Chelid Turtles from the Miocene Freshwater Limestones of Riversleigh Station, Northwestern Queensland, Australia

EUGENE S. GAFFNEY,¹ MICHAEL ARCHER,² AND ARTHUR WHITE²

ABSTRACT

The early to middle Miocene freshwater limestones of Riversleigh Station, northwestern Queensland, have yielded three taxa of side-necked turtles, or pleurodires, of the family Chelidae: *Pseudemydura* sp., *Chelodina* sp., and a member of the *Emydura* group. The *Pseudemydura* specimen, a portion of the skull roof, is the first fossil of this rare and endangered genus and the first record outside its present small range near Perth, Western Australia. The *Chelodina* specimen, a plastron, is the first Miocene record and oldest fossil of this living Australian genus.

INTRODUCTION

Turtles are often common elements of both living and extinct faunas, and they have the potential to provide significant perspectives on biogeography, habitat, and evolutionary relationships. The fossil record of turtles in Australia is still not well known compared with some groups like mammals, and new discoveries can often result in important alterations to distributions and phylogeny. Turtles were discovered in the Carl Creek Limestone at Riversleigh Station by Tedford (1968) along with other elements of the Riversleigh local fauna. Since then, further work by teams led by M. Archer, S. Hand, and H. Godthelp to more remote areas of Riversleigh Station has resulted in discovery of more than 80 additional local faunas spanning in time the ?Oligocene to Pleistocene (e.g., Archer et al., 1986; Archer et al. 1989).

This paper announces the discovery of three taxa of fossil turtles from these deposits that extend the temporal and geographic range of

¹ Curator, Department of Vertebrate Paleontology, American Museum of Natural History.
² University of New South Wales, Kensington, N.S.W. 2033, Australia.
living Australian turtle taxa and give a better glimpse than was previously available of the diversity of the Australian turtle fauna during the Tertiary. The turtle specimens described here are fragmentary, and this report should be considered a preliminary account of taxa that will hopefully become better known in the future. The Riversleigh deposits, the source of these fossils, have become famous in recent years for yielding a diversity of well-preserved specimens, and with further collection, well-preserved turtles should come to light. The Riversleigh collection contains three taxa of chelids and one meiolaniid. The chelids are described here while the meiolaniid will be described along with other mainland meiolaniids in a paper being prepared by Gaffney.

The three chelids, or side-necked turtles, found at Riversleigh represent the three main generic-level groups found in the recent Australian chelid fauna. *Pseudemydura* is a very rare living form, consisting of a single endangered species restricted to two small swamps north of Perth, Western Australia. *Pseudemydura* is autapomorphic among chelids in having a skull largely lacking temporal emargination. Gaffney (1977) has suggested that *Pseudemydura* may be the sister group to all chelids; thus the discovery of a fossil belonging to this taxon is of considerable interest. *Chelodina*, represented in the collection by a plastron, has been hypothesized as being closely related to South American chelids (Gaffney, 1977), and a better fossil record for this form will be useful.

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**LOCALITIES, LOCAL FAUNAS, AND AGES**

Fossils described herein were collected from Ringtail Site and Gag Site, Ray's Amphitheatre, Riversleigh Station, northwestern Queensland. Gag Site has produced the Dwornamor Local Fauna (Archer and Hand, 1984). Ringtail Site has produced the Ringtail Local Fauna. Precise location details of both localities, based on laser surveys, have been recorded by the University of New South Wales research team. These may be made available on request to M. Archer and/or the
Queensland Museum. Gag Site and Ringtail Site are excavations in two levels of a thick sequence of lacustrine carbonates. Our present understanding leads us to conclude that Gag Site is stratigraphically lower than the Ringtail Site. D-Site (source of the Riversleigh Local Fauna; Tedford, 1968) comes from the Carl Creek Limestone exposed along the western margin of the Riversleigh/Lawn Hill road. Current evidence (work in preparation) suggests that Gag Site and Ringtail Site are contained within younger unnamed freshwater carbonates separated from the older Carl Creek Limestone by at least one angular unconformity.

Some of us previously interpreted the sequence of deposits at Riversleigh to span middle Miocene to late Pleistocene time (e.g., Archer et al., 1986) partly on the basis of intracontinental correlation of marsupials (Tedford, 1968; Archer et al., 1986; Archer et al., in press) and rodents (Godthelp, in prep.). The Dwornamor Local Fauna, from deposits near the base of the Ray's Amphitheatre system in the Riversleigh sequence, contains Djilgaringa gillespieae, a pilkipildrid marsupial congeneric with D. thompsoniana from the Yanda Local Faunas of South Australia (Archer et al., 1987). Similarly, the Ringtail Site Local Fauna contains a species of Obdurodon (Archer et al., 1986), an ornithorhynchid monotreme genus previously recorded from the Ditijimanka and Pinpa Local Faunas of central South Australia (Woodburne and Tedford, 1975).

Although it has become customary to interpret these central Australian deposits to be middle Miocene in age (approximately 12-15 m.y.; Woodburne et al., 1985), more recent work with foraminifera (Lindsay, 1987) suggests that at least some of these deposits may be as old as late Oligocene. This assessment was based on the abundant presence of the foraminiferan Buliminoides sp. in the Etadunna Formation at Lake Palankarina. This older age assessment is supported by Norrish and Pickering (1983) who reported a late Oligocene Rb-Sr date for illite from the Etadunna Formation. Further, intercontinental comparisons of Riversleigh bats from Microsite (the Nooraleeaba Local Fauna; Sige et al., 1983) led to the conclusion that the Riversleigh hipposiderid Brachiposideros nooraleebus was most probably Aquitanian (late Oligocene) to Burdigalian (early Miocene) in age based on comparisons with European congeners. Ringtail Site and Gag Site, as presently understood, are stratigraphically higher in the Riversleigh Tertiary system than is Microsite. In view of these considerations, we suggest that it is probable that the Dwornamor and Ringtail local faunas are between late Oligocene and middle Miocene in age. Because the ornithorhynchid is considerably larger and the pilkipildrid somewhat more derived than their presumably late Oligocene central Australian counterparts, it seems probable that the Dwornamor and Ringtail local faunas are early to middle Miocene in age.

**SYSTEMATICS**

ORDER TESTUDINES LINNAEUS 1758
INFRAORDER PLEURODIRA COPE 1863
FAMILY CHELIDAE GRAY 1825
SUBFAMILY PSEUDEMYDURINAE
Gaffney 1977

For diagnoses of these taxa and the following higher taxa and for a more complete classification of turtles, see Gaffney (1977, 1984), Gaffney and Meylan (1988), and Gaffney (in press).

*Pseudemydura*, sp. (fig. 1)

**LOCALITY:** Ringtail Site, Riversleigh Station (fig. 3), northwestern Queensland.

**MATERIAL:** QM F17415, posterior part of skull roof, consisting of supraoccipital, posterior parts of right and left parietals, and right and left squamosals.

**DESCRIPTION:** The Riversleigh specimen identified as *Pseudemydura* consists of the entire posterior margin of the skull roof. Portions of the right and left squamosals, right and left parietals, and the supraoccipital are preserved, largely free of matrix. A dark black plastic covers much of the bone surface but the sutures are nonetheless clear. The anterior and ventrolateral portions of the specimen are represented by broken edges but the lateral and posterior edges are mostly natural.

The right and left squamosals lack their anterior and ventrolateral portions. They both preserve the posterodorsal area of the antrum.
postoticum and part of the posterolateral trough where the depressor mandibulae muscle attaches on the outside of the skull (see Gaffney, 1979a). These areas are virtually identical in recent *Pseudemydura umbrina* and the Riversleigh *Pseudemydura*. The squamosals have a flat plate extending medially to meet the other skull roofing bones and form the posterolateral margin of the skull.

Only small portions of the right and left parietals are preserved in the Riversleigh *Pseudemydura* specimen, but they reveal useful morphology and are of considerable interest. One of the more obvious autapomorphies of *Pseudemydura* (Gaffney, 1977) is the presence of a laterally expanded dorsal plate of the supraoccipital. In other chelids and in nearly all other turtles, the supraoccipital rises from the foramen magnum as a vertical, sagittal plate articulating with the medially meeting parietals dorsally and being exposed as a narrow bar posterior to the skull roof (Gaffney, 1977, 1979a). In *Pseudemydura*, however, the supraoccipital forms a horizontal plate on the skull roof that separates the posterior part of the parietals along the midline. In the recent *Pseudemydura umbrina*, figured by Burbidge et al. (1974) and Gaffney (1977, 1979a), the supraoccipital forms a roughly equilateral triangle, apex pointing anteriorly, that has relatively wide contacts with the squamosals posterolaterally. In the Riversleigh *Pseudemydura*, however, the dorsal plate of the supraoccipital is not equilateral but narrower than long and the posterior portions of both parietals separate the supraoccipital from the squamosals. A narrow strip of the parietals reaches the posterior edge of the skull roof. In what is interpreted as the primitive condition of the chelid skull (Gaffney, 1977), the parietals widely separate the squamosals from contact with the very narrow supraoccipital. Thus the Riversleigh *Pseudemydura* condition may be interpreted as primitive in relation to the recent *Pseudemydura*.

However, is this condition significant enough to designate a new taxon? Because *Pseudemydura umbrina* is so rare, a good-sized sample of skulls is unavailable. One of us (ESG) was able to find only four specimens of the recent *Pseudemydura umbrina* that had skulls prepared so that the skull roof could be studied. In two of these (WAM R29341, figured in Gaffney, 1977, 1979a; and WAM R29338) the supraoccipital widely contacts both squamosals. In WAM R21859 there is a wide contact on the left side but on the right side the parietal narrowly separates supraoccipital and squamosal. In WAM R21858 (fig. 1) there is a very narrow supraoccipital-squamosal contact on the left side while on the right side the parietal narrowly separates the two bones. Nevertheless, all four recent *Pseudemydura* do have the dorsal plate of the supraoccipital relatively wider than in the Riversleigh specimen.

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**Fig. 1.** A. *Pseudemydura umbrina*, WAM 21858, Recent, Bullsbrook Reserve, Perth, Western Australia; ventral view of posterior part of skull roof. B. *Pseudemydura* sp., QM F17415, early to middle Miocene, Riversleigh Station, Queensland; ventral view of posterior part of skull. C. Same as B; dorsal view. D. *Pseudemydura umbrina*, WAM 29341, Recent, Twin Swamp Reserve, Perth, Western Australia; dorsal view of skull. Sutures have been enhanced; all specimens coated for photography. Abbreviations: pa, parietal; so, supraoccipital; sq, squamosal.
Even though the sample of recent *Pseudemydura* is very small, the apparent high proportion of variation in the supraoccipital-squamosal contact makes this a difficult character to use alone to diagnose a new taxon.

The Riversleigh *Pseudemydura* also differs from recent *Pseudemydura* in the depth of the vertical plate, the crista supraoccipitalis (Gaffney, 1979a: fig. 9). In recent *Pseudemydura* the crista is relatively shallow and the cavum cranii and skull roof are close together. Although it is not particularly well preserved, the crista in the Riversleigh *Pseudemydura* seems to be at least slightly deep so that the cavum cranii is separated from the skull roof to some extent. This feature, however, varies within species of turtles and in the absence of better material it is very difficult to evaluate systematically.

**?Pseudemydura** sp.

**LOCALITY:** Ringtail (AR 10442).

**MATERIAL:** QM F17416, a pygal bone.

**DESCRIPTION:** The shell of *Pseudemydura* has a number of diagnostic features but only one fragment seen to date in the Riversleigh material may be referable to that genus. A pygal bone, AR 10442, has a small caudal notch and is bent convex dorsally on the mid-line as seen in *Pseudemydura umbrina*, and in contrast to other Australian chelids. The posterior width of the bone is much narrower as in recent *Pseudemydura*. In the absence of larger samples of both recent and fossil *Pseudemydura*, the significance of this distinction is unknown.

**DISCUSSION:** The genus *Pseudemydura* has had a very unusual taxonomic history. In 1839, a German collector, J. A. L. Preiss, brought to the Natural History Museum in Vienna, the stuffed specimen that would become the type. The specimen remained incognito until 1901 when the great turtle systematist and anatomist Friedrich Siebenrock used it as the basis for the taxon *Pseudemydura umbrina*. In 1907 Siebenrock figured and described the type specimen, but recorded no additional specimens or locality data (other than Australia). The species was “lost” taxonomically until 1954 when L. Glauert named a new species, *Emydura inspectata*, on the basis of a specimen collected near Perth by a schoolboy and exhibited in a local pet show (Burbidge, 1983; Goode, 1967). E. E. Williams (1958) rediscovered *Pseudemydura umbrina* by comparing the descriptions of Siebenrock and Glauert. The osteology of *Pseudemydura umbrina*, however, was not figured until the work of Burbidge et al. (1974) and Gaffney (1977). Other information on the genus can be found in Goode (1967), Burbidge (1981, 1983), and Ovington (1978).

*Pseudemydura umbrina* is possibly the world’s rarest turtle and is on the brink of extinction. Burbidge (1981, 1983) has studied the ecology of *Pseudemydura* and has led the effort that resulted in establishing two reserves for wild populations and a captive breeding program. Unfortunately, the reserves have declining habitats due to suburban encroachment and carnivorous mammal predation, and the captive breeding program has been very slow to produce results. Recently, both reserves have been deteriorating even more rapidly (G. Kuchling, personal commun.) and the future of the 25
Pseudemydura was hypothesized by Gaffney (1977) as the sister group of all other chelids. Only one character was found to support this contention: in all chelids except *Pseudemydura* the anterior process of the frontal at least partially separates the nasals. In *Pseudemydura* the nasals slightly separate the frontals and the typical chelid frontal process is absent. The condition in *Pseudemydura* is very similar to that in other turtles with nasals, including *Proganochelys*, and is hypothesized as primitive. The alternative hypotheses for *Pseudemydura*, that it is the sister group only of *Emydura*, or that *Emydura* is the sister group of *Pseudemydura* plus all other chelids, were discussed in Gaffney (1977) and found to have no synapomorphies in their favor.

The prediction of the favored hypothesis in terms of stratigraphy is that *Pseudemydura* should be at least as old as any other chelid, but we can never be sure that the fossil record is complete enough to test this hypothesis. Nonetheless, considering how sparse the Australian fossil record is, it is gratifying to find a mid-Tertiary *Pseudemydura*.

The discovery of the first fossil *Pseudemydura* considerably extends the temporal and zoogeographic range of this enigmatic turtle, but it presents more questions than it answers. It does demonstrate what had been presumed, that *Pseudemydura* was once more widespread and is now occupying only a fraction of its former range. It also shows that the taxon is geologically old. The fragmentary nature of the *Pseudemydura* material precludes detailed morphologic comparisons, particularly in the taxonomically important nasal region, so we are unable to provide new tests of Gaffney's (1977) phylogenetic hypothesis.

### SUBFAMILY CHELINAE GRAY 1825
### INFRAFAMILY EMYDURODD GAFFNEY 1977

**Emydura group** (including Elseya and Rheodytes)

**Locality:** Same as QM F17415. Found in the same block of matrix as QM F17415, QM F17420, and QM F17419.

**Material:** A left parietal, QM F17417.

**Description:** Found in the same block of
matrix with the *Pseudemydura* skull fragment (QM F17415) are a series of chelid skull fragments. One of these, a complete left parietal (QM F17417), duplicates a portion of the *Pseudemydura* skull roof (QM F17415) and is identifiable as *Emydura* group (sensu Gaffney, in press), demonstrating the presence of at least two taxa in the block. This parietal can be closely compared with the one in the skull of *Emydura macquarii* figured in Gaffney (1977: fig. 2). The anterior margin of the Riversleigh material shows the transverse suture with the frontal and the short, anterolateral suture with the postorbital. The lateral margin is a natural finished edge, parallel with the midline, showing the extent of lateral emargination seen in the *Emydura* group. This is very different from *Pseudemydura*, which has a long postorbital contact and an extensive lateral development of the parietal. *Chelodina* has a greatly developed lateral emargination that separates parietal and squamosal and produces a very long, narrow parietal in contrast to the Riversleigh parietal. The Riversleigh parietal has a natural margin at its posterolateral corner for a contact with the squamosal. The posterior margin is a natural edge, curved concave anteriorly, as in the *Emydura* group, to form the edge of the limited temporal emargination typical of the *Emydura* group, and significantly different from *Pseudemydura* and *Chelodina*. The posteromedial edge of the Riversleigh specimen has a short contact area for the supraoccipital. Ventrally, this parietal (QM F17417) has some of the processus parietalis inferior preserved and it is very similar to that of the *Emydura* group.

**Discussion:** In the living Australasian fauna there are about nine species (possibly more, depending on the authority) of chelids that are very similar in osteology and general habitus. Most of these species are usually placed in the genera *Emydura* (sensu stricto) and *Elseya* (see Goode, 1967; Cogger, 1975; Cann, 1978). In 1980, Legler and Cann named a new genus and species, *Rheodytes leukops*, that also is very similar to *Emydura* (sensu stricto) and *Elseya*. The phylogenetic relationships of these species have never been analyzed using character distribution and Gaffney (in press) refers to them as the *Emydura* group, a term also used here. The *Emydura* group has only one hypothesized synapomorphy, the relatively heavy lower jaws with wide triturating surfaces and a slightly developed symphylial "hook" (Gaffney, 1977). This condition is absent in all other chelids but does occur in some pelomedusids. The rest of the features used to characterize the *Emydura* group are primitive for chelids; in fact, the *Emydura* group is very close to the morphotype for the family (Gaffney, 1977). It is quite possible that the *Emydura* group is paraphyletic, but unlikely that it is polyphyletic.

In order to determine generic allocation of the species in the *Emydura* group, it would be necessary to develop a hypothesis of relationship among these species and then recognize monophyletic groups using genera and other categories. Unfortunately, this has not yet been done. *Elseya* does have some characters that can be considered synapomorphies (Burbidge et al., 1974; Gaffney, 1977, in press) and *Rheodytes* is a single species, monophyletic by definition. Therefore, the present division of the *Emydura* group into three genera does not reflect a coherent systematic hypothesis of the included species. Rather, it reflects the recognition of a few species that are more readily distinguishable on the basis of unanalyzed characters.

The *Emydura* group has been identified in the Australian fossil record from a number of shells and partial skeletons. The best materials are skulls, shells, and limb elements from South Australia described by Gaffney (1979b, 1981), and Burke et al. (1983). Although these specimens are very similar to recent species of the *Emydura* group, it must be kept in mind that the *Emydura* group is characterized almost entirely by features that are plesiomorphic for Chelidae. Therefore, it is to be expected that any primitive chelid taxon will look like the *Emydura* group (except for the heavy lower jaws), and the identification of a fossil as *Emydura* is often just saying "primitive chelid."

The recognition of an *Emydura* group specimen in the Riversleigh deposits extends the geographic range of fossils of this taxon but it is within the range of the living *Elseya dentata* and possibly *Emydura kreftiii* (fide Cogger, 1975). Nonetheless, it is interesting to find a specimen of this taxon sympatric with *Pseudemydura*, a condition that does not occur today.
INFRAFAMILY CHELODD GRAY 1825, EMENDED RANK, GAFFNEY 1977
TRIBE CHELINI GRAY 1825, EMENDED RANK, GAFFNEY 1977
SUBTRIBE CHELINA GRAY 1825, EMENDED RANK, GAFFNEY 1977
INFRA TRIBE HYDROMEDUSAD GAFFNEY 1977

Chelodina sp. (fig. 2)

LOCALITY: Gag Site, Riversleigh Station, northwestern Queensland.

MATERIAL: Nearly complete plastron and some carapace fragments, QM F17418.

DESCRIPTION: One of the acid-prepared blocks of matrix has yielded a number of fragments (QM F17418) that have been piece-fitted into a partial plastron (fig. 2) and some carapace fragments identifiable as Chelodina. The anterior lobe of the plastron is the most diagnostic shell region for this genus and enough of the lobe is preserved in QM F17418 for identification. There is a very large intergular scute that is separated from the anterior edge of the plastron by medially meeting gular scutes. Although the sulcus for the medially meeting gular is not preserved in QM F17418, the intergular scute sulcus is preserved up to the midline on the right side, and it does not reach the plastron edge. As in recent Chelodina, the large intergular scute covers most of the entoplastron and completely separates the humeral scutes and the anterior part of the pectoral scutes. In the Emydura group the intergular scute is much smaller, reaches the anterior edge of the plastron, separates the gular scutes, separates the humeral scutes only slightly, and does not even contact the pectoral scutes.

Pseudemydura resembles Chelodina in having a large intergular scute that separates the humerals and part of the pectorals as in Chelodina, but it differs in having the intergular reach the anterior edge of the plastron and separate the gular scutes. Gaffney (1977) considered the anterior lobe scale morphology to be an autapomorphy for Chelodina.

Goode (1967) and Cogger (1975) used plastral shape to distinguish among some of the recent species of Chelodina. It is somewhat difficult to apply these characters because the total length of QM F17418 is not precisely known. However, with some extrapolation and side-to-side restoration of edges, it is possible to obtain a length/width ratio of about 1.8, unfortunately intermediate between Cogger's (1975: 127) two alternatives of 1.4–1.7 (steindachneri, novaguinae, longicollis) and <1.9 (oblonga, expansa, rugosa). The intergular scute of QM F17418 is only slightly longer than the midline contact of the pectoral scutes, a feature of the second species group listed above. There have been no studies of Chelodina that corroborate the use of these characters to delimit natural groups nor have there been convincing studies of the range of variation of these features.

The few carapace fragments associated with the plastron QM F17418 include two medial fragments of costals demonstrating the absence of neurals.

DISCUSSION: Chelodina is rare in the fossil record. Gaffney (1981) noted a plastron that is probably Pliocene from Tara Creek, northeastern Queensland. The lectotype of "Chelodina insculpta" is a Chelodina entoplastron (Gaffney, 1977) with unknown stratigraphic and locality data (probably eastern Queensland, Neogene). The new Riversleigh Chelodina provides the oldest record of the genus and a further extension of its geographic distribution, although the living Chelodina rugosa comes close to the Riversleigh area (Cogger, 1975).

The relationships of Chelodina appear to be with the South American rather than the Australian chelids (Gaffney, 1977, in press). The new Riversleigh specimen provides no new test of this hypothesis.

CHELIDAE INDETERMINANT

LOCALITY: Ringtail site, Riversleigh Station, northwestern Queensland.

MATERIAL: The block of limestone that contains the Pseudemydura skull roof fragment, QM F17415, and the Emydura parietal, QM F17417, also contained the anterior part of a crushed skull, QM F17420, and disarticulated skull bones, QM F17419.

DESCRIPTION: The anterior part of a crushed skull (QM F17420) is either Emydura group or Pseudemydura. Most of the dorsal part of the skull is missing and the preserved surface is covered with a dark plastic. Ventrally, more bone is exposed but most of the elements are incomplete and separated to some extent from each other. Portions of both maxillae are
present but the right one is better preserved, being nearly complete. The premaxillae appear to be either absent or obscured by the plastic. This is unfortunate because the premaxillae-maxillae contact areas provide features for differentiating the *Emydura* group from *Pseudemydura*. The only feature suggesting *Pseudemydura* rather than the *Emydura* group is the relatively narrow maxillary triturating surface. However, although narrower than in the *Emydura* group, it is not as narrow as in *Pseudemydura*. The front part of this specimen has an outline in dorsal view that could be considered more characteristic of *Pseudemydura* than the *Emydura* group, but this is of dubious value.

QN F17420 preserves some fragments of the pterygoid and palatine bones but they are badly broken and disconnected from surrounding elements. Part of the basisphenoid is also present. Both prootics form the posterior part of the specimen and these are relatively well preserved. The ventral surface and the cavum labyrinthicum of both prootics are free of matrix and invisible. The *Emydura* group and *Pseudemydura* are very similar in these areas.

Also in this block of matrix were other disarticulated bones, given the group number QM F17419. Included in these are an articulated right pterygoid and quadrate that duplicates the partial right quadrate preserved in the anterior skull fragment of QM F17420, showing that it is from a different individual. The processus trochlearis pterygoidei of a right and left pterygoid, a fragment of a basisphenoid, and a possible opisthotic fragment are also present. All appear to be chelid but further identification requires better material.

**DISCUSSION:** The anterior skull fragment, QM F17420, is either *Emydura* or *Pseudemydura*, certainly not *Chelodina*. Some features are more suggestive of *Pseudemydura* but this is all that can be said at present.

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