

Eocene chelid turtles from Redbank Plains, Southeast Queensland, Australia

France de LAPPARENT de BROIN

Laboratoire de Paléontologie, UMR 8569 du CNRS,
Muséum national d'Histoire naturelle,
8 rue Buffon, F-75231 Paris cedex 05 (France)
fdelap@mnhn.fr

Ralph E. MOLNAR

Queensland Museum, P.O. Box 3300,
South Brisbane, Queensland (Australia)
barbmolnar@hotmail.com

Lapparent de Broin F. de & Molnar R. E. 2001. — Eocene chelid turtles from Redbank Plains, Southeast Queensland, Australia. *Geodiversitas* 23 (1) : 41-79.

ABSTRACT

The rich fauna of freshwater turtles from Redbank Plains (Brisbane), Queensland, Eocene (or less probably Palaeocene) includes only Chelidae (Pleurodira). Besides an indeterminate form, five taxa are attributed to two of the three extant groups: three taxa to the *Chelodina* group, and one or two to the *Emydura* group, all new, but allowing the erection of only one new species, *C. alanrivi*. They show the degree of differentiation that had already occurred here in the evolution of several of the extant lineages of the two groups, consistent with the age of the two groups of genera within the family, which has been recorded from the Early Cretaceous of southern Argentina. It reflects the origin of the Chelidae on a single landmass, Gondwanaland, the family representing the southern component of the Pleurodira.

KEY WORDS

Turtles,
Chelidae,
Chelodina,
Emydura,
Eocene,
Australia,
new species.

RÉSUMÉ

Tortues chélidées de l'Éocène de Redbank Plains, Queensland du sud-est, Australie.

La région de Redbank Plains, à côté de Brisbane, Queensland, a livré une importante faune de tortues d'eau douce, attribuée aux seuls Chelidae, Pleurodira, avec deux des trois groupes de genres australiens actuels de la famille. Outre une forme indéterminée, trois taxons sont attribués à *Chelodina* s.l. et un ou deux à *Emydura* s.l. Seule l'espèce *C. alanruxi* est créée, les autres espèces reposant sur du matériel insuffisant quoique nouveau dans le contexte des Chelidae connus. La localité, paléogène, est attribuée à l'Éocène au plus tard. La différenciation déjà nette de plusieurs lignées au sein des deux genres confirme son ancienneté, étant en accord avec l'âge de la famille, représentée depuis le Crétacé inférieur du Sud de l'Argentine. Elle reflète l'origine des Chelidae sur un continent unique, le Gondwana, la famille représentant le composant sud des Pleurodira.

MOTS CLÉS

Tortues,
Chelidae,
Chelodina,
Emydura,
Éocène,
Australie,
nouvelles espèces.

INTRODUCTION (TABLE 1)

In 1990, Dr Alan Rix, of the University of Queensland, discovered and collected new chelonian material from the Eocene deposits at Redbank Plains, Southeast Queensland. This included the most complete turtle material yet collected from this site. A further specimen was collected in 1993. Turtles were first mentioned at Redbank Plains by Jones (1926) who mentioned "Tortoise remains [...] apparently identical with *Chelodina insculpta* De Vis [...]". Riek (1952) figured a fragmentary impression of "skin of ? turtle" and mentioned "Fragments of the carapace and plastron of a turtle [...] but they are possibly only those of a recent specimen". The turtle material from Redbank Plains was considered as "Testudines indeterminant" in the first synthesis of fossil turtles of Australia (Gaffney 1981: fig. 5). Part of the newly collected material has been mentioned as "chelid material" and figured by Rix (1991). Study of the new material in this paper shows that the Redbank Plains turtles are chelids, belonging to at least five taxa. Other possibly Eocene chelid material from Queensland has been found at Rockhampton, Proserpine and Cape Hillsborough. The geology of this region is still poorly understood and undergoing further description, thus some units

still lack formal stratigraphic names and correlation is tentative. What Gaffney (1981) termed "Testudines indeterminant" and then "chelid material being in press" (Gaffney 1991) comes from Queensland geological Survey bore number 2, Rockhampton, of the mid to late Eocene Rundle Formation (Henstridge & Coshell 1984). This bore is actually just outside Gladstone (Henstridge & Coshell 1984) where abundant turtle remains have recently (August, 1999) been collected from a bonebed in the Kerosene Creek Seam of the Rundle Formation, near Gladstone. This material consists of articulated and disarticulated shells, isolated limb elements and girdles, and at least one mandible. The fossils seem to occupy a single level only a few centimetres thick, and only sporadic bones or teeth (crocodilian) occur outside this level. The collected material suggests at least five individuals per square metre. A broken shell (QM F14318) from the Condor oil shale near Proserpine, between Bowen and Cape Hillsborough, is still under preparation. This shell pertains to *Emydura* s.l. sp. (see below) but its age relative to the Redbank Plains specimens is unclear. It is given as "lower Tertiary", with palynological studies giving a range of "Palaeocene to middle Oligocene" or "Eocene to Miocene" (Paine 1972; Green & Bateman 1981) depending where in the strata the specimen has

TABLE 1. — Oldest chelid or possible chelid records in Palaeogene of Australia.

Name	First mention	Palaeocene	Eocene	Oligocene
Chelidae indet.?		Boongerooda Greensand, WA		
<i>Chelodina alanrxi</i> n. sp. a, sp. b, sp. c, <i>Emydura</i> s.l. sp. a and b?, 1 indeterminate	pro parte <i>Chelodina</i> <i>insculpta</i> De Vis in Jones, 1926, pro parte “indeterminant” (Gaffney, 1981)	Redbank Plains, Q	
<i>Emydura</i> s.l. sp.	Chelidae (Gaffney, 1991; McNamara, 1994)	15.5 km SSE Proserpine Q, (Palaeocene to middle Oligocene)	Cape Hillsborough B.
Chelidae? (not studied)	“indeterminant” (Gaffney, 1981)		Eight Mile Plains, Runcorn, near Brisbane, Q, Corinda F. (?Eocene)	
Chelidae (not studied)	Chelidae (Gaffney, 1991)		Wedge Island at Cape Hillsborough, Q, Cape Hillsborough B., Wedge Island beds, middle Eocene. Rockhampton, near Gladstone, Q, Rundle Formation (mid- to late Eocene)	
<i>Chelodina</i> sp.	<i>Chelodina insculpta</i> De Vis, 1897 given as <i>Chelodina</i> sp. in Gaffney, 1981		Eocene to Pleistocene: mixed Eocene of Eight Mile Plains, Q + Plio-Pleistocene of Darling Downs, SQ, and Warburton River, SA (lectotype and other figured material from Darling Downs)	

come from and on the exact location of the specimen. The Condor oil shale may be part of the Cape Hillsborough Beds or the Plevna beds. Turtle shell fragments (QM L1190), attributed to Chelidae, also derive from the “Wedge Island beds”, the lower unit of the Cape Hillsborough Beds, of middle Eocene age, at Wedge Island, Cape Hillsborough (McNamara 1994). Other, nearly contemporaneous material from Southeast Queensland, is either very fragmentary or yet unprepared and thus has not been revised. Fragments of both carapace (UQF 17494-UQF 17510) and plastron (UQF 24020), some over 1 cm thick, were collected in 1954 from a well penetrating the Corinda Formation in the Brisbane suburb of Eight Mile Plains (Cranfield

et al. 1989; Willis & Molnar 1991). They are believed to be Eocene (Hill & Denmead 1960). De Vis (1897) mentioned other material from Eight Mile Plains including it in the description of *Chelodina insculpta*, along with material from the Plio-Pleistocene of the Darling Downs, Queensland, and the Warburton River, South Australia. Unfortunately, he did not specify which specimens came from which locality, so it is not possible to confirm the presence of *Chelodina* at Eight Mile Plains. However, his figures (De Vis 1897) show that he did not confuse the *Emydura* and *Chelodina* groups, the two main Australian chelid groups, so that the presence of *Chelodina* in Eight Mile Plains is possible, even if the figured material is only from

Darling Downs (Thomson in prep.) and, particularly, the lectotype designed by Gaffney (1981). Regarding the Warburton River material, Plio-Pleistocene sediments of the Katipiri Sands, which yielded *Chelodina insculpta* (fide Vickers-Rich & Rich 1993: fig. 259) proceed from the margins of this river. Gaffney (1981: fig. 18A) figured as "Chelidae" a specimen attributable to *Chelodina*, from the Katipiri Formation at Lake Kanunka, South Australia, Southwest of the Warburton River in the same area.

Two turtle fragments have been collected (by John Long, Western Australian Museum) in the Palaeocene Boongerooda Greensand, at Pilbara, just South of Exmouth Gulf, western Australia. They are indeterminable although probably chelids fragments. One is thick and smooth as are several *Emydura* s.l. including *Pelocomastes* De Vis, 1897 (an *Elseya* specimen, Thomson pers. comm.). The other is thinner and decorated with small polygons, like those observed in chelids.

With the exception of the shell from near Proserpine (QM F14318) and the newly collected material from Gladstone, none of this material is as complete as that from Redbank Plains.

There is much material of older Australian turtles, from the Early Cretaceous. Following careful observation of the specimens in 1993, we think that all this material is clearly cryptodiran, not pleurodiran. On the one hand there is marine Chelonioidea (*sensu* Hirayama & Chitoku 1996), including *Cratochelone* Longman, 1915 and *Notochelone* Lydekker, 1889, from the Albian Toolebuc Formation, Queensland, the latter attributed to the protostegid lineage (Gaffney 1991). There is also a new cryptodiran form, from the Toolebuc near Boulia, western Queensland (Queensland Museum). On the other hand, there are freshwater taxa, also belonging to Cryptodira. There is a new form (Molnar 1991: pl. 1), from the Cenomanian Winton Formation near Winton, Queensland (Queensland Museum). There are also various elements from the late Aptian and early Albian of Victoria (Rich & Rich 1989; Dettmann *et al.* 1992) (Museum of Victoria and Monash University) and from the Early Cretaceous Griman Creek

Formation of Lightning Ridge, New South Wales (Warren 1969b; Molnar 1980; Dettmann *et al.* 1992) (casts in the Australian Museum, Museum of Victoria and Queensland Museum). *Chelycarapookus* Warren, 1969, from the Casterton neighbourhood, Victoria, is definitely a primitive cryptodire, not a pleurodire contrarily to a previous assessment: a hypothesis still erroneously given (Manning & Kofron 1996) in spite of recent work to the contrary (Gaffney 1991) recently confirmed (Gaffney *et al.* 1998). Observation of the holotype specimen allows a reconstruction of a rounded-oval shell, with pleiomorphic characters such as anteriorly- and posteriorly-wide intervertebral canal, wide vertebrae (much wider than the costals) and wide nuchal and cervical; the plastron has short plastral lobes, rounded (relatively derived state), a primitive long entoplastron and no central plastral fontanelle. In Victoria, there are also primitive cryptodiran turtles including *Otwayemys* Gaffney *et al.*, 1998, from the Slippery Rock site, Dinosaur Cove, Otway group, Aptian-Albian, Cape Otway, and an unnamed form from Eagles Nest, Cape Patterson, Strzelecki group, Aptian (Victoria Museum). *Otwayemys* is considered by its authors (Gaffney *et al.* 1998) as close either to the Meiolaniidae (Late Cretaceous-Pleistocene, Patagonia, Australia and neighbouring islands) or to some Asiatic genera from Early Cretaceous (*Sinemys*, *Dracochelys*-*Hangaemys*, *Ordosemys*), on the base of the evolutionary grade of the isolated elements attributed to *Otwayemys*. These taxa are cryptodiran turtles of an evolutionary grade without mesoplastra and with vertebrae with formed joints (condyles, cotyles). The material from the Otway retains some primitive characters in the proportions of the elements (shell, vertebrae) which allow us to think that they are more primitive than the compared Asiatic taxa. The difference between *Chelycarapookus* and *Otwayemys* is established. Some turtle elements from the Early Cretaceous of Lightning Ridge, New South Wales (Molnar 1980; Dettmann *et al.* 1992) show the possible presence of *Otwayemys* in opisthocoelous (AM F72276) and amphicoelous (AM F68245) cervical vertebrae, short and high,

with a dorsal spine and double transverse processes (separated tuberculum and capitulum for a double headed cervical rib). However, one specimen of cervical vertebra 4 from Lightning Ridge (AM F68254) is distinct from *Otwayemys*, represented by the preserved cervical 8 (unfortunately, the cervical 5 attributed to *Otwayemys* is not figured in Gaffney *et al.* 1998). It has a longer and lower centrum and a lower neural spine than the other vertebrae from Lightning Ridge and the cervical 8 attributed to *Otwayemys*; it has a strong transverse apophysis, not a double headed cervical rib; it is biconvex as in some cryptodires (third, fourth, eighth) and – and this is interesting – as in some pleurodiran cervical vertebrae: as in Chelidae (fifth and eighth) and in Pelomedusoides (axis); the transverse apophysis is at the anterior-mid length of the neurocentral suture, as in some cervicals of primitive cryptodires (only) and as in vertebrae of the Eupleurodira (Chelidae and Pelomedusoides). However, as it cannot be an axis (because of the different position of the prezygapophyses and the absence of an anteriorly protruded neural spine) and as it lacks a common pedicle for the postzygapophyses, it cannot be attributed to the Eupleurodira (including the Chelidae). Although it has a more lowered neural spine, it resembles the fourth cervical of the cryptodiran *Ordosemys leios* Brinkman & Peng, 1993, from the Early Cretaceous of Mongolia, better than the vertebra 8 attributed to *Otwayemys* resembles to the eight of this Asiatic genus. All of these Early Cretaceous turtles are peculiar to Australia. They may have common ancestors with Asiatic forms (Gaffney *et al.* 1992, 1998) or Late Jurassic North American forms (Gaffney 1981), in other words they are related to taxa developed in the Laurasiatic part of the Pangea.

It has already been shown (Gaffney 1981; Gaffney *et al.* 1989) that the comparative study of the osteology of the extant Australian chelids remains to be done so that is not possible to distinguish between the taxa – genera or species – of the extant Australian chelids from the postcranial skeleton. Neither the definition of the characters (morphology of the elements, their decoration),

allowing a distinction between the taxa nor the research of their phylogenetical relationships, is yet available. This explains why much fossil chelid material is considered indeterminate (Gaffney 1979, 1981) although some identification is possible by comparison with material of extant chelid taxa. Study of the Redbank Plains material presents the opportunity of revealing some new distinguishing features, although it does not pretend to resolve all problems.

The material described here is not only the oldest described Australian Cenozoic turtle material, but also the oldest Australian specimens definitely attributable to freshwater chelids. It shows that by this time the Australian group was already diverse with large and small forms of the *Chelodina* and *Emydura* groups. It supports the current palaeoecological interpretation of the Redbank Plains Formation as having been deposited in a large, shallow lake.

OCCURRENCE AND AGE

The fossils occur in large ironstone nodules found in the soil at Redbank Plains and clearly deriving from the Redbank Plains Formation. This unit consists of mudstones, clays and fissile shales, with white to light grey sandstones (Staines 1960). A basalt from the overlying Silkstone Formation has been dated at 45 my. (Green & Stevens 1975; Cranfield *et al.* 1989), so that the Redbank Plains Formation is at least Eocene in age. This age is generally accepted, although it may be as old as Palaeocene. The vertebrate fossils usually occur in ironstone nodules, weathered out of the shales, and often the bone originally within the nodules has been lost to weathering, so that only fragments and natural molds remain. As the matrix of the nodules is fine-grained, these molds preserve fine detail.

This locality has yielded a fauna of fish (mostly teleosts, but with a dipnoan) and invertebrates, including insects, ostracods and a bivalve (*Unio* sp.) (Riek 1954; Staines 1960; Kemp 1991). A report of crocodylian material, including impressions of the skin (Riek 1952), so far has not been substantiated, however the impression of the foot

of a large, ground-dwelling bird was recovered in 1989 (Vickers-Rich & Molnar 1996).

Beasley (1945) reconstructed the environment of deposition of the Redbank Plains Formation as a shallow, permanent lake with a floor of "mud, decayed vegetable matter and algae" (Beasley 1945: 122). This conclusion is supported by large specimens of teleosts and the dipnoan and is consistent with the turtle material described herein.

MATERIAL

The Queensland Museum collection includes several specimens collected on the slopes East of Jones Road, Redbank Plains, near Brisbane (notably QM F18344) and on the slope above (West of) the former Redbank Plains refuse tip (QM F31697). Five individuals belong to four to five different species (Table 2) and the two other specimens examined either belong to one of these species or are indeterminate.

The specimens have been compared with the extant and fossil Pleurodira, from Triassic to present times, particularly with the extant Australian chelid genera: the comprehensive *Emydura* Bonaparte, 1836 s.l., a group including *Emydura* Bonaparte, 1836, *Elseya* Gray, 1867 and *Rheodytes* Legler & Cann, 1980 (and *Elusor* Cann & Legler, 1994, and not observed); *Pseudemydura* Siebenrock, 1901; and *Chelodina* Fitzinger, 1826. The characters allowing to distinguish the genera of the *Emydura* group are not yet established and given together in a comparative cladistic study. The comparative material, consisting of some prepared shells and mainly unprepared shells (with scutes and with plastron sutured to carapace) is principally that of the Zoology and Palaeontology departments of the Australian Museum, Sydney, the Queensland Museum, Brisbane, the South Australian Museum, Adelaide, the Western Australian Museum and the collection of the Dr Gerald Kuchling, University of Western Australia, Perth, the Muséum national d'Histoire naturelle, Paris, the Natural History Museum, London. Also examined were specimens from the National Museum of Victoria, Melbourne, the American

Museum of Natural History, New York, the Departamento Nacional da Produção Mineral, Rio de Janeiro, the Museu de Zoologia da Universidade de São Paulo, the Museo de Ciencias Naturales de Buenos Aires, the Museo de Ciencias Naturales de La Plata, the Museum für Naturkunde, Humboldt-Universität zu Berlin, the Naturmuseum Solothurn, the Staatliches Museum für Naturkunde-Stuttgart, the Zoologische Staatssammlung München.

ABBREVIATIONS

QM	Queensland Museum, Brisbane;
MNHN	Muséum national d'Histoire naturelle, Paris (AC, Anatomie comparée; H, Zoologie des Reptiles et Amphibiens; P, Paléontologie);
BMNH	the Natural History Museum, London;
UQF	University of Queensland Geology Museum, Brisbane;
UWA	University of Western Australia, Nedlands, Perth;
WA	Western Australian Museum, Perth.

SYSTEMATICS

Order CHELONII Brongniart, 1800
 Sub-Order PLEURODIRA Cope, 1864
 Family CHELIDAE Gray, 1825
 Genus *Chelodina* Fitzinger, 1826

Chelodina alanrixi n. sp.

HOLOTYPE. — QM F18344, a nodule with a part of the external and internal impressions of the carapace (Figs 1-3; Table 2).

ETYMOLOGY. — In honour of Prof. Alan Rix, of the University of Queensland, in recognition of his contributions to both invertebrate and vertebrate palaeontology of the Early Cenozoic in Australia.

LOCALITY AND STRATIGRAPHIC HORIZON. — The specimen was collected on the slopes East of Jones Road, Redbank Plains, near Brisbane, Queensland, Australia. Redbank Plains Formation, Early Cenozoic, at least Eocene if not Palaeocene time.

DIAGNOSIS. — A new large species of *Chelodina* without particular widening or narrowing of the carapace and narrowing of the vertebral 5, but with very narrowed vertebrals 2 to 4. Similar to the extant *C. expansa* Gray, 1857, by its large size and shell pro-

portions, the high degree of pygal-peripheral overlap by the costals and vertebral 5, the nearly flattened posterior border slightly pointed and not medially raised, the iliac scar shape and the presence of a strong iliac scar crest. More primitive than *C. expansa* by the smaller polygons, the wider vertebral 5, still completely wider than the suprapygal, and by the complete series of neurals, although not contacting the suprapygal; more derived than *C. expansa* by the relatively more narrowed vertebrals 2 to 4 as in the extant elongated *C. oblonga* Gray, 1841 and in *C. longicollis* (Shaw, 1802). Different from the Redbank Plains form 2 of *Chelodina* which is a small rounded form. Different from *C. insculpta* De Vis, 1897, in the greater size of the shell and the relatively smaller size and morphology of the polygons and the greater width of vertebral 5. Presumably distinct from form 3 of *Chelodina* from Redbank Plains, in the greater size of the shell, the relatively smaller polygons and the presumed absence of an upwardly-curved border.

DESCRIPTION

Material (Figs 1-3; 10; Tables 2; 3)

Form 1 of *Chelodina* from Redbank Plains, *C. alanruxi* n. sp., is represented by QM F18344. It consists of a single nodule, broken in several parts by weathering. The principal elements are the external impression of the dorsal face of the right lateral and posterior part of a shell (Fig. 1B) in reversed relief, the impression of the ventral face of the posterior part of the shell, superposed on the external impression of some shell plates, in reversed relief (Fig. 1A) and a fragment with the ventral aspect of the medial part of the shell.

Measurements (in cm)

Preserved longitudinal length of shell: 37.5.

Estimated total longitudinal length of shell: c. 40-41.

Preserved posterior width of shell: 26.

Estimated posterior width of shell: 30.

Vertebral 4, maximal width: 4.9.

Vertebral 5, maximal width: 10.2.

Suprapygal, maximal width: 8.3.

Peripheral 10, anterior length/external width: c. 4.8/5.1 = c. 94%.

Decoration

This consists of very well-marked, small, salient, elongate or rounded polygons. These appear here, owing to the reversal of relief, as elongate

and rounded pits separated by sharp crests. The polygons, narrow, vary from c. 9-2 mm long over c. 2.5-1 mm wide. Medially, in the area of the vertebrals, they are longitudinally elongate; on the lateral part of the shell, in the area of the costals, they are transversally elongate; on the last pleurals they are obliquely oriented and their elongation follows the external margin on the peripherals. The polygons are uniformly distributed on the carapace. As in *Chelodina* and in *Pseudemydura*, they are more marked and more evenly distributed than in those *Emydura* s.l. with a partly polygonal decoration. In those forms, the polygons of the carapace are weakly developed and poorly formed, a derived condition relative to the primitive decoration (see below); there are dichotomous sulci, smooth areas, granulations, pits, sharp crests or rounded ridges characteristic of the *Emydura* s.l. lineage, whether or not polygons are present. Examples of the decoration of the *Emydura* group can be seen in Gaffney (1981: figs 10-12) and in the figures of De Vis (1897: pls I-IV), showing the polygons weakly developed, crests and ridges; figures of finely ridged specimens of *Emydura* s.l. from the Miocene of South Australia are given by Gaffney (1979, 1991). Another part of the fossil material of De Vis (1897: pl. V) attributed to *Chelodina insculpta* De Vis, 1897 shows a typical decoration of extant species of *Chelodina*. But some of the carapace fragments referred to the species (pl. V, H, a suprapygal) show polygons smaller than usual in extant *Chelodina* and than in the other referred fragments, including the lectotype designed by Gaffney (1981) and more similar in size to those of the Redbank Plains material of *Chelodina*. The small, marked, well-distributed dorsal polygons of *Pseudemydura* are all rounded (not elongate) in form and, as a whole on the shell, smaller than in the other living species.

The plastral polygons are less different in *Chelodina* and *Pseudemydura* than in the *Emydura* group, when present in the latter. The polygons are, in general, more weakly developed and more elongate in *Emydura* s.l. Comparison may be made using Gaffney (1981), specimens from the Miocene of South Australia, fig. 15,

with the more elongate polygons, and fig. 18B-C, with the more elongate polygons and fine ridges, compared to fig. 18A (Pleistocene of South Australia), all being given as *Emydura*. The latter is in fact a *Chelodina* specimen, as shown by the rounded posterior form of the ischiadic scar on the xiphiplastron (derived character state found in extant *Chelodina*), as opposed to the posteriorly-pointed form in *Emydura* s.l. and *Pseudemydura* (plesiomorphic character state). The decoration of the plastron of *C. insculpta* De Vis, 1897 (pl. VI), with rounded polygons, is also typical of *Chelodina*, with polygons intermediate in size between old specimens of *C. expansa* and *C. longicollis*. The lectotype (designed by Gaffney 1981) of *C. insculpta* De Vis, 1897, 5 cm long, shell around 27 cm long, bears around 30 polygons along the medial line, the entoplastron of *C. longicollis* (MNHN AC 1911-181), 3.7 cm long, shell 20 cm long, bears around 35 narrower polygons while the entoplastron of the specimen of *C. expansa* (MNHN AC 1914-178), 6.2 cm long, shell 37.5 cm long, bears only 22 larger polygons along the medial line. Granulate and well-marked plastral polygons are also found in a specimen from Redbank Plains, possibly belonging to *Chelodina* sp. c (see below), but the polygons are more clearly longitudinally oriented and smaller than in *C. insculpta*.

Confusion of isolated parts (those with rounded polygons) of the shells of *Chelodina* for those of *Pseudemydura* is possible. In the present case, the other associated parts of the shell indicate that the Redbank Plains specimens do not pertain to *Pseudemydura*. A polygonal or granulate decoration is primitive for turtles, found in Triassic specimens from Germany (*Proganochelys*, *Proterochersis*). It is retained in *Notoemys* (weakly developed polygons), a pleurodiran from the Late Jurassic of Argentina. The decoration consisting of dorsal and ventral polygons that radiate from a center is probably primitive for chelids, as polygons so oriented are found in nearly all chelids, from the Late Cretaceous (of Argentina) to the present. The decoration of polygons is however very little developed in the first known chelids (Aptian-Albian of Argentina) (Lapparent de

Broin, Fuente & Calvo 1997). They, however, represent only a part of the chelid groups and the polygonal decoration is more widely distributed in the various species of the Late Cretaceous that belong to all the chelid groups. The decoration of polygons is particularly developed in the groups including *Hydromedusa*, *Chelodina* and *Pseudemydura*, it is variably developed in the *Phrynops* and *Emydura* groups and is nearly completely absent in some fossil forms: the primitive arrangement of the polygons evolved independently in the lineages, either weakening or developing and, as shown above, it is possible to distinguish the three Australian groups. The shell on the whole has narrower and more marked polygons in *C. alanruxi* n. sp. than in *C. expansa*, the living species of *Chelodina* of equivalent size. They are distinct from the fragments attributed to *Chelodina insculpta* De Vis, 1897. In this species, as previously noted, De Vis (1897) included material from the Eocene of Eight Mile Plains, Queensland, as well as from the Plio-Pleistocene of Darling Downs, Queensland, and of the Warburton River area, South Australia. Some of the material therefore could be contemporaneous with *C. alanruxi* n. sp. and could be conspecific with it. However, the figured fragments of *C. insculpta* are relatively smaller, from a carapace about 27 cm long for the entoplastron (lectotype) of 5 cm. The shell of the reconstructed plastron in De Vis (1897) has 30 cm (Thomson pers. comm.). It is a little longer than, for example *C. longicollis*, with shells 18-22 cm long, within the limits of *C. expansa*, with shells up to 42.3 cm long (Goode 1967) and *C. alanruxi* n. sp., shell around 40-41 cm long. The decoration of the posterior elements of the carapace of *C. insculpta* which are comparable to those of *C. alanruxi* n. sp. has relatively more rounded and wider polygons (pleurals, peripherals) and more rounded and smaller polygons (suprapygals), more similar to those of the living *C. longicollis* than to *C. expansa* (see Fig. 10D) and *C. alanruxi* n. sp. (Fig. 1B).

Carapace shape

The shell is that of a fully adult animal, well-grown with well-sutured plates. It was probably

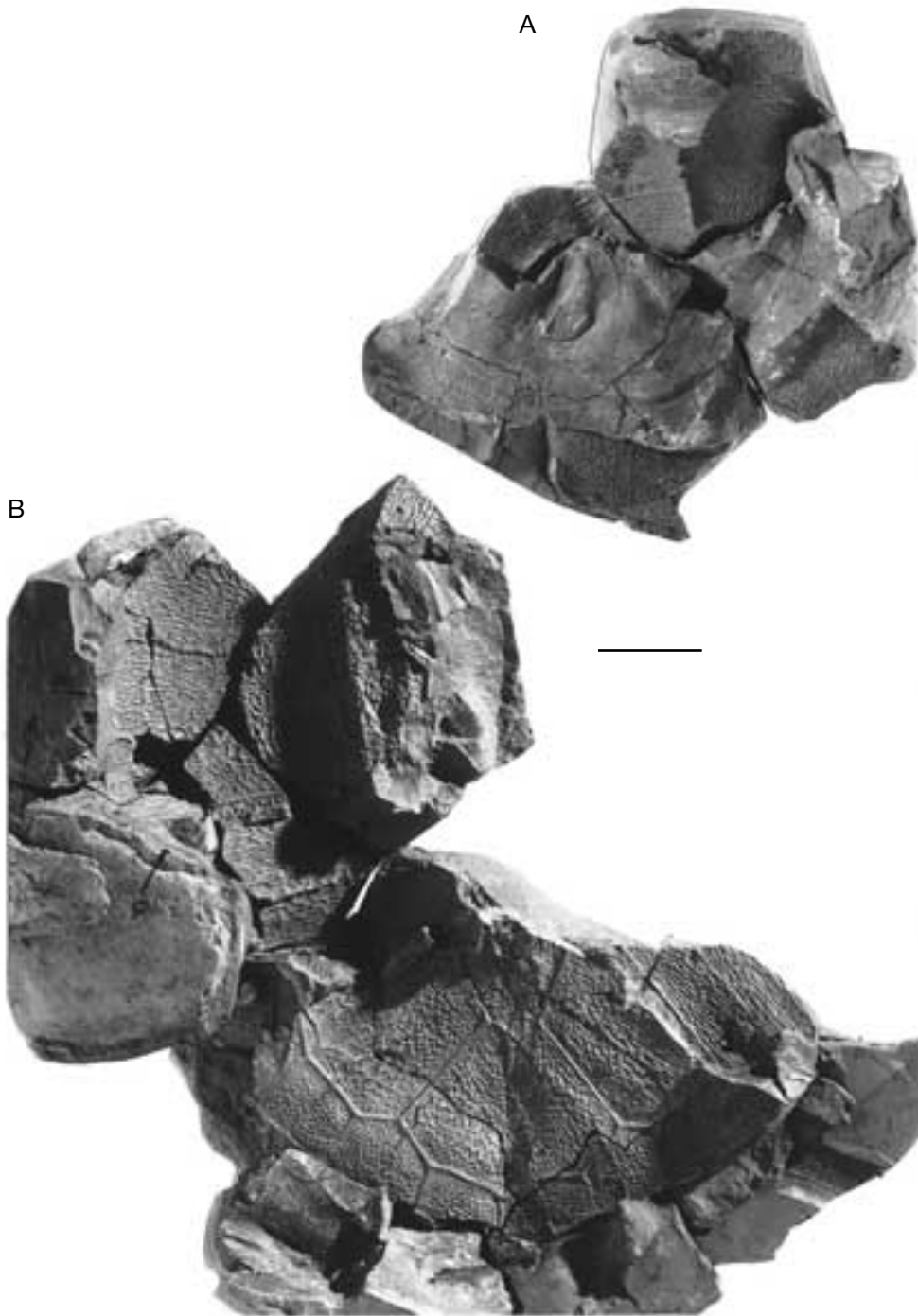


FIG. 1. — *Chelodina alanixi* n. sp., form 1, Redbank Plains, Queensland, Eocene (QM F18344); **A**, posterior part of the shell, impression of the superposed internal and external parts; **B**, lateroposterior part of the shell, impression of the external face. Scale bar: 5 cm.

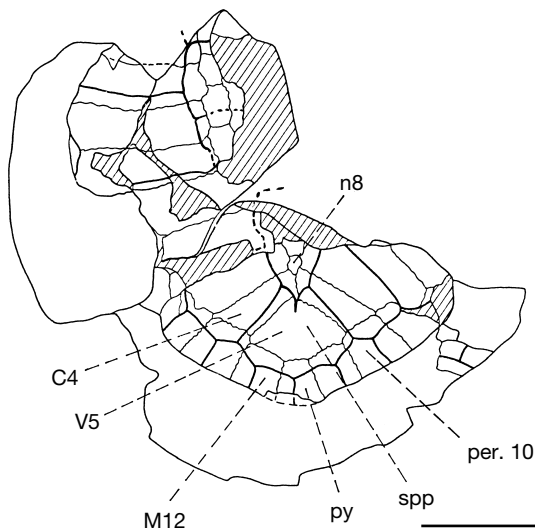


FIG. 2. — *Chelodina alanruxi* n. sp., form 1, Redbank Plains, Queensland, Eocene (QM F18344), lateroposterior part of the shell, impression of the external face. Abbreviations: C4, costal scute 4; M12, marginal scute 12; n8, neural 8; per. 10, peripheral 10; py, pygal; spp, suprapygals; V5, vertebral scute 5. Scale bar: 10 cm.

moderately elongate (Fig. 10A), probably showing the primitive condition for shell elongation in *Chelodina*, the ratio of width to (presumed) length estimated as 73–75%. This percentage (Table 3) is that of moderately elongate living *Chelodina*, such as the largest, *C. expansa* and the smaller *C. longicollis*; it also enters in the range of the still shorter species, *C. reimanni* Philippen & Grossmann, 1990, *C. pritchardi* Rhodin, 1994 and *C. mccordi* Rhodin, 1994 (the distinguishing osteological shell characters of these species remain unknown). The percentage is in the lower range for the small *C. novaeguineae* Boulenger, 1888, and of the rounded *C. steindachneri* Siebenrock, 1914. It is in the higher range for the medium-size, more elongated or narrowed species, the *C. rugosa* Ogilby, 1890 – *C. siebenrocki* Werner, 1901 group and *C. oblonga* (see shells figured in Burbidge *et al.* 1974; Goode 1967; Philippen & Grossmann 1990; Rhodin 1994a, b; Rhodin & Mittermeier 1976). Individual variations, including sexual and ontogenetic variation, and overlap between species are all possible. The estimated ratio of *C. alanruxi* n. sp. indicates that

it was not a short rounded form nor a very elongate or narrow form. It, therefore, has a relatively undifferentiated shell form within the genus in this respect. The posterior border is short, rounded and slightly medially pointed as *C. expansa* (borders of both not as short as in *C. oblonga*) (pointed as in males of *C. expansa*, more than in females), not convex and raised at the pygal as in *C. longicollis* and not particularly convex, curved and narrowed ventrally as in *Pseudemydura*. It is also not elongated and posterolaterally expanded as in the *Emydura* group.

Dermal bones

From the right side of the shell – that is on the left side in Figs 1B and 2, a partial impression of the eight pleurals is preserved. Only the posterior border of pleural 1 may be seen, but pleurals 2–4 are nearly complete, 5–6 lack the medial border and 7–8 are complete. On the left, pleurals 6 (incomplete) and 7–8 are preserved. These pleurals were connected to the medial neurals. The neurals 1 (incomplete), 2–4, 7 (also incomplete) and 8 are preserved. It is evident that there was a complete series of eight neurals, the first quadrangular, the following hexagonal-short-sided in front, and the last pentagonal: the series does not contact the suprapygals, instead the pleurals 8 meet behind the small pentagonal neural 8.

The presence of a complete neural series is primitive and, furthermore, also plesiomorphic for each South American chelid genus, as demonstrated by the early fossil record (from the Albian and Senonian-Maastrichtian of Argentina, Broin & Fuente 1993; Lapparent de Broin *et al.* 1997; Fuente *et al.* 2001). In the primitive chelonian series, known since Late Jurassic, neural 1 or neurals 1 and 2 are hexagonal short sided behind and the first quadrangular neural is 2 or 3. Neural 8 contacts the suprapygals. In Patagonian chelids, reduction of the neural series is already shown by the Albian in a form similar to the small species of the group *Phrynops* Wagler, 1830 – *Acanthochelys* Gray, 1873 (Lapparent de Broin *et al.* 1997). In Late Cretaceous times, Senonian-Maastrichtian, it appears in forms without living relatives and in forms related to *Phrynops* and

Hydromedusa Wagler, 1830, at least (Broin & Fuente 1993). In South American chelids, complete reduction appears only in the *Phrynops* complex: in *Platemys* Wagler, 1830, *Acanthochelys* and in some species of *Phrynops* s.l. (Bour & Pauler 1987; Broin & Fuente 1993; Fuente 1988, 1992; Fuente & Ledesma 1985; Kischlat 1991; Perea *et al.* 1996; Pritchard & Trebbau 1984; Sanchez-Villagra *et al.* 1995a, b; Wood 1976; Wood & Moody 1976; specimens of visited Museums). In Australian chelids (Boulenger 1889; Burbidge *et al.* 1974; Cann & Legler 1994, Legler & Cann 1980; Rhodin & Mittermeier 1976, 1977; Thomson & Georges 1996; specimens of visited Museums), the tendency for neural reduction is common to all the genera, but each genus has done so at a different rate. In Australia, reduction of the neural series is more marked (complete) in *Pseudemydura*. It is complete or nearly complete in the members of the *Emydura* complex, as early as Eocene. Neurals are lost in *Emydura* s.l. sp. from the Condor oil shale near Proserpine (QM F13687). Neurals are rare, and often incomplete, in specimens given as *Emydura* sp. from Tasmania (Warren 1969a) and in some specimens of the extant *Elseya latisternum* Gray, 1867 and *E. novaeguineae* (Meyer, 1874) (see Rhodin & Mittermeier 1977), *Elseya* sp. aff. *latisternum* from Manning River and *Elseya* sp. from South Alligator River (Thomson & Georges 1996; a new determination is given in Thomson in prep., pers. comm.) and only the ventral part of the posterior neurals remains in *Emydura* s.l. sp. a (Redbank Plains form 5). In the specimens of *Chelodina*, examined, the reduction is either always complete and not submitted to individual variations (*C. expansa*, see Fig. 10B, *C. rugosa*, *C. steindachneri*), much pronounced (*C. siebenrocki*, *C. novaeguineae*) or slightly pronounced (*C. oblonga*). In the former, the ventral layer of the neurals is preserved below the pleurals which meet over them as in *Emydura* s.l. sp. a (Redbank Plains form 5) and this may be present in many South Australian chelids (Thomson & Georges 1996). This shows that the reduction occurred independently in each lineage of *Emydura* s.l. as well as of *Chelodina* and that

C. alanruxi n. sp. has a primitive character state with a complete series of neurals, but already with the first neural quadrangular and neural 8 not contacting the suprapygal. This morphology indicates that it may be at the base of one of the lineages leading to extant *Chelodina* species.

The posterior border is represented by the peripherals 8-11, on the right side and the pygal and the peripherals 9-11 on the left. The pleurals are well-sutured with the peripherals and the dorsal rib extremities well-fused in the dermal plates, without any salient ventral part and any free rib extremity, appropriate for a large adult without permanent fontanelles with their intercalated cartilaginous tissue. The peripherals are relatively wide, for example for peripheral 10 the ratio of anterior length to external width is 94%. Among extant forms, this ratio is comparable to that of *Chelodina* (84% in *C. oblonga*, 106% in *C. steindachneri*, 107% in *C. expansa*, 116% in *C. longicollis*) and *Pseudemydura* (93% and 121%, from two specimens). The value is higher in the *Emydura* group although a slight overlap between the two groups exists: 105% in *Elseya latisternum*; 115% and 141.5% in *E. novaeguineae*; 137% in *E. dentata* (Gray, 1863); 120%, 129% (holotype, MNHN H 9409) and 137% in *Emydura macquarrii* (Gray, 1831); 140% in the specimen QM J31703 attributed to *Rheodytes leucops* Legler & Cann, 1980; 171.5% in a specimen from the MNHN (H) coll. attributed to *E. australis* (Gray, 1841), a specimen apparently conform to the holotype, BMNH 47-3-4-36; see Goode 1967 (Thomson pers. comm. suggests that the specimens identified here as *E. australis* are of *E. victoriae* [Gray, 1842] that he separates from the former with which it was synonymized). The posterior peripherals have the most derived condition, for Australian chelids in the *Emydura* group – narrower and more elongated – although they are as wide as in some *Chelodina* in the less derived specimens such as in *Elseya latisternum* and in some specimens of *E. novaeguineae*. However, in all the *Emydura* group species, they are more elongate than in *C. alanruxi* n. sp. The measurements of the peripherals of *C. alanruxi* n. sp. are fully concordant only with those of *Chelodina* and *Pseudemydura*

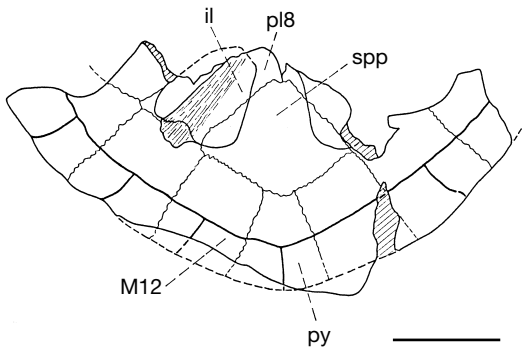


FIG. 3. — *Chelodina alanrivi* n. sp., form 1, Redbank Plains, Queensland, Eocene (QM F18344), posterior part of the shell, impression of the internal face of the Fig. 1A. Abbreviations: **il**, iliac scar below pleural 8 and suprapygal; **M12**, marginal scute 12; **pl8**, pleural 8; **py**, pygal; **spp**, suprapygal. Scale bar: 5 cm.

specimens. Actually, the primitive turtle form of the border, and the original form in the pleurodires in particular, is not expanded anteriorly or posteriorly. These include *Proterochersis* Fraas, 1913, from the Triassic of Germany (specimens in the Staatliches Museum für Naturkunde-Stuttgart), *Notoemys Cattoi* & Freiberg, 1961, from the Late Jurassic of Argentina (specimens from Museo de Ciencias Naturales de La Plata, Museo de Ciencias Naturales de Buenos Aires; Fuente & Fernandez 1989; Fernandez & Fuente 1994), and *Platycheilus* Wagner, 1853, from the Late Jurassic of Germany and Switzerland (specimens in Naturmuseum Solothurn; Bräm 1965). The shell border is slightly elongated anteriorly and posteriorly in *Pseudemydura*, much more elongated anteriorly and slightly posteriorly in *Chelodina* and slightly elongated anteriorly and much more elongated and expanded posteriorly in *Emydura* s.l. Parallel evolution produced similar forms in each of the South American chelid groups as well as in the northern Gondwanian Pelomedusoides but, linked to other characters, these still represent important diagnostic features for each genus or group of species.

The suprapygal and pygal are similar to those of *C. expansa*: the suprapygal is pentagonal but nearly rhomboid and the pygal is more narrowed anteriorly. The suprapygal shape is also more

anteriorly triangular in *C. alanrivi* n. sp. than in *C. insculpta* De Vis, 1897. That suprapygal of that species, rather similarly to that of *C. longicollis*, bears the borders of the vertebral 5, this scute being narrowed as in the extant relatively elongated forms, including *C. longicollis* (see below) and different from that of *C. alanrivi* n. sp. The figures 1A and 3 show the scars for the sutural attachment of both ilia below the posterior carapace. This is a typically pleurodiran character in the suture of the pelvis to the shell: in the Pleurodira, relative to the primitive state in turtles, the pelvis is reduced in width at least to the size of the posterior lobe (or even narrower). This has become bifid to receive the points of the ischia (Lapparent de Broin & Fuente 1996). The dorsal surface of the iliac blade is widened and shortened and sutures to the carapace. The pubis and ischia become vertical and their ventral extremities suture with the plastron. The shape of the iliac scar of *C. alanrivi* n. sp. is a trapezoid with rounded angles, the anterior side directed medially, as long as wide and occupying most of the surface of pleural 8 and overlapping the suprapygal by a wide, rounded triangular area. The shape of the iliac scar is variable in chelids. It is primitively triangular in chelids and it remains so or rather triangular in *Emydura* s.l., becomes more elongate and rounded-oval in *Pseudemydura* and it is most often oval or triangular (but much rounded) in *Chelodina*. There is parallel evolution in each South American chelid group. The length of the scar below pleurals 7 and 8 and the suprapygal varies much. If the scar is wider or both shorter and wider, it is more derived: the primitive pleurodiran scar being narrow and prolonged from pleural 7 to the peripherals. In chelids the scar has a tendency to be reduced anteriorly so that it does not contact pleural 7 any more. The ilium also tends to maintain – but eventually to expand in width – its contact with the suprapygal (the pelvis becoming more posteriorly sutured to the shell). This condition is different from that of the Pelomedusoides where the tendency is to reduce the contact with the suprapygal (the contact most often disappears, with the pelvis more anteriorly sutured to the shell) (Lapparent

de Broin & Fuente 1996; Lapparent de Broin & Murelaga 1999). The anterior contact of the scar under pleurals 7-8 is not preserved in *C. alanruxi* n. sp., but, judging from the part preserved, the scar ought to be little developed in pleural 7 or limited to the suture between the two pleurals, as in *C. expansa*.

The scar is a depressed region on the pleurals, well-delimited and nearly smooth. But dorsal rib 9, which is enveloped in pleural 8, within the scar, develops in a ventral, strong and salient crest in *C. alanruxi* n. sp., as in every other observed *Chelodina*, strong as in *C. expansa* and particularly wide. The crest is also developed in *Emydura* s.l. (for example in *E. macquarrii*), although less developed than in *Chelodina expansa* and doubled in some specimens, *Pseudemydura* (shallow rib) and South American chelids, such as many species of *Phrynops* and *Hydromedusa* (narrow or thin, sharp or rounded in the scar). The character is subdued (shallow with a short or thin crest) or absent in many other species of *Emydura* s.l. and of *Phrynops*. In the *Emydura* group, instead of a crest of rib 9, there are often rugosities, for example in *Elseya novaeguineae* and *E. latisternum*, or a triangular zone of sutural tubercles, as for example in specimens attributed, in collections, to *Emydura australis*. A zone of tubercles around the crested rib is present in the South American *Chelus* Duméril, 1806. In the present case, the scar and rib conform those of *C. expansa*.

Scutes

The costals and vertebral 5 much overlap the peripherals and pygal as in *Chelodina*, dorsally (Figs 1B; 2; 10) particularly as in *C. expansa* (Fig. 10B); ventrally (Fig. 3), the marginals overlap the peripherals more than in that species. Vertebrales 1 (at least in the preserved posterior part), 2, 3 (certainly, although lacking) and 4 are strongly narrowed. Although the vertebrales are incomplete, the narrowing is shown by the close proximity of the lateral vertebral border to the lateral neural border (a narrow pleural covered by the vertebrales). Vertebral 5 is narrow anteriorly and wide posteriorly. It is wider than the supra-

pygal, which it fully covers as well as covering a part of pleurals 8 and of peripherals 10, 11 and pygal. This particularly strong narrowing of the vertebrales from the posterior part of the first to the anterior part of the fifth is derived and particular in chelids to the relatively elongated extant species of *Chelodina* (shell moderately elongate to elongate), particularly *C. oblonga* and *C. longicollis*, although a regular narrowing of the series is common in all chelid forms, including all *Chelodina* species. But in the extant *C. expansa*, with less narrowed vertebrales (Fig. 10B), and at least *C. siebenrocki*, *C. parkeri* Rhodin & Mittermeier, 1976, *C. rugosa*, *C. oblonga* and *C. longicollis*, with more narrowed vertebrales, vertebral 5 is so much narrowed anteriorly that it is narrower than the suprapygal (in most examined specimens), or as wide as the suprapygal only posterior to the suprapygal (at least some specimens of *C. longicollis* and *C. oblonga*). In the fossil suprapygal which is part of the specimens attributed to *C. insculpta* De Vis, 1897, vertebral 5 is also narrowed relatively to the plate. On the pleurals, which are also parts of those specimens, the preserved parts of the vertebrales are also narrowed. They are not as narrow as in *C. alanruxi* n. sp., *C. longicollis* and *C. oblonga*, but as in *C. expansa* for example (Fig. 10B). In the short rounded *C. steindachneri*, the vertebrales also look narrow compared to the costals, but the costals are widened, owing to the widening of the shell, thus giving a narrowed aspect to the vertebrales. In the other forms not showing narrowing, the vertebrales are, primitively, little differentiated on the whole, although they tend to be narrowed from the anterior one posteriorly; sometimes there are subdivisions of the second or of the fourth in a short and narrow supplementary scute as in the other group of elongate forms. In these forms that are not elongated as in *C. alanruxi* n. sp. and unlike all the other fossil and extant species of *Chelodina*, the vertebral 5 is wider than the pygal, which is the primitive condition. We think therefore that, for the character of narrowed vertebrales, *C. alanruxi* n. sp. is also separated from the group with rounded shells such as *C. steindachneri* and probably also from Redbank

Plains form 2. *C. alanruxi* n. sp. may be just at the base of a group including extant *Chelodina* forms with vertebral 5 narrower, at least anteriorly, than the suprapygal, the character of narrowed vertebrals 2 to 4 being shared in common. If this character, of vertebral 5 narrowed relative to the suprapygal, developed only once, then *C. alanruxi* n. sp. is the sister group of the latter and the group with rounded shells such as *C. steindachneri* their common sister group. In this case, the shortening of the sulcus between the pectoral was produced twice, once in *C. longicollis* and once in the *C. steindachneri* group (see Discussion below). But the character of vertebral 5 narrow relative to the suprapygal may have developed several times and we lack too much of *C. alanruxi* n. sp. (plastron, skull, neck) to detect the possible homoplasies and define exactly the phylogenetic relationships of the fossil form.

In chelids, it sometimes happens that instead of covering the peripherals and pygal, vertebral 5 is posteriorly reduced in length and marginals 12 developed, at least medially, over the suprapygal. This happens in *Emydura* sp. aff. *E. macquarrii* from the Oligo-Miocene of Tasmania (Warren 1969a) as well as in some South American extant species of *Phrynops* and the Cretaceous chelids from the Area Loma de la Lata and Ocho Hermanos (Broin & Fuente 1993; Lapparent de Broin & Fuente in prep). Sometimes also, marginals 12 meet vertebral 5 just at the pygal-suprapygal suture, which is more like the primitive condition in turtles. But the more frequent state in chelids is that of a moderate overlapping for the peripheral border by the costo-vertebral scutes. *C. alanruxi* n. sp. is therefore well-developed in this state, as is *C. expansa*. It differs, on this point, from *C. oblonga* which has a relatively short posterior border (apomorphic) with a short scute overlap, as compared to *C. expansa*. On the other hand, *C. oblonga* is much more elongate anteriorly (longer nuchal relative to shell length) than *C. expansa* and probably *C. alanruxi* n. sp.

We note that vertebral 5 is partly longitudinally divided anteriorly, in *C. alanruxi* n. sp.: this is an individual variation sometimes present in specimens of all extant turtles.

DISCUSSION

Chelodina alanruxi n. sp., clearly pleurodiran as shown by the pelvis sutured to the shell, is a *Chelodina* species because of the shape of the shell; its decoration; its posterior border, elongate but not too much; its iliac scar morphology and extension; its narrowed vertebrals 2 to 4, as in some extant species of *Chelodina*.

The genus *Chelodina* is well-defined, in extant species, principally on two excellent derived characters that are not preserved here:

- 1) on the anatomy of the skull, with a complete dorsal skull fenestration, beginning from the lateral emargination and prolonged backwards, cutting the supraoccipital-parietal contact with the squamosal;
- 2) on the intergular scute, withdrawn backwards from the epiplastral border, allowing the gular scutes to meet anteriorly to the intergular, or to nearly meet in the holotype of *Chelodina intergularis* Fry, 1915 (a deformed *C. rugosa* fide Thomson pers. comm.) (Wermuth & Mertens 1961; Goode 1967). Posteriorly, the enlarged intergular completely separates the humeral scutes and a part of the pectorals. For this character, the more derived forms are the shorter forms (including the rounded *C. steindachneri*) where the intergular is more backwards prolonged and the suture between the pectorals shorter, but *C. longicollis*, a relatively elongated form judging by the skull (see below) and without a widened carapace, also approximates them (short hyoplastral suture and interpectoral sulcus). For the intergular position, the less derived are the elongated-narrowed forms and among them the *C. siebenrocki-rugosa* group, including *C. intergularis*, and *C. oblonga*. A short skull is the primitive condition and an elongation of the palate, correlated with a flattening of the skull, is produced in the elongated-narrowed forms. The elongation can be measured by the ratio of the lateral ventral length of the pterygoid, between its suture with the jugal and the maxillary and its suture with the quadrate, on the skull width, at the quadrate ventral border below the tympanic meatus. The ratio is the shortest in *Pseudemydura*. Then, the ratio elevates a little in the *Emydura* group. According to the figures of the authors, the

forms of *Chelodina* with a medium-sized and short, more or less rounded carapace, including *C. reimanni*, *C. pritchardi* and *C. mccordi*, have the same proportions for the skull characters: all of them have the lowest percentage in *Chelodina*, which in part (*C. steindachneri*) covers that of some *Emydura* s.l. species. Their higher percentage (*C. novaeguineae*) is below that of *C. longicollis* and that of the other forms with a moderately elongated or clearly elongated shell: within this group, the skull elongation is visually noticeable from *C. longicollis* and it is maximum in *C. expansa*. A less transverse position of the trochlear pterygoid processes is partly correlated with the skull elongation. The neck is also longer in the longer skull forms than in those with short skull forms. There are overlaps between the species.

The living species of *Chelodina* are often classified in two groups, following a dichotomous system which is very useful, although fully phenetic: it is principally based on the length of the plastron relative to the width (plastral length generally about one time and a half maximum width, rarely exceeding one time and three-fourth the maximum plastral width, or usually greater than 1.9 time the maximum width of plastron (Cogger 1992; Goode 1967). This system does not take into account: 1) the way the various parts of the plastron (anterior lobe or all the posterior lobe or xiphiplastral points only or all the plastron as a whole) are widened and enlarged, relative to the primitive chelid narrow short state with narrow xiphiplastral points; 2) the way the plastron is widened, relative to the way the shell is elongated or rounded (widened). Also are considered other characters such as the skull (broad or narrow), the contact between the pectorals (short in forms with broad plastron or long in forms with long plastron), some other characters (barbels, head and neck skin surface, odour, etc.) and some relative proportions which are variable and with overlap between the two groups. The primitive and the derived states and the intergradations are not taken into account. The plastral size and the evolution of the intergular posteriorly do not coincide with the other characters of the skull

(elongation and flattening, position of the trochlear pterygoid processes, etc.), neck elongation, changes in plastral proportions, neural reduction, border proportions, vertebrals narrowing (see above), etc.

The characters of the two phenetic groups do not coincide with those used here to distinguish the fossil species. For example, in the phenetic dichotomous system, *C. longicollis* is placed by the authors with the short forms of the type of *C. steindachneri* and *C. novaeguineae*. However, it has a relatively elongate skull as *C. siebenrocki*, narrowed vertebrals as *C. oblonga*, vertebral 5 narrower than suprapygals as the large *C. expansa* and as the long forms, and it has not a widened or narrowed-elongated shell although it has a widened plastron. Cladograms of *Chelodina* species are given (Rhodin 1994a, b) supporting the phenetic system, but they are not verifiable or refutable because they are given without the matrix and list of the characters. Other phylogenetic studies are based on electrophoretic data or on mitochondrial and nuclear gene sequence variation (Georges & Adams 1992, 1996; Georges *et al.* 1999), not useful in our study of fossils (see also White 1997). Their results, not including fossils, do not present the evolution in all the forms from Triassic to present times. They are useful overall in separating paraphyletic taxa at the generic level, according with the osteological results: for example *Elseya*. As far as *Chelodina* is concerned, these analysis correspond together and with the phenetic system, grouping species mostly on synplesiomorphic characters, but not with our observations: in one analysis, *C. longicollis* is placed with *C. steindachneri* and *C. novaeguineae* (two rounded short forms), with *C. oblonga* as sister group, and the whole with *C. rugosa* and *C. expansa* as outgroup (Georges & Adams 1992). In another paper, *C. oblonga* and *C. longicollis* have *C. rugosa* as outgroup, *C. steindachneri* not being integrated (Georges *et al.* 1999). Thomson (pers. comm.) supports an independent acquisition of skull lengthening and a possible reversion to a short skull in various extant species and the separation in the two *Chelodina* groups of the authors, A and B, on

TABLE 2. — Comparative elements of five specimens (1 to 5) from Redbank Plains, Queensland, Queensland Museum. Abbreviations: **app.**, approximately; **n**, neural; **part 7, 8**, posterior part of pleural 7, pleural 8; **per. 10 L/w**, peripheral 10, anterior length on external width; **PL**, posterior lobe of plastron; **PL w/L**, plastral posterior lobe, width at abdomino-femoral sulcus on maximal length; **py**, pygal; **spp**, suprapygal; **V**, vertebral scute.

Forms, taxa from Redbank Plains	Decoration	Posterior shell shape Neural number; continuous	Iliac suture under pleurals and spp; pubis, ischiadic scars	Vertebrales
1: <i>Chelodina alanruxi</i> n. sp., (sp. a) (QM F18344), carapace: width c. 30 cm; length c. 41 cm; per. 10 L/w = c. 94%	Strong dorsal; very small polygons, elongate: transversally (lateral parts), longitudinally (medial parts) and obliquely (posteriorly)	Slightly pointed in open rounded V. n1 to partial n8; yes, without spp contact	Trapezoid, part 7, 8, wide good part spp; strong wide rib 9; ?	V1?, V2 to V4 very narrow << V5 > spp; V5 long on py
2: <i>Chelodina</i> sp. b (QM F18214), carapace: width c. 14 cm; length c. 16,5 cm; per. 10 L/w = 95%	Strong dorsal; very small polygons, at least elongate transversally on lateral parts	Rounded. ?, without spp contact	? ?	V1-V3?, V4 V5 narrow, V5 app. = spp; V5 long on py
3: <i>Chelodina</i> sp. c (QM F18216-18215): carapace length c. 25 cm; upwardly-curved narrow bridge peripherals as in various <i>Chelodina</i>	Strong dorsal; small polygons regularly distributed, as in <i>Chelodina</i>	? ?	? Pubis scar diamond-oval shaped, ischiadic scar posteriorly rounded as in <i>Chelodina</i>	?
4: <i>Chelodina</i> sp. c? (QM F18212) plastral length c. 18 cm?, carapace length c. 22 cm? PL w/L = 91.95% (as in <i>Emydura</i> s.l., < to extant <i>Chelodina</i>); preserved part PL = shape as in some <i>Emydura</i> s.l. and as in some <i>Chelodina</i>	Strong ventral; plastral granulate polygons regularly distributed, particularly as in <i>E. (Elseya) dentata</i> , longitudinally elongate on posterior hypoplastron and on hypo-xiphi-plastral suture areas; polygons very small; dorsal polygons as in <i>Chelodina</i>	? ?	? Pubic scar oval as in some <i>Emydura</i> s.l., at least <i>E. (Elseya) latisternum</i> and <i>E. (Elseya) novaeguineae</i>	?
5: <i>Emydura</i> s.l. sp. a (QM F31697), carapace: width c. 15.5 cm; length c. 20 cm; PL w/L = c. 94 to 100%	Weak dorsal decoration (some weak dichotomous sulci); plastral weak polygons	Rounded. 0 dorsal (n 6-8 preserved ventrally); no	Trapezoid-rounded triangle, part 7, 8, rounded part spp; rugosities on rib 9; ?	V1-V3?, wide (angulate lateral borders) V4 < wide V5 >>

osteological characters. It will be interesting to see if the characters shared by each group are synapomorphic or synplesiomorphic, if we can detect the homoplasies and conciliate the contradictions with the present statements.

In fact, the distribution of the derived characters preserved here appears as a mosaic type. In the absence of the skull, neck and plastron, we cannot establish a cladogram to show the phyletic position of *C. alanruxi* n. sp.

We just can take the obvious characters in *C. alanruxi* n. sp., which are principally those of the evolutionary states of neurals, of width of vertebrals 2-4 and of anterior width of vertebral 5. The combination of these characters shows that the species is new, compared to the fossil and living species, and that it is rather primitive.

The diagnosis shows it is similar (same derived state of characters) to *C. expansa* (see Fig. 10) by its large size, the posterior slightly pointed flattened border (overall in males), the strength of the iliac scar crest and the posterior plate proportions and scute covering, all characters in which it particularly differs from *C. oblonga*. Its peculiarities are never found as individual variations in extant *C. expansa*. But it is more primitive than *C. expansa*, *C. longicollis* and the relatively elongated and elongated-narrowed living forms by the width of the vertebral 5, not anteriorly reduced, differing there as well as from the fossil suprapygial attributed to *C. insculpta*.

Relative to *C. expansa*, it differs also by the presence of a prolonged neural series. In this character, it is similar to *C. oblonga*, that retains one to seven neurals (although the first one is incomplete in front, when present), but this is a primitive character not allowing a privileged phyletic relation between them. On the other hand, the fossil form 1 shares with *C. oblonga* a very derived character, the higher degree of narrowing of vertebrals 2 to 4. However, it lacks the shortened posterior border of *C. oblonga* and the vertebrals are also often much narrowed in *C. longicollis*, which lacks an elongated-narrowed shell: narrowing of the vertebrals, present in a higher degree in *C. alanruxi* n. sp., is not linked to the carapace elongation and modification of the posterior border.

The dorsal elements are sufficient to separate this species from *C. insculpta* De Vis, 1897. In the absence of a preserved plastron for the Redbank Plains form 1, we cannot analyse its differences from the plastron of the living and fossil species. In the former (and composite) species, the anterior and posterior preserved plastral parts are consistent with the belonging to only one species of a single age, owing to the decoration and the



FIG. 4. — *Chelodina* sp. b, form 2, Redbank Plains, Queensland, Eocene (QM F18214), right lateral and posterior part of the shell, impression of the external face. Scale bar: 2 cm.

proportions of the elements. The preserved part of the anterior plastron is more similar to that of *C. longicollis* in the relative distances between sutures and scutes than to the elongated forms; in particular, the suture between the two hyoplastra and the sulcus between the pectoral scutes are relatively short, compared to the elongated forms with a long suture, being closer to the rounded forms with a short suture, but the plastral anterior lobe is much narrower than in *C. longicollis*. The posterior part is also much less widened, anteriorly and posteriorly, so closer to the primitive chelid state: it is still narrow at the hypoplastra and anterior part of xiphiplastra and less widened at the posterior part of the xiphiplastra below the anal scutes. It is different from the extant species although most of them have still narrowed anals.

In summary, the Redbank Plains form 1, *C. alanruxi* n. sp., is therefore a new species primitive relative to extant and fossil *Chelodina* species, although much derived in having the vertebrals narrowing as in the moderately elongated and very elongated forms. It is different from the rounded species, including the following

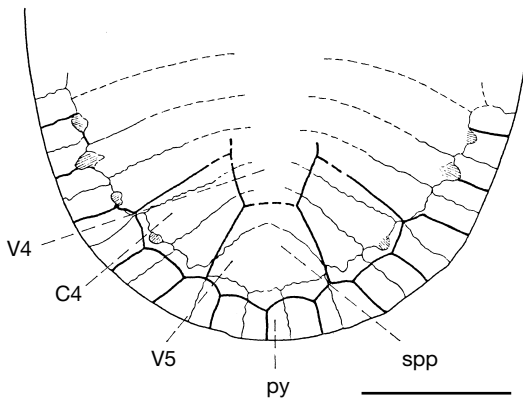


FIG. 5. — *Chelodina* sp. b, form 2, Redbank Plains, Queensland, Eocene (QM F18214), reconstruction of the lateroposterior part of the shell. Abbreviations: C4, costal scute 4; py, pygal; spp, suprapygal; V4, V5, vertebrals scutes 4 and 5. Scale bar: 5 cm.

Redbank Plains form 2, and from the extant species without vertebrals narrowing. It differs also from the Redbank Plains form 3 by its elongate and smaller (relatively) polygons, its larger size and the presumed absence of an upwardly-curved border.

Chelodina sp. b

DESCRIPTION

Material (Figs 4; 5; Table 2) (Rix 1991: fig. 2A)

Redbank Plains form 2 is represented by the specimen QM F18214. It is an external impression of a fragmentary carapace, of the right lateral and posterior parts. It includes the impression of the lateral border from the peripheral 4, the impression of the right peripherals 5 (a part) to peripheral 11, of the pygal and of a part of the left peripheral 11, of the lateroposterior part of the pleurals 3-8 and a part of the suprapygal.

Measurements (in cm)

Oblique anterior preserved border: *c.* 13.8.

Width at the peripherals 5: 14.

Estimated medial length: *c.* 16.5.

Maximal suprapygal width: 3.6.

Maximal vertebral 5 width: 3.6.

Peripheral 10 anterior length on external width: $1.9/2 = 95\%$.

Decoration

The decoration is similar to that of *Chelodina alanruxi* n. sp. except that the size of the polygons is much reduced, in proportion with the much reduced carapace size. The polygons are *c.* 0.5-1 mm wide and 0.1-4 mm long. The polygons are very well-marked and uniformly distributed on the shell part preserved as in all the *Chelodina* species, including *C. alanruxi* n. sp. as well as the rounded extant form *C. steindachneri*. They are very elongate on the lateral extremities of the pleurals and on the posterior extremity of the suprapygal, at the boundary with the peripherals and the pygal, more elongate there than in *C. alanruxi* n. sp. and in the extant species. The polygons are slightly smaller than in the *C. steindachneri* and *C. novaeguineae* (they are not known in the relatively short and medium sized recently described other extant species). As in *Chelodina*, the polygons of the peripherals are elongate in the direction of the lateral border of the carapace. The polygons of the suprapygal are equivalent in size to those of the suprapygal attributed to *C. insculpta* De Vis, 1897 (pl. V, H) but those are not drawn obliquely oriented and not posteriorly elongate. However, the other fragments attributed to this species have coarser polygons, as in the extant species of *Chelodina*. As shown above (Table 1), these fragments, including the lectotype selected by Gaffney (1981), are not precise as to their origin and age: Pliocene-Pleistocene of Darling Downs and Warburton River and Eocene of Eight Mile Plains. They could therefore include a specimen equivalent in age to a Redbank Plains form. Thomson (pers. comm.) thinks that all the figured specimens are from Darling Downs.

Shell shape

Of the parts preserved, the width of the posterior preserved part and the shortness of the preserved pleurals, make it possible to reconstruct a rounded oval carapace, like that of a rounded form of *Chelodina* such as the extant *C. steindachneri* Siebenrock, 1914. Figure 5 shows the reconstruction of the posterior part of the carapace reconstructing the left side symmetrical to the preserved right side.

TABLE 3. — Comparative carapace ratio of width to length in the carapace of some living *Chelodina*.

Taxon	Carapace length	% carapace width/length
<i>C. alanruxi</i> n. sp.	c. 40-41 cm (estimated)	73 to 75?
<i>C. expansa</i>	up to 42.3 cm	78 (MNHN AC 1914-178); 70.5 to 76.12 (Goode 1967)
<i>C. longicollis</i>	up to 32 cm	71.21 (MNHN AC 1911-181); 77.87 (MNHN AC A 5190)
<i>C. reimanni</i>	up to 20.6 cm	68.93 to 76.66 (Philippen & Grossmann 1990)
<i>C. pritchardi</i>	22.8 cm	72.83 to 81.36 (Rhodin 1994a)
<i>C. mccordi</i>	21.3 cm	76.05 to 79.35 (Rhodin 1994b) (young 73.36)
<i>C. novaeguineae</i>	up to 18 cm	77.77 (BMNH 46.1.22.36); 74.73 to 78.10 (Goode 1967)
<i>C. steindachneri</i>	up to 22 cm	80.24 (WA R 29375); 84.92 (WA R 113100); 84.61 (WA R 113101); up to 86.79 (Goode 1967)
<i>C. rugosa</i>	20.2 cm	75.74 (MNHN H 1983-378)
<i>C. siebenrocki</i>	up to 27.5 cm	67.27 to 75.49 (Goode 1967)
<i>C. oblonga</i>	up to 28 cm	60.97 (UWA); 66.66 (BMNH 64.12. 22.6); 67.34 (WA R 29382); 63.14 to 72.34 (Goode 1967)

The shell, with well-sutured plates, is that of a young adult with still uncovered rib extremities or of an adult of a species keeping free lateral rib extremities in the peripherals, visible dorsally, as in various extant chelid species and in particular as in many *Chelodina*. The shell is estimated to have been rather rounded, the width relative to the presumed length being estimated as c. 85%. This percentage is that of *C. steindachneri* Siebenrock, 1914 (up to 86.79%, see Table 3). The rounded posterior border of the pleural disc is comparable to that of *C. steindachneri* and *C. novaeguineae*, not as narrow as in most of the other extant species and not cordiform as in *Pseudemydura*. The posterior border of the carapace is short, rounded and not slightly medially pointed, as it is in extant *C. expansa* and in *C. alanruxi* n. sp. (and still more pointed in *C. longicollis* and *C. mccordi*). As in *C. alanruxi* n. sp., *C. expansa* and some other species such as *C. steindachneri* and *C. pritchardi*, it is not raised at the pygal, convex from side to side, as in the extant *C. longicollis* and *C. mccordi*. It is not so as markedly convex, inwardly recurved and ventrally narrowed as in *Pseudemydura*. It is not elongated and expanded as in the *Emydura* group.

Laterally, nothing indicates the presence of the beginning of an upwardly-curved border as in *C. sp. c.*, *C. longicollis* and in some other *Chelodina* species and as in *Pseudemydura*.

Dermal bones

The length of the preserved pleurals is short compared to the lateral pleural borders in contact with the peripherals. This allows the reconstruction of a rounded form as *C. steindachneri*. The free rib extremities are clearly visible in the impression of the external dorsal view, more than in most extant adult forms. It might therefore be a sub-adult of a slightly larger adult form. The plates of the border are not very elongated. The pygal and peripherals 11 and 9 are as wide externally as long anteriorly, the peripheral 10 is wider externally than long and the peripherals 8 and anterior (preserved to peripheral 5) have their external border progressively elongated relative to the shortened anterior and posterior borders. The ratio length/width of the peripheral 10 is 95%, approximately as in *C. alanruxi* n. sp. As seen above, it is a low ratio in *Chelodina*, just higher than in *C. oblonga* and closer to that of *C. steindachneri* and *C. expansa*, as well as that of *Pseudemydura*,

and far from the higher ratios of the *Emydura* group. Also, it indicates a moderate expansion of the posterior border, distinct from the tendency developed in the *Emydura* group.

The suprapygal is pentagonal, more or less pointed anteriorly (missing in part).

Scutes

The vertebral 5 and costals 4 overlap the peripherals and pygal less than in *C. alanruxi* n. sp., *C. expansa* and *C. longicollis*, as in *C. steindachneri* and more than in *C. oblonga*. More anteriorly, the sulcus of the costal 3-marginals remains a little external to the peripheral-pleural suture and then is nearly united with it. We do not know how it was in *C. alanruxi* n. sp. In extant *Chelodina*, the osteology of which is known, either all the costals remain overlapping the peripherals laterally (*C. expansa*) or the costal 2 alone is united with the suture (*C. longicollis*) or nearly united to the suture (*C. steindachneri*, *C. oblonga*). It therefore may have a specific value. In the Redbank Plains form 2, the morphological stage is closer to that of the forms with a rounded posterior border than to that of *C. expansa*, *C. longicollis* and other elongate forms.

Part of the medial carapace, anterior to the suprapygal, is missing. We know nothing about presence of neurals and width of vertebrae, except that the vertebral 5 is just as wide as the maximum width of the suprapygal. It is therefore narrower than in *C. alanruxi* n. sp. and *C. steindachneri* (not known in *C. novaeguineae* but probably wide as in *C. steindachneri*). But it is still wider than in forms without a widened shell and with narrowed vertebral 5, including *C. longicollis*, *C. expansa* and *C. oblonga*.

DISCUSSION

The posterior part of carapace QM F18214 shows the decoration of *Chelodina*. The shape of the preserved part agrees with *Chelodina* and not with *Emydura* s.l. and *Pseudemydura*.

Within *Chelodina*, the specimen better agrees with the rounded form *C. steindachneri* but also with some extant forms without a pointed and medially raised posterior border (the primitive condition) such as *C. reimanni* and *C. novaeguineae*.

It differs from *C. alanruxi* n. sp. in the relatively smaller size of the polygons, owing to the smaller size of the carapace. The size of the polygon is also smaller than in another fragment of turtle from Redbank Plains, studied below and attributed also to *Chelodina*, undefined species, from a carapace slightly larger than the Redbank Plains form 2. The size of the polygons is also smaller than in the dorsal shell of extant species (smaller polygons exist in plastral part of extant species such as *C. steindachneri*). It is similar to that of the suprapygal referred to *C. insculpta* De Vis, 1897. But this has a clearly narrowed vertebral 5, narrower than the suprapygal, as in the extant *C. longicollis*, *C. expansa* and the elongated species. In return, in this character, the Redbank Plains form 2 is less derived, intermediate between them and the short *C. steindachneri* which has a vertebral 5 wider and even much wider (enlarged in some specimens) than the suprapygal and *C. alanruxi* n. sp.: the vertebral 5 is here slightly narrower and shortest on the external border plates.

It differs also from *C. alanruxi* n. sp. by the more rounded shape of the carapace with relatively shortest pleurals, the smaller size of the carapace and of the polygons.

It seems to differ also from the Redbank Plains form 3, undefined sp. of *Chelodina*. This is larger (maybe because an older individual) with relatively larger dorsal polygons. Furthermore, the latter has a recurved lateral border, as in many extant species, which does not seem to be present here.

In summary, it is probable that it belongs to the *C. steindachneri* lineage and to a new species, but the elements are insufficient to define it. Furthermore, as long as the osteology of all the extant species is not known, it is not possible to satisfactorily address this question.

Chelodina sp. c

DESCRIPTION

Material (Table 2)

The Redbank Plains form 3 consists of specimens QM F18216 and 18215, the impression of a

fragment of carapace, comprising some dislocated plates in which we recognize three right bridge peripherals, four or five fragments of pleurals and a plastral bridge element, with the fragmentary left pubis and ischium.

Measurements (in cm)

Right peripheral 7: posterior ventral width: 2.2; lateral length: 2.6; anterior ventral width: 1.5.
 Right peripheral 6: posterior ventral width: 1.2; lateral length: 2.6; anterior ventral width: 0.9.
 Right peripheral 5: posterior dorsal width: 1.5; lateral length: 2.5; anterior dorsal width: 1.5.
 Pleurals anteroposterior length: 2.2 to 2.4.
 Length of the bridge: 5.2 (and *c.* 2 mm more of hyoplastron hidden under the hypoplastron).
 The elements belonged to a carapace of 24 or 25 cm long, estimated by comparison with *C. longicollis*.

Decoration

Size of the polygons (approximate), on pleurals: 3-4 over 1-1.5 mm, on peripherals: 1 over 1 mm, on plastral bridge part: 0.5 over 1 mm.
 The decoration is made of small well-marked polygons (strong decoration), most of them rounded and well-distributed, as in *Chelodina* and *Pseudemydura*. The carapace polygons are similar to those of the shell of *C. oblonga* and *C. longicollis*, for example within the extant species, and to those of the figured specimens attributed to *C. insculpta*. But the polygons are smaller for a shell of equivalent size to that of *C. longicollis*, *C. oblonga* and *C. insculpta*, although larger than in the two other species of *Chelodina* from Redbank Plains. The plastral bridge element bears still much smaller polygons than the carapace, arranged in transversal elongate lines and in radiate lines. The carapace decoration is also similar to that of *Pseudemydura*, but the plastral polygons are smaller than in this extant genus and the other elements prevent the attribution to this genus.

Dermal bones of the carapace

The preserved right peripherals 7 and 6 are seen in ventral and medial views. The seventh is the

last of the bridge and, then, less open than the sixth. Besides, the right peripheral 5 is shown only in dorsal view, associated with a fragment of corresponding pleural 3. Two superposed fragments of even pleurals (with the sulcus between two costals) are preserved besides.

The plates have the morphology of the corresponding plates in the extant *C. longicollis*. The external dorsal border of the fifth peripheral is narrow and upwardly-curved. In medial view of the peripherals 7 and 6, the hole for the free rib is well-visible and the medial width (between dorsal and ventral borders of the plate) is equivalent to that of *C. longicollis*. But their ventral width is slightly less than that of the corresponding plates in *C. longicollis*: the peripheral border was less expanded. It is also nearly similar to that of *C. oblonga*, but less narrowed and more curled.

Plastron

A small part is seen under the peripherals. It consists of the bridge part of the hyoplastron and hypoplastron and does not show any determinant characters except its very fine and granulate unusual decoration, as in the following specimen, form 4, from Redbank Plains.

Pelvis

The left pubis is seen in inferoposterior view. The pubic ventral suture with the xiphiplastron is diamond shaped, nearly oval: anterior and posterior sharp angle, with rounded lateral borders. The type of pelvic scar on xiphiplastron has not been observed in every Australian chelid, owing to lack of the preparation of the material. But this type of pelvic scar has been seen in *Chelodina oblonga*. It is different from that of *C. expansa*, long, narrow posteriorly and wide anteriorly, from that of *C. longicollis*, short, triangular, wide anteriorly, and from that of *C. steindachneri*, short, oval and nearly round. In the *Emydura* group, some species have an oval shaped suture, very similar but without extreme sharp angles. In *Pseudemydura*, the suture is similar to that of *C. longicollis*, a short rounded-triangle, wide anteriorly.

The ischium is represented by the ventral part, in inner and ventral view. The ventral suture for the

xiphiplastron is incomplete medially but fortunately complete posterolaterally: its posterior extremity is well-rounded. This is typical of *Chelodina*, as seen in the *C. alanruxi* n. sp. section in its differing from the other chelid forms with an angulate posterior part (primitive condition). In the Pleistocene example of *Chelodina*, fig. 18A of Gaffney 1981, given above, the rounded scar is closer to the lateroposterior border of the plate than in *Emydura* s.l. If the scar is rounded posteriorly in all the examined species of *Chelodina*, its position varies. The scar is still closer to the lateroposterior border of the plate in *C. oblonga* (narrowed form), farther laterally and posteriorly in *C. longicollis* (form with enlarged xiphiplastron and a reduced anal notch) and farther posteriorly in *C. steindachneri* (narrow xiphiplastron but short anal notch). In the Pleistocene form, the scar is situated as in *C. expansa*, within the *Chelodina* species, but we do not know its position in the Redbank Plains form 3.

DISCUSSION

This specimen belongs clearly to *Chelodina* by the set of obvious characters:

- the complete cover of polygons on the dorsal shell. When there are polygons on the dorsal carapace in *Emydura* s.l., there are also ridges or granulations or smooth areas: the polygons are not well-marked and well-distributed over all the dorsal shell, a difference from the plastron which has often a cover of well distributed polygons (although it is probable that the primitive *Emydura* group members had a more polygonal carapace);
- the curled peripherals: there is a slight upwardly-curved border in some *Emydura* s.l. such as *E. macquarrii*, but the width of the bridge peripherals is much larger and the border is not so curled;
- the well-rounded posterior border of the ischiadic suture with the xiphiplastron.

The two first characters are also shared by *Pseudemydura*, the first one being a primitive character in chelids, the second a derived character but homoplastic in turtles. The third is autapomorphic in the observed material of *Chelodina*,

and the set is diagnostic of the genus. But it is impossible to define the species. It is different from *C. alanruxi* n. sp., which is much larger and has relatively small (owing to the larger size) and narrower polygons. In the latter, the bridge peripherals are not preserved so that we do not know if they were upwardly-curved. But the relatively wide and flat posterior border does not indicate that the peripherals had to become recurved at the bridge; they had to be flat or scarcely recurved as in *C. expansa*. The undefined species is probably also different from the form 2, smaller with smaller polygons and probably also without upwardly-curved border. It does not seem a rounded species of the lineage of *C. steindachneri*. It might better belong to an elongated species (such as in *C. oblonga* or *C. siebenrocki-rugosa* lineages) or to a moderately elongated species (such as in *C. longicollis* lineage).

Chelodina sp. c?

Emydura s.l. sp. ? Possible synonymy.

DESCRIPTION

Material (Fig. 6) (Rix 1991: fig. 2B)

Redbank Plains form 4 is represented by the specimen QM F18212. It consists of a broken nodule with the impression of half of the plastron, posterior part, without the bridge, with an impression (natural mold) of a part of the right pelvis in external view and parts of two or three right posterior peripheral plates.

Measurements (in cm)

Maximal length and width of the fragment: 13.6 and 10.4.

Maximal length and width of the preserved part of the plastron: 12.5 and 7.8.

Maximal length of the half posterior plastron (from hypo-hyoplastral suture): 10.5.

Maximum length of posterior lobe (from abdomino-femoral sulcus): 8.7.

Width of posterior lobe at abdomino-femoral suture: c. 8.

Ratio of width to estimated length of posterior plastral lobe: c. 92%.

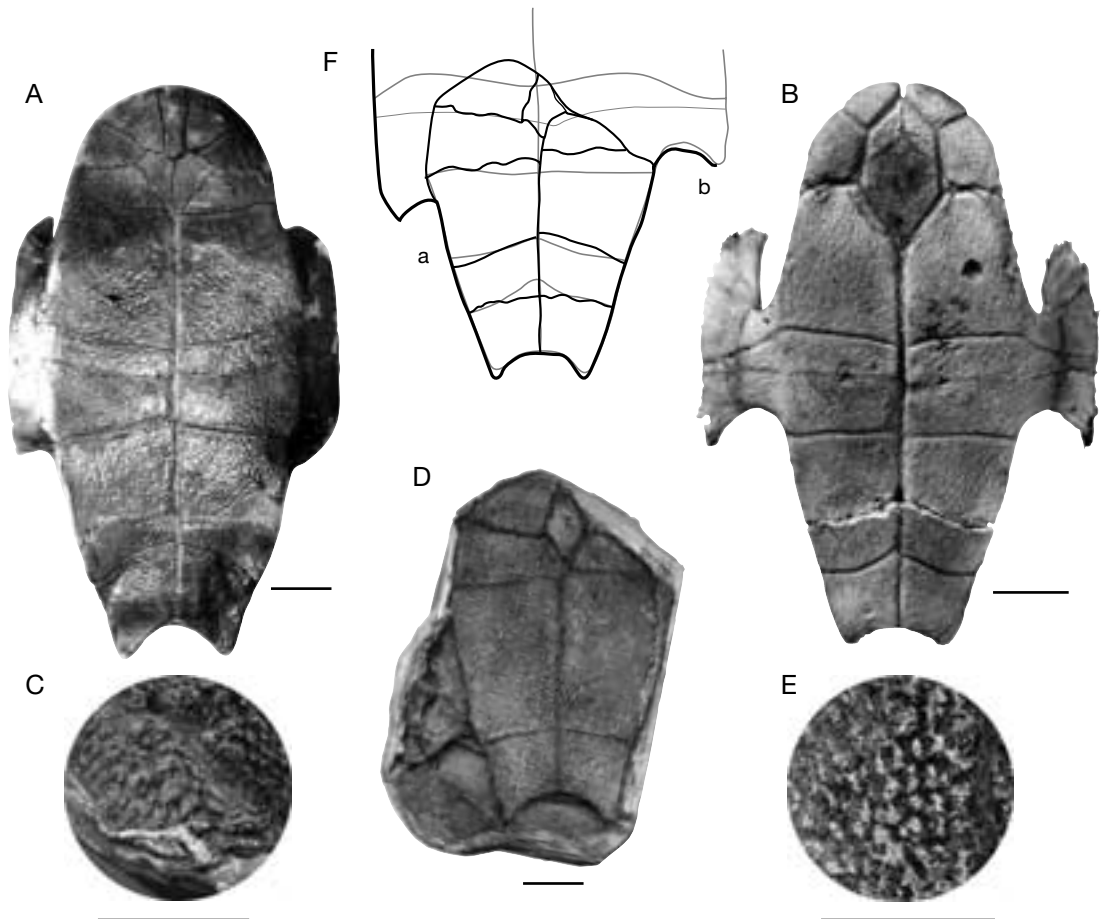


FIG. 6. — **A**, plastron of *Euseya dentata* (BMNH 76-5-19-77); **B**, plastron of *Chelodina oblonga* (BMNH 64-12-22-6), ventral views; **C-E**, *Chelodina* sp. c?, Redbank Plains, Queensland, Eocene (QM F18212), positive of the posterior mid-part of plastron, partial right pelvis and small part of shell; **C**, enlargement of the shell part, showing the polygons similar to those of *Chelodina*; **D**, the specimen, ventral view; **E**, enlargement of a plastral part showing the small granulate polygons; **F**, posterior mid-part of the plastron, superposed to that of *Chelodina oblonga*, with reconstruction of the inguinal notch. Abbreviations: **a**, left, as in *Euseya*; **b**, right, as in *Chelodina*. Scale bars: A, B, D, 2 cm; C, E, 1 cm.

Width at the femoro-anal sulcus: 5.5.
 Preserved height of the pelvis (dorsal part of ilium incomplete): 3.6.
 Anal notch, width and length: 3.4 and 1.

Decoration

All the preserved part of the plastron (Fig. 6D, E) is covered with small polygons, elevated, well-marked (strong), well-separated, most of them rounded, *c.* 1 × 1 mm wide, giving a granulate appearance to the positive (mold) of the speci-

men: but the fossil impression of the fig. 2B of Rix 1991, which is reversed, shows small pits separated by fine crests. As indicated above, a cover of polygons is present in the plastron of *Chelodina* and *Pseudemydura* as in various *Emydura* s.l. The polygons are arranged in lines, oriented from a center at the lateral border of the abdomino-femoral sulcus and quite longitudinally elongate in the hypo-xiphiplastral suture area. The plastral polygons (Fig. 6E) are relatively smaller than in *Pseudemydura*. In *Chelodina*, we

have seen relatively as small polygons in the plastron of *C. steindachneri* and in the preserved part of bridge of form 3, *Chelodina* sp. c. But, as seen above, the polygons are not as longitudinally elongate in those two genera and this is rather a character of the *Emydura* group. In the latter, a similar decoration has been observed in *Elseya dentata* (BMNH 76-5-19-77), although the polygons are slightly smaller in the fossil, for a similar plastral size (Fig. 6A).

The fragmentary peripherals have also well-marked, small and granulate polygons. One of them also shows small polygons (Fig. 6C), high as in *Chelodina* and particularly as in *Chelodina* sp. c. They are also similar to the polygons of the plastron of *C. oblonga* (Fig. 6B) and we consider them as apomorphic for *Chelodina*.

Plastron (Fig. 6D, E)

The plastron impression has a central rhomboid fontanelle, as observed in juveniles, for example in *Elseya latisternum* (BMNH 71-9-25-8). It is preserved from the pectoro-abdominal sulcus, anteriorly, to the anal notch, posteriorly. The exact shape and proportions of the posterior lobe are not possible to determine. The fragment is cut short, laterally, so that we do not see where the inguinal notch was positioned nor do we know how long the bridge was. If the inguinal notch was situated at the lateral extremity of the abdomino-femoral sulcus (Fig. 6F, a), it was a fragment of *Emydura* s.l. as in Fig. 6A. In the two Redbank Plains forms attributed to the *Emydura* group, the sulcus finishes in the bottom of the inguinal notch and the bridge was relatively long, as in the other *Emydura* species. But if the bridge was shortened, the abdomino-femoral sulcus would not end in the bottom of the inguinal notch, but backwards on the border of the lobe (Fig. 6F, b) and the fragment would belong to a *Chelodina* species as in Fig. 6B.

The posterior lobe is elongate with proportions known in Australian chelids in the *Emydura* group. The percentage ratio of width to length of the posterior lobe (measured from the extremity of the abdomino-femoral sulcus) is c. 92%, which conforms to the *Emydura* group, measuring bet-

ween 84.69 (*Rheodytes leucops*) and 97 to 103% (*E. macquarrii*) as seen above in the study of the *Emydura* s.l. sp. a: the ratios are higher in *Pseudemydura* (141%) and *Chelodina* (103 to 138%) which have relatively shorter posterior lobes. In *Pseudemydura*, the plastral lobe is short and much rounded with a very small and narrow anal notch. It is very different from the lobe of the Redbank Plains forms 5 and 6. Here, as in *Emydura* s.l. sp. a, form 5, the two borders of the posterior lobe clearly converge, from the bottom of the inguinal notch, at the abdomino-femoral sulcus, towards the xiphiplastral extremities in a straight line, without strong narrowing at the femoro-anal sulcus. Just a small indentation for a slight posterior anal narrowing is noticeable at this sulcus. The anal notch is very widely rounded and short, as in most of species of *Emydura* s.l., except some forms such as *Elseya latisternum* and *E. novaeguineae* which have a less rounded anal notch. But this shape of the posterior lobe is also similar to that of *C. oblonga* (Fig. 6B) with its slightly convergent straight lateral borders and a wide and short anal notch. The anal notch of the fossil is relatively shorter than in *Emydura* s.l. but longer than in *C. oblonga*, as shown in the Fig. 6E. The percentage ratio "width/length of the posterior lobe" is elevated as in some *Emydura* s.l., known in *E. macquarrii*, but not different from the lower one in *Chelodina*, in *C. oblonga* (103.44%). *C. oblonga* is the more elongated species of *Chelodina*, with the relatively more elongate posterior lobe.

Right pelvis

It is visible in external view, the inferior part being anteriorly positioned lateral to the plastron. The upper part of the ilium is missing. The acetabulum is slightly posteriorly dilated as in most of adult chelids. Anteriorly, the posterior part of the ventral suture of the pubis with the xiphiplastron is preserved: it is oval but apparently without a sharp posterior angle, different from the specimen of *Chelodina* sp. c described above. The problem is that this extremity of the pubic scar may be eroded. Such an oval suture and xiphiplastral corresponding scar, primitive in its evolutionary

stage, is known in some specimens of the *Emydura* group such as *Elseya latisternum* and *E. novaeguineae*. It differs from that known in one specimen of *Emydura macquarrii* where it is nearly rectangular with a sharp anterior angle, and of one specimen of *Elseya dentata* where it is very narrow. As in *Chelodina* there are differences, unfortunately not studied at the specific or group of species level. No *Chelodina* and no *Pseudemydura* are known with this oval morphology but it is known in the *Emydura* group. The ventral face of the ischium is hidden below the xiphiplastron.

DISCUSSION

It is better to attribute the specimen of the Redbank Plains form 4 to *Chelodina* sp. c than to *Emydura* s.l., owing to the granulate plastral decoration and polygonal dorsal decoration that is exactly similar to those of the form 4. The small size of the polygons better conforms with those of *Chelodina*, in the context of the Redbank Plains Eocene forms and, in particular, the apomorphic decoration of the preserved peripheral bone is consistent with that of *Chelodina* and not with the *Emydura* group. But the extant *Elseya dentata* has a similar granulate plastral decoration and the proportions of the posterior lobe are consistent with those of the *Emydura* group. The oval pubic scar, if correctly preserved, could better be consistent with attribution to the *Emydura* group, as it is known at present. But the granulate decoration of oriented small polygons and the oval pubic ventral suture may be primitive for both groups. In the absence of the inguinal notch bottom, we cannot be certain.

Emydura Bonaparte, 1836 s.l.

Emydura s.l. sp. a

DESCRIPTION

Material (Figs 7-9C, D; Table 2)

The single specimen of the Redbank Plains form 5 (QM F31697) consists of a broken nodule

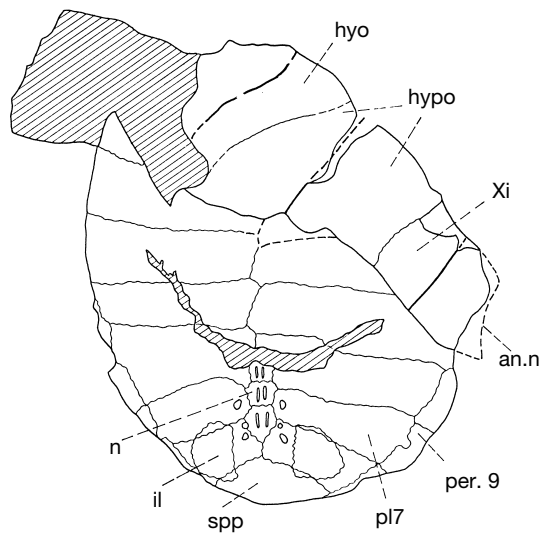


FIG. 7. — *Emydura* s.l. sp. a, form 4, Redbank Plains, Queensland, Eocene (QM F31697), internal cast of the carapace, anteriorly covered by the external impression of the left latero-posterior part of the plastron. Abbreviations: **an.n**, reconstruction of the anal notch; **hyo**, partial hyoplastron; **hypo**, partial hypoaplastron; **il**, iliac scar; **n**, ventrally preserved neural; **per. 9**, partial peripheral 9; **pl7**, pleural 7; **spp**, partial suprapygals; **Xi**, partial xiphiplastron. Scale bar: 5 cm.

showing two parts of an incomplete carapace: the external impression of the scutes and plates of the partial left lateral border and posterior border of the pleural disc and a part of the peripherals (Figs 8; 9D); the internal cast showing the impression of the ventral part of the plates of the pleural disc, at the anterior border in an oblique line, from left side at the pleural 2 to right side at the pleural 3 to 5 (Figs 7; 8C). The anterior part of the pleural disc is hidden by the impression of the external part of the partial left half plastron.

Measurements (in cm)

Preserved length and width of the internal cast (i.e. approximately of the pleural disc): 17.5 and 15.5.

Presumed approximate length and width of the carapace: 20 and 15.8.

Ratio of width to estimated length of posterior plastral lobe: 6.6/6-7, percentage ratio *c.* 94-100%.

Decoration

The external impression shows only a very weak decoration of some shallow, thin and short sulci, some of them dichotomous. A small part of the ventral decoration of the right marginal scutes 9 and 10 is preserved on the cast of the fragmentary peripherals 9 and 10: some small dichotomous sulci, shorter and closer together than in the pleurals, are also visible. The decoration could be slightly different at the level of the missing vertebrae.

The impression of the plastron shows a stronger decoration of rather large polygons, not elevated (weakly marked), elongate, oriented from a center near the inguinal notch, longitudinally on the posterior lobe and radially forward on the anterior hypoplastral part. Below the preserved femoral scute, the polygons are 7-5 mm long on 4-1 mm wide.

Such an attenuated decoration of the carapace is often seen in the *Emydura* group, for example in *Elseya latisternum* and in young *E. novaeguineae*. In other forms, the carapace may be covered by irregular polygons, not as well-formed and as closed as in *Chelodina* and *Pseudemydura*, oriented in transverse or oblique (lateral part) and longitudinal lines (medial part). For example a specimen (MNHN AC 1887 814), attributed to *Emydura macquarrii*, has some longitudinal fine lines, in the medial part and some lateral pits and short weak ridges. But the holotype of *E. macquarrii* (MNHN H 9409) and a specimen of the Natural History Museum (BMNH 86-8-26-5) correctly attributed to this species, have strong, wide, flat and long ridges separated by grooves, oblique below the costals and radiating from a medioposterior center below the vertebrae. In most of forms, the carapace is ornamented with granulations, pits, sulci and ridges, more or less wide, rounded or sharp, longitudinally and transversally oriented, also depending on the part of the carapace. The decoration of ridges is strong in the extant specimens of the MNHN collections attributed to *E. krefftii* and *E. australis*, the ridges being less oblique and medially finer than in the holotype of *E. macquarrii*, at least in some specimens of *E. krefftii* (MNHN H 1883-380 and 381) (the synonymy of *E. krefftii* with *E. mac-*

quarrii is admitted by Thomson pers. comm., but the holotype of the former is not conform to the holotype of the latter: the study of the individual and sexual variation of the species, from specimens collected in the area typica of each species could verify this assertion). But the ornamentation seems variable within the species, more or less pronounced, and varies with age. For example there may or may not be granulations and pits on the dorsal carapace of *E. krefftii*, but there are granulations in young *Elseya latisternum* (BMNH 71-9-25-8) and pits in adult (MNHN H 7973). The plastron is always more ornamented, often more granulate and with well-formed and well-distributed polygons as in *Pseudemydura* and *Chelodina*, although more oriented in lines on the posterior lobe. For example *Elseya dentata* (NHM specimens) has very well marked, granulate and small polygons on the plastron and *Emydura macquarrii* (holotype) has plastral granulate polygons, longitudinally oriented medially, below the pectorals, the abdominals and the femorals. As seen above, if polygons (the primitive design) are shared by all the chelid forms, only the *Emydura* group has longitudinal lines, sulci and ridges, sometimes much developed. And some fossil forms with ridges described by De Vis (1897) and considered as Testudines or Chelidae indeterminate by Gaffney (1981) are evidently forms of the group *Emydura* s.l. (Thomson in prep.). This is important because in the Cape Hillsborough Beds, near Proserpine (between Bowen and Cape Hillsborough), Queensland, an area considered as Palaeogene and probably Eocene, possibly contemporaneous of Redbank Plains, a partial carapace is preserved (Queensland Museum, in prep.). It has a typical *Emydura* decoration of fine longitudinal ridges on the pleural disc, laterally and medially, and weak polygons on the peripherals. It is much more decorated than the Redbank form 4 which is devoid of longitudinal lines (at least in the preserved parts), different as a species and probably from a different group of species. It is similar to Miocene South Australian *Emydura* specimens figured in Gaffney 1979 and 1991 (such as the specimen of *Emydura* sp. from the Ngapakaldi

Lake, Miocene), and described *in* Burke *et al.* 1983; but fine longitudinal medial and lateral lines are also present in adult *Elseya novaeguineae* (BMNH 13-6-9-20). Longitudinal lines are also present in the holotype of *E. macquarrii*, as said above, but they are coarser. A study of extant material would be necessary to precisely diagnose the decoration of the *Emydura* s.l. forms, as nearly all the specimens in the visited museums are not prepared. But we can hypothesize that, owing to the decoration, the two Eocene (or Palaeogene) fossil forms were representatives of two already separated *Emydura* s.l. species lineages. The fossil Oligo-Miocene form from Tasmania described by Warren 1969a, and attributed to *Emydura* sp. aff. *E. macquarrii*, has a weak decoration of polygons and, besides, some fine longitudinal medial lines under the vertebrals, a decoration differing from that of the holotype of the species. The decoration of its plastron is not given. This species may be possibly closer to the Redbank Plains form than to the Proserpine form.

Carapace: shell shape

The pleural disc is oval, slightly narrowed posteriorly but not cordiform, the posterior border being rounded and rather short, not pointed. Its anterior part is missing, hidden below the plastral part. The shape of the carapace was elongate, longer than wide, but not much elongated relative to the primitive stage, probably as in the fossil form of *Emydura* from Tasmania (Warren 1969a) and less elongate than the Proserpine form. We cannot say if it was dentate or not nor how much its peripheral border was expanded, although possibly more than the minimum given in the reconstructed drawing (Fig. 8).

Scutes

The external impression shows the sulci of the costals 1, 2 (partly), 3 and 4, vertebrals 4 and 5 and a part of some marginals sulci. They are straight and well-marked. The vertebral 4 is just slightly narrower than the vertebral 5, which is much wider than the suprapygal. The vertebral 4 is also much wider than the costal 4: there is no

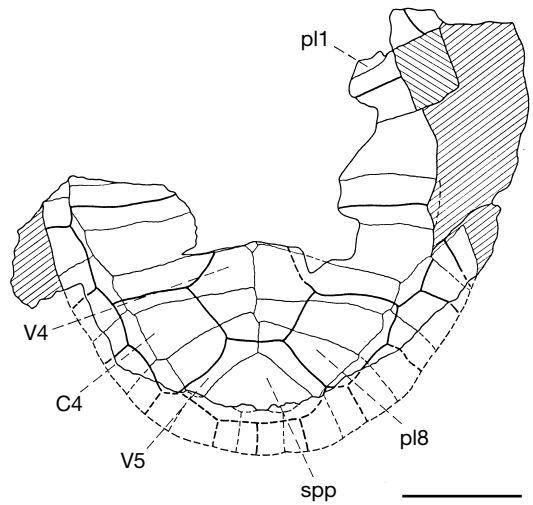


FIG. 8. — *Emydura* s.l. sp. a, form 5, Redbank Plains, Queensland, Eocene (QM F31697), impression of the external left lateral and posterior part of the carapace. Abbreviations: **C4**, costal scute 4; **pl1**, **pl8**, pleurals 1, 8; **spp**, suprapygal; **V4**, **V5**, vertebrals 4 and 5. Scale bar: 5 cm.

narrowing of the vertebrals. The lateral borders of the vertebral 4 are united in a sharp angle, as in many extant *Emydura* s.l. (see Goode 1967), particularly in small and young forms, and also as in the fossil *Emydura* from Tasmania. But at the difference with the latter, the marginals 12 do not overlap the suprapygal medially, the vertebral 5 covering all the suprapygal. The costals 3 and 4 overlap the peripherals, as in *Elseya novaeguineae*, for example, and less than in *Emydura macquarrii* and in the Tasmanian form.

Dermal bones

The bones are firmly linked, without fontanelles between pleurals and peripherals, which indicates an adult form.

There are no neurals appearing in dorsal view (Figs 8; 9D), but the centra of the dorsal vertebrae corresponding to neurals 6, 7 and 8 are preserved and visible in the cast (Figs 7; 9C), between the pleurals 6, 7 and anterior half of 8 which do not contact on the mid-line. This also happens in some living specimens of *Emydura* s.l. and in many specimens of living *Chelodina* (see

above). It is the last remnant of the primitive series of the dorsal vertebrae linked to the neurals and still intercalated between the pleurals ventrally. In this case, only the inferior layer of the neural remains, attached to the vertebra. But here we have only the internal cast of the carapace with the inferior part of the vertebrae (centrum). We do not see the upper part with the neural inferior layer which was surely present in the complete specimen. In the other living taxa as in the anterior part of the fossil carapace of Redbank Plains, the neurals have completely disappeared and the dorsal arch of the vertebrae is separated from the carapace, just united at the medial line, the pleurals of each pair meeting in the mid-line dorsally and ventrally. As seen above, rare and often incomplete neurals have been mentioned in the *Emydura* sp. from Tasmania (Warren 1969a), in some specimens of extant *Elseya latisternum* Gray, 1867 and *E. novaeguineae* (Meyer, 1874) and extant specimens of *Elseya* sp. aff. *E. latisternum* from Manning River and *Elseya* sp. from South Alligator River (Rhodin & Mittermeier 1977; Thomson & Georges 1996).

The suprapygal is pentagonal, much wider than long.

The internal cast shows the scars of the ilia below the carapace. Each scar is trapezoido-triangular with rounded angles, pear-shaped, as long as wide, similar to that of the specimen (MNHN AC 1887-814) attributed to *Emydura macquarrii* but not similar to the specimen (BMNH 86-8-26-5) which is consistent with the holotype in external view (internal characters not known in the holotype): in the second specimen, the scar is triangular trilobate and shorter. The scar of the *Emydura* s.l. sp. a covers a wide very short part of the pleurals 7, a wide part of the pleurals 8 and a small angular part of the suprapygal (as in *Elseya latisternum* fide Thomson pers. comm., but not as in NHM specimens attributed to *E. latisternum*). It is depressed, well-delimited by a denticulate border, with shallow rugosities inside. In the middle part of the scar, there is a rounded zone of stronger rugosities, on the central part of the rib 9, corresponding to a rugose excavated zone in

the iliac surface, as in specimens attributed to *E. australis* (MNHN) and to *E. aff. australis* (WA). *Emydura macquarrii* (BMNH 86-8-26-5 and MNHN AC 1887-814 specimens, not known in holotype) has an apparent rib 9, as in *Chelodina*, thin and sharp. The scar zone is very weakly rugose in a specimen of *Elseya novaeguineae* (MNHN P 1880-467), variably rugose in *Rheodytes leucops* and *Emydura krefftii*. It is not prepared in the Natural History Museum specimens of *E. dentata* and *E. novaeguineae*. As we have seen above in the section on *Chelodina alanrivi* n. sp., the shape of the iliac scar is quite variable in chelids and it derived independently in all the lineages, with some homoplasies. It is triangular with rounded angles to oval in *Chelodina*, rounded-oval in *Pseudemydura* and most often triangular, inverted or not, in *Emydura* s.l., sometimes also with rounded angles. The longer triangular shape is primitive in Eupleurodira and the more rounded or oval shape is derived. In most of observed specimens of the *Emydura* group (*Emydura* and *Elseya*), the scar is limited to the pleural 8 and suprapygal and it does not contact the pleural 7 any more. White (1997) noted that “the pelvic scars on pleurals 8 and the suprapygal are more typical of *Elseya*”. We observed a scar reduced to pleurals 8 and suprapygal in *Emydura macquarrii* (BMNH 86-8-26-5, specimen externally consistent with the holotype of the species), *Rheodytes leucops* (Queensland Museum and Australian Museum specimens) and *Emydura krefftii* (Queensland Museum specimens and MNHN H 1983-380 and 381). The scar is still on the pleurals 7 in a specimen of the Queensland Museum attributed to *Elseya dentata* (while not in most other specimens attributed to this species, including QM J47911, attributed now to *E. lava-rockorum* [Thomson pers. comm.]) as in the specimen attributed to *Emydura macquarrii* (MNHN AC 1887-814) and observed specimens attributed to *E. australis* (MNHN) and *E. aff. australis* (WA). Actually, the iliac scar, in the Redbank Plains form 5, which clearly covers the suprapygal and hardly the pleural 7, is similar to many chelids and conforms to *Emydura* s.l. in the rugosities and shape.

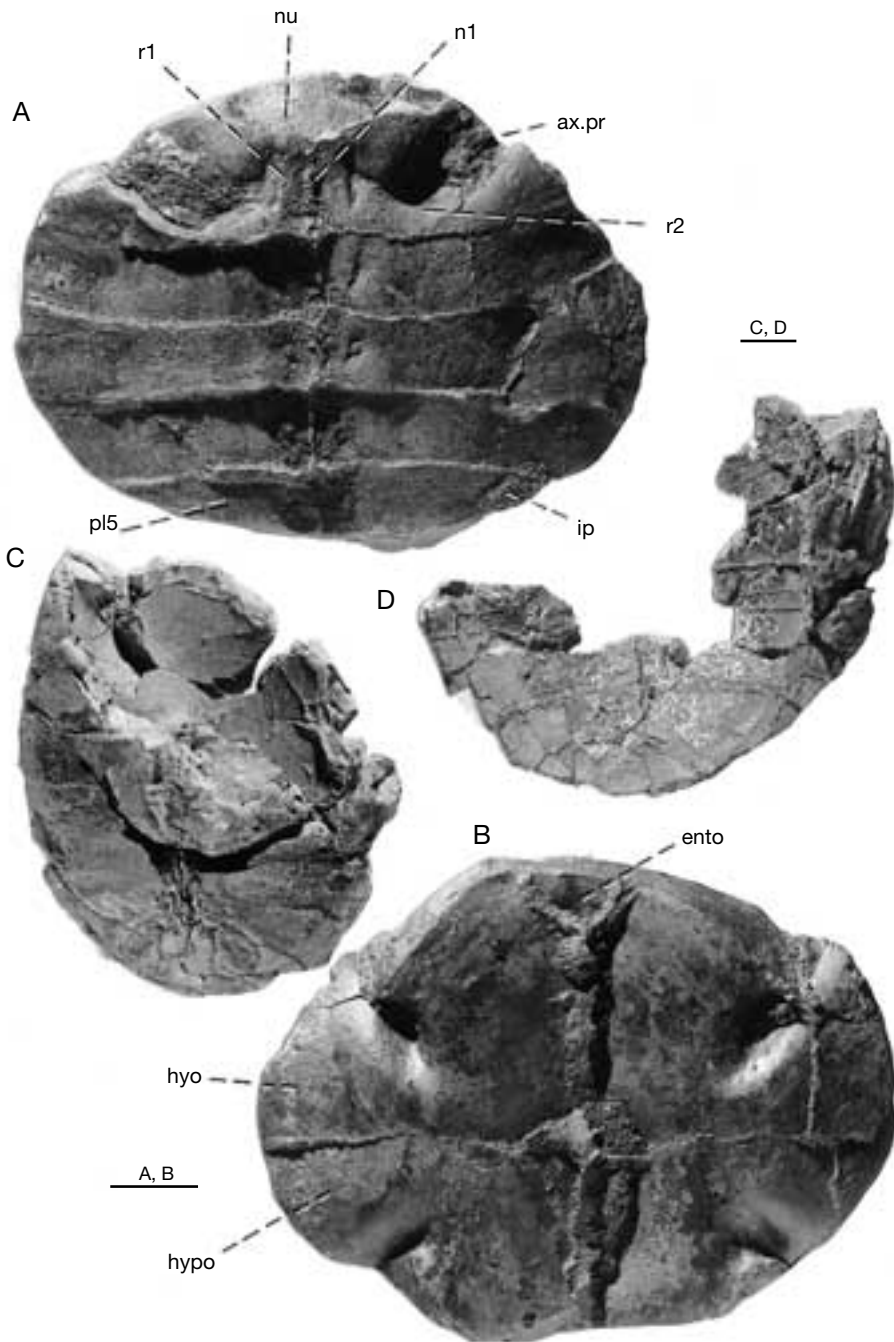


FIG. 9. — Redbank Plains, Queensland, Eocene; **A-B**, *Emydura* s.l. sp. a or b?, form 6 (QM F37913), internal mold of an anterior part of the shell; **A**, dorsal part; **B**, ventral part; **C-D**, *Emydura* s.l. sp. a, form 5 (QM F31697); **C**, internal mold of the left lateral and posterior part of the shell, anteriorly covered by the external impression of the left lateroposterior part of the plastron; **D**, impression of the external left lateral and posterior part of the shell. Abbreviations: **ax.pr**, axillary process; **ip**, inguinal process; **n1**, remnant of neural 1; **nu**, nuchal; **pl5**, pleural 5; **r1**, **r2**, thoracic ribs 1 and 2; **ento**, posterior part of the entoplastron; **hyo**, hyoplastron; **hypo**, hypoplastron. Scale bars: 2 cm.

Plastron

The part of left plastron superposed to the cast of the internal carapace (Figs 7; 9C) consists of the posterior medial part of the hypoplastron and of the medial part of the hypoplastron (the axillary and inguinal processes are incomplete laterally) and the xiphoplastron, less its posterior extremity at the anal notch.

The posterior lobe is narrow without widening forward of the anals at the femoro-anal sulcus and without narrowed pointed xiphoplastral points. The lateral border of the femoral scute is slightly incomplete, but the posterior lobe border was nearly straight, only slightly converging towards the anal notch (Fig. 7), less than in the species studied above, form 4, *Chelodina* sp. c? The anal notch, from the marks on the broken nodule, had to be relatively wide and short as in the above form 4.

The posterior lobe is elongate, relatively long for its width (and may be still longer than reconstructed in the Fig. 7), with an estimated ratio width/length of 94-100%. The elongated posterior lobe is a derived character of the *Emydura* group among the Australian chelids, immediately observable in figures (see Goode 1967), and different from *Chelodina* and *Pseudemydura* with short posterior lobes. The posterior lobe ratio, width at abdomino-femoral sulcus to full length, measured in some specimens, is: 84.69% in *Rheodytes leucops*; c. 95% in *Elseya latisternum*, 97% in *E. novaeguineae* and 102% in *E. dentata*; 97%, 97.17% (holotype) and 103% in *E. macquarrii* and c. 98% in a specimen attributed to *E. australis*. The ratio is 141% in *Pseudemydura*. In *Chelodina*, the ratios vary from 103% (103.44%, 103.17% and 111.76%) in *C. oblonga* to 138% in *C. novaeguineae*. The plastron had no reduced bridge length. The abdomino-femoral sulcus finishes in the bottom of the inguinal notch instead of further backwards on the lobe border, as it occurs in *Chelodina* (see above, *Chelodina* sp. c?, Fig. 6). The posterior lobe is not much rounded and widened relative to the base as it occurs in *Pseudemydura* (see Burbidge *et al.* 1974).

DISCUSSION

The Redbank Plains form 5 is clearly a member of the *Emydura* group. Owing to the very weak decoration (although eventually not completely preserved in the dorsal part of the shell) we can differentiate it from the species from Proserpine (Cape Hillsborough Beds) which has a stronger decoration of longitudinal lines, although fine and not the strongest possible in the group (see the figures in De Vis 1897; Gaffney 1979, 1981; Goode 1967; Burke *et al.* 1983). The Redbank Plains form is surely different from the extant species *E. macquarrii* s.s., in being more rounded (shortest behind), less decorated and without a mark of rib 9 in the iliac scar. Because of its rounded shape, its "faded" decoration and its vertebrals wide and with angulate lateral angles, it is similar to the specimen from Tasmania (Warren 1969a) (a *latisternum* group member *vide* Thomson pers. comm.) It specifically differs from the latter by the marginals 12 not overlapping the suprapygal. But, although possible, it is not sure that they both belong to the *E. macquarrii* group, to which the Tasmanian form is referred. The Redbank Plains *Emydura* s.l. sp. a is also surely different from the Redbank Plains form 4, described above, doubtfully attributed to *Chelodina* sp. c?, although possibly belonging to the *Emydura* sp. group, in the strong difference in the plastral ornamentation of the latter, with smaller granulate polygons like those of *Elseya dentata*, for example, instead of wider medial polygons like those of *Emydura macquarrii*, for example.

Emydura s.l. sp. a or b?

DESCRIPTION

Material (Fig. 9A, B)

The specimen of the Redbank Plains form 6 is represented by QM F37913. It consists of a rounded nodule with the ventral view of a partial shell, with the natural mould and some bone fragments of pleurals 4-8 and the suprapygal and, on the other side, the impression of the medial part of the plastron, without the most anterior

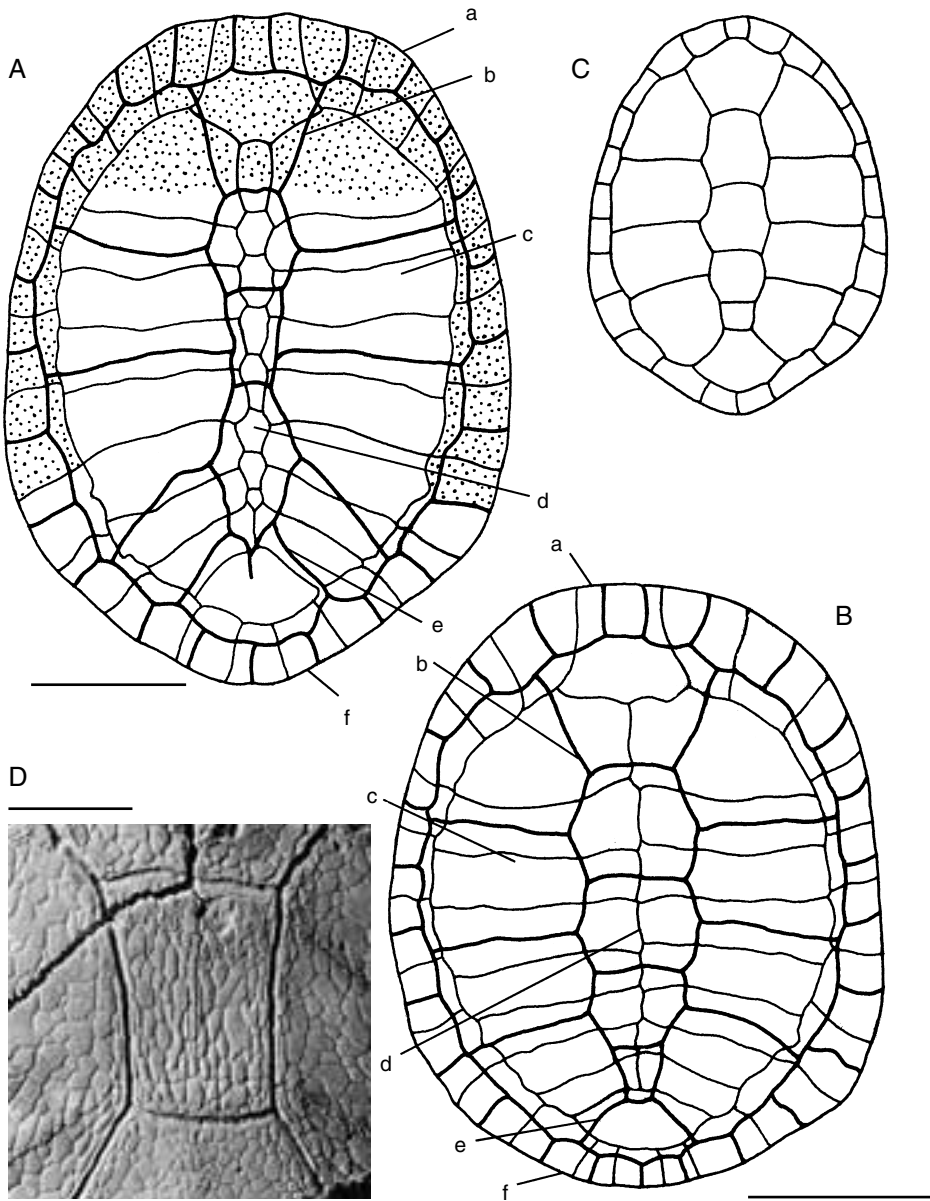


FIG. 10. — **A**, *Chelodina alanixi* n. sp., form 1, Redbank Plains, Queensland, Eocene (QM F18344), 40-41 cm long, reconstruction of the carapace, dorsal view, missing parts dotted, presenting generic identities and specific differences with *C. expansa* in B-D; **a**, flat-tented, large and wide carapace as in *C. expansa*; **b**, narrow vertebrals, the first one narrower than the nuchal bone, the second to fourth narrower than the first and fifth, the third particularly narrow, vertebrals narrower than in *C. expansa* except the fifth that is wider than the suprapygal bone; **c**, polygons of the decoration c. 1/3 smaller than in *C. expansa* (see D and compare with Fig. 1B); **d**, 8 neurals present, against no one in *C. expansa*; **e**, vertebral 5 wider than the suprapygal contrarily to *C. expansa*; **f**, long and flat posterior extremity, as in *C. expansa*, slightly pointed as in males in *C. expansa*; **B**, *C. expansa*, extant (MNHN AC 1914-178), 37.5 cm long; **a**, large and wide carapace as in *C. alanixi* n. sp. (anteriorly narrower in males); **b**, wide vertebral 1 wider than the nuchal bone, the vertebrals 2 to 4 (the fourth subdivided) progressively narrowing; **c**, large polygons (see D); **d**, no neurals (never); **e**, vertebral 5 narrower than the suprapygal; **f**, long and flat posterior extremity, slightly pointed as in *C. alanixi* n. sp. but more rounded border (a female); **C**, *C. expansa* Gray, 1856 (pl. XII), holotype, from Goode (1967) and Wermuth & Mertens (1961), 35 cm long, a male (anteriorly narrower and posteriorly pointed, plastron with a concavity); **D**, *C. expansa*, extant (MNHN AC 1914-178), 37.5 cm long, detail of the decoration of the carapace in the area of the vertebral 4 (subdivided here), compare with Fig. 1B. Scale bars: A, B, 10 cm; D, 2 cm.

part (epiplastra, entoplastron) and the most posterior part (xiphiplastra).

Measurements (in cm)

Maximum preserved length and width of the fragment: 10.8 and 15.

Estimated length and width of the carapace: *c.* 21 and 17.5.

Plastral bridge length: *c.* 4.2.

Anterior lobe width at its base: 7.6.

Maximum estimated entoplastral length: 2.

Medial hyoplastral length: 5.2.

Decoration

It is not preserved.

Shell shape

The plates were relatively thick for their length and there is no indication of fontanelles. It was fully adult. Based on the preserved parts, i.e. the scars of the thoracic ribs 1 and 2, the axillary process, the entoplastral size, the distance between the entoplastron and the hyo-hyoplastral suture and the bridge proportions, the species belongs to the *Emydura* group. It is therefore possible to reconstruct a carapace of *Emydura* s.l. shape. This is not much variable in the group, i.e. there is always a carapace particularly elongated relative to the primitive length and expanded posteriorly and slightly narrowed anteriorly, with a narrow plastron a little smaller than the carapace, with an open U-shaped anterior lobe, a relatively long bridge and a long posterior lobe.

In the *Emydura* group, the posterior border of the carapace is more expanded in some species than in others, some are more rounded and some are more elongated. The anterior lobe may be more narrowed and the posterior lobe may be more or less narrowed posteriorly at the femoro-anal sulcus, depending on the species to which it belonged.

Dermal bones of the shell

The nuchal is moderately wide (the anterior part is missing) and the pleurals 1 are moderately long. There are no neurals between the preserved pleurals 1 to 5 which are wide for their length.

Between the two pleurals 1, the neural arch of the dorsal vertebra 1 is preserved in its medial part (reduced anteriorly and posteriorly) which means that dorsal vertebra 1 was still intercalated between the plates while between pleurals 2 to 5 there are no more intercalated vertebrae and no more neurals at all. The axillary process enters pleural 1 at the mid posterior part of peripheral 2 and at the beginning of peripheral 3, anterior to rib 2. It covers *c.* 2/3 of the width of pleural 1, being well-rounded and well-overlapping thoracic rib 2 at that place. The lateral part of the impression of the right pleural 5 bears the short rounded extremity of the inguinal process.

Plastron

The impression of a good part of the entoplastron is preserved and easy to reconstruct in its length. It was small and largely separated from the hypoplastra (slightly more than two times its length) as in *Emydura* s.l. This is the difference from *Chelodina* where the entoplastron is large in the anterior lobe and closer to the hypoplastra (distance of a little more than its length in *C. expansa* and *C. oblonga*, less than its length in *C. longicollis* or in *C. steindachneri*). The situation in *Pseudemydura* is intermediate; the entoplastron is small, but the anterior lobe is wide and short and the entoplastron is separated from the hypoplastra by a distance of a little more than its length. As in *Emydura* s.l., the bridge is long relative to the width of the plastral lobes at their base, its length being clearly more than the half the plastral width, different from *Chelodina* and *Pseudemydura* where it is as long or shorter.

DISCUSSION

As seen above, the specimen belongs clearly to the *Emydura* group in light of these features: the characters of the pleurals 1, the entoplastral size, the distance between the entoplastron and the hyo-hyoplastral suture and the bridge length relative to the width of the lobes. In the *Emydura* group, the axillary processes generally enter the pleural 1 from forward, at peripherals 1 to 3 depending on the taxa (it is more derived where

it is more forwardly positioned). Within the Chelidae, *Emydura* s.l. is particularly derived in its long bridge and more forwardly prolonged axillary processes. The axillary process enters pleural 1 and goes obliquely backwards to join thoracic rib 2 that it covers, up to half the width of pleural 1. It is forward positioned relative to the primitive condition which is still found in *Chelodina* and *Pseudemydura*, where the process enters at peripheral 3 and directly covers thoracic rib 2. In the *Emydura* group, the more primitive condition is that of *Elseya latisternum*, *Rheodytes leucops* and *Elusor macrurus* (see Thomson *et al.* 1997; QM and BMNH specimens) where the process enters at peripheral 3 just forward but close to thoracic rib 2, that it covers up to the mid-width of the plate, i.e. more widely than in the primitive condition seen in most of *Chelodina* species and in *Pseudemydura*. In *Chelodina* and *Pseudemydura*, the process, entering at peripheral 3, either is still short laterally but, directed obliquely backwards, may cover a small part of pleural 2 (for example *C. steindachneri*, *C. longicollis*, *Pseudemydura*), or it is also prolonged up to pleural 2 and furthermore it is wide up to the mid-width of pleural 1 (*C. expansa*, with the more derived condition in *Chelodina*). In the Redbank Plains form, the position of the axillary process which enters pleural 1 at the posterior part of peripheral 2 and beginning of peripheral 3, anterior to rib 2, is consistent with that of various species of the *Emydura* group moderately derived on that point: that of *Elseya dentata* (BMNH 765-19-77, Thomson *et al.* 1997), *Emydura macquarrii* (BMNH 86-9-26-5, MNHN 1897-814), specimens attributed to *E. kreffii* (White & Archer, 1994), *E. novaeguineae* (BMNH 1835-5-10-177), extant *Elseya lavarackorum* in Thomson *et al.* 1997, *Emydura* sp., fossil from Lake Tarkarooloo, Miocene, Burke *et al.* 1983. In these forms, the process is more or less thin where it contacts with pleural 1 and either situated in front of the posterior part of peripheral 2 or just backwards, at the limit of both peripherals 2 and 3. It is clearly situated more backwards than in the fossil *Elseya lavarackorum* White & Archer, 1994,

Pleistocene from Riversleigh, figured in Thomson *et al.* 1997, *Emydura subglobosa* (Thomson *et al.* 1997) and young (MNHN P 1880-467), where it is positioned at mid-length of peripheral 2. It is still more backwards situated than in "*E. australis*" (AM, R26581), where it enters pleural 1 at peripheral 1, which is the more derived condition in the *Emydura* group. But it is more forward positioned than in *Rheodytes leucops* (see Thomson *et al.* 1997) and *Elseya latisternum* (White & Archer 1994; BMNH 71-9-25-8) where the process enters at peripheral 3.

The specimen, adult, is approximately the same size as the other *Emydura* s.l. specimen from Redbank Plains described above and the doubtful specimen of *Chelodina* sp. c? (possibly a specimen of *Emydura*?), also adults: c. 20 cm in sp. a, c. 23 cm in "*Chelodina* sp. c?", and c. 21 cm in form 6. The presence of the remains of the neural arch 1 between the pleurals 1 can be compared to the presence of the remains of neurals 6 to 8 between the pleurals 6 to 8 in *Emydura* s.l. sp. a, thus showing that both forms could belong to the same species without a complete neural reduction. The possible shape of the plastron of form 6 conforms to the plastron of form 5. It is possible that the carapace was slightly wider than in form 5. This species cannot be of the same group as the species from Proserpine nor the same as the species of the form 4, if it is a *Emydura* s.l. instead of a *Chelodina*.

Even if only one species of *Emydura* s.l. existed in Redbank Plains, two species of two distinct groups existed in the Palaeogene of Queensland. In fact many more extant species exist than were known in the last Century (Cann 1978; Wells & Wellington 1985; Iverson 1992) and a rediagnosis of each species ought to be given, based on the anatomy of the skeleton, allowing better definition of the new subgroups of *Emydura* s.l.

Chelidae indet.

DESCRIPTION

This is a fragment of a rather large shell, QM F12361, in ventral view with three median

pleurals and adjacent fragments, with the lateral part of corresponding neurals and fragmentary corresponding plastral part in ventral view. There are important lateral fontanelles between peripherals and buttresses. It cannot belong to *Chelodina* owing to the absence of decoration. The preserved fragment is c. 14 cm long.

CONCLUSION

The Redbank Plains turtle fauna is, in the present state of knowledge, limited to Family Chelidae; no cryptodiran turtles are yet recognized.

The Redbank Plains fauna is well-differentiated with representatives of two of the three groups of living Australian chelids: *Chelodina* and *Emydura* s.l. There are three species of *Chelodina*, belonging to two or three groups of extant species. There are one or two species of *Emydura* s.l. and one indeterminate chelid. The oldest known species of *Emydura* s.l. are represented here, older than the Oligocene form from Tasmania (Warren 1969a) and that the Oligo-Miocene forms from Riversleigh (Gaffney *et al.* 1989; White 1997). With the *Emydura* s.l. form from Proserpine, also from the Palaeogene and maybe contemporaneous, there were during Palaeogene times in Queensland two species of the *Emydura* group, belonging to two already differentiated different lineages. As far as *Chelodina* is concerned, the Redbank Plains forms may be also the oldest members of the genus if we exclude the material attributed to *Chelodina insculpta* by De Vis (1897) which possibly includes Eocene material of Eight Mile Plains (but not the figured material, see Thomson in prep.). *Pseudemydura* is not represented at Redbank Plains and the oldest attested representative of the genus is that of Riversleigh Station, Oligo-Miocene of northern Queensland (Gaffney *et al.* 1989). In *Emydura* s.l. as in *Chelodina*, the decoration is an important character. The age of the fauna is shown by the small size of the polygons, smaller in *Chelodina* from Redbank Plains than in the extant species, as well as in the dubious *Chelodina* sp. c? (or *Emydura* sp?). In *Chelodina*, it is also

seen in the wide vertebral 5 relative to the pygal when, in the later species, the vertebral 5 is reduced in the forms with narrowed vertebrals 1 to 4. But, surprisingly, *C. alanruxi* n. sp., the form of *Chelodina* with narrowed vertebrals 1 to 4, has the most derived condition for the character, which indicates a possibility of homoplasy for the narrowing of the vertebrals 1 to 4 as well as of the vertebral 5. Also primitive is the character of the peripherals, not much expanded posteriorly. In *Emydura* s.l., the carapace of the form was not much elongated and narrowed but it was well-derived by the reduced decoration.

This material reveals the differentiation of the forms as already well-established in Early Palaeogene time and a suite of lineages allowing for the erection of several genera for each group of species, *Chelodina* as *Emydura* s.l. thus representing higher taxonomical categories. Several authors have recently argued for the subdivision of the *Emydura* group. Legler & Cann (1980) erected *Rheodytes leucops* and Cann & Legler (1994) erected *Elusor macrurus*. Thomson *et al.* (1997) estimate that the *Emydura* group includes, besides *Rheodytes* and *Elusor*, three subdivisions of the group: *Emydura* s.s. and two subdivisions of *Elseya*, one for the *dentata-novaeguineae* group and one for the *latisternum* group. As observed above, the attribution of the Redbank Plains material to one of these subdivisions is impossible until the diagnostic apomorphic osteological characters, applicable to our fossils, are defined and given with a well-established cladogram in a comparative work, based on the type specimens of the species. Wells & Wellington (1985) revived the subdivisions of Gray and erected new genera, as well for *Chelodina* as for *Emydura* groups. There is no solid argument in their work. The diagnosis of the future subdivisions would have to include not only autapomorphic characters but also their integration in the evolutionary stage of the genera, all of which is completely missing in the data, and integrate the South American forms with the South Australian forms. We are not only waiting for the study of the osteology and the external characters of the extant species, but also for the research into the primitive and derived states of

each character. This requires taking outgroups outside Australia: in primitive Pleurodira and in Pelomedusoides, following the evolution of each genus. In this way the homoplasies will be made clear.

The Redbank Plains material is insufficiently preserved to resolve the problems and this study is just a first step. For the moment, we do not know: 1) if *Chelodina alanrivi* n. sp. is or not part of the *Chelodina* group with narrowed vertebrals, because of the contradiction between the wide vertebral 5 and the much narrowed vertebrals 1 to 4, and if *Chelodina* form b is or is not part of a monophyletic group with *C. steindachneri*; 2) the group to which *Emydura* s.l. sp. a belongs and if the specimen from Proserpine is a member of the *E. macquarrii* group.

It is certain that at this Palaeogene time several species were differentiated. It is also certain that the three Australian genera were differentiated before the Palaeocene, as suggested by the discovery in the Palaeocene of western Australia. It is evident if we follow the cladistic study of the family by Gaffney (1977), although within this study the problems of vicariance between Australia and South America could be examined and clades could be established instead of grades, when homoplasies are taken into account. Overall, the age of the group in Argentina has been confirmed by the discovery of the very differentiated chelid forms in the Cretaceous (Aptian to Maastrichtian) of Patagonia (Broin 1987, 1988; Broin & Fuente 1993; Lapparent de Broin *et al.* 1997; Lapparent de Broin & Fuente 1999; Fuente *et al.* 2001), with the extant genera, *Phrynops*, *Chelus* and *Hydromedusa*, already defined beside *Emydura*-like forms and more primitive forms. The absence of Chelidae in Early Cretaceous times in Australia may be, therefore, a problem of continental barrier between West and East of Gondwana: actually, in the southern Gondwana fauna of the Early Cretaceous, the South American chelids appear as an Occidental group and the fauna of Victoria, South Wales and Queensland as an Oriental group. It may be a problem of availability of geologically adequate localities in convenient latitudes. As they are

fresh-water turtles, the Chelidae may be found in continental beds, or exceptionally in marine layers near the shore. As poikilothermic animals, Chelidae require a minimal yearly temperature ratio, with a short period of high temperatures or with a longest period of more moderate temperatures, higher than for birds and mammals. And as pleurodiran turtles, although they are more tolerant than Pelomedusoides, they never became accustomed to the cold weather that can affect the Cryptodira, although they can hibernate in the mud (as well as estivate). In the most southern part of Australia, their most southern habitat, they presently live in an area from around 10° minimum in July (the same minimum as in their southern habitat in Argentina, in the North of Buenos Aires Province) or, exceptionally, even less than 10 °C (Thomson pers. comm., for *C. longicollis*) up to 18° C minimum in January. But the question is whether the low temperature period of the year has to be short relative to the higher temperature period, to allow the eggs to mature. On the other hand, it is possible that some extant Australian Quelidae such as *C. longicollis* must to be more adapted to cooling than the primitive Mesozoic forms and other extant forms (they have had much time to adapt), as some Trionychidae did. The problem of a sufficiently high yearly temperature ratio, besides the problems of structural barriers and of the possibilities of a stable fluvial network, is probably an important part of the reason they do not appear in the southern Cretaceous localities of Australia (see Dettmann *et al.* 1992: fig. 24).

Acknowledgements

We first warmly thank Dr Alan Rix for the discovery of the specimens, their gift to the Queensland Museum, and for his help in the present study, particularly concerning the geological references about the fossil localities and references on fossil and living Australian chelids. For their help for the comparative material, we are grateful to Dr J. Covacevich and P. Couper, Vertebrates, Zoology, Queensland Museum, Brisbane; Dr A. Greer, Department of Zoology,

Dr A. Ritchie and R. Jones, Department of Palaeontology, Australian Museum, Sydney; Dr M. Hutchinson, Department of Zoology and Dr N. Pledge, Department of Palaeontology, South Australian Museum, Adelaide; Dr G. Kuchling, University of Western Australia, Department of Zoology, Nedlands; Dr J. Long, Department of Palaeontology and Dr L. Smith, Department of Zoology, Western Australian Museum, Perth; Dr T. Rich, National Museum of Victoria, Natural History Division, Melbourne; Dr P. Vickers-Rich and Mrs L. Kool, Monash University Department of Earth Sciences, Clayton, Melbourne; Dr A. Warren, Zoology Department, La Trobe University, Bundoora; Arthur White, University of New South Wales. In Argentina, we warmly thank for his welcome Prof. J. Bonaparte, Museo de Ciencias Naturales de Buenos Aires and Dr M. S. de la Fuente, Museo de Ciencias Naturales de La Plata. At the Natural History Museum, London, we kindly thank Dr C. McCarthy, Department of Zoology, Reptiles, and Sandra Chapman, Department of Palaeontology. At the Muséum national d'Histoire naturelle de Paris, we are particularly grateful to R. Bour, Laboratoire de Zoologie des Reptiles et Amphibiens, for his help and commentaries, to F. Pilard and H. Lavina (figures) and L. Merlette (photographs), Laboratoire de Paléontologie, and to F. Renoult, Laboratoire d'Anatomie comparée (osteological material). We also thank the authors of the reviews sent to *Geodiversitas* and including S. Thomson. At the moment this paper is sent to press, various important papers on chelids of S. Thomson (pers. comm., in prep. or in press but references not communicated) and others (including Megirian & Murray 1999), are not received here and, therefore, not available for the present study.

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Submitted on 11 October 1999;
accepted on 14 September 2000.