

Systematic palaeontology (Vertebrate palaeontology)

Euclastes acutirostris, a new species of littoral turtle
(Cryptodira, Cheloniidae) from the Palaeocene phosphates
of Morocco (Oulad Abdoun Basin, Danian–Thanetian)

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Abstract

A new species of the littoral cheloniid turtle *Euclastes*, *E. acutirostris*, is proposed, on the basis of a skull from the Palaeocene Phosphates of Morocco, the first turtle record from the Sidi Chennane area. It is estimated to be Danian–Thanetian in age, possibly younger than the previous Danian Moroccan specimens of *Euclastes*. It differs from the other species of *Euclastes* mainly by a more elongated and narrower snout, forming a small hook, the presence of a long and narrow spur-shaped postero-inferior process of the jugal, better delimiting the lateral skull emargination and the medially shorter palate, in relation to American Palaeogene specimens. This study indicates the necessity for a world-wide revision of the “*Euclastes* group” in order to redefine the taxa. It shows the potential interest of the group in the radiation and dispersion of the faunas of the Tethysian and Atlantic margins during the Cretaceous–Tertiary turnover. **To cite this article:** N.-E. Jalil et al., C. R. Palevol 8 (2009).

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Résumé

Euclastes acutirostris, une nouvelle espèce de tortue littorale (Cryptodira, Cheloniidae) des phosphates paléocènes du Maroc (Bassin des Oulad Abdoun, Danien–Thanétien). Une nouvelle espèce de la tortue littorale cheloniidée *Euclastes*, *E. acutirostris*, est proposée, sur la base d’un crâne provenant des phosphates paléocènes du Maroc, premier reste de tortue de Sidi Chennane. Son âge estimé est Danien–Thanétien, peut-être plus jeune que celui des spécimens marocains antérieurs d’*Euclastes*, daniens. Elle diffère des autres espèces d’*Euclastes*, principalement par son museau plus allongé et plus étroit et formant un petit bec, la présence d’un processus postéro-inférieur du jugal long et étroit et délimitant mieux l’échancrure latérale du crâne et par l’étendue plus courte du palais médialement par rapport aux spécimens américains paléogènes. Son étude met en évidence la nécessité d’une révision du « groupe *Euclastes* » à l’échelle mondiale, dans le but de redéfinir les taxons. Elle montre aussi l’intérêt potentiel du

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groupe dans la radiation et la dispersion des faunes des marges téthysiennes et atlantiques, au tournant Crétacé-Tertiaire. **Pour citer cet article** : N.-E. Jalil et al., C. R. Palevol 8 (2009).

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Keywords: Turtles; *Euclastes acutirostris* n. sp.; Cheloniidae; Africa; Moroccan phosphates; Sidi Chennane; Palaeocene

Mots clés : Tortues ; *Euclastes acutirostris* n. sp. ; Cheloniidae ; Africa ; Phosphates du Maroc ; Sidi Chennane ; Paléocène

1. Introduction

1.1. Historical background and geographical and geological setting

The phosphates of Morocco are part of the Mediterranean Tethyan phosphogenic province, a complex of warm and shallow-marine platforms characterized by intense phosphatic sedimentation along the southern margin of the Tethys during the Late Cretaceous and Early Palaeogene [35]. Phosphatic deposits are currently exposed from North Africa to the Middle East, where they are an economically valuable resource (Fig. 1).

The phosphatic deposits of Morocco, known since 1908, have been exploited since 1920 [47]. They crop out in several basins, the main ones being those of the Oulad Abdoun and the Ganntour (Fig. 1A). Stratigraphically, they extend from the Late Cretaceous (Maastrichtian) to the Middle Eocene (Lutetian), spanning the longest interval of time of all Tethyan phosphates [35].

In the Oulad Abdoun Basin, the main currently exploited areas are, from north to south, Daoui, Meraa El Arach and Sidi Chennane (more recently exploited) (Fig. 1B). Compared to other basins, the Oulad Abdoun phosphatic series is highly condensed [47]. The series includes several phosphatic levels named respectively from base to top: level III (Maastrichtian), level II (Danian-Thanetian), levels I and 0 and sillons A and B (Ypresian). The phosphatic series ends in the basal Lutetian and is overlapped by the so-called “*Dalle à Thersitées*” (Lutetian).

Fossils occur throughout the series, both in the phosphatic levels and in the intercalary layers of phosphatic limestones. The level II involves two phosphatic sub-levels, IIa (Danian) and IIb (Thanetian) eventually separated by intercalary beds. From the base to the top, the Danian-Thanetian represents a considerable time interval. The Upper Maastrichtian level III is close from the level II, but both are separated by a sedimentation gap at the K/T limit, and phosphatic levels eventually by intercalary layers above and below the gap. In Daoui, at the base of the Danian, there is an intercalary layer with reworked Maastrichtian elements (*couche à mélanges*): material from the level IIb with reworked Maastrichtian elements could have been considered as Maastrichtian, when dated by the presence of reworked selachian teeth. Similarly, above the Danian-Thanetian series, mammal material from the base of the Ypresian has also been first dated as Thanetian because of the presence of reworked Thanetian selachians. This phosphatic series corresponds to a shallow marine environment open westwards to the Atlantic Ocean the depth of which varied over time (see [22] for details).

These Oulad Abdoun Basin phosphates are characterized by their richness in marine vertebrate remains, especially selachians, bony fishes, marine and littoral reptiles (including squamates, plesiosaurs, crocodylians

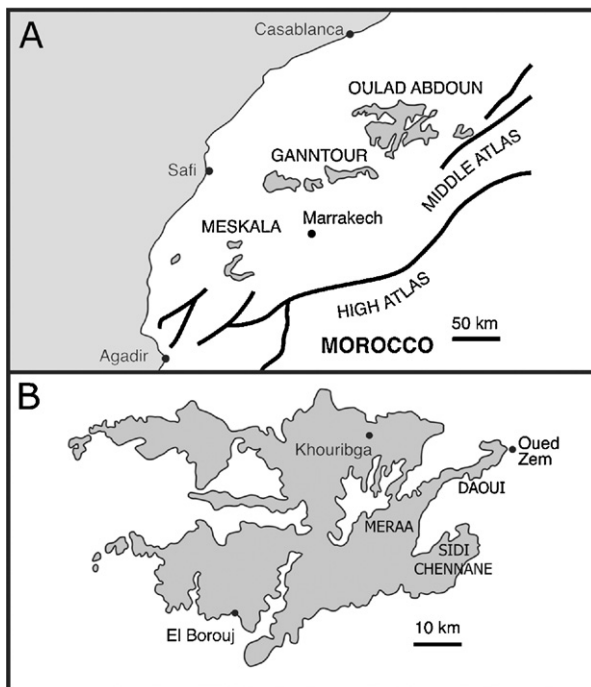


Fig. 1. Geographical location of the phosphates of Morocco. **A**. Main basins: Oulad Abdoun, Ganntour and Meskala. **B**. Main exploited zones of the Oulad Abdoun Basin: Daoui, Meraa El Arach, Sidi Chennane. OCP.DEK/GE 408 comes from Sidi Chennane zone.

Fig. 1. Localisation géographique des phosphates du Maroc. **A**. Principaux bassins : Oulad Abdoun, Ganntour et Meskala. **B**. Principales zones exploitées dans le Bassin des Oulad Abdoun : Daoui, Meraa El Arach, Sidi Chennane. OCP.DEK/GE 408 provient de la zone de Sidi Chennane.

and turtles: see below) and birds [3,6,7,10,28,29,46,53]. Unexpected continental taxa have also been found in these shallow-marine environments. They consist of Maastrichtian pterosaurs and dinosaurs [51,52] and Palaeogene mammals [22,56]. As far as turtles are concerned, they are highly diverse in all levels of the Moroccan phosphates, representing a significant component of the marine-littoral reptile faunas. The present specimen of *Euclastes* is the first turtle record from the Sidi Chennane area (Fig. 1).

1.2. Turtles

Since the first study of Moroccan fossil turtles [1], and the up-dated overview by Lapparent de Broin [32] of Moroccan fossil turtles, abundant new material has been obtained from the Maastrichtian to the Ypresian phosphatic basins of Morocco. Phosphate turtles belong to the two major groups of extant turtles: Pleurodira, mostly represented by the fossil Bothremydidae (more than ten Palaeogene different genera) [19,20,40], and Cryptodira, represented by a Maastrichtian “Dermochelyidae” indet. [58], and fossil cheloniids: *Tasbacka ouledabdounensis* Tong & Hirayama, 2002, Thanetian [57], *Argillochelys africana* Tong & Hirayama, 2008, Ypresian [59] and “*Euclastes* group” elements, including “Aff. *Rhetechelys* sp.” estimated as Maastrichtian in age [23] and two Palaeocene species recently attributed to *Euclastes wielandi* Hay [24] and estimated as Danian [24,27,30,38,49]. In the framework of an active French-Moroccan collaboration including the mining company exploiting the phosphatic deposits, the Office chérifien des phosphates (OCP), the ministère de l’Énergie, des Mines, de l’Eau et de l’Environnement (Rabat), the Muséum national d’histoire naturelle (Paris) and the Universities Cadi Ayyad (Marrakech) and Chouaïb Doukkali (El Jadida), a large collection of turtle fossils has been made, among which a skull of a new species of *Euclastes*, the object of this note.

Euclastes belongs to the “Osteopyginae”, a group of basal Cheloniidae s.l. (sensu Lapparent de Broin 2001 [33]), which developed a secondary palate associated with a lower jaw with a diagnostic particularly long and wide triangular symphysis. In the last few years, interpretation of this group underwent important changes [38,49,50].

The “Osteopyginae” have been first defined as part of the Toxochelyidae family by Zangerl [63], essentially on the basis of the lower jaw, together with fragmentary anterior skull and shell morphology, of specimens attributed to *Osteopygis* Cope, 1869 (Upper Creta-

ceous to Palaeocene, New Jersey). Later, Zangerl [64] emended the taxon on the basis of the rather completely known skeleton of *Erquelinnesia gosseleti* (Dollo, 1886) [14,15], (Thanetian, Belgium), and to which was added the poorly known *Glossochelys planimentum* (Owen, 1842) (Ypresian, England) [48,55]. It should be noted that *Euclastes platyops* Cope, 1867 [11] (Palaeocene, New-Jersey), type species of the genus was first not included into the “Osteopyginae” because it was considered, under the name *Rhetechelys*, Hay 1908 [24] as *incertae sedis* [63]; next, *Euclastes* name was considered to be a synonym of *Erquelinnesia* because it was thought to be preoccupied [64] (*in errore*). Afterwards, more material was found and new taxa or cranial specimens have been added to the “Osteopyginae” [4,5,13,16,17,21,27,30,38,49].

Recently, Lynch and Parham [38,49] claimed that the specimens attributed to *Osteopygis emarginatus*, the type-species of *Osteopygis*, represent in fact a chimera and correspond to two different taxa. The authors reattributed the type-specimen of *O. emarginatus*, a partial shell, to the “Macrobaenidae” (a poorly defined group of cryptodires, representing a grade) and all cranial material historically attributed to *Osteopygis* to the Cheloniidae. As a result, these authors refer all cranial material previously attributed to *Osteopygis* (= *Lytoloma* Cope, 1870, in part) *emarginatus* to a new combination *Euclastes wielandi* (Hay, 1908) [24,38,49]. This includes American material from the Late Cretaceous [5,17] and Palaeocene [16,24,60,61] of California, New Jersey and Maryland, as well as from the Palaeocene phosphates of Morocco [27], the latter material also including *Osteopygoides priscus* Karl et al., 1998 [27,30]. All the other *Osteopygis* species and related genera, *Erquelinnesia* Dollo, 1887 [15,64], *Glossochelys* Seeley, 1871 [55] and *Pampaemys* de la Fuente & Casadio, 2000 [13], are provisionally included by the authors within the genus *Euclastes*, *sensu lato de facto* [38,49].

According to the ICZN, Article 11.7.1.1. [2], the names Osteopyginae or Osteopygidae are no longer valid for *Euclastes* and its relatives. It is clear that a profound revision of all the members of this assemblage is required. Careful new morphological work must be carried out and accurate diagnoses erected for all valid taxa before any phylogenetic analysis can be performed. This is beyond the scope of our paper which is to describe the skull of the new *Euclastes* species from Morocco. The name “*Euclastes* group” is used to designate “Osteopyginae” related to the type species *E. platyops*, the group for which the other related original genus names are maintained here.

“*Euclastes* group” were near-shore cheloniids, littoral like the Moroccan Bothremydidae, with a durophagous diet. It is estimated that they were not as much adapted to sea swimming as the Cheloniidae s.s. and more restricted in areas than extant turtles which are worldwide: from the limb bone anatomy ([64]: Fig. 16), they were probably not yet able to cross the high seas because their shorter paddles were not yet as long and rigid (and their shell not as hydrodynamic [24]: Fig. 196, [63]) as in true marine forms which swim with more efficiency and during a longer time, helped by a synchronous movement of the anterior limbs [54]. Like bothremydids [8,20,34], the *Euclastes* s.l. group occurred from Late Cretaceous to Palaeogene time along the coastlines of the young Atlantic and its appendices, as well as on the northern and southern margins of the Tethys; after a long gap, their last known record is from the Miocene of California [27,38,49]. We think they developed independently during Palaeogene times on each side of the Atlantic, like other turtles and crocodylians ([20,29,32,63] and others), and (according to Cheloniidae and Bothremydidae at least) differently between Phosphate basins of Tunisia [32] and Morocco [20,27,57,59], with an exceptional diversity in various ecological niches, as for the five extant species of *Podocnemis* in the Amazon basin.

Abbreviations. AMNH, American Museum of Natural History, New York; ANSP, Museum of the Academy of Natural sciences, Philadelphia; MNHN, Muséum national d’Histoire naturelle, Paris; NJSM, New Jersey State Museum, Trenton, New Jersey; OCP, Office Chérifien des Phosphates, Morocco; YPM, Yale Peabody Museum, New Haven, Connecticut.

2. Systematics

Order Chelonii Latreille, 1800

Superfamily Cheloniodea Opper, 1811

Family Cheloniidae Opper, 1811 s.l.

“*Euclastes* group” (Subfamily “Osteopyginae” Zangerl, 1953)

Genus *Euclastes* Cope, 1867 s.l.

Type species genus s.l.: *Euclastes platyops* Cope, 1867 [11]

Locality and age: Hurffville, Camden County, New Jersey, Vincenton Formation, Late Palaeocene.

Holotype, ANSP 10187, an incomplete skull figured by Cope, 1871 [12] and Hay, 1908 [24].

Principal synonymy pro parte: *Osteopygis* Cope, 1869; Zangerl, 1953 [63]; *Lytoloma* Cope, 1870; Hay, 1908; *Rhetechelys*, Hay, 1908 [24]; *Erquelinnesia* Dollo,

1887; Lynch & Parham, 2003, Parham 2005 [38,49]; see additional details in [49].

Euclastes s.l. *acutirostris* n. sp.

Etymology: from “*acuti*” (latin): acute, and “*rostris*” (latin): snout, because of the shape of the snout which is more pointed and narrowed than in other “*Euclastes* group” species.

Locality and age: Sidi Chennane, Oulad Abdoun Basin, level II, Lower Palaeogene, Palaeocene (Danian–Thanetian) (Fig. 1). The matrix, a fine white phosphatic sand, did not include any selachian teeth. The age could be either Thanetian or Danian: If Thanetian, it would be younger than the other specimens of *Euclastes* up to now reported from Morocco. The derived condition of the snout, in relation to the Danian *Euclastes* skulls from Morocco, argues in favor of this hypothesis.

Holotype: OCP.DEK/GE 408, an almost complete skull (Figs. 2 and 3).

2.1. Diagnosis

A member of the “*Euclastes* group”, sensu “Osteopyginae” [49,64], of moderate size, differing from all other adequately known species by the following characters: **Autapomorphies:** (1) A derived more elongated and narrower snout, with its associated features: narrow anteriorly forming a small premaxillary-maxillary hook (visible in lateral and anterior views); external nares occupying nearly all the width of the extremity of the snout; narrow interorbital bar; suborbital bar narrow in dorsal view, maxilla narrowed so that the prefrontal-maxilla lateral limit is confluent with the antero-lateral border of the orbit; pterygoids medially narrowed making the *processus pterygoideus externus* more protruding in the *fossa temporalis inferior* and accentuating the heart-shaped form of the latter; and the premaxillae longer than the vomer ventrally; snout index of about 72%. (2) Presence of particularly long and narrow inferoposterior processes on the jugals, protruding posteriorly and partly ventrally enclosing the cheek emarginations of the skull, which are posteriorly deeper. (3) Narrow triturating surface of the palatine ending well anterior of the posterior border of the triturating pterygoid surface of the palate which is relatively long posterior to the maxillary part. **Additional diagnostic characters:** prefrontal meeting postorbital at the orbit; low suborbital bar; rather flat premaxillary-vomerine ventral surface, slightly sagittally depressed. Vomer hexagonal ventrally, clearly widened at the level of the extremities of the anterior triturating palatine surface; wide open U shaped border of the choanae; ventral base of the vomerine pillar not apparent in ventral view; maxilla

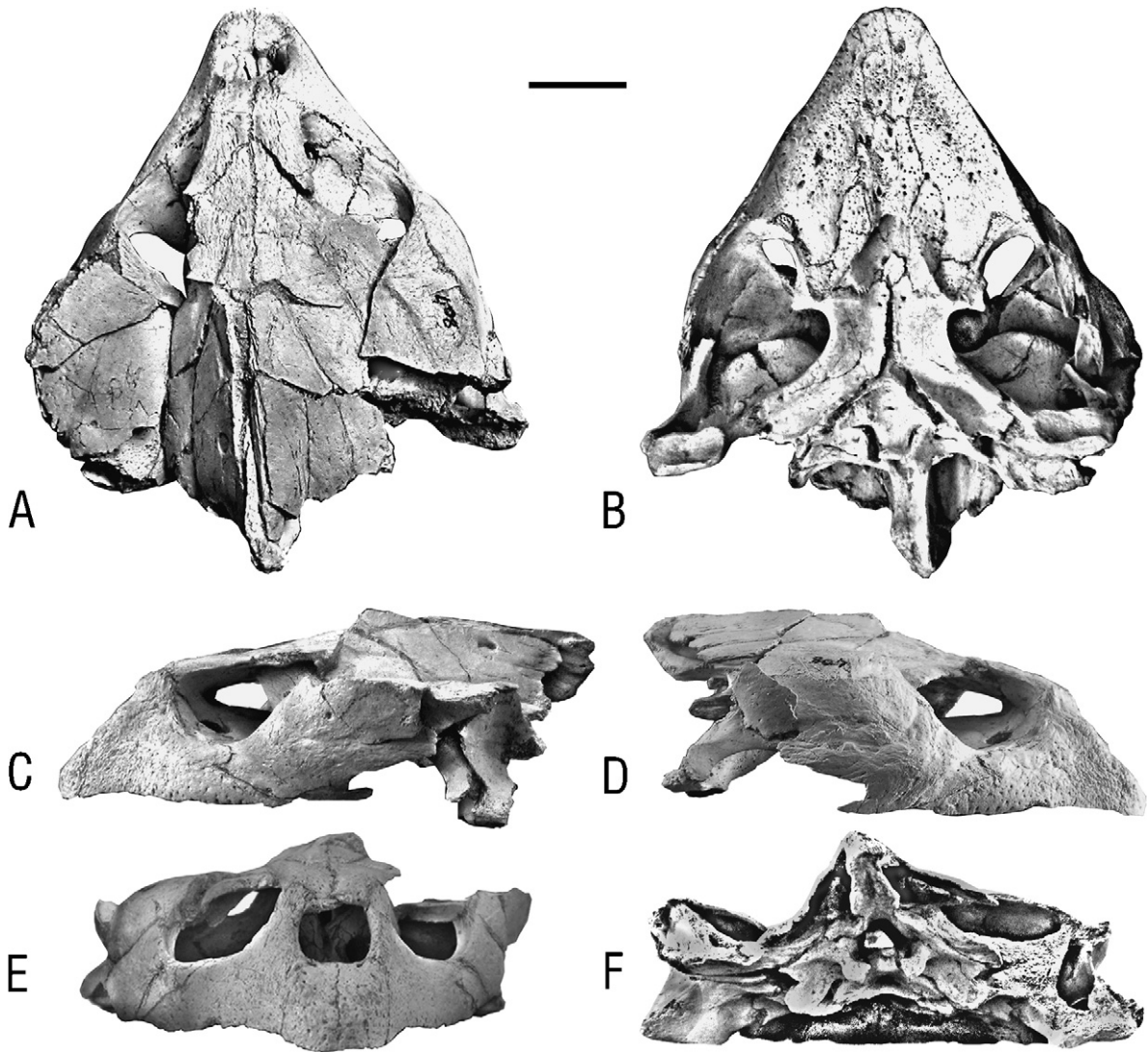


Fig. 2. *Euclastes acutirostris* n.sp. Oulad Abdoun Basin, Morocco, Palaeocene (Danian-Thantetian), holotype OCP.DEK/GE 408, skull in: A, dorsal, B, ventral, C, D, left and right lateral, E, anterior and F, posterior views. Photographs. Scale bars: 3 cm.

Fig. 2. *Euclastes acutirostris* n.sp. Bassin des Oulad Abdoun, Maroc, Paléocène (Danien-Thanétiens), holotype OCP.DEK/GE 408, crâne en vues : A, dorsale, B, ventrale, C, D, latérales gauche et droite, E, antérieure et F, postérieure. Échelles : 3 cm.

participating in the margin of the orbito-nasal foramen. Medially, the secondary palate nearly reaches the ventral anterior extremity of the *fossa temporalis inferior*, not extending beyond it (secondary palate index: 72.4%).

2.2. Description

2.2.1. Preservation

E. acutirostris n.sp. is known only by the holotype, DEK/GE408, an almost complete skull with well preserved anterior and palatal regions. The sutures

and scute sulci are mostly clearly discernible. Most bones are nearly complete but some are broken, partly displaced or lost and the posterior preserved part of the roof is crushed. The posterior-most part of the skull including the squamosals and the posterior part of the right quadrate are missing. Both orbits are incomplete posteriorly. The ventral surface of the skull is well preserved with only slight displacement of some bones, in particular the articulating branches of the quadrate. The inner cerebral cavity structure is barely visible and partly crushed dorsally (Figs. 2 and 3).

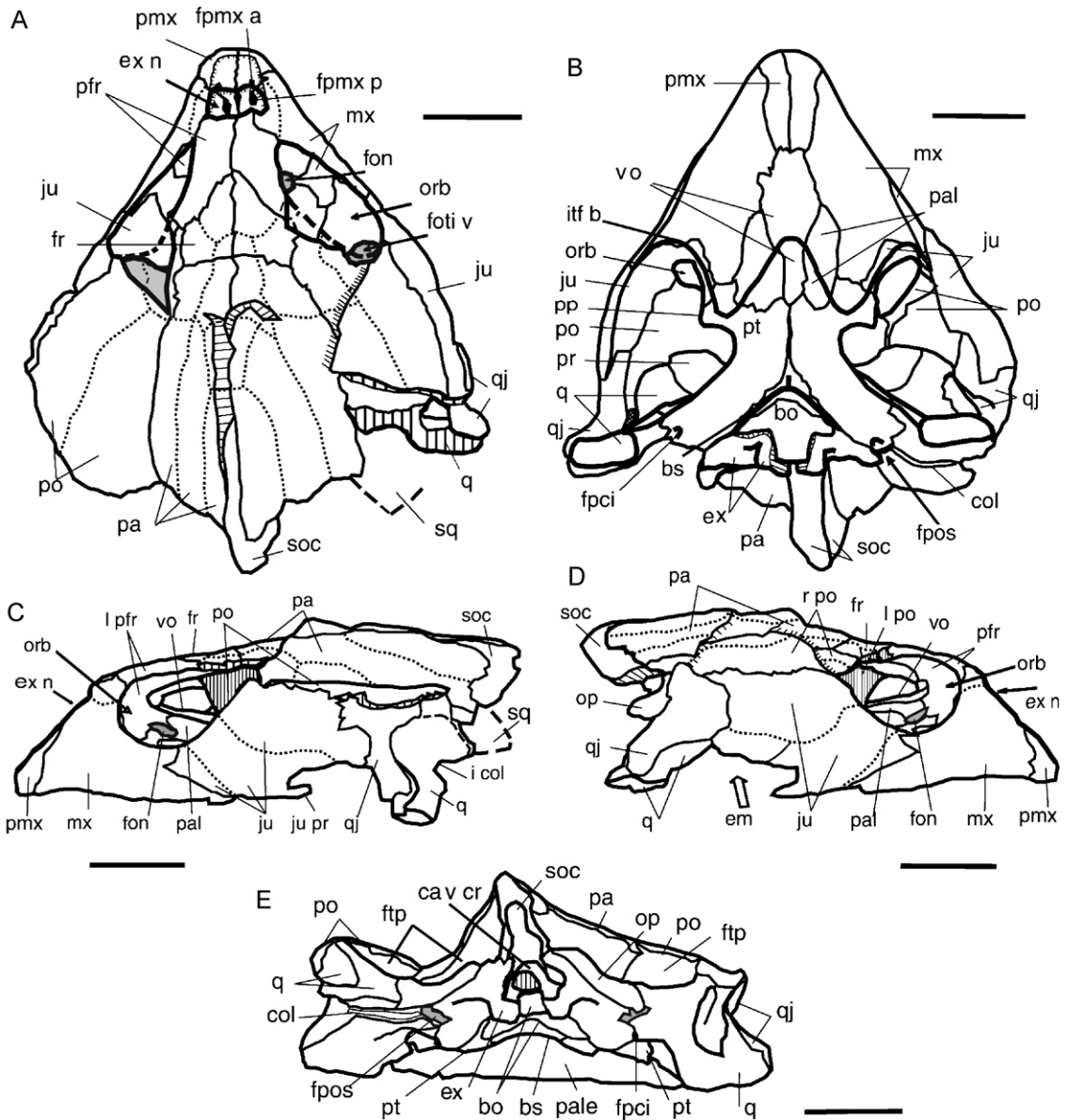


Fig. 3. *Euclastes acutirostris* n.sp. Oulad Abdoun Basin, Morocco, Palaeocene, (Danian-Thanetian), holotype OCP.DEK/GE 408, skull in: **A**, dorsal, **B**, ventral, **C**, **D**, left and right lateral, and **E**, posterior views. Interpretive drawings. Scale bars: 3 cm.

bo, basioccipital; bs, basisphenoid; cav cr, *cavum cranii*; col, *columella auris*; em, ventral emargination; ex, exoccipital; ex n, odd external nares; fon, *foramen orbitonasale*; fpos, *fossa postotica*; foti v, view on the *fossa temporalis interior* or palatal fossa; fpci, *foramen posterior canalis carotici interni*; fr, frontal; fpmx a, *foramen premaxillare supero-anterius*; fpmx p, *foramen premaxillare supero-posterius*; ftp, *fossa temporalis posterior* (or “superior”); i col, *incisura columellae auris*; itf b, inferior temporal fossa anterior border; ju, jugal; ju pr, infero-posterior jugal process; l pfr, left prefrontal; l po, left postorbital; mx, maxilla; op, opisthotic; orb, orbit; pa, parietal; pal, palatal; pale, anterior palate in ventro-posterior view; pfr, prefrontal; pmx, premaxilla; po, postorbital; pp, *processus pterygoideus externus*; pr, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; r po, right postorbital, sq, squamosal, soc, supraoccipital; vo, vomer.

Fig. 3. *Euclastes acutirostris* n.sp. Bassin des Oulad Abdoun, Maroc, Paléocène (Danien-Thanéien), holotype OCP.DEK/GE 408, crâne en vues : **A**, dorsale, **B**, ventrale, **C**, **D**, latérales gauche et droite et **E**, postérieure. Schémas. Échelles : 3 cm.

Table 1

Skull measurements, *Euclastes acutirostris* n.sp., Sidi Chennane, Palaeocene, phosphates of Morocco, holotype OCP.DEK/GE 408 (in mm).

Tableau 1

Mesures du crâne, *Euclastes acutirostris* n.sp., Sidi Chennane, Paléocène, phosphates du Maroc, holotype OCP.DEK/GE 408 (mm).

Length	
Full sagittal preserved up to <i>crista praoccipitalis</i> extremity	178
To basioccipital condyle	137
To the ventral anterior <i>fossa temporalis inferior</i> extremity	64
To the posterior vomer extremity at choanae	63
To the <i>processus pterygoideus externus</i> extremity	94
Premaxillae, sagittal ventral	34
Vomer, sagittal ventral	32
Width	
At ventral anterior <i>fossa temporalis inferior</i> extremity	89
At vomerine choanae border	87
At <i>meati quadrati</i>	140
Full distorted preserved width at articular quadrate facets	146
At <i>processi pterygoidei externi</i>	60
At ventral perygoids narrowing	35
Distance between posterior vomer border at choanae and posterior maxillary triturating surface suture	15

2.2.2. Measurements

Tables 1 and 2.

2.2.3. General characteristics

In dorsal view, the skull of *E. acutirostris* n. sp. (OCP.DEK/GE 408, Figs. 2 and 3A), is triangular in shape with a wide and rounded posterior region, mod-

Table 2

Snout index (ratio of the sagittal length, from the premaxillae anterior extremity up to the ventral anterior extremity of the *fossa temporalis inferior*, on the snout ventral width at this extremity) of *E. acutirostris* n. sp., Sidi Chennane, Palaeocene, phosphates of Morocco, holotype OCP.DEK/GE 408, other “*Euclastes* group” members and cheloniids with long secondary palate.

Tableau 2. Index du museau (rapport de la longueur sagittale, de l'extrémité du prémaxillaire jusqu'à l'extrémité antérieure ventrale de la *fossa temporalis inferior*, sur la largeur ventrale du museau à cette extrémité) de *E. acutirostris* n. sp., Sidi Chennane, Paléocène, phosphates du Maroc, holotype OCP.DEK/GE 408, d'autres membres du « groupe *Euclastes* » et des Cheloniidae à long palais secondaire.

<i>Euclastes acutirostris</i> n. sp.	Ca. 72%
<i>E. platyops</i> (ANSP 10187)	Ca. 100%
<i>E. wielandi</i> (AMNH 30022)	Ca. 60%
<i>E. wielandi</i> (AMNH 30030)	Ca. 56%
<i>E. wielandi</i> (NJSM 11872)	Ca. 50%
<i>E. hutchisoni</i> (LACM 103351)	Ca. 51%
<i>Erquelinnesia gosseleti</i> (Zangerl, 1971; MNHN 2008-1-1)	Ca. 56 to 63%
<i>Tasbacka ouledabdounensis</i> Tong & Hirayama, 2002	Ca. 70.5%
<i>Puppigerus</i> [39]	Ca. 100%

erate cheek (lateral) and weak posterior emarginations (hidden *foramen stapedio-temporale*). The anterior part of the skull, up to the frontals is faintly sculptured and pierced by numerous nutrient foramina, particularly for the ramphoteca. The position of the supraoccipital crest and the symmetry of the skull in occipital view, indicate that the height of the skull, which is rather low, is not greatly affected by postmortem dorso-ventral compression. As indicated by its specific name, the snout is more pointed and narrower than in any other member of the “*Euclastes* group”, although it is also pointed in *E. platyops* [12] and *Erquelinnesia* [64]. However in these, the skull proportions are different: in *E. platyops*, the snout is as long as wide at the lower temporal fossae (Table 2) while the skull is very wide for its length; the snout is narrower in *Erquelinnesia* and *E. acutirostris*, in which the premaxillae are longer than the vomer; but the snout is relatively shorter for the skull in the former; in the latter (the skull not being widened as in *E. platyops*), the snout is relatively longer and the snout index (72%) is higher than in *E. wielandi* and *Erquelinnesia* skulls (as in *Eretmochelys* within the extant Cheloniidae). In the “eochelyine” *Puppigerus*, the snout is particularly long for the skull length but as long as narrow at the temporal fossae. The snout of *E. acutirostris* forms an apomorphic hook, together premaxillary and maxillary (visible laterally and anteriorly, Fig. 2, C–E) as the bony hook present in some extant genera below the hook constituted by the horny ramphoteca (bony hook absent or only premaxillary hook in others) ([18,62]; MNHN collections). The narial opening is quadrangular, occupying nearly all the snout width, and dorso-anteriorly directed. Its plane forms, in lateral view, an angle of 40° with the ventral plane of the premaxillae (Figs. 2 and 3, C, D) (53° in *E. wielandi* from the Palaeogene of Morocco phosphates) [27]; 64° in a French specimen of *Erquelinnesia*, from the Bracheux sands, Thanetian, MNHN 2008 1-1 [33]; Figs. in [13,49], 46° in *Euclastes hutchisoni* [38] from the Miocene of California). The lateral surfaces of the snout converge anteriorly and are flat and inclined; with the flat dorsal surface, they give to the snout a trapezoidal form in transverse section. The orbits are longer than high and face latero-dorsally. The infra-orbital bar, comprised of the maxillary and the jugal (Figs. 2 and 3), is narrow in dorsal view and low in lateral view. The preserved part of the skull roof is dominated by the parietals and the postorbitals, and posteriorly relatively few emarginated taking into account the missing squamosals (Fig. 3A). The *crista supraoccipitalis* extends slightly beyond the parietals.

Numerous small to large nutrient foramina cover the surface that bore the horny bill (Fig. 2A–D). As in other

cheloniiids with a developed secondary palate, there are no *foramina praeopalatina*. When present, these foramina are formed by the vomer and the premaxilla and transmit the anterior nasal arteries from the palate into the nasal tissue. Instead, as in extant marine forms, two pairs of anterior foramina are present on the dorsal surface of the premaxillary: two foramina on the floor of the nasal cavity on both sides of medial line (Fig. 3A, fpmx p) and the second pair, elongate, in front of the narial opening (fpmx a, Figs. 2 and 3A).

Cranial scute sulci are visible on the skull roof (Figs. 2 and 3), conforming to the “*Euclastes* group” as a whole [16,27]: medially, the posterior limits of an anterior fronto-prefrontal scute; a somewhat rectangular medial fronto-parietal; medial hexagonal parietal 1 and pentagonal parietal 2; laterally, a wide fronto-postorbital-parietal (up to the orbit), a narrow rectangular parietal, and a wider and external rectangular parieto-postorbital; on the lateral face, an elongated postorbital-jugal and a jugal ventrally.

2.2.4. Dorsal and lateral views (Figs. 2 and 3 A, C, D)

The premaxillae are primitively unfused, unlike those of *Erquelinnesia gosseleti* from the Erquelinnes sands, Belgium [18,64] and Bracheux, France (MNHN 2008 1-1) and the partly fused ones of *E. hutchisoni* Lynch & Parham, 2003 [38]. They comprise a pair of elongated bones forming the tip of the snout and flooring medially the *fossa nasalis* up to the ascending processes of the vomer which are short. The inter-premaxillae suture is dilated into a short slit. Anteriorly to the narial opening, the smooth premaxillae area is relatively long.

Both prefrontals are preserved in OCP.DEK/GE 408. They are elongated and form the dorsal border of the narial opening and the anterodorsal corner of the orbits: there are no nasals. The prefrontals contact the frontals alongside an anteriorly directed V-shaped suture. Two weak swellings are present on the prefrontals, just above the narial opening. The vertical descending processes of the prefrontals form the posterior wall of the nasal cavity and the lateral margins of the *fissura ethmoidalis* (for the transmission of the olfactory [I] nerve) and the anterior orbit border, partly limiting the orbito-nasal foramen. The *fissura ethmoidalis* (Fig. 2E) is heart-shaped and widely enlarged dorsally. The orbito-nasal foramen is visible in dorsal (Figs. 2 and 3 A) and lateral views (Figs. 2 and 3, C, D). It is short and nearly horizontal as in *Erquelinnesia* and in the specimens of Fastovsky, 1985 and Hirayama and Tong, 2003 [16,27] attributed to *Euclastes wielandi*. In the orbit, the anterior limit between the maxilla and the prefrontal is at the border of

the orbit and the maxilla contributes to the orbito-nasal foramen in front of the palatines, as in *Erquelinnesia* of Bracheux and a Moroccan *E. wielandi* [27] but unlike Fastovsky’s specimen [16] (variable contribution in extants).

The frontals are flat dorsally, roofing the *fossa orbitalis* posteriorly to the prefrontals. Their ventral surface has parasagittal crests that separate the *sulcus olfactorius* for the olfactory nerve (I). The sutural areas are preserved on the frontal, left prefrontal and left postorbital showing that the frontal was excluded from the orbital margin by a postorbital-prefrontal contact, a derived condition also seen in *Euclastes platyops* and “*Argillochelys*” *africana* [59]; MNHN 2005-7; OCP coll.). This condition may be subject to individual variations in turtles [18]; the exception is rare and occurs in few specimens: frontal exclusion, only present in *E. acutirostris* n. sp. among specimens of *Euclastes* from phosphates in which the frontal is known (including at least 5 Danian skulls), may be considered as diagnostic. *E. acutirostris* n. sp. possesses a posterior process on the jugal (Figs. 2 and 3, C and D), which antero-inferiorly surrounds the lateral cheek emargination. This process is narrow and long enough to allow definition of the contour of the emargination, showing that it is deeper posteriorly than in any another known member of *Euclastes*. A shorter and more massive process is seen only in one of the other Moroccan skulls ([27], text-fig. 2, on one side) reattributed to *E. wielandi* [49].

2.2.5. Palatal structure (Figs. 2 and 3, B)

The dominant feature in palatal view is the well-developed secondary palate, much longer than in extant Cheloniidae [62] and “*Argillochelys*” *africana* [59] but less than in *Erquelinnesia* [61] and *Tasbacka ouledabdounensis* [56]; it involves the premaxillae, the maxillae, the vomer and the palatines; medially, it extends to the anterior border of the *fossa inferior temporalis* and, laterally, to the root of the *processus pterygoideus externus*. The secondary palate index (ratio of the length up to the vomerine choanae medial border on width at this point) is 72, 4%, nearly identical to the snout index (72%). The triturating surface is shallow and wide with a low (short) tomial ridge. The pterygoid is integrated in the triturating surface. The premaxillae are longer than the vomer and their anterior width is slightly greater than that of the vomer at its widest level. The vomer-premaxillary contact is wide in relation to extant Cheloniidae and narrower than the widest part of the vomer. A shallow median depression is present in the ventral surface of the vomer. This is surrounded by two low longitudinal swellings on the maxillae, converging medially.

The vomer is hexagonal in ventral view. It is I-shaped in medial cross-section with ventral and dorsal horizontal blades connected by a vertical pillar. The vomerine pillar is nearly as long as the ventral vomerine blade and its dorsal attachment is faintly visible in palatal view as in all the *Euclastes* members, including *E. wielandi* (NJSM 11872 [16] and *E. hutchisoni* [38]; but its base is not, unlike in these two American forms. The dorsal blade is narrow and contributes slightly to the dorsal roof of the choanal passageways with the palatines. It extends much further posteriorly beyond the choanal margin up to the pterygoids. The choanae angle is an open U-shape (60°). Its vomer border is very slightly in front of the anterior border of the *fossa inferior temporalis*, approximately as in all the Morocco specimens. The position of the choanae in relation to the fossae border is characteristic in cheloniid genera. This medial extension of the secondary palate is variable in *E. wielandi* sensu Parham, 2005 [16,27,38,49], longer and posterior to the fossa border (ca.18% longer) in the American *wielandi* specimens [16,24,60] and in *E. platyops*. As in other phosphate specimens, the vomerine pillar, although prolonged inwards as in all the previously examined *Euclastes*, has its base not visible at the choanae border. The palatine of OCP.DEK/GE 408 is distinct from that of other “*Euclastes* group” cheloniids. Its triturating surface is narrow and converges strongly posteriorly to end in front of the posterior border of the triturating surface of the palate. In other “*Euclastes* group” members, the palatine is broader and is confluent with or ends close to the posterior border of the triturating surface.

The pterygoid processes are prominent in the fossae. Their vertical lateral facets are well marked. They appear as well developed particularly because the anterior pterygoid borders are narrowed just anteriorly to them and the pterygoids are well narrowed behind, at their mid length; these processes seem variably developed in the group but, actually, they are often damaged. Posteriorly, the *processus trochlearis oticus* is well developed and is constituted nearly equally by the prootic and the quadrate. The pterygoid has a medial longitudinal crest, the basisphenoid is small, triangular and crested, and the basioccipital is concave; the entrance of the carotid foramen is posterior in the pterygoid.

2.2.6. Braincase

In spite of the crushed roof, a wide *processus inferior parietalis* is preserved and is visible anteriorly. It unites with the narrow and short ascending *crista pterygoidea* and the well-developed epipterygoid to form a relatively wide anterior part of the braincase wall, in front of the *foramen nervi trigemini*. This foramen (for

the exit of the branches V2 and V3 of the trigeminal nerve [V] and the *arteria mandibularis*), is bordered by the prootic posteriorly, the epipterygoid ventrally and infero-anteriorly and the parietal dorsally and antero-superiorly. It is narrow and dorso-ventrally elongated. *Erquelinnesia* differs from *E. acutirostris* n. sp. in having a narrower wall in this part of the braincase and a wider foramen V. In other *Euclastes* species, this area has not been described. These proportions are variable among modern cheloniids, but always with a shorter anterior *cavum cranii* wall and a larger foramen V. On the dorsal basisphenoid surface, the area of the *sella turcica*, laterally limited by the ossified *trabeculae*, and its posterior wall, the *dorsum sellae*, is barely visible from the right orbit, but the exit of the left *canalis cavernosus* in the *sulcus cavernosus* is clearly visible: the *sella turcica* seems wide and not reduced in diameter as in modern cheloniids. As in Fastovsky’s specimen [16], a Moroccan specimen described by Hirayama & Tong [27: Text-Figs. 2 and 3], and *Erquelinnesia* (MNHN 2008 1-1), the *dorsum* seems moderately high, not strongly inclined with a median ridge up to the fine crest of separation of the anterior carotid foramina. The anterior extremity of the *trabeculae* is clearly visible, protruding anteriorly: they are fused into a double *rostrum basisphenoidale*, as figured in Fastovsky’s specimen (partly hypothetical), but the anterior rostrum extremity is flattened and wide, as in *Erquelinnesia*. In modern cheloniids, the *dorsum* is always high, although variably, all have strong *processi clinoides*, a median ridge on the long and inclined surface of the *dorsum*, a very small *sella turcica* pit and a protruding *rostrum basisphenoidale*, which is rodlike in shape at its anterior tip. In *Erquelinnesia*, the *trabeculae* are also narrow and well separated in dorsal view and their base is flat where united anteriorly; the *dorsum* points into the *sella turcica* where the anterior carotid foramina appear, separated by a fine and short crest, as figured in *E. wielandi* [16,27].

2.2.7. Postero-lateral structures (Figs. 2 and 3 C–E)

The *foramen magnum* is floored by the basioccipital with the participation of the exoccipitals. The exoccipitals are separated from each other below the wide inferiorly tectiform *crista supraoccipitalis* and are well developed in comparison with the relatively small basioccipital. A pair of foramina *nervi hypoglossi* (XII) pierce the lateral wall of the exoccipital. The quadrate is moderately bent over itself and is posteriorly directed (angle ca 50°) (Fig. 3C). There is no contact between the quadrate and the jugal or the postorbital. The *processus articularis* extends below the ventral border of

the maxillary. The left *columella auris* is preserved and is well exposed in posterior view inside a well-opened *incisura columellae auris* (Figs. 2F and 3E). It is a thin and slightly curved bony rod extending from the *cavum tympani* to the *fenestra postotica*.

2.3. Discussion and diagnostic comparisons

In the absence of the lower jaw, on which the group was first defined, and of any post-cranial element, OCP.DEK/GE 408 can be referred to the “*Euclastes* group” of Cheloniidae on the basis of the shared derived character states of the skull:

Derived character states shared with Cheloniidae: skull scutes: presence and general pattern; loss of the *foramen palatinum posterius*; pterygoid with slight medial sagittal crest; small triangular basisphenoid with a wide and anteriorly directed V-shaped crest and basioccipital concave behind; prominent *processus trochlearis oticus* comprised of the quadrate and prootic (variable in strength in Cheloniidae and homoplastic in littoral turtles such as *Solnhofia*); *foramen posterior canalis carotici interni* situated well posteriorly on the pterygoid border (homoplastic in Eucryptodira).

Derived character states shared with the “*Euclastes* group”: precise scute pattern, skull low and triangular in dorsal view and flat lateral snout surfaces, with wide post-orbital region; large posterior width, skull nearly as wide as long (sagittal width 80% of the length up to the extremity of the *crista supraoccipitalis* and 97% up to the extremity of the basioccipital condyle); well developed secondary palate prolonged up to the *processus pterygoideus externus* and integrating the pterygoid in the triturating surface (homoplastic in the “eochelyine” Eocene Anglo-Belgium *Puppigerus* [39,42] and in the Palaeocene Kazakh and Moroccan *Tasbacka* [44,45,57]; shallow and wide triturating surface with low tomial ridge; short orbito-nasal foramen nearly horizontal, mostly bordered by the ventral branch of the prefrontal anteriorly, with participation of the maxilla in its external margin as in Moroccan *E. wielandi* (but not participating in Fastovsky’s specimen) and of the palatine medially and posteriorly [16,25,26,31,39,42,43,57].

Euclastes acutirostris n. sp. differs from all the other “*Euclastes* group” members by the conjunction of its skull autapomorphies within the *Euclastes* group, and additional characters (see diagnosis and Table 2). The other *Euclastes* species differ from *E. acutirostris* by their autapomorphies and some principal additional characters: Type species *E. platyops* (very large holotype skull, 280 mm long [12,24], looks similar to *E.*

acutirostris by a relatively pointed snout with elongated maxillae and premaxillae, but this snout is shorter and the skull is very wide; premaxillae not longer than the vomer, elongating the external nostril area; snout not hooked, with wide surrounding maxillae and a premaxillary ventral pit; greater extension of its secondary palate: the ventral vomer border of the choanae is posteriorly situated in relation to the anterior edge of the *fossa inferior temporalis*; palatal concavity on each side of the rounded sagittally raised vomer, which protrudes posteriorly between the two choanae foramina; V-shaped posterior part of the triturating surface of the maxillae, ending at the level of the choanae); *E. hutchisoni* [38] (short snout, partly fused premaxillae with incised palatal and orbitae few dorsally facing because of the wide interorbital bar, premaxillary-vomer sagittal ventral crest, ventral base of vomerine pillar clearly evidenced in ventral view, exposing the two choanae conduits; dubious very short nasals – their morphology does not conform to that in *Erquelinnesia*); *E. roundsi* Weems, 1988 [60] from the Danian of Maryland (anterior portion of the palate blunt and wide, prominent medial keel on the vomer; poorly preserved and unknown position of the anterior edge of the inferior temporal fossa); *E. wielandi* from North America, when known [16,24,64] (short snout, longer palate prolonged behind the anterior extremity of the inferior temporal fossa as in *E. platyops*, maxilla not reaching the orbito-nasal foramen); *E. wielandi* from Moroccan phosphates (figured AMNH 30022, 30030 in [27,30], OCP collections: short snout, more massive, and higher below the orbits, see the diagnosis); *Erquelinnesia gosseti* ([64]; MNHN 20081-1 [33]) (rather long snout, more developed secondary palate, with palatines united behind the rhomboid-pentagonal vomer, extending beyond the mid-length of the *fossa inferior temporalis*, presence of nasals, a wide *foramen nervi trigemini* (V) with a narrow *processus inferior parietalis* in front of it). By its high snout index, *E. acutirostris* differs from the other *Euclastes* species, among which it is closer to *Erquelinnesia* and meets *Tasbacka ouledabdounensis*, both separated from *Puppigerus* (Table 2). Although these two latter genera share a long secondary palate with the *Euclastes* group, they lack its other apomorphies and diagnostic features [42,39,44,45,57].

Various characters are distributed in mosaic, either homoplastic or synapomorphic, but some are possibly variable individually. For example: (1) in *E. acutirostris*, the frontal excluded from the orbit, as in the Late Palaeocene *E. platyops* and the Ypresian “*Argillochelys*” *africana* [59], as well as *Dermochelys* and most *Caretta* specimens in extant marine forms (prefrontal-postorbital contact just by a point in 1

Caretta specimen on 7); (2) in *E. roundsi*, *E. platyops* and unpublished Palaeogene skulls from Phosphates or already attributed [58] to *E. wielandi sensu* Parham, 2005 [27,49], the medially widened ventral vomer; 3) in American *E. platyops* and *E. wielandi* (snouts YPM 913a [18,24,61] and USNM 412113 [60]), a sagittal ventral vomerine swelling protruding between the choanae foramen; others have a sagittal ventral vomerine crest (*E. wielandi* from Morocco, *E. roundsi* and perhaps the American *E. wielandi* NJSM 12273); and (4) the narial opening is variably rounded (American *E. wielandi*) or quadrangular [12,16,25,27,30,60].

Glossochelys planimentum (Ypresian, London Clay) differs from *E. acutirostris* by its extensive secondary palate, as long as that of *Erquelinnesia gosseleti* (Thanetian) [36,37,41,48,55]. Moody [41] has synonymised *Glossochelys* with *Erquelinnesia*, but on the basis of unclear indexes, and without detailed morphological comparisons or new illustrations other than those of Owen and Bell and Lydekker [36–48]. As figured, the skull, which is geologically younger, is apparently massive, higher and narrower for its length.

The Miocene *E. hutchisoni*, which differs from the Palaeogene American specimens by its primitively shorter secondary palate (as Phosphate skulls), ought to be the result of a different branch of *Euclastes* [38]. Other “*Euclastes* group” remains from Russia, America and phosphates of Morocco are too poorly figured or preserved to be adequately compared with *E. acutirostris* [4,5,9,13,17,21,30].

3. Conclusion

OCP.DEK/GE 408 is referred to *Euclastes* since it has a low and wide skull, broad and flat palatal surface with a low tomial ridge and other diagnostic characters. It is attributed to a new species, *Euclastes acutirostris* n. sp., on the basis of cranial autapomorphies and the combination of diagnostic features. These have the same value as those which differentiate the extant Cheloniidae. Thus, among the autapomorphies: the elongation and acute shape of the snout (similar to those which characterise *Eretmochelys*); the presence of a hook and its conformation; the height and outline of the lateral emargination; the relative position of the choanae and inferior temporal fossae, etc.: the extants have their own diagnostic relative proportions of vomer, premaxillae, other snout elements and emarginations [18,62].

All recent studies agree to include the “*Euclastes* group” in the Cheloniidae. Nevertheless, the content of this assemblage and its interrelationships are far from being well-understood. A profound revision of

this grouping is needed. Detailed morphological work must be carried out, and accurate diagnoses erected for all valid taxa of the group. The possible synonymy of *Erquelinnesia* and *Glossochelys* with the number of included species [33] must be resolved. The variability among specimens attributed to *Euclastes wielandi* deserves attention [16,25,27,30,38,49]. In particular, the character of the relatively short medial development of the palate, in relation to the ventral anterior borders of the inferior temporal fossae (*E. acutirostris* n. sp. and all the other skulls from Morocco including those attributed to *E. wielandi* [27]) versus the derived longer medial palate development in North American *E. wielandi* (in which the snout is well enough preserved [16,24,60]) and *E. platyops* [12].

The braincase characters of the “*Euclastes* group” (“*Osteopygis*”) members require more attention in the cladistic analysis, instead of considering the global presence in these taxa of a unique “cheloniid configuration”; the variability of the basicranium in cheloniids might be re-evaluated [16,25,26,31,43] as well as the participation of the maxilla in the orbito-nasal foramen. The description of the Maastrichtian specimen from the phosphates of Benguerir (Ganntour Basin) [23] will provide a new information to the question (Gmira & Lapparent de Broin in prep.). The littoral pattern and the possibly restricted dispersion of the “*Euclastes* group” during a long interval of time enable a specific differentiation between the western and eastern Atlantic margins, as for others tetrapod vertebrate taxa [20,29]. *E. acutirostris* n. sp. is an additional cheloniid described from the phosphates of Morocco [23,30,57–59] and confirms the exceptional palaeobiodiversity of these outcrops [20,28], which justifies the presence of a new *Euclastes* species in Sidi Chennane, whatever its geological age. The “*Euclastes* group” contributes to the knowledge of the palaeobiogeographical events which affected the Tethys and Atlantic margins during the Cretaceous-Tertiary turnover.

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