

A new dermochelyid turtle from the Late Paleocene–Early Eocene of Saudi Arabia

Nouvelle tortue dermochélyidée du Paléocène supérieur–Éocène inférieur d'Arabie Saoudite

Haiyan Tong^a, Eric Buffetaut^a, Herbert Thomas^b, Jack Roger^c, Mohammed Halawani^d, Abdallah Memesh^e, Patrick Lebret^c

^a UMR 5561, 16, cour du Liégar, 75013 Paris, France

^b Collège de France et laboratoire de paléontologie, UMR 8569, Muséum national d'histoire naturelle, 8, rue Buffon, 75005 Paris, France

^c BRGM, SGN, 3, avenue C.-Guillemin, BP 6009, 45060 Orléans cedex 2, France

^d Ministry of Petroleum and Mineral Resources, Deputy Ministry for Mineral Resources, Jeddah, Kingdom of Saudi Arabia

^e BRGM Mission, Ministry of Petroleum and Mineral Resources, DMMR Jeddah, Kingdom of Saudi Arabia

(Received 9 September 1998, accepted after revision 8 November 1999)

Abstract — A new dermochelyid sea turtle, *Arabemys crassiscutata* n. gen. n. sp., is described on the basis of epithelial shell mosaic ossicles from the Late Paleocene–Early Eocene of Saudi Arabia. This is the oldest and the most primitive known representative of the dermochelyids having an epithelial shell mosaic. (© 1999 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS.)

Testudines / Dermochelyidae / *Arabemys crassiscutata* n. g. n. sp. / Late Paleocene–Early Eocene / Saudi Arabia

Résumé — Une nouvelle tortue marine de la famille des Dermochelyidae, *Arabemys crassiscutata* n. gen. n. sp., est décrite d'après des plaques épithéliales provenant du Paléocène supérieur–Éocène inférieur d'Arabie Saoudite. C'est le plus ancien et le plus primitif représentant connu des dermochélyidés possédant une carapace épithéliale en mosaïque. (© 1999 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS.)

Testudines / Dermochelyidae / *Arabemys crassiscutata* n. g. n. sp. / Paléocène supérieur / Éocène inférieur / Arabie Saoudite

Version abrégée (voir page 918)

1. Introduction

Recent geological mapping in northern Saudi Arabia by BRGM/DMMR (*figure 1*) has resulted in the discovery of a new marine vertebrate fauna east of the Nafud, in dolomitised shales belonging to the top unit of the Aruma Formation (the Lina Member), usually referred to as the Maastrichtian. Both a preliminary analysis of this

fauna, which includes remains of a dozen taxa of selachian and actinopterygian fishes, as well as a giant marine turtle, and a reinterpretation of the stratigraphic position of the Lina Member, have led us to assign a much younger, Late Paleocene to Early Eocene, age to this unit (Thomas et al., 1999).

Note communicated by Yves Coppens.

* Correspondence and reprints

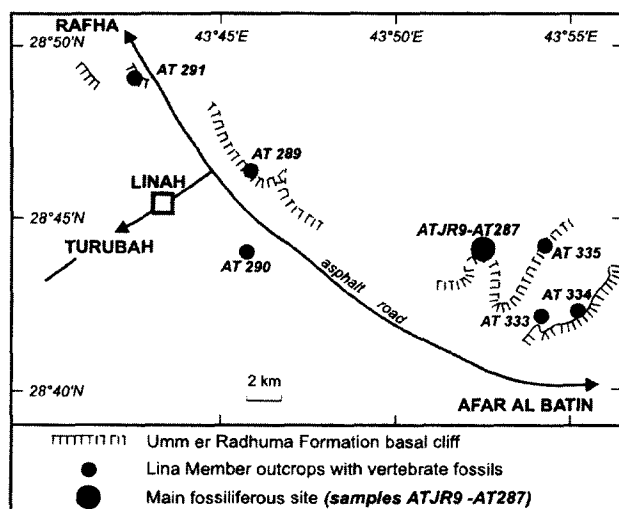


Figure 1. Location sketch map of fossil localities of *Arabemys crassiscutata* with indication of BRGM field sample numbers.

Carte de situation des localités fossilifères à *Arabemys crassiscutata*, avec indication des numéros des échantillons collectés par le BRGM.

The fauna from the Lina Member is heavily dominated by remains of the marine turtle, represented mostly by hundreds of epithelial ossicles characteristic of the family Dermochelyidae, for which a new genus and species are erected.

The family Dermochelyidae is represented by one living species, *Dermochelys coriacea*, the leatherback turtle, which is the largest living reptile and the only living turtle in which the thecal shell is replaced by an epithelial shell mosaic consisting of thousands of small ossicles. Although the family is recorded since the Late Cretaceous, dermochelyids with an epithelial shell mosaic were not known earlier than the Mid-Late Eocene.

2. Systematics

Order Testudines
Suborder Cryptodira
Superfamily Cheloniodea
Family Dermochelyidae

Arabemys crassiscutata, n.g., n.sp. (figure 2, 1–8)

Derivatio nominis: generic name from Saudi Arabia, and *emys*, Greek for turtle. Specific name from the Latin *crassus*, thick, and *scutum*, shield.

Diagnosis (for genus and species): Dermochelyid turtle with epithelial shell mosaic composed of a large number of bony ossicles; different from *Cosmochelys dolloi* Andrews, 1919, in having a carapace without anteroposterior ridges and bony ossicles bulging and very thick (up to more than 20 mm) with the external surface deeply sculptured with wrinkles and tubercles radiating outward from the centre of each ossicle, and without a spongy layer in cross-section.

Holotype: an isolated bony ossicle (n° AT JR9-3, figure 2, 1)

Hypodigm: several hundred isolated ossicles.

Locus typicus: east of Linah village, Linah quadrangle, northern Saudi Arabia. Main fossiliferous site (samples ATJR9 – AT287): 28°44'02"N/43°52'25"E.

Stratum typicum: Lina Member, Aruma Formation, Late Palaeocene/Early Eocene.

Description:

The material consists of several hundred isolated bony ossicles, in several groups corresponding to different collecting points in the field. Most specimens are eroded and broken, probably as a result of post mortem transport, while some of them are fresh. The external surface of uneroded ossicles is deeply sculptured with wrinkles and tubercles radiating outward from the centre of the ossicle. The visceral surface of the ossicles is smooth with several tiny nutritive holes. The lateral sides of the ossicles are marked with corrugations corresponding to the suture with the adjacent one. The ossicles have a polygonal shape, from tetragonal to heptagonal, most being pentagonal or hexagonal. Their size is variable, ranging from about 20 mm up to 45 mm in largest diameter, most of them being between 25 and 35 mm, with the length only slightly larger than the width. There are a few (four or five) elongate ossicles for which the length is about 1.5 times the width (45 × 30 mm). The thickness of the ossicles is greatly variable, ranging from 6 mm up to more than 20 mm, the thickest one being 23 mm thick. Most ossicles are more or less bulging on the external side, with the visceral side flat, so the greatest thickness is usually in the middle or near the middle of the ossicle, but rarely on the border. No keeled ossicle is present. In cross-section, the bone is homogeneously dense, without a spongy layer. Some of the ossicles present a free smooth rim, separated from the sculptured area by a groove, which probably corresponds to the edge of the shell (figure 2, 2 and 4).

It is difficult to decide whether a given ossicle belongs to the carapace or to the plastron. No reconstruction is possible since none of these ossicles can be fitted together. Some ossicles are clearly thicker than others, but all intermediate thicknesses exist. The differences in size and thickness between the ossicles may reflect different positions on the shell or different individuals of different sizes. It is likely that the swellings were arranged in some regular manner on the shell surface, but our material is too fragmentary to reconstruct such a pattern.

3. The dermochelyid fossil record

The family Dermochelyidae is recorded from the Late Cretaceous to the Recent, mainly on the basis of shell mosaic ossicles or humeri, which are characteristic elements for the family. Recently, Wood et al. (1996) reviewed the dermochelyid record, but some European data were omitted. The fossil record of the Dermochelyidae is summarized below (figure 3).

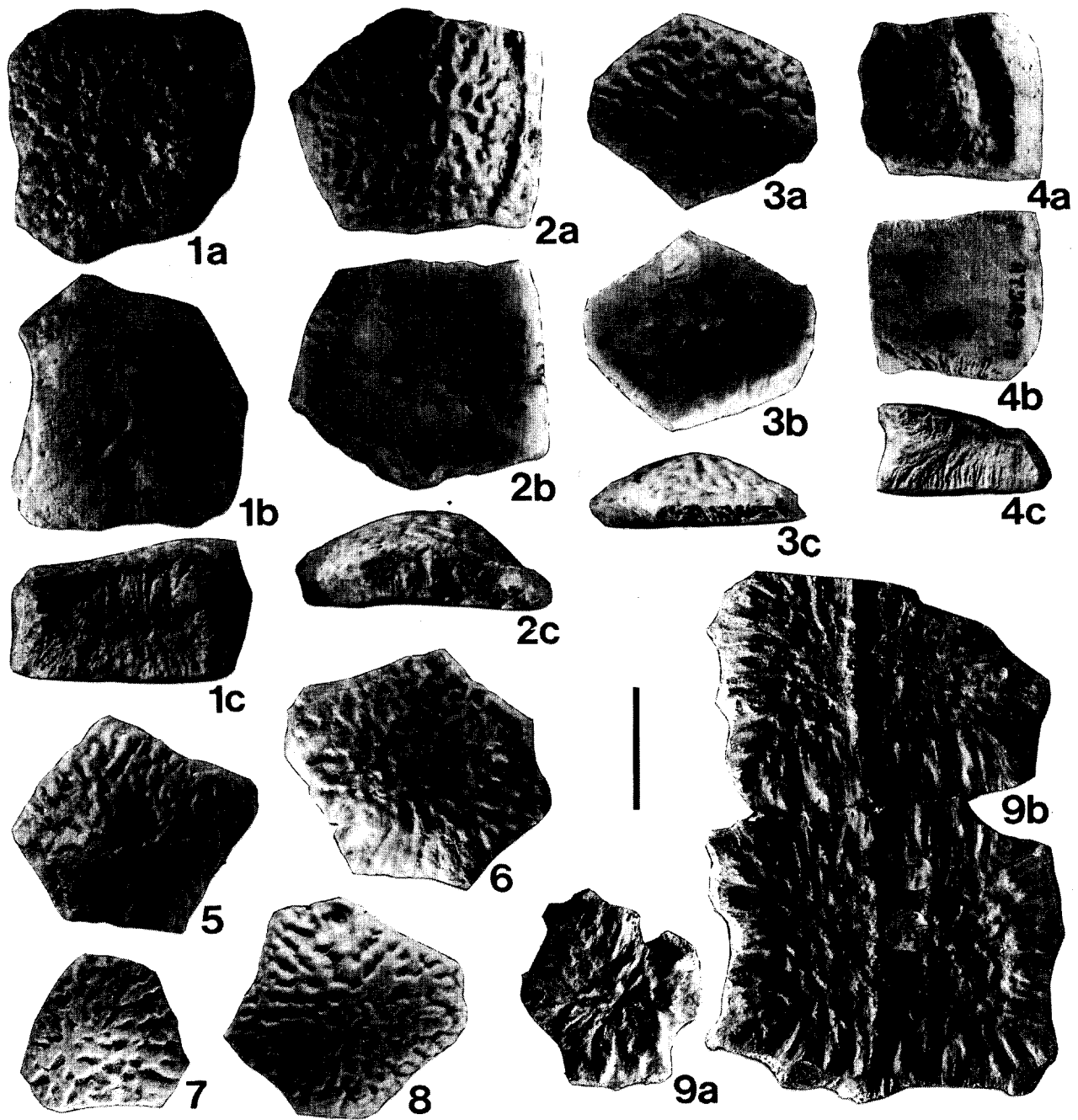


Figure 2. 1–8: *Arabemys crassiscutata* n. g. n. sp.; 1: ATJR9-3, holotype, 1a: external view, 1b: visceral view, 1c: lateral view; 2: ATJR9-1; 3: ATJR9-8; 4: ATJR9-10; 5: ATJR9-5; 6: ATJR9-2; 7: AT287-11; 8: ATJR9-7; 9: *Cosmochelys dolloi* Andrews, 1919; R/4338, Natural History Museum, London, 9a: plate without keel, 9b: keeled plates. Scale bar: 2 cm.

1–8 : *Arabemys crassiscutata* n. g. n. sp. ; 1 : ATJR9-3, holotype, 1a : vue externe, 1b : vue interne, 1c : vue latérale ; 2 : ATJR9-1 ; 3 : ATJR9-8 ; 4 : ATJR9-10 ; 5 : ATJR9-5 ; 6 : ATJR9-2 ; 7 : AT287-11 ; 8 : ATJR9-7. 9 : *Cosmochelys dolloi* Andrews, 1919 ; R/4338, Natural History Museum, London, 9a : plaque sans crête, 9b : plaques avec crête. Barre d'échelle : 2 cm.

Cretaceous. Two dermochelyids are known from the Late Cretaceous: *Corsochelys haliniches* from the Campanian of Alabama, USA (Zangerl, 1960; Hirayama, 1994) and *Mesodermochelys undulatus*, from the Maastrichtian of Japan (Hirayama and Chitoku, 1996). Both include skull fragments and shell material. These primi-

tive dermochelyids possess a thecal shell without an epithelial shell mosaic.

Paleocene. Wood et al. (1996) recorded no dermochelyids from the Paleocene. Hirayama and Chitoku (1996) mentioned Late Paleocene dermochelyids, but the source of this record is unspecified. *Eosphargis breineri*

(Nielsen, 1959; 1963) is from the Fur Formation of Denmark, originally considered as Early Eocene in age, but now placed in the latest Paleocene (Bonde, 1987).

Eocene. *Eosphargis* is a dermochelyid without an epithec shell mosaic from the Latest Paleocene to early Eocene of Europe, with *E. gigas* from England (Owen, 1880; Lydekker, 1889) and Belgium (Quintart and Plisnier-Ladame, 1968). Lydekker (1889) referred ossicles, probably from the Middle Eocene of Sussex, England, to *Psephophorus* sp.

In Africa, fragments of shell mosaic from the Eocene of Nigeria were described as *Cosmochelys dolloi* by Andrews (1919) (figure 2, 9). A humerus, a partial shell mosaic and some other elements were described from the Late Eocene of Egypt as *Egyptemys eocaenus* (Andrews, 1901; Wood et al., 1996). A skull from the Lower Ypresian (Early Eocene) phosphates of Gafsa, Tunisia, originally described as *Thalassochelys testei*, a supposed cheloniid, by Bergounioux (1956), was later identified as a dermochelyid by Moody and Buffetaut (1980).

In North America, dermochelyids are recorded from Alabama, USA (Müller, 1849; Wood et al., 1996).

In New Zealand, a partial *Psephophorus* humerus (Köhler, 1994) and an undescribed fragment of shell mosaic (Wood et al., 1996) have been reported from an Eocene locality.

In Antarctica, dermochelyid ossicles have been described from the Eocene of Seymour Island as cf. *Psephophorus* (De la Fuente et al., 1995).

Oligocene. *Natemys peruvianus*, from the Late Oligocene of Peru is based on a partial shell mosaic (Wood et al., 1996). '*Psephophorus*' *rupeliensis*, represented by several well-preserved specimens from Belgium, has not been fully described (Van Beneden, 1883; Dollo, 1888; Wood et

al., 1996) and has been considered as a new genus (Wood and Moody, 1998). Dames (1894) described a partial skull from the Late Oligocene of Germany as *Pseudosphargis ingens*, and isolated shell mosaic ossicles from the Early Oligocene as *Psephophorus* sp. Nielsen (1959) suggested that the skull may belong to *Psephophorus* or to *Eosphargis*. Undescribed specimens are known from South Carolina, USA (Wood et al., 1996).

Miocene. All Miocene dermochelyid remains, most of them from Europe, are referred to the genus *Psephophorus*. The type species, *P. polygonus* Meyer was described from present-day Slovakia, on the basis of a portion of shell mosaic and several vertebrae (Seeley, 1880). A fragment of shell mosaic from Vendargues (Hérault, France) was described as *P. pseudostracion* (Gervais, 1872). A fragment of carapace mosaic was described from Italy as *P. sp.* (de Broin and Pironon, 1980) and isolated shell mosaic ossicles were reported from the Miocene of Germany (Dames, 1894). A humerus is reported from Belgium as *P. scaldii* (Van Beneden, 1871). *P. calvertensis* is based on a portion of shell mosaic, and a scapula fragment, from the Middle Miocene of Maryland, USA (Palmer, 1909; Weems, 1974). A skull and a shell mosaic fragment were described from the Miocene (not Eocene as erroneously mentioned by Wood et al., 1996) of Oregon as *Psephophorus* (?) *oregonensis* by Packard (1940) and later referred to the genus *Egyptemys* on the basis of shell morphology (Wood et al., 1996).

Pliocene. A single undetermined ossicle from Florida, USA (Dodd et al., 1992), and several limb bones from the Pliocene of Belgium referred to *Psephophorus scaldii* (Dollo, 1888).

Recent. The living *Dermochelys coriacea*.

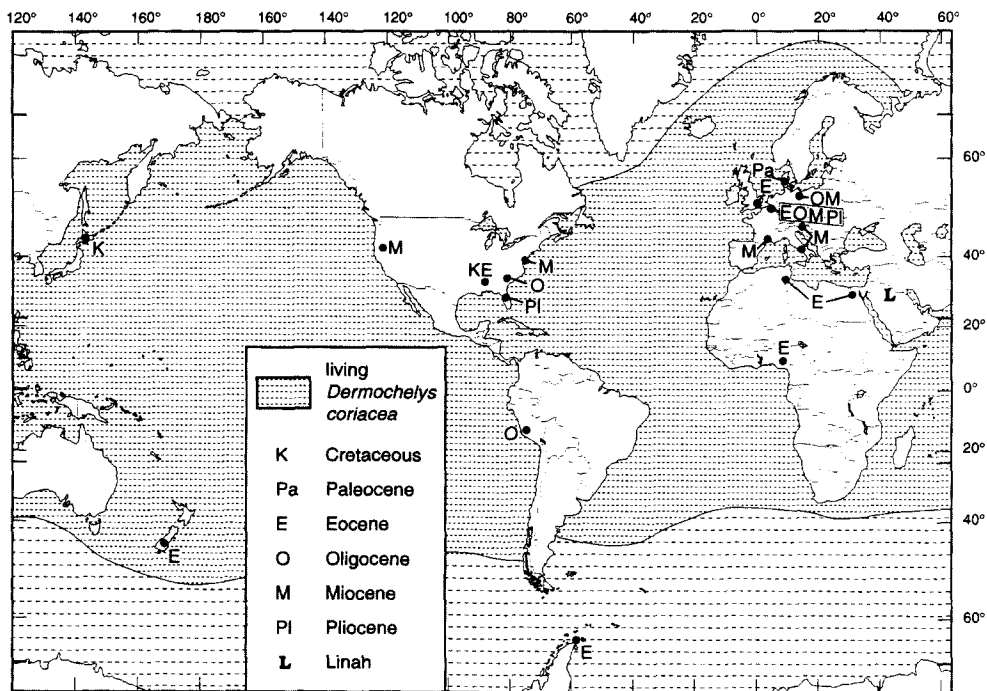


Figure 3. Fossil dermochelyid localities and present distribution of *Dermochelys coriacea*.

Localités à dermochelyidés et répartition de l'actuelle *Dermochelys coriacea*.

4. Comparisons and discussion

Fragments of shell mosaic and humeri represent most fossil dermochelyids. Until recently, with only one exception (*Cosmochelys*), all fossil dermochelyids in which the shell mosaic is known were referred to the genus *Psephophorus*. Wood et al. (1996) recognised four dermochelyid genera possessing an epithelial shell mosaic: *Cosmochelys* (Eocene), *Egyptemys* (Eocene and Miocene), *Natemys* (Oligocene) and *Psephophorus* (Eocene to Pliocene). The latter is probably a 'wastebasket' taxon to which most shell mosaic ossicles have been referred. By comparison with these taxa, the dermochelyid remains from Saudi Arabia reveal some distinctive features:

– **a deeply sculptured external surface**; the ornamentation on the external surface of the shell mosaic seems to be diagnostic among dermochelyids although this feature should be treated with caution because of possible post mortem erosion; *Natemys* and some *Psephophorus* (such as those from the Miocene of France and Italy) have ossicles with a smooth or nearly smooth external surface (Gervais, 1872; de Broin and Pironon, 1980; Wood et al., 1996); it has been suggested that the ossicles of some dermochelyids, such as *Egyptemys eocaenus* (Wood et al., 1996) and *Psephophorus calvertensis* (Palmer, 1909), were ornamented before they became worn; the ossicle ornamentation most similar to that of *Arabemys* is found in *Cosmochelys*, where it consists of "a series of irregular tuberosities in the middle bordered by ridges more or less radially arranged, and running to the margin..." (Andrews, 1919, p. 315); the sculpture in our specimens is more homogenous and more vermiculated; the Miocene *Psephophorus polygonus* has only radial ridges (Seeley, 1880), less pronounced than in *Cosmochelys* (Andrews, 1919); '*Psephophorus*' *rupeliensis* also shows some slight ornamentation apparently similar to that of *P. polygonus*;

– **the absence of anteroposterior ridges on the carapace**, since no keeled ossicle is present among the abundant specimens from Saudi Arabia; most dermochelyids with a shell mosaic have five or seven anteroposterior ridges or keels: at least seven in *Cosmochelys* (Andrews, 1919), five in *Egyptemys eocaenus* (Wood et al., 1996), seven in *Dermochelys*; these ridges may be weak and expressed only on the external surface of the carapace mosaic (*Egyptemys*, *Cosmochelys* and *Psephophorus*), or strong, with an upward flexure of both external and visceral surfaces as in *Dermochelys* (Wood et al., 1996); according to Wood et al. (1996), '*Psephophorus*' *rupeliensis* and *Natemys* have no anteroposterior ridges, but have clusters of ossicles forming a sunflower pattern with a large, scallop-edged central ossicle surrounded by an array of smaller ossicles; our material does not suggest great size differences between the ossicles;

– **bulging external surface of ossicles**; other known dermochelyids have ossicles with a flat or nearly flat external surface, except for the keel-bearing ones (absent in

our material) in which the keel extends along the whole length of the ossicle;

– **very thick ossicles**; in our specimens, the thickness of the ossicles may exceed 20 mm (23 mm for the thickest); they are thus the thickest known dermochelyid ossicles; the thickness of the ossicles is 10 mm in the middle of the carapace, and up to 16 mm at the level of the ridges in *Cosmochelys* (Andrews, 1919); up to 18 mm in cf. *Psephophorus* from the Eocene of Seymour Island (De La Fuente et al., 1995); 7 to 12 mm in *Egyptemys eocaenus* from the Eocene of Egypt (Wood et al., 1996); up to 10 mm in *Psephophorus polygonus* (Seeley, 1880), 5 to 10 mm in *P. sp.* from the Miocene of Italy (de Broin and Pironon, 1980). *Psephophorus calvertensis* from the Miocene of Maryland is the only one in which the keel-bearing ossicles may be more than 20 mm thick (21 mm according to Palmer, 1909);

– **bone of ossicles dense, without a spongy layer**; other dermochelyids, such as *Cosmochelys*, show two layers in cross-section; a dense outer layer and a spongy inner one.

The Saudi Arabian specimens cannot be included in any known dermochelyid taxon, hence the erection of a new genus and species, *Arabemys crassiscutata*. It is most similar to *Cosmochelys* (figure 2, 9) from the Eocene of Nigeria by the sculptured external surface of the ossicles, but differs from it by the absence of anteroposterior ridges on the carapace, its thicker, denser and bulging ossicles, and the different sculpturing on their external surface.

Wood et al. (1996) have proposed a tentative phylogeny of the Dermochelyidae on the basis of shell mosaic. They recognise several groups among forms with a shell mosaic: a *Natemys* – '*Psephophorus*' *rupeliensis* group from the Oligocene, characterized by the lack of carapace keels plus the presence of rows of clusters of ossicles with a distinctive 'sunflower' pattern; an *Egyptemys*–*Cosmochelys* group from the Eocene and Miocene, characterized by weakly developed and closely-spaced ridges; and an Eocene to Recent group, including *Dermochelys*, characterized by more prominent and widely-spaced keels produced by flexure of the entire shell. Five evolutionary trends in shell morphology have been recognised in the latter group including: 1) a decrease in mosaic shell thickness over time; 2) a concomitant decrease of the size of individual ossicles; 3) an increase in the prominence of the carapace ridges; 4) the development of undulating crests along the ridges; 5) an increase in the number of ossicles intervening between adjacent ridges. Andrews (1919) had noticed that from the Eocene (*Cosmochelys*) to the Miocene (*Psephophorus*), there is a multiplication of the ossicles between the ridges and the sculpture of the surface becomes less marked. Within the phylogenetic scheme proposed by Wood et al. (1996), *Arabemys* is the most primitive dermochelyid having an epithelial shell mosaic, because of the deeply sculptured external surface and the great thickness of the ossicles, and of the absence of antero-

posterior ridges on the carapace. These primitive features suggest that *Arabemys* is probably older than the Mid–Late Eocene, from which dermochelyids with a more derived epithelial shell mosaic are recorded. Out of some ten dermochelyid genera currently known since the Late Cretaceous, more than half possess a shell mosaic. As pointed out by Wood et al. (1996), their evolutionary history is much more complicated than was previously believed, with several lineages; the exact relationships of *Arabemys* are obscure because of the fragmentary nature of the material.

Little can be said about the mode of life of *Arabemys*. The thick and dense ossicles suggest a heavy shell, not

adapted to rapid swimming. Dollo (1901) suggested that primitive dermochelyids may have been coastal forms. According to Andrews (1919), in *Cosmochelys* “the presence of this strongly marked ornament seems to show that this turtle was not adapted for rapid motion through the water, but was probably a littoral or even a swamp-living form like *Trionyx*”. In contrast, the living dermochelyid species, *Dermochelys coriacea*, is a truly pelagic sea turtle (Prichard and Trebbau, 1984), with the broadest geographical distribution of any extant reptile. *Arabemys crassiscutata*, with its very heavy epithelial shell, in all likelihood was not as much adapted to pelagic life as the leatherback turtle.

Version abrégée

Une faune inédite de vertébrés marins a été découverte dans le Nord de l'Arabie, dans des dépôts de l'unité sommitale de la formation Aruma — le membre Lina —, classiquement considéré comme d'âge Maastrichtien (figure 1). L'analyse de cette faune, qui comprend une douzaine de poissons sélaciens et actinoptérygiens, ainsi qu'une tortue marine géante, conjuguée à des considérations géologiques, nous ont conduits à rajeunir cette unité en lui attribuant un âge Paléocène supérieur à Éocène inférieur (Thomas et al., 1999). La faune du membre Lina se distingue surtout par l'abondance des plaques osseuses épithéliales d'une tortue marine, caractéristiques de la famille des Dermochelyidae.

La famille des Dermochelyidae est représentée par une seule espèce vivante, la tortue luth (*Dermochelys coriacea*), seule tortue actuelle chez laquelle la carapace thécale soit remplacée par une carapace épithéliale composée de milliers de petites plaques osseuses en mosaïque. Bien que cette famille soit connue depuis le Crétacé supérieur, les formes possédant une carapace épithéliale en mosaïque n'étaient pas connues avant l'Éocène moyen-supérieur. Nous décrivons ici un nouveau taxon de Dermochelyidae provenant du Paléocène supérieur–Éocène inférieur d'Arabie Saoudite.

Arabemys crassiscutata n.g., n. sp. (figure 2, 1–8)

Holotype: une plaque épithéliale isolée (AT JR9-3, figure 2, 1).

Hypodigme: plusieurs centaines de plaques épithéliales isolées.

Derivatio nominis: le nom du genre provient du pays, Arabie Saoudite; le nom de l'espèce du latin *crassus*, épais, et *scutum*, bouclier.

Locus typicus: à l'est du village de Linah, Nord de l'Arabie Saoudite. Localité principale, échantillons ATJR9 – AT287: 28°44'02"N/43°52'25"E.

Stratum typicum: membre Lina, formation Aruma, Paléocène supérieur à Éocène inférieur.

Diagnose: Dermochélyidé à la carapace composée d'un grand nombre de plaques osseuses épithéliales en mosaïque; diffère de *Cosmochelys dolloi* Andrews, 1919 par l'absence de crêtes antéro-postérieures sur la carapace, et des plaques très épaisses, pouvant dépasser 20 mm, avec face externe bombée

et fortement sculptée de bourrelets et de tubercules disposés de façon radiaire à partir du centre de chaque plaque, et ne montrant pas de couche spongieuse en coupe.

Le matériel est constitué de plusieurs centaines de plaques osseuses isolées, réparties en lots correspondant aux points de récolte sur le terrain. La plupart des spécimens sont usés et cassés, résultat d'un transport *post mortem*, mais certains sont encore frais. La surface externe des plaques non usées est fortement sculptée, avec des bourrelets et des tubercules vermiculés disposés de façon radiaire à partir du centre de chaque plaque. La face interne des plaques est lisse, avec quelques minuscules forams nutritifs. Les faces latérales des plaques portent des plis, correspondant aux sutures avec les plaques voisines. Les plaques sont polygonales, pour la plupart pentagonales ou hexagonales. Leur diamètre varie de 20 à 45 mm; il est la plupart du temps compris entre 25 et 35 mm. Il y a peu de plaques allongées. L'épaisseur des plaques varie de 6 à plus de 20 mm (épaisseur maximum: 23 mm). La face externe est généralement bombée, la face interne plane. Aucune plaque ne porte une crête. En coupe, les plaques montrent une densité homogène, sans couche spongieuse. Certaines plaques, correspondant au rebord de la carapace, montrent un rebord libre, avec un bourrelet et un sillon interne.

Ces plaques isolées ne permettent pas une reconstitution d'ensemble. Il est vraisemblable que des bombements étaient disposés de façon régulière sur la carapace, mais notre matériel est trop fragmentaire pour le déterminer.

Les Dermochelyidae sont connus du Crétacé supérieur à l'Actuel, principalement par des plaques osseuses épithéliales ou des humérus, éléments caractéristiques de la famille. Quatre genres possédant une carapace épithéliale en mosaïque sont connus: *Cosmochelys* (Eocène), *Egyptemys* (Eocène et Miocène), *Natemys* (Oligocène), et *Psephophorus* (Éocène à Pliocène). Par comparaison avec ces taxons, les spécimens d'Arabie Saoudite révèlent certaines particularités: sculpture très marquée sur la surface externe des plaques; absence de crêtes antéro-postérieures sur la carapace; surface externe des plaques bombée; plaques très épaisses pouvant dépasser 20 mm d'épaisseur, homogènes en densité, sans couche spongieuse.

Les spécimens d'Arabie Saoudite ne pouvant être placés dans un taxon connu, le nouveau taxon *Arabemys crassiscu-*

tata n. g. n. sp. est créé ici. Par l'ornementation de ses plaques, le taxon le plus proche est *Cosmochelys* (figure 2, 9), de l'Éocène du Nigéria. *Arabemys* s'en distingue par l'absence de crêtes longitudinales sur la carapace, ses plaques bombées, plus épaisses et homogènes en densité, et l'ornementation différente de la surface externe des plaques.

Wood et al. (1996) ont proposé une phylogénie des Dermochelyidae fondée sur les caractères de la carapace en mosaïque. Dans cette optique, *Arabemys*, par la forte orne-

mentation et la grande épaisseur de ses plaques osseuses et l'absence de crêtes antéro-postérieures, est le plus primitif des Dermochelyidae possédant une carapace épithéciale en mosaïque. Ces caractères suggèrent, pour *Arabemys*, un âge plus ancien que l'Éocène moyen-supérieur, époque à laquelle on connaît des Dermochelyida possédant une carapace épithéciale plus évoluée. Les plaques épaisses et non-spongieuses suggèrent qu'*Arabemys* possédait une carapace lourde peu adaptée à une nage rapide.

Acknowledgements. This study was carried out within the framework of an agreement between the Saudi Arabian Deputy Ministry for Mineral Resources and the French Bureau de recherches géologiques et minières. Publication of these results was made possible thanks to the support and authorization of Dr. M.A. Tawfiq (Assistant Deputy Ministry for Survey and Exploration, Deputy Ministry for Mineral Resources), to whom the authors express their grateful thanks. We also wish to thank Roger Wood, Eugene Gaffney, Ren Hirayama and Ella Hoch for information and comments, Pascal Godefroit, Angela Milner and Sandra Chapman for access to comparative material, and Patrick David for bibliographic research.

5. References

- Andrews C.W. 1901. Preliminary note on some recently discovered extinct vertebrates from Egypt (Part II), *Geol. Mag.*, 8, 436–444
- Andrews C.W. 1919. A description of New Species of Zeuglodont and of Leatherback Turtle from the Eocene of Southern Nigeria, *Proc. Zool. Soc. London*, 1, 309–318
- Bergounioux F.M. 1956. Les reptiles fossiles des dépôts phosphatés du Sud-Tunisien, *Ann. Min. Géol. Tunis*, 1–105
- Bonde N. 1987. *Moler-its origin and its fossils especially fishes*, Skamol, Nykobing Mors, 53 p.
- Broin de F. and Pironon B. 1980. Découverte d'une tortue dermochélyidée dans le Miocène d'Italie centro-méridionale (Matese Oriental), province de Benevento, *Riv. Ital. Paleont.*, 86, 3, 589–604
- Dames W. 1894. Die Chelonier der norddeutschen Tertiärformation, *Geol. Paleont. Abhandl.*, n. s., 2 (4), 137–200
- De la Fuente M.S., Santillana S.N. and Marensi S.A. 1995. An Eocene leatherback turtle (Cryptodira: Dermochelyidae) from Seymour Island, Antarctica, *Stud. Geol. Salmant.*, 31, 21–34
- Dodd C.K. and Morgan G.S. 1992. Fossil sea turtles from the Early Pliocene Bone Valley Formation, central Florida, *J. Herpetol.*, 26, 1–8
- Dollo L. 1888. Première note sur les reptiles oligocènes et néogènes de la Belgique, *Bull. Mus. Roy. Hist. Nat. Belg.*, 5, 59–96
- Dollo L. 1901. Sur l'origine de la tortue luth (*Dermochelys coarctata*), *Bull. Soc. roy. Sc. Med. & Nat. Bruxelles*, 1–26
- Gervais P. 1872. Ostéologie du *Sphargis luth*, *Nouv. Arch. Mus. Nat. Paris*, 8, 2, 199–228
- Hirayama R. 1994. Phylogenetic systematics of chelonoid sea turtles, *The Island Arc*, 3, 270–284
- Hirayama R. and Chitoku T. 1996. Family Dermochelyidae (Superfamily Chelonioidae) from the Upper Cretaceous of North Japan, *Trans. Proc. Palaeont. Soc. Jpn.*, N.S., 184, 597–622
- Köhler R. 1994. An Eocene turtle humerus (Dermochelyidae, *Psephophorus*) from New Zealand, *Studia Geol. Salman.*, 30, 101–106
- Lydekker R. 1889. *Catalogue of fossil reptilia and amphibia in the British Museum (Natural History)*, vol. 3, Trust. Brit. Mus. (Nat. Hist.), London, 239 p.
- Moody R.T.J. and Buffetaut E. 1980. Notes on the systematics and paleoecology of the crocodiles and turtles of the Metlaoui Phosphates (Eocene) of Southern Tunisia, *Tertiary Res.*, 3 (3), 125–140
- Müller J. 1849. *Über die fossilen Reste der Zeuglodonten von Nordamerika, mit Rücksicht auf die europäischen Reste aus dieser Familie*, G. Reimer, Berlin, 38 p.
- Nielsen E. 1959. Eocene turtles from Denmark, *Medd. Dansk. Geol. Foren*, 14 (2), 96–114
- Nielsen E. 1963. On the post-cranial skeleton of *Eospargis breineri* Nielsen, *Medd. Dansk. Geol. Foren*, 15 (3), 281–313
- Owen R. 1880. Monography on the first Reptilia of the London clay, *Mon. Pal. Soc.*, 2, 1.
- Packard E.L. 1940. A new turtle from the marine Miocene of Oregon, *Oregon St. Col. Stud. Geol.*, 2, 1–31
- Palmer W. 1909. Description of new species of leatherback turtle from the Miocene of Maryland, *Proc. US Nat. Mus.*, 36, 369–373
- Prichard P.C.H. and Trebbau P. 1984. The turtles of Venezuela, *Contrib. Herpetol.* 1, 403 p.
- Quintart A. and Plisnier-Ladame F. 1968. *Eosphargis gigas* (Owen, 1861). À propos d'une tortue géante récemment exposée dans les salles de l'I.R.Sc.N.B., *Les Naturalistes belges*, 49, 366–381
- Seeley H.G. 1880. Notes on *Psephophorus polygonus* v. Meyer, a new type of Chelonian reptile allied to the leatherback turtle, *Quart. J. Geol. Soc. London*, 36, 406–413
- Thomas H., Roger J., Halawani M., Memesh A., Lebre P., Bourdillon C., Buffetaut E., Cappetta H., Cavalier C., Dutheil D., Tong H. and Valet D. 1999. Late Paleocene to Early Eocene marine vertebrates from the uppermost Aruma Formation (Northern Saudi Arabia): implications for the K–T transition, *C. R. Acad. Sci. Paris*, 329, série IIa, 905–912
- Van Beneden P.J. 1871. Les reptiles fossiles en Belgique, *Bull. Acad. Roy. Belg. Sc. Lettr. Beaux-Arts*, 2 (31), 9–16
- Van Beneden P.J. 1883. Note sur des ossements de *Sphargis* trouvés dans la terre à briques du pays de Waas, *Bull. Acad., Roy. Belg. Sc. Lettr. Beaux-Arts*, 3 (6), 665–684
- Weems R.E. 1974. Middle Miocene sea turtles (*Syllomus*, *Procolpochelys*, *Psephophorus*) from the Calvert Formation, *J. Paleont.*, 48, 278–303
- Wood R.C., Johnson-Gove J., Gaffney E.S. and Maley K.F. 1996. Evolution and Phylogeny of Leatherback Turtles (Dermochelyidae), with Descriptions of New Fossil Taxa, *Chelonian Conservation and Biology, International Journal of Turtle and Tortoise Research*, 2, 2, 266–286
- Wood R.C. and Moody R.T.J. 1998. Fossil leatherback (dermochelyid) turtles from the Tertiary of Belgium, *J. Vert. Paleont.*, 18, 3 suppl., 88
- Zangerl R. 1960. The vertebrate fauna of the Selma formation of Alabama. Part 5. An advanced chelonian sea turtle, *Fieldiana Geol., Memoirs*, 3, 281–312