemys*, uniquely among Paleogene podocnemidids, was able to spread across the salt waters of the Atlantic to South America and from there across the Caribbean region to Puerto Rico and the southeastern United States (Fig. 18.13).

There is another possible factor that may have contributed to the successful spread of *Bairdemys* across the Caribbean. There may have existed, around the beginning of the Oligocene, a land-bridge that connected the Greater Antilles islands with South America along the course of the present-day submerged Aves Ridge (GAARlandia of Iturralde-Vinent and MacPhee 1999). If this land bridge (or a chain of closely spaced islands in the same location) did exist then, it would have greatly reduced the distances that *Bairdemys* needed to navigate across salt water to reach North America from South America during the Oligocene.

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