

New fauna of archaeocete whales (Mammalia, Cetacea) from the Bartonian middle Eocene of southern Morocco



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ABSTRACT

Six genera and species of archaic whales are present in a new fauna from the Aridal Formation at Gueran in the Sahara Desert of southwestern Morocco. Three of the archaeocete species represent semiaquatic Protocetidae and three species are fully aquatic Basilosauridae. Protocetids are characteristic of Lutetian lower middle Eocene strata, and basilosaurids are characteristic of Priabonian late Eocene beds. Similar representation of both families is restricted to intervening Bartonian strata and indicative of a late middle Eocene age. Archaeocetes from Gueran include (1) a small protocetid represented by a partial humerus, teeth, and vertebrae; (2) a middle-sized protocetid represented by a partial innominate and proximal femur; (3) the very large protocetid *Pappocetus lugardi* represented by teeth, a partial innominate, and two partial femora; (4) a new species of the small basilosaurid *Chrysoctetus* represented by a dentary, teeth, humeri, and many vertebrae; (5) a new species of the larger basilosaurid *Platyosphys* (resurrected as a distinct genus) represented by a partial braincase, tympanic bulla, and many vertebrae; and (6) the large basilosaurid *Eocetus schweinfurthi* represented by teeth, a tympanic bulla, and lumbar vertebrae. The Gueran locality is important geologically because it constrains the age of a part of the Aridal Formation, and biologically because it includes a diversity of archaic whales represented by partial skeletons with vertebrae in sequence and by forelimb and hind limb remains. With further collecting, Gueran archaeocete skeletons promise to clarify the important evolutionary transition from foot-powered swimming in Protocetidae to the tail-powered swimming of Basilosauridae and all later Cetacea.

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1. Introduction

The evolutionary transition of fully aquatic cetaceans from their land-mammal ancestors can be traced in stages from early artiodactyls that made their first appearance in the fossil record during the Paleocene-Eocene thermal maximum or PETM (Rose, 1982, 1996; Gingerich, 2006) to semiaquatic Pakicetidae in the early Eocene (Gingerich et al., 1983; Madar, 2007), semiaquatic Protocetidae in the early middle Eocene (Gingerich et al., 1994, 2001a, 2009), and fully aquatic Basilosauridae in the late middle Eocene (Kellogg, 1936; Gingerich et al., 1990; Uhen, 2004; Martínez-Cáceres and Muizon, 2011). Gaps in documentation remain in the transition from artiodactyls to the first semiaquatic Pakicetidae, and in the transition from foot-powered swimming in Protocetidae

to tail-powered swimming in Basilosauridae (Gingerich, 2012). We recently described a late Eocene archaeocete fauna from Dakhla in southwestern Morocco with five species, all basilosaurids (Zouhri et al., 2014). Here we provide initial documentation of a new archaeocete fauna that includes both protocetids and basilosaurids. With further field work and recovery of more complete skeletons the new fauna has the potential to clarify the transition from foot-powered swimming in Protocetidae to tail-powered swimming in Basilosauridae.

2. Geological setting

The new archaeocete fauna comes from Gueran (also called Guerran, Garouaz, Punta Güera, and Krebb Afedeira), a remote uninhabited depression in the Sahara Desert of southwestern Morocco (Fig. 1). Geologically this is in the middle of a much larger southwest-to-northeast trending structural basin paralleling the Atlantic coast. The basin is variously called the Aaiun-Tarfaya Basin (Ranke et al., 1982), the Tarfaya-Laayoune-Dakhla Basin (Davison

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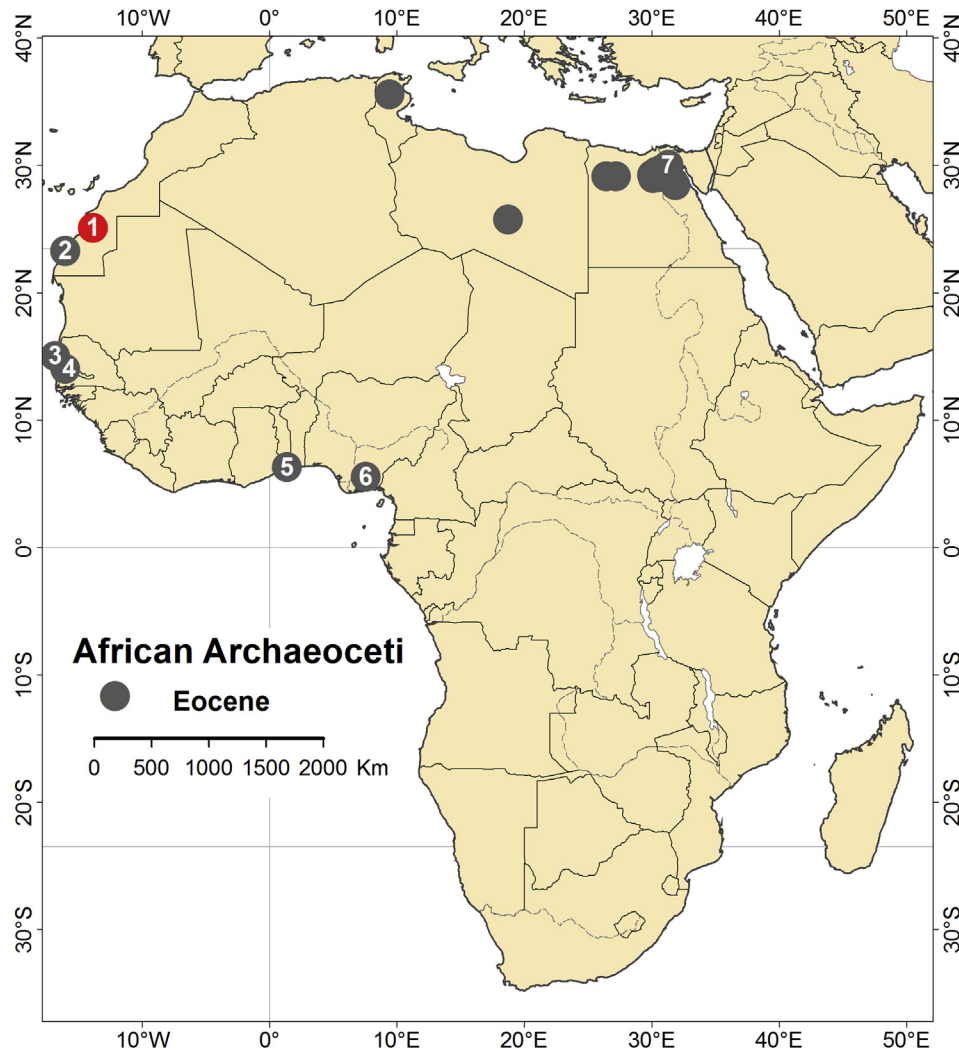


Fig. 1. Map showing the geographic distribution of Eocene Archaeoceti on the African continent. The principal localities of interest are numbered from 1 to 7. 1, Gueran locality in southwestern Morocco yielding protocetids and basilosaurids of Bartonian age documented here. 2, Garitas and nearby sites south of Dakhla in southwestern Morocco yielding basilosaurids of Priabonian age (Zouhri et al., 2014). 3, Ndomor Diop site near Taïba Ndiaye in Senegal yielding a protocetid innominate of Lutetian age (Hautier et al., 2014). 4, Tiavandou in Senegal where the partial skeleton of a *Dorudon*-like basilosaurid of Priabonian age was found (Elouard, 1981). 5, Kpogamé in Togo that yielded *Togocetus traversei* and other protocetid remains of Lutetian age (Gingerich and Cappetta, 2014). 6, Ameke in southern Nigeria yielding dentaries and vertebrae of the protocetid *Pappocetus lugardi* of Bartonian age (Andrews, 1920; Halstead and Middleton, 1974, 1976). 7, Gebel Mokattam near Cairo in Egypt, which yielded a mixture of protocetid and basilosaurid teeth and vertebrae of Bartonian age resembling some specimens reported here.

and Dailly, 2010), or sometimes simply the Boujdour Basin. Gueran is approximately 125 km inland from Boujdour, which is the nearest town on the coast (Fig. 2).

Lafitte et al. (1952) and Gévin (1962) mapped the Gueran depression as Cretaceous. Medina et al. (1958) mapped this as 'Neogene.' Ratschiller (1967, 1970) published a more detailed geological map and discussion of stratigraphy. He placed the strata of interest here in the Gueran Member of his Samlat Formation. The Gueran Member was named for strata exposed at Gueran, and the Samlat Formation as a whole was named for strata exposed at Samlat Amgrach farther to the west. Ratschiller regarded the Samlat Formation as Paleocene through Oligocene in age, possibly even Miocene, and he regarded the Gueran Member of interest here as Eocene based on studies of foraminifera (Ratschiller, 1970, p. 25).

The type section of the Gueran Member is on the eastern flank of the Gueran depression, where Ratschiller reported an outcrop thickness of 45 m in a section lacking both the base and top of the member. Much of this is chalk, but Ratschiller (1970, p. 75) also

mentioned an intercalation in the lower chalk of white, coarse-grained conglomeratic sandstone up to 1.5 m thick that contains shark teeth, fish bones, and coprolites, which is the sandstone yielding archaeocete remains.

Lindner and Querol (1971) published a map of Spanish Sahara in which they included a new Aridal Formation. This was named for exposures at Aridal east of Boujdour (Fig. 2). Aridal is a large internally-drained, sebkha- or sabkha-filled solution crater perforating the surrounding Mio-Pliocene hamada. Aridal is also the name of an early astronomical observation point south of Sabkha Aridal on the original track connecting Laayoune and Dakhla ('Aaiun and Cisneros'). Lindner and Querol (1971) mapped the Aridal Formation over a large area including Gueran. At Gueran the Aridal Formation of Lindner and Querol (1971) is clearly equivalent to the Gueran Member of the Samlat Formation of Ratschiller (1967, 1970). Aridal Formation is the name used on the current *Carte Géologique du Maroc* (Hollard et al., 1985).

Lindner and Querol (1971) regarded the Aridal Formation as late

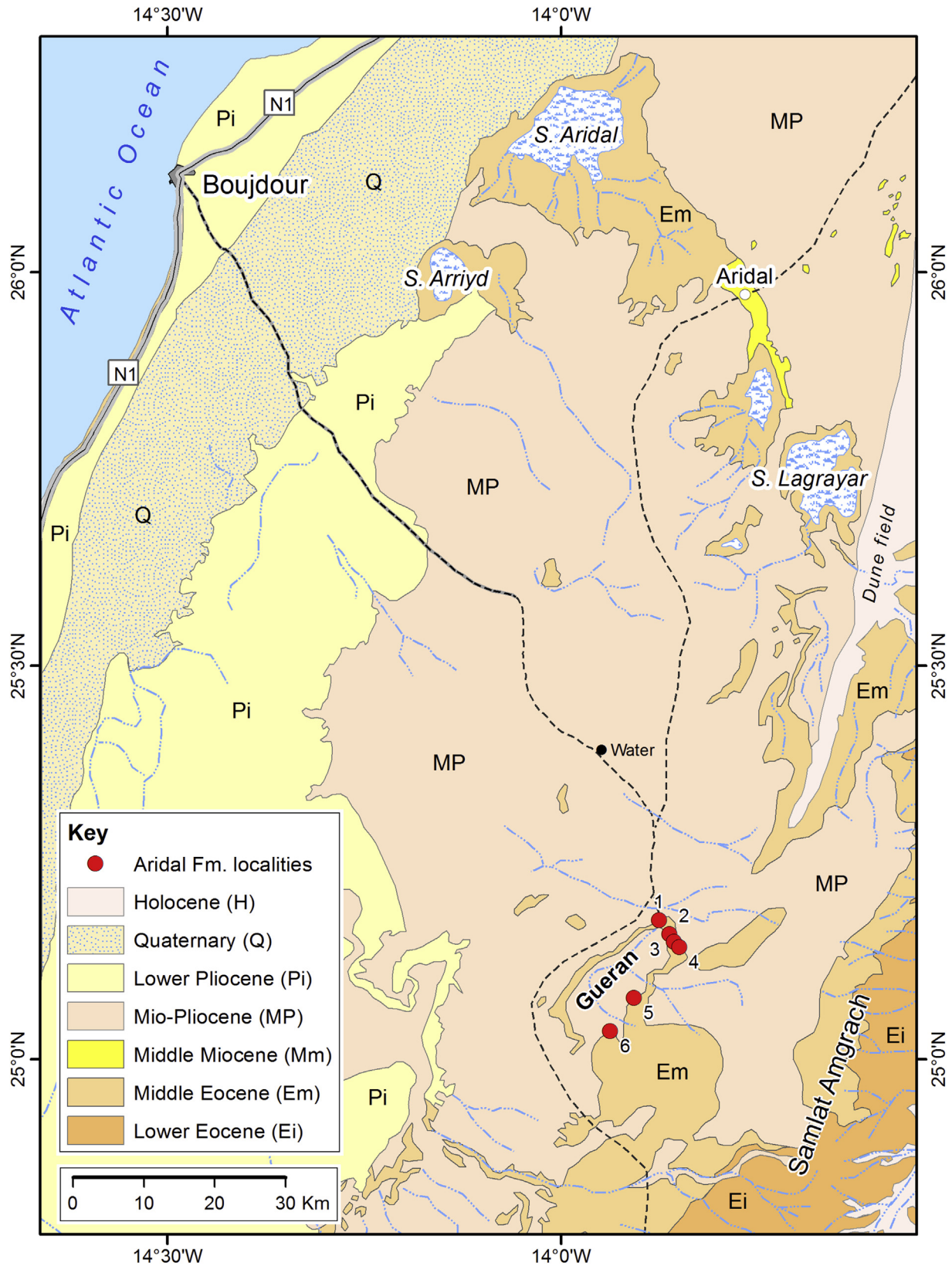


Fig. 2. Geological map of the desert south and east of Boujdour in southwestern Morocco. Red symbols at Gueran mark sites yielding the archaeocete remains described here. These are numbered 1–6 from north to south. Aridal east of Boujdour is the type section of the Aridal Formation named by Lindner and Querol (1971). Gueran itself is the type section of the Gueran Member of the Samlat Formation named by Ratschiller (1967, 1970). ‘S. Aridal,’ etc., are internally-drained sebjet or sabkha depressions in the surrounding Mio-Pliocene hamada. Geology is from Hollard et al. (1985) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Eocene in age without explanation. Subsequent authors have generally considered the Aridal Formation to represent the middle and late Eocene (Hollard et al., 1985), or sometimes more generally to span the combined Paleocene and Eocene (Rjimati et al., 2011). Ranke et al. (1982) located Gueran in the neritic zone of a shallow shelf paleoenvironmentally, with marine carbonates accumulating farther offshore to the northwest and terrestrial clastics accumulating onshore farther to the southeast.

All of the fossils described here came from a single sandstone that can be traced for many kilometers near the base of the escarpments surrounding the Gueran depression (Fig. 3). The sandstone is white to light gray in color, clayey, silty, poorly-sorted, and very fine to coarse in grain size ($\Phi = +4$ to -1). The larger sand grains include clear quartz grains and opaque lithic fragments, all subrounded to rounded, and polished. Sandstone cement is calcareous. Marl and clay casts up to several centimeters in diameter are common, and fish coprolites on the order of 1.0–1.5 cm long and 4–5 mm in diameter are present.

Archaeocetes at Gueran are preserved as associated skeletons and partial skeletons, partially articulated and disarticulated. Some of the larger bones were clearly broken before burial, and their freshly broken surfaces are preserved embedded in matrix. Bones are also commonly bored by an unknown organism making a tubular burrow. Selachian teeth are frequent, including large 10 cm diameter teeth of *Otodus* or *Carcharocles*. Minute teleost vertebrae are present, as are occasional bones of larger fish, turtles, and crocodiles. Sirenian bones and teeth are conspicuously absent.

Bone breakage and compression fractures on unbroken bones suggest predation or scavenging – by other archaeocetes or by large sharks. Some multi-element specimens are clearly associated, while elements from others are seemingly isolated. Disarticulation, breakage, and boring indicate that some bones were exposed on the sea bed before burial. However, preservation in poorly sorted sediment suggests rapid burial, possibly in a storm surge.

3. Materials and methods

The study area was discovered by commercial fossil collectors in 2014, and we carried out a 10-day reconnaissance in November, 2014, salvaging specimens whenever possible. We were assisted by experienced collectors Amer Ait Ha and M'Barek Fouadassi. Commercial collectors are primarily interested in teeth and tooth-bearing crania and dentaries. Our interest included postcranial remains as well. Vertebrae and limb bones are often as diagnostic as tooth-bearing crania and dentaries for identification of protocetids



Fig. 3. Panoramic view of the Gueran depression in southwestern Morocco. View is to the southwest. An archaeocete excavation in the foreground (arrows) is at M'Barek site 2 (site 2 in Fig. 2). Note the two collectors standing in the lower right excavation providing scale. White sediment below the excavation is the Gueran Member lower white chalk of Ratschiller (1970).

and basilosaurids, and they are important for understanding the mode of swimming of early cetaceans. Cranial terminology generally follows Mead and Fordyce (2009), and postcranial terminology follows Kellogg (1936).

Specimens described here are permanently archived in the Department of Geology, Faculty of Sciences Ain Chock, University Hassan II, in Casablanca. Casts of some specimens are archived in the University of Michigan Museum of Paleontology, Ann Arbor.

Museum abbreviations: *FSAC Bouj*, Faculty of Sciences Ain Chock, Boujdour collection, Casablanca (Morocco); *NHML*, Natural History Museum, London (England); *SCSM*, South Carolina State Museum, Columbia (U.S.A.); *SFNF*, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt; *SMNS*, Staatliches Museum für Naturkunde, Stuttgart (Germany); *USNM*, U. S. National Museum of Natural History, Washington (U.S.A.).

4. Systematic paleontology

Protocetid archaeocetes are distinguished from basilosaurids in having premolar and molar teeth that are simpler in shape, lacking accessory denticles; in retaining an upper third molar (M^3); in lacking well-developed pterygoid sinuses in the basicranium; in having cervical and thoracic vertebrae with relatively small neural canals; and in having the large innominates and femora required of a foot-powered swimmer. Basilosaurids in contrast are distinguished in having more complex premolar and molar teeth with accessory denticles; in lacking M^3 ; in having well-developed pterygoid sinuses; in having cervical and thoracic vertebrae with relatively large neural canals; and in having the reduced innominates and femora consistent with tail-powered swimming (Kellogg, 1936; Gingerich, 2010).

Archaeocetes grow ontogenetically like other mammals to reach a definitive adult size. Young individuals can be recognized by the presence of deciduous teeth that have distinctive shapes compared to adult teeth, and by the presence of porous skeletal bone retaining juvenile cartilage. Fusion of long-bone and vertebral epiphyses is an indication of adulthood, but in marine mammals the epiphyses do not always fuse in adults. Judging from tooth form and bone texture, all of the specimens described here are full-grown subadults to adults. Differences in the reported sizes of long bones and vertebrae are not due to ontogenetic differences.

Class Mammalia.

Order Cetacea.

Suborder Archaeoceti.

Family Protocetidae Stromer, 1908.

Protocetid species A.

Figs. 4A–B, 5A–E.

The smallest of three protocetid species at Gueran is represented by (1) a left distal humerus, FSAC Bouj-12 (Fig. 4A–B); (2) a left upper molar M^1 , FSAC Bouj-13 (Fig. 5A–B); and (3) a middle thoracic vertebra, FSAC Bouj-4 (Fig. 5 C–E). All three specimens are similar in size to comparable elements of the Lutetian protocetids *Protocetus*, *Artiocetus*, *Rodhocetus*, *Maiacetus*, and *Togocetus* (Fraas, 1904a; Gingerich et al., 2001a, 2009; Gingerich and Cappetta, 2014). The distal humerus of Protocetid A is similar in size to that of *Rodhocetus balochistanensis*, but it is distinctive in two ways: first, the distal medial and lateral condyles are more rounded; and second, the deltopectoral crest is virtually absent. Both are seemingly primitive traits in protocetids. The humerus measures 9.6 cm in length as preserved, 2.9×2.2 cm in cross section at the midshaft of the diaphysis, and 3.6 cm in width across the distal end. The condyles are 2.8 cm in width.

The upper molar, M^1 , has a prominent paracone and a smaller metacone posterior to the paracone. There is a small parastyle on the enamel crest anterior to the paracone. The protocone is missing

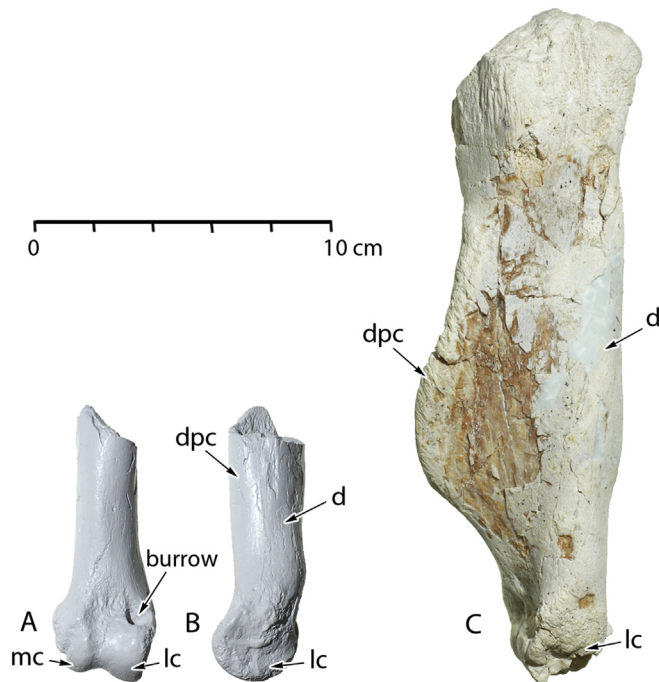


Fig. 4. Distal humeri of the smallest of three protocetids and smallest of three basiliosaurids found at Gueran in southwestern Morocco. **A–B**, left distal humerus of Protocetid sp. A, FSAC Bouj-12, in anterior and lateral view (cast of original). A tubular burrow of unknown origin is visible above the lateral torus of the trochlea. Note the virtual absence of a deltopectoral crest. **C**, left humerus of *Chrysocetus fouadassii*, FSAC Bouj-3, in lateral view (proximal epiphysis is missing). Note the great development of a deltopectoral crest on the humerus of Protocetid sp. A at left, and the virtual absence of a deltopectoral crest on the humerus of *C. fouadassii* at right. Both specimens are shown at $0.4 \times$ natural size. Abbreviations: *d*, diaphysis; *dpc*, deltopectoral crest; *lc*, lateral condyle; *mc*, medial condyle.

but, judging from the shape of the remaining crown, the protocone was positioned medial to the paracone and not posteromedial to it, a feature distinguishing M^1 from M^2 . The full anteroposterior length of the crown is 2.3 cm, making it similar in size to M^1 in *Protocetus*, *Artiocetus*, and *Maiacetus*, but the width of the crown cannot be measured. Enamel on the surface of the crown is finely crenulated.

The thoracic vertebra has a roughly 'D-shaped' centrum, and capitular facets for rib articulations are well developed on the front and back of the centrum. The neural arch is robust. It is distinctive in enclosing a relatively small neural canal. A prominent diapophysis is preserved on the left side of the vertebra, rising from the neural arch, with a tubercular facet for articulation with a rib tubercle. The diapophysis is surmounted by a distinct metaphysis. The neural spine is broken but appears to have been posteriorly inclined. All of these characteristics point to a position in the middle of the thoracic series of vertebrae. Centrum length, anterior width, and anterior height are 3.73, 5.21, and 3.70 cm, respectively. The neural canal measures 2.05×1.75 cm in width and height.

Recovery of the small Protocetid species A is encouraging but the specimens at hand do not permit detailed comparison with other small protocetids.

Protocetid species B.

Fig. 5F–I.

The middle-sized protocetid species at Gueran is represented by (1) a right partial innominate, FSAC Bouj-14 (Fig. 5F–G); and (2) a left proximal femur, FSAC Bouj-15 (Fig. 5H–I). The innominate is similar in size to innominates of *Georgiacetus* and *Qaisracetus* (Hulbert et al., 1998; Gingerich et al., 2001b), and while not

identical compares most closely in form to the innominate of *Georgiacetus*. The acetabulum of Protocetid B has the concavity to accommodate a femoral head with a diameter of about 3.8 cm, and the dorsal surface of the innominate above the acetabulum is 2.75 cm wide in Protocetid B and 2.73 cm wide in *Georgiacetus*. Both have a smooth capsular surface dorsal to the acetabulum itself, both have a deep acetabular fossa for the round ligament or ligamentum teres and a well developed acetabular notch, and both have a relatively sharp ischiatic spine. A very short segment is preserved of the border of the obturator foramen.

The proximal femur is referred here because the femoral head is the right size to articulate with the acetabulum of the innominate. Salient features are a shallow fovea for the teres ligament, a relatively short femoral neck, an angled neck, and a prominent lesser trochanter. The trochanteric crest is broken, but clearly it defined a deep trochanteric fossa. The femoral head is spherical and measures 3.5 cm in diameter. The midshaft of the femur is circular in cross section and measures 3.2 cm in diameter.

Genus *Pappocetus* Andrews 1920.

Revised diagnosis: Largest protocetid, with M_1 in the type measuring $44 \text{ mm} \times 18.5 \text{ mm}$. P_1 single-rooted. Deciduous premolar dP_3 has two weakly developed accessory cusps, unusual for a protocetid, following the apical cusp. Molars are elongated, with a single apical cusp, the protoconid, followed by a robust hypoconid.

Included species: *Pappocetus lugardi* Andrews (1920; type species).

Pappocetus lugardi Andrews 1920.

Fig. 5J–P.

The largest of the three protocetid species at Gueran is represented by (1) the talonid of a left lower molar M_2 , FSAC Bouj-16 (Fig. 5J–K); (2) a left partial innominate, FSAC Bouj-17 (Fig. 5L–M); (3) a right proximal femur, FSAC Bouj-25 (Fig. 5N–O); and (4) the head of a second femur, FSAC Bouj-18 (Fig. 5P). These are protocetids because the talonid of M_1 is simple, and because the innominate and the more intact femur retain the form of comparable elements in protocetids and in land mammals.

The talonid of M_1 is large, measuring 1.64 cm in transverse breadth, and it is simple in form in having a single prominent hypoconid cusp well separated from the trigonid. The trigonid remnant and the talonid both have heavy attritional wear on the buccal side of the tooth crown. The talonid described here matches those of M_1 in the holotype dentary, NHML M–114114, and in a referred dentary, NHML M–11086, very closely in form and size.

The left innominate is large and robust, with the concavity to accommodate a femoral head with a diameter of about 5.2 cm. This is the largest acetabulum known for any archaic cetacean. The dorsal surface of the innominate is 4.45 cm wide above the acetabulum, as compared to 2.75 cm recorded above for Protocetid B. This innominate has a conspicuous, slightly rugose capsular surface extending 1.7 cm out of the acetabulum dorsally. There is a deep acetabular fossa for a teres ligament, and a well developed acetabular notch. Much of the border of the obturator foramen is preserved posterior to the acetabular notch.

Parts of two femora are known. The most complete femur preserves the head, greater trochanter, and diaphysis extending distally as far as the lesser trochanter. The femoral neck is longer and set at a greater angle to the diaphysis than is seen in Protocetid species B. The head of the second femur is difficult to position accurately, but it does have a distinct fovea for the teres ligament. This ligament anchors the femoral head within the acetabulum, and the presence of a fovea on the femoral head is consistent with the presence of a deep acetabular notch on the innominate. The femoral head of FSAC Bouj-18 measures 5.0 cm in diameter.

Pappocetus lugardi is distinguished from other protocetids at Gueran and indeed from all other protocetids by its large size.

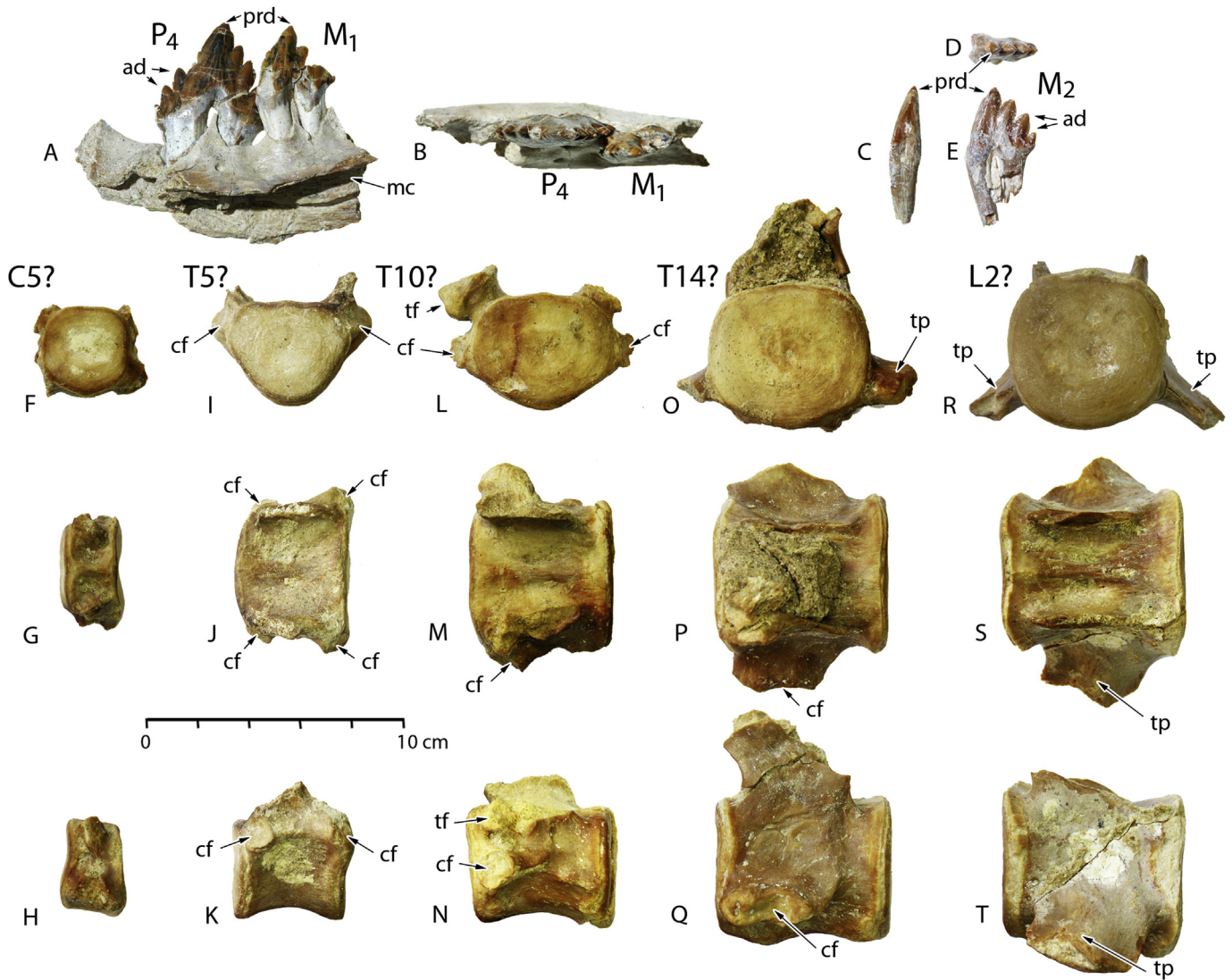


Fig. 6. Teeth and representative vertebrae of the smallest basilosaurid, *Chrysoctetus foudassii*, new species, found at Gueran in southwestern Morocco. **A–B**, left dentary with P₄–M₁, FSAC Bouj-1 (holotype), in lateral and occlusal view. **C–E**, isolated left M₂, FSAC Bouj-19, in occlusal, anterior, and lateral view. **F–H**, cervical vertebra C5 (?). **I–K**, thoracic vertebra T5 (?). **L–N**, thoracic vertebra T10 (?). **O–Q**, thoracic vertebra T14 (?). **R–T**, lumbar vertebra L2 (?). Vertebrae in **F–T** are part of FSAC Bouj-2, with each shown in anterior, dorsal, and left lateral view. Vertebral positions are uncertain because the vertebral column of FSAC Bouj-2 is incomplete. Measurements of FSAC Bouj-2 vertebrae are listed in [Table 1](#) and graphed in comparison to *Chrysoctetus healyorum* in [Fig. 6](#). Neural arches and transverse processes on centra of vertebrae are broken. All illustrations are 0.4 × natural size. Abbreviations: *ad*, accessory denticles; *cf*, capitular facet for rib; *mc*, mandibular canal; *prd*, protoconid; *tf*, tubercular facet for rib; *tp*, transverse process.

length of the anterior surface of the diaphysis. The greatest anteroposterior development of this crest occurs about two-thirds of the distance from the proximal end of the bone. The two humeri of *C. foudassii* measure 22.5 and 22.8 cm long, respectively, without their proximal epiphyses. Apart from length, they resemble the humerus of *C. healyorum* in other measures of size ([Uhen and Gingerich, 2001](#), p. 16).

The holotype dentary preserves crowns of the teeth P₄ and M₁ ([Fig. 6A–B](#)). Both have relatively smooth enamel. P₄ has a long, narrow, straight, and high crown, with five accessory denticles on the carina anterior to the central protoconid (counting the denticle broken from the anterior cingulum) and five accessory denticles on the carina posterior to the protoconid. It is followed by an M₁ with a smaller high, narrow crown. There is a distinct groove on the anterior surface of the crown bordered by two vertical crests of enamel. The lateral crest has a small denticle at the base and two more in the middle of the crown before ascending to the protoconid. The carina posterior to the protocone is damaged but it

clearly had three accessory denticles. M₂ is better preserved than M₁ and very similar in most characteristics, but differing in lacking denticles on the anterior lateral crest ([Fig. 6C–E](#)). The dentary itself has much of the ramus broken away, with tooth roots extending into what was formerly a large mandibular canal. In the holotype, P₄ measures 4.72 × 1.32 × 4.30 cm in anteroposterior length, buccolingual width, and crown height, and M₁ measures 3.28 × 1.16 × 2.86 cm in length, width, and height.

Representative vertebrae of *Chrysoctetus foudassii* are illustrated in [Fig. 6F–T](#), and those of the best vertebral column of *C. foudassii* (FSAC Bouj-2) are compared to vertebrae of *C. healyorum* in [Fig. 7](#). Vertebrae of the two species compare closely in form and size, with one notable exception: cervical vertebrae of *C. foudassii* are significantly longer than those of *C. healyorum*. Measurements of vertebrae of *C. foudassii* are listed in [Table 1](#).

Genus *Platyosphys* Kellogg 1936.

Revised diagnosis: Species of *Platyosphys* are distinctive among Basilosauridae in being relatively large and in having posterior

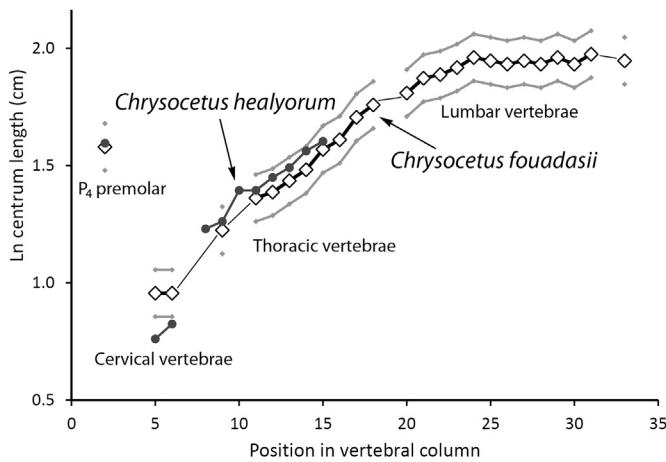


Fig. 7. Premolar P₄ tooth length and vertebral centrum length of *Chrysocetus foudassii*, new species (FSAC Bouj-1 and Bouj-2; open diamonds) compared to those of *Chrysocetus healyorum* Uhen and Gingerich, 2001 (SCSM 87.195, P₃ or P₄; solid circles). Light gray points and lines enclose a 95% confidence band for centrum length in *C. foudassii* based on the empirical observation that linear measurements have a standard deviation averaging 0.05 on a natural-logarithm scale. Note that the one tooth that can be compared, premolar P₄, is similar in mesiodistal crown length in the two species. Cervical vertebrae of *C. foudassii* are significantly longer than those of *C. healyorum*, while thoracic vertebrae are similar in length.

Table 1

Measurements of vertebrae of specimen FSAC Bouj-2, *Chrysocetus foudassii*, new species, from Gueran in southwestern Morocco. Associated vertebrae are from site II-1: ‘Site d’Ali’ (locality numbered ‘5’ on the map in Fig. 2). Vertebral positions are uncertain because the series is not complete. See Fig. 7 for a graphical profile. Measurements are in cm; those with asterisks are estimates. Abbreviations: Vert., vertebral position; Len, centrum length; AW, anterior centrum width, AH, anterior centrum height; PW, posterior centrum width; PH, posterior centrum height; NCW, neural canal width; NCH, neural canal height.

Vert.	Len	AW	AH	PW	PH	NCW	NCH	Illustration
C5?	2.6	3.5	3.5	3.7	3.6	2.6	—	Fig. 6F–H
C6	2.6	3.9	3.8	4.4	3.9	2.8	—	—
T2?	3.4	4.7	3.5	4.4	3.7	3.2*	—	—
T4?	3.9	4.5	3.6	—	3.6	3.0*	—	—
T5?	4.0	4.6	3.6	4.5	3.6	3.7	—	Fig. 6I–K
T6?	4.2	4.7	3.8	4.8	3.8	3.8	—	—
T7?	4.4	4.7	3.8	5.2	4.1	3.9	—	—
T8?	4.8	4.8	3.7	5.4	3.7	3.3	—	—
T9?	5.0	5.1	4.3	5.9	4.5	3.5	—	—
T10?	5.5	5.6	4.6	5.9	4.7	3.5	—	Fig. 6L–N
T11?	5.8	5.8	4.7	5.9	5.1	3.6	—	—
T13?	6.1	5.9	5.0	5.9	5.4	3.1	—	—
T14?	6.5	5.9	5.3	6.2	5.4	3.0	2.0	Fig. 6O–Q
L1?	6.6	5.9	5.6	6.4	5.8	3.2	—	—
L2?	6.8	6.1	6.0	6.4	6.4	3.2	—	Fig. 6R–T
L3?	7.1	6.1	5.7	6.5	5.8	3.4	—	—
L4?	7.0	6.5	6.2	6.8	6.4	3.3	—	—
L5?	6.9	6.0	6.0	6.7	6.1	3.3	—	—
L6?	7.0	5.9*	5.9	6.5	5.9	3.1	—	—
L7?	6.9	5.9	5.6	6.2	5.8	2.8	—	—
L8?	7.1	6.2	5.8	6.5	6.0	3.5*	—	—
L9?	6.9	6.3*	6.3	6.9	6.3	3.3	—	—
L10?	7.2	6.3	6.3	7.0	6.3	3.0	—	—
L12?	7.0	6.6	6.3	6.7	6.4	2.5	—	—

thoracic, lumbar, and anterior caudal vertebrae that are conspicuously elongated. Lumbar vertebrae have broad and flat transverse processes that arise along virtually the entire anteroposterior length of the centrum. Cranial and vertebral bone is unique among archaeocetes in being pachyostotic and osteosclerotic. Pachyostosis gives vertebrae a swollen appearance, and nutrient canals opening at the surface add a pock-marked texture.

Included species: *Platyosphys paulsonii* (Brandt, 1873a); *P. wardii* (Uhen, 1999), and *P. aithae* (new). *Platyosphys einori* Gritsenko (2001) and *P. uheni* (Gol’din and Zvonok, 2013) may be valid or may be synonyms of *P. paulsonii*.

The generic name *Platyosphys* refers to the broad transverse processes of the lumbar vertebrae. *Platyosphys Kellogg* (1936) is considered a valid genus, contrary to Gol’din and Zvonok (2013); see Discussion.

Platyosphys aithai, new species.

Figs. 8, 10F.

The middle-sized basilosaurid species at Gueran is represented by (1) a partial cranium, FSA–C Bouj-20 (Fig. 8A–B); (2) a left tympanic bulla, FSAC Bouj-26 (Fig. 10F); and (3) vertebrae of several specimens including FSAC Bouj-6 (Fig. 8C–J), FSAC Bouj-7 (Fig. 8K–L), and FSAC Bouj-11 (Fig. 8M–R).

Holotype: associated thoracic vertebrae T1–T4 of FSAC Bouj-6 (Fig. 8C–J) constitute the type specimen. Should there be any concern about the integrity of the series, the largest vertebra with the diapophysis (Fig. 8I–J) is the holotype.

Etymology: named for the experienced collector Amer Ait Ha, who guided us in the field in 2014.

Diagnosis: *Platyosphys aithai* is a small species of *Platyosphys* (Fig. 9). *P. wardii* (Uhen, 1999) from North America is similar in size but slightly larger. The species *P. paulsonii* and *P. uheni* from eastern Europe are much larger. *P. aithai* is distinct from all other species of *Platyosphys* in having a distinct diapophysis arising from the vertebral centrum on middle thoracic vertebrae that is not seen in other species of *Platyosphys*.

Description: The partial cranium of *Platyosphys aithai* (Fig. 8A–B), found in association with vertebrae, is the first cranium described for the genus. Six bones are represented: the right squamosal, part of the right periotic with an intact posterior process, the right exoccipital, the supraoccipital, and parts of both the left and right parietal. The squamosal contacts the exoccipital and supraoccipital posteriorly, and has a dorsal projection that rises high on the corresponding parietal. The squamosal includes a portion of the glenoid fossa and the external auditory meatus. Much of the squamosal is fully osteosclerotic with a texture more typical of the periotic. The body of the periotic is not well preserved, but what remains rests in the periotic fossa of the squamosal. The posterior process of the periotic is intact and solidly wedged between the squamosal and exoccipital. The lateral margin of the exoccipital is sharply squared. The midline supraoccipital is notable in being approximately 3.0 cm thick above the foramen magnum. Left and right parietals meet dorsally to form a low sagittal crest. Posterolaterally the parietals are wedged tightly between the supraoccipital and dorsal extensions of the overlying squamosals. The intertemporal midcranial pons is thick, measuring 6.6 cm from side to side, and this is very densely ossified lending both weight and rigidity to the cranium. The parietals are broken ventrally along the rising course of the long olfactory stalk, and the parietals are broken anteriorly before contacting the frontal shield. The width of the cranium, estimated by doubling the distance from the midline to the lateral surface of the glenoid fossa, is minimally 32.0 cm.

The braincase as a whole has the conformation typical of basilosaurids, but the bone is exceptionally thick and dense. Some bones like the periotic and squamosal are osteosclerotic. Surrounding bones are thick and dense, but not fully osteosclerotic. All are brittle in the sense that they seemingly fracture in large pieces rather than deform. The thick, dense cranial bone of *P. aithai*, and its breakage into large pieces rather than deforming by microfracturing are important differences from the type cranium of *Eocetus schweinfurthii* (Fraas, 1904a), which is a microfractured basilosaurid sometimes interpreted as being related to *Platyosphys*

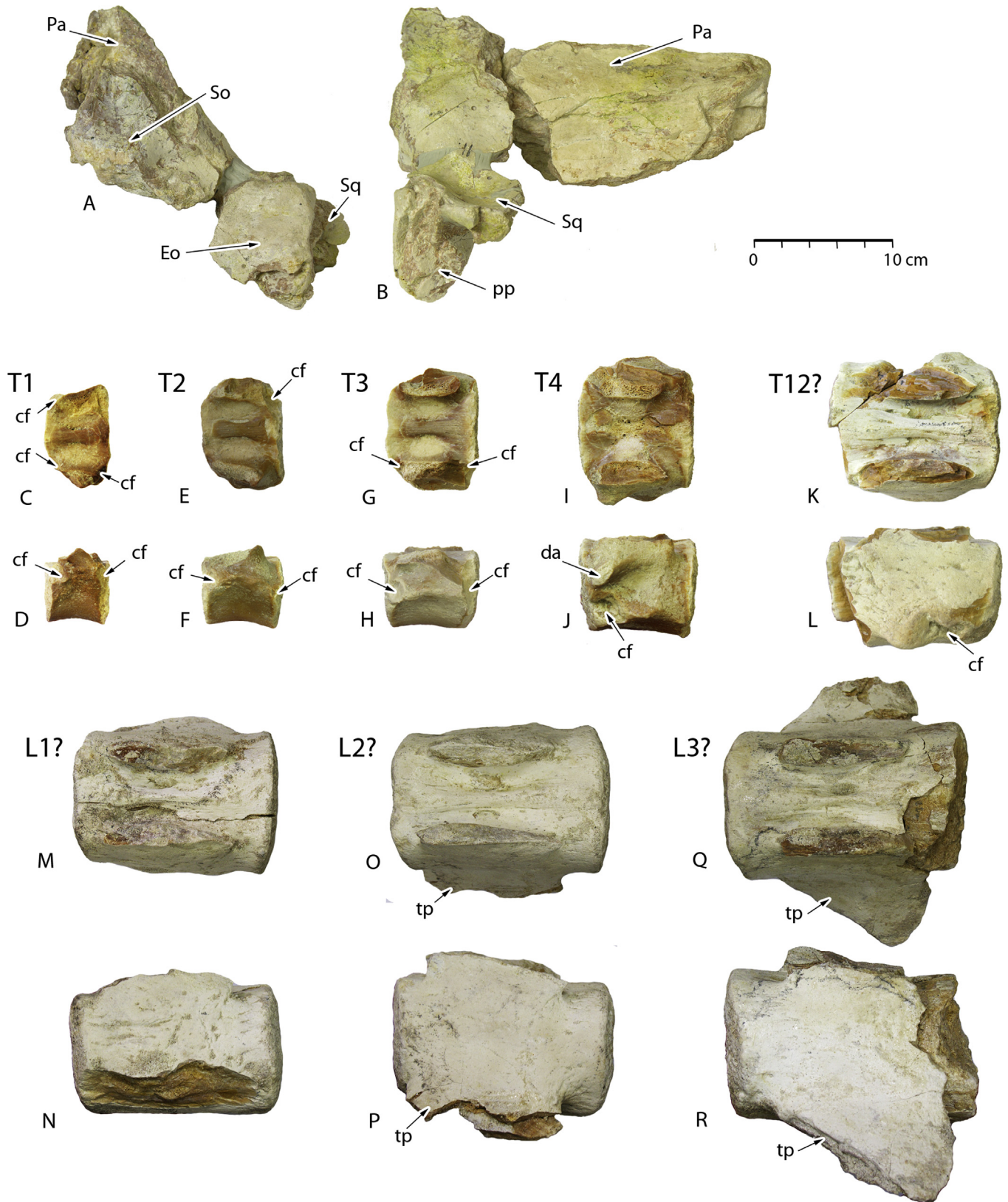


Fig. 8. Cranial remains and representative vertebrae of *Platyosphys aithai*, new species, found at Gueran in southwestern Morocco. **A–B**, posterior parts of cranium, FSAC Bouj-20, in posterior and right lateral view. **C–D**, thoracic vertebra T1. **E–F**, thoracic vertebra T2. **G–H**, thoracic vertebra T3. **I–J**, thoracic vertebra T4. **K–L**, thoracic vertebra T12?. **M–N**, lumbar vertebra L1? **O–P**, lumbar vertebra L2? **Q–R**, lumbar vertebra L3? Vertebrae in **C–J** are FSAC Bouj-6 (*P. aithai* holotype). Vertebra in **K–L** is FSAC Bouj-7. Vertebrae in **M–R** are FSAC Bouj-11. Each is shown in dorsal and left lateral view. All specimens are shown at 0.25 × natural size. Measurements of vertebrae are listed in Table 2. Abbreviations: *cf*, capitular facet for rib; *da*, diapophysis with tubercular facet for rib; *Eo*, exoccipital bone of cranium; *Pa*, parietal; *pp*, posterior process of petiotic; *So*, supraoccipital; *Sq*, squamosal; *tp*, transverse process.

(see Discussion). Fracture patterns depend on burial history to some extent, but these also depend on the thickness and density of original bone.

Two large tympanic bullae of slightly different sizes and shapes are known from Gueran. Both are osteosclerotic, and the smaller appears to belong to *P. aithai* (Fig. 10F). Neither is complete. The tympanic of *P. aithai* measures 7.3 cm in anteroposterior length and approximately 4.8 cm in transverse diameter. Salient characteristics distinguishing the smaller tympanic from the larger one are its smoothly rounded rather than squared inner posterior prominence, its shallow but distinct interprominental notch, and its shallow but distinct medial prominental notch. Both have a distinct, centimeter-sized, circular feature interrupting the smooth texture of the posterodorsal surface of the involucrum, the inner process of the posterior pedicle (Tsai and Fordyce, 2015).

Vertebrae of *Platysphys aithai* are distinctive compared to those of other archaocetes. Anterior thoracic vertebrae, such as T1–T4, taper anteroposteriorly, with the posterior surface of the centrum being notably wider than the anterior surface. T1–T3 have capitular facets for the heads of ribs on both the anterior and posterior ends of the centrum, but by T4 there is a capitular facet at the anterior end of the centrum but not at the posterior end (Fig. 8J). This vertebra is the first to have a diapophysis arising from the centrum for articulation with the rib tubercle, and the capitular articulation is less a facet than a pit. The diapophysis is lost on posterior thoracics, and the rib articulation is now a large pit on an elevated parapophyseal surface (Fig. 8L). Lumbar vertebrae of *P. aithai* are not complete but show the anteroposteriorly long, robust transverse processes extending virtually the entire length of the centrum (Fig. 8M–R) that are characteristic of the genus *Platysphys* (Kellogg, 1936, p. 97).

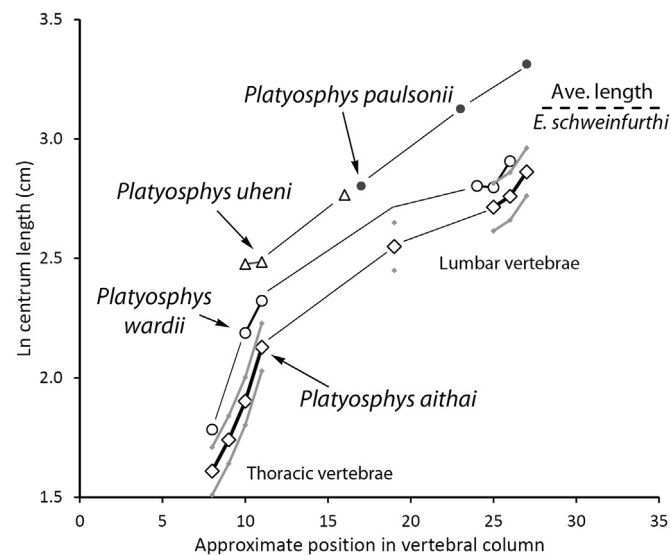


Fig. 9. Comparison of the vertebral centrum length profile of *Platysphys aithai*, new species (open diamonds), with those of *Platysphys paulsonii* (Brandt, 1873a,b; solid circles), *Platysphys* or *Basilotritus wardii* (Uhen, 1999; open circles), and *Platysphys* or *Basilotritus uheni* (Gol'din and Zvonok, 2013; open triangles). Vertebrae of *P. aithai* are illustrated in Fig. 8 and measurements are listed in Table 2. Light gray points and lines enclose a 95% confidence band for centrum length in *P. aithai* based on the empirical observation that linear measurements have a standard deviation averaging 0.05 on a natural-logarithm scale. Note that vertebrae of *P. aithai* are slightly smaller than those of *P. wardii*, and both have vertebrae significantly smaller than those of *P. paulsonii* and *P. uheni*. Measurements of the type specimen of *P. wardii*, USNM 310633, are from Uhen (1999). The average length for nine lumbar vertebrae of Gueran *Eocetus schweinfurthi* (Table 3) is shown by the dashed line in the upper right portion of the figure.

Table 2

Measurements of vertebrae of *Platysphys aithai*, new species, from Gueran. Three specimens are represented: FSAC Bouj-6 (T1–T4, holotype), Bouj-7 (T12?), and Bouj-11 (L1?–L3?), all from site II-1: 'Site d'Ali' (locality numbered '5' on the map in Fig. 2). Some vertebral positions are uncertain because the series is not complete. See Fig. 9 for a graphical profile. Measurements are in cm; those with asterisks are estimates. Abbreviations: *Vert.*, vertebral position; *Len.*, centrum length; *AW*, anterior centrum width, *AH*, anterior centrum height; *PW*, posterior centrum width; *PH*, posterior centrum height; *NCW*, neural canal width; *NCH*, neural canal height.

Vert.	Len	AW	AH	PW	PH	NCW	NCH	Illustration
T1	5.0	5.4	4.9	6.3	4.8	4.4*	–	Fig. 8C–D
T2	5.7	6.6	5.1	8.0*	5.5	4.9*	–	Fig. 8E–F
T3	6.7	6.7	5.6	8.4*	5.8	4.9*	–	Fig. 8G–H
T4	8.4	8.6	6.7	8.9	7.0	4.6*	–	Fig. 8I–J
T12?	12.8	9.7*	8.2*	9.6	7.7	4.3	–	Fig. 8K–L
L1?	15.1	10.0	8.8	10.9	8.9	4.4	–	Fig. 8M–N
L2?	15.8	10.4	8.7	11.1	9.4	4.4	–	Fig. 8O–P
L3?	17.5	11.1	10.1	10.8	10.2	4.2	–	Fig. 8 Q–R

Vertebrae of *P. aithai* are unusual in having anterior and posterior cones of cancellous bone tapering toward the center of the centrum, with intervening parts of the cylindrical diaphysis filled with laminae of denser cortical bone. This distinctive architecture is best seen when vertebrae are broken (but it can be seen too at the posterior end of L3? in Fig. 8Q–R). Nutrient foramina penetrating the laminae of this dense cortical bone are responsible for the pock-marked surface typical of *Platysphys* (and *Eocetus*). Measurements of vertebrae of *Platysphys aithai* are listed in Table 2.

Genus *Eocetus* Fraas 1904b.

Revised diagnosis: Large basilosaurid with posterior thoracic, lumbar, and anterior caudal vertebrae elongated and cylindrical. Differs from *Basilosaurus* in having a neural arch and neural spine that are longer anteroposteriorly, with prezygapophyses or metapophyses projecting to or beyond the anterior face of the centrum. Differs from *Platysphys* in having more cylindrical posterior thoracic, lumbar, and anterior caudal vertebrae, with pachyostosis and nutrient foramina less developed; differs too in having vertebrae with anteroposteriorly-shorter transverse processes.

Included species: *Eocetus schweinfurthi* (Fraas, 1904a) and *Eocetus drazindai* (Gingerich et al., 1997).

Eocetus schweinfurthi (Fraas, 1904a)

Fig. 10A–E, G.

The largest of the three basilosaurid species at Gueran is represented by (1) teeth including right upper premolar P³, FSAC Bouj-22 (Fig. 10A–B), and right upper premolar P⁴, FSAC Bouj-23 (Fig. 10A–B); (2) a right tympanic bulla, FSAC Bouj-21 (Fig. 10G); and (3) lumbar vertebrae, including FSAC-8 (Fig. 10D) and FSAC-9 (Fig. 10E). These differ from vertebrae of *Platysphys aithai* in being substantially larger (dashed line in Fig. 9) and in lacking the anteroposteriorly elongated transverse processes characteristic of *Platysphys*. They are referred to *Eocetus schweinfurthi* because of their large size, relatively long vertebral centra, and retention of prezygapophyses reaching anteriorly to a point above the anterior articular surface of the centrum. The latter characteristic is a clear distinction from *Basilosaurus isis* and *Basilosaurus cetoides*.

Teeth referred to *Eocetus schweinfurthi* include a partial upper premolar P³ and a complete P⁴ (Fig. 10A–B). Both are double-rooted. The crowns are heavily worn as is characteristic of mature larger basilosaurids. P³ has three denticles decreasing in size posterior to the large central cusp (Fig. 10A–B), and a fourth very small denticle near the base of the crown (Fig. 10C). P⁴ is similar to P³ but there is no fourth denticle. The anterior part of the crown of P⁴ is too worn to reveal the number of denticles. The crown of P³ is 2.65 cm wide buccolingually, and the crown of P⁴ is 5.76 cm long anteroposteriorly and 3.00 cm wide buccolingually. The

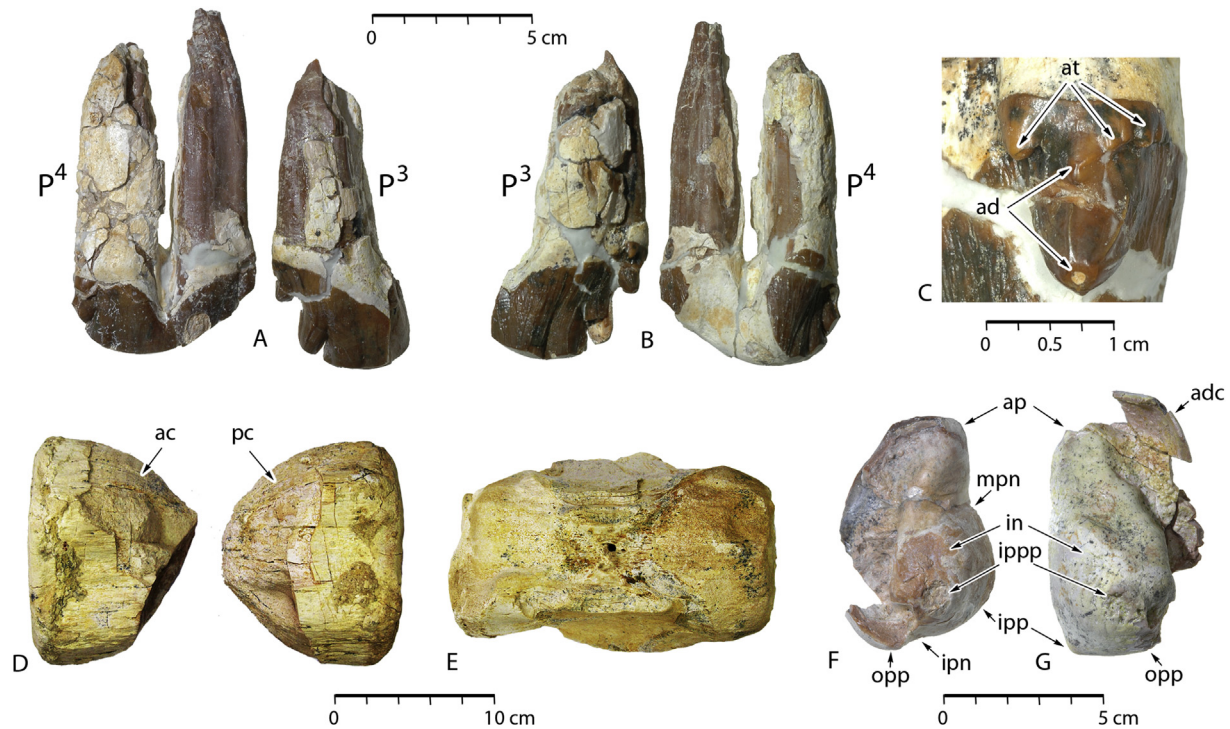


Fig. 10. Teeth and representative vertebrae of *Eocetus schweinfurthi* found at Gueran in southwestern Morocco, with a comparison of tympanic bullae of *Platyosphys aithai* and *E. schweinfurthi*. **A–B**, right upper premolars P^3 and P^4 of *E. schweinfurthi*, FSAC Bouj-22 and Bouj-23, in buccal and lingual view. **C**, close-up of the posterior margin of P^3 , FSAC Bouj-22. Note heavy wear on upper premolars, and the presence of accessory tubercles bordering the accessory denticle near the base of the crown. **D**, lumbar vertebra of *E. schweinfurthi*, FSAC Bouj-8, in dorsal view. Note cones of cancellous bone. **E**, caudal vertebra of *E. schweinfurthi*, FSAC Bouj-9, in dorsal view. **F**, left tympanic bulla of *P. aithai*, FSAC Bouj-26, in dorsal view. **G**, right tympanic bulla of *E. schweinfurthi*, FSAC Bouj-21, in dorsal view. Note the presence of a medial and posterior prominent notch on the bulla of *P. aithai* not seen on that of *E. schweinfurthi*. **A–B** are 0.5 \times natural size; **C** is 2 \times natural size; **D–E** are 0.25 \times natural size; and **G–H** are 0.5 \times natural size. Abbreviations: *ac*, anterior cone of cancellous bone; *ad*, accessory denticle on carina of premolar; *adc*, anterodorsal crest of outer lip; *ap*, anterior prominence; *at*, accessory tubercle; *in*, involucrum; *ipn*, inner prominent notch; *ipp*, inner posterior prominence; *ipp*, inner process of posterior pedicle; *mpn*, medial prominent notch; *opp*, outer posterior prominence; *pc*, posterior cone of cancellous bone.

posterior surfaces of both of these premolars have small accessory tubercles in addition to the accessory denticles. These are reminiscent of accessory tubercles seen on upper premolars of *Platyosphys* or *Basilotritus uheni* (Gol'din and Zvonok, 2013; Gol'din et al., 2014), but differ in that they are on the base of the crown as an incipient or remnant cingulum rather than on the denticles themselves (Fig. 10C).

The tympanic bulla referred to *Eocetus schweinfurthi* (Fig. 10G) is a little smaller but otherwise similar to the tympanic of *Basilosaurus isis* (Gingerich et al., in prep.). It measures 8.2 cm in anteroposterior length and 4.9 cm in transverse diameter. It is a little larger than the tympanic of *Platyosphys aithai*, and differs in lacking the rounded inner posterior prominence, the interprominential notch, and the medial prominent notch seen in *P. aithai*.

Vertebrae of *Eocetus schweinfurthi*, like those of *Platyosphys aithai*, are unusual in having anterior and posterior cones of cancellous bone tapering toward the center of the centrum (*ac* and *pc* in Fig. 10D), with intervening parts of the cylindrical diaphysis filled with laminae of denser cortical bone. This laminar bone has spalled away in FSAC-8 (Fig. 10D). A vertebra of *E. schweinfurthi* from the Giushi Formation of Gebel Mokattam in Egypt, SMNS 10934 described by Stromer (1903, p. 83–85; 1908, p. 109) appears to be similar in this respect. The surface of vertebral bone in *E. schweinfurthi* is often pock-marked like the surface of vertebral bone in *Platyosphys* (Uhen, 1999, fig. 2). Two series of more complete lumbar vertebrae measured to calculate the average centrum length shown by the dashed line in Fig. 9 are not illustrated because they are not yet fully prepared. Vertebral measurements are listed in Table 3.

5. Discussion

Several points bearing on the Gueran archaeocetes and on their geological and paleontological significance merit further discussion.

Table 3

Measurements of lumbar and caudal vertebrae of *Eocetus schweinfurthi* (Fraas, 1904a) from Gueran in southwestern Morocco. FSAC Bouj-8, Bouj-27, and Bouj-28 are lumbar, and Bouj-9 and Bouj-10 are caudals. Bouj-8 is from site II-1: 'Site d'Ali' (locality numbered '5' on the map in Fig. 2). Bouj-27 is from site I (locality numbered '1' on map in Fig. 2). Remaining specimens are from unknown localities at Gueran. Vertebral positions within the lumbar and caudal series are uncertain because these are not complete. Average lumbar centrum length of 22.9 cm is compared to lumbar centrum length for *Platyosphys aithai* in Fig. 9 and to Egyptian *Eocetus schweinfurthi* in Fig. 11. Measurements are in cm; those with asterisks are estimates. Abbreviations: *Bouj.*, specimen number; *Len*, centrum length; *AW*, anterior centrum width; *AH*, anterior centrum height; *PW*, posterior centrum width; *PH*, posterior centrum height; *NCW*, neural canal width; *NCH*, neural canal height.

Bouj.	Len	AW	AH	PW	PH	NCW	NCH	Illustration
8	—	14.5	11.8	14.7	12.0	—	—	Fig. 10D
9 (c)	20.2*	11.2*	9.0*	10.7*	9.1*	3.7	—	Fig. 10E
10 (c)	15.4	12.0*	7.3*	11.8*	6.8*	—	—	—
27	24.0*	14.0	11.5	—	—	—	—	—
27	23.0*	—	—	—	—	—	—	—
27	24.0*	—	—	—	—	—	—	—
28	22.5	—	—	16.0	13.0	—	—	—
28	21.0	—	—	15.0	12.5	—	—	—
28	23.5	—	—	15.5	13.5	—	—	—
28	24.0	—	—	16.0	13.5	—	—	—
28	22.5*	—	—	16.0*	13.5*	—	—	—
28	21.5	—	—	15.5	13.0	—	—	—

5.1. Size relationships of Gueran archaeocetes

It is not yet possible to make quantitative estimates of body size for all of the Gueran archaeocetes, but we can group the species into five size categories that give some sense of their possible ecological relations. From smallest to largest, the groups are:

- (1) Protocetid species A
- (2) Basilosaurid *Chrysocetus foudassaii*
- (3) Protocetid species B
- (4) Protocetid *Pappocetus lugardi* and basilosaurid *Platyosphys aithai*
- (5) Basilosaurid *Eocetus schweinfurthii*.

Protocetids are generally smaller than basilosaurids, but in the Gueran fauna the families overlap considerably in size.

5.2. Age of the Gueran archaeocete fauna

The combination of three species of protocetids with three species of basilosaurids preserved in the same sandstone unit is clear evidence of a Bartonian-age fauna. Protocetid teeth and basilosaurid cranial and vertebral remains are found together in the Giushi Formation of Bartonian age at Gebel Mokattam in Egypt (Fraas, 1904a; Stromer, 1908), and the two families are found together in the Drazinda Formation of Bartonian age flanking the Rodho anticline in Pakistan (Gingerich et al., 1995, 1997). Archaeocetes from the Gueran locality are important geologically because they constrain the age of the Aridal Formation sandstone to be Bartonian late middle Eocene in age.

5.3. Systematic position of *Platyosphys*

Lumbar vertebrae like those in Fig. 8M–R are typical of ‘*Zeuglodon paulsonii* Brandt (1873a,b) from Ukraine, which Kellogg (1936) placed in the new genus *Platyosphys*. Kellogg (1936, p. 97) distinguished *Platyosphys* as an archaeocete having elongated lumbar vertebrae and transverse processes on the lumbar vertebrae nearly as long anteroposteriorly as the length of the vertebral centrum. *Platyosphys* has been little discussed in the archaeocete literature because the morphology of the vertebrae is so distinctive, the age was long thought to be Oligocene, and few new specimens were forthcoming from eastern Europe. This changed when Uhen (1999, 2001) described new specimens from North America as *Eocetus wardii*, and Gol'din et al. (2012) recognized *Eocetus* sp. in upper Lutetian to Bartonian strata in Ukraine. Gol'din and Zvonok (2013) reinterpreted all of these remains, named a new genus and species *Basilotritus uheni*, and reclassified ‘*Eocetus wardii* as a species of *Basilotritus*.

Gol'din and Zvonok (2013) did not clearly state their reason for separating *Basilotritus* from *Eocetus*, but this separation appears justified based on observations presented here (see 5.4). Gol'din and Zvonok's separation of *Basilotritus* from *Platyosphys* depended on setting the genus and species *Platyosphys paulsonii* (Brandt, 1873a) aside as a nomen dubium – in spite of its stated similarity to *Basilotritus uheni* – because “this type specimen is considered to be lost” (Gol'din and Zvonok, 2013, p. 263). The validity of a genus and species does not depend on the continued availability of a type specimen, but rather on existence of an indication of the morphology involved and the source of a tangible specimen, whether lost or not. Both are clearly provided by Brandt (1873a,b) and by Kellogg (1936, p. 97).

Vertebrae identified as *Platyosphys aithai* here are smaller than those of *P. paulsonii* and *P. uheni*, but they conform closely in morphology to specimens described from Ukraine (Brandt, 1873b;

Gol'din et al., 2012, 2014; Gol'din and Zvonok, 2013) and from the southeastern United States (*P. wardii*; Uhen, 1999, 2001). Detailed comparison will require more complete vertebral columns than are presently available.

5.4. Vertebrae of *Eocetus schweinfurthii*

The type specimen of *Eocetus schweinfurthii* (Fraas, 1904a) is a large cranium, ‘St. 1’ or SMNS 10986, from the Giushi Formation of Gebel Mokattam in Egypt. This measures 96.0 × 40.0 cm in length and width (Kellogg, 1936, p. 247). Fraas regarded the cranium as enabling identification of the large 24.5 cm long lumbar and an accompanying vertebra described and illustrated by Stromer from the same stratigraphic interval (Stromer, 1903, p. 83–85: ‘St. 2’ or SMNS 10934). Stromer later added two additional vertebrae of the same skeleton as SMNS 10934 (Stromer, 1908, p. 109: ‘Fr. 1’ or SFNF 4470). In addition, Stromer (1908, p. 109) mentioned three smaller vertebrae (‘St. 3’) that he interpreted as subadult representatives of a third specimen of *E. schweinfurthii* (Stromer, 1908, p. 109: ‘St. 3’ or SFNF unnumbered). Stromer characterized the best vertebra of ‘St. 3’ as a centrum that is minimally 13.5 cm long, with transverse processes arising along the whole lower margin of the centrum that protrude slightly forward and slightly downward.

Uhen (1999, fig. 2) interpreted Stromer's ‘St. 3,’ mislabeled as SFNF 4470, to represent *Eocetus schweinfurthii*, in contrast to the larger vertebra of ‘St. 2’ (SMNS 10934), which he referred to *Basilosaurus drazindai* Gingerich et al. (1997). Here we offer an alternate solution (Fig. 11). We know the size of the *E. schweinfurthii* type skull (see above), which represents a mature adult. We know the size of the skulls and the lumbar vertebrae of *Basilosaurus cetoides* and *B. isis* (Kellogg, 1936; Gingerich et al., in preparation), which are

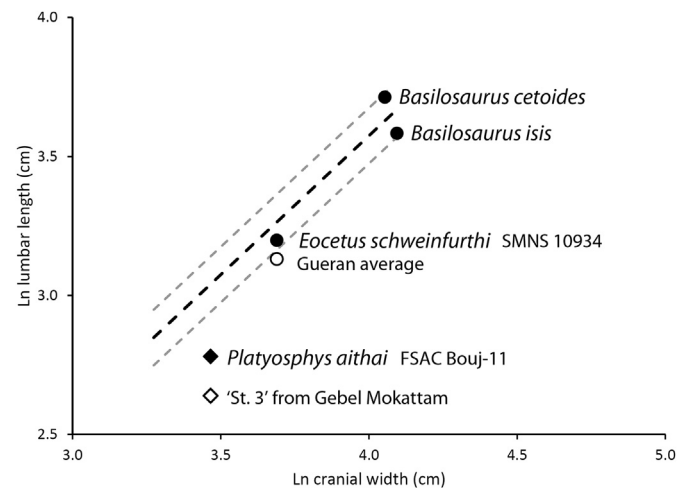


Fig. 11. Comparison of the relative lengths of lumbar vertebrae of Gueran *Platyosphys aithai* (Morocco) and Gebel Mokattam *Eocetus schweinfurthii* (Egypt) to the length expected from isometric scaling of lumbar length to cranial width in Egyptian and North American *Basilosaurus isis* and *B. cetoides* (dashed lines enclose a 95% confidence band for centrum length in *Basilosaurus* based on a 0.05 natural-logarithm-unit standard deviation). Note that the largest vertebra from Gebel Mokattam, the elongated *Basilosaurus*-like vertebra described by Stromer (1903, p. 83–85 and fig. 1), is a little longer than the average from Gueran (open circle, which lacks a corresponding cranial width). The Gebel Mokattam vertebra is the right length to belong with the type skull of *E. schweinfurthii* named by Fraas (1904a,b), which corroborates Stromer's referral of the vertebra to *E. schweinfurthii* (Stromer, 1908, p. 109). An *Eocetus*-like lumbar vertebra would be too long to belong with a skull the width of the cranium of *Platyosphys aithai* described here, which corroborates association of the cranium and vertebrae shown in Fig. 8. Measurements for *B. cetoides* and Gebel Mokattam *E. schweinfurthii* are from Kellogg (1936), those from *B. isis* are from Gingerich et al. (in preparation), and the average for Gueran *E. schweinfurthii* is from Table 3. All of these crania represent adult individuals.

again both mature adults). Thus we can ask how large a *Basilosaurus*-like lumbar vertebra of *E. schweinfurthi* is expected to be in proportion to the size of its skull? The resulting estimate for lumbar size compared to skull width (bizygomatic breadth) is shown by the dashed lines in Fig. 11 (we use skull width because this is all we can estimate for comparison in adult *Platyosphys aithai*). The SMNS 10934 vertebra lies within the dashed lines, corroborating interpretation that it represents *Eocetus schweinfurthi* (Fraas, 1904a; Stromer, 1908; Kellogg, 1936). An alternative approach, projecting the lumbar-to-cranial-width relationship for *Platyosphys aithai* to the cranial width for *E. schweinfurthi*, shows that SMNS 10934 is too large to represent *P. aithai*, and too large to represent 'St. 3' from Gebel Mokattam.

The partial cranium of *Platyosphys aithai* described here is relevant too in showing that *Platyosphys* had a more heavily built skull than that of *Eocetus*, making it less susceptible to the compression seen in the type skull of *Eocetus*. Thus, following Fraas (1904a), Stromer (1908), Kellogg (1936), and Van Valen (1968), we interpret *Eocetus schweinfurthi* as a basilosaurid, with vertebrae proportioned like those of *Basilosaurus* but lacking reduction of the neural arch and zygapophyses seen in *Basilosaurus* itself. *Basilosaurus drazindai* from Bartonian strata of Pakistan has lumbar vertebrae substantially larger than those of *E. schweinfurthi*, with a long neural arch and zygapophyses reaching the anterior limit of the centrum (Gingerich et al., 1997). We now regard *B. drazindai* as a large species of *Eocetus*.

5.5. Paleobiogeography of Gueran archaeocetes

Protocetid and basilosaurid archaeocetes had broad, essentially global geographic distributions by the later part of the middle to late Eocene, being known from Asia, Europe, Africa, North America, and South America (Uhen, 2010; Martínez and Muizon, 2011). Basilosaurids are also known from this interval in New Zealand and Antarctica (Borsuk-Bialynicka, 1988; Köhler and Fordyce, 1997). The new fauna from Gueran is interesting in bringing together in one fauna *Pappocetus*, previously known only from Nigeria in West Africa; *Cynthiacetus*, previously known only from North America; *Eocetus*, previously known with certainty only from North Africa; and *Platyosphys*, previously known principally from Ukraine in eastern Europe. This reinforces the idea of cosmopolitanism in Bartonian and Priabonian whales, and it highlights the centrality of Gueran biogeographically for understanding the diversity and Bartonian history of Archaeoceti.

6. Conclusions

The fossils recovered from Gueran in 2014 indicate that the Aridal Formation sandstone producing the fossils is Bartonian late middle Eocene in age. Archaeocetes of the family Protocetidae are represented by three species, including the first record of *Pappocetus lugardi* outside Nigeria. Archaeocetes of the family Basilosauridae are also represented by three species. *Chrysocetus foudassii* is a small, new, generalized basilosaurid with gracile teeth and vertebrae of normal proportions. *Platyosphys aithai* in contrast is a larger species, also new, with a skull and elongated vertebrae composed of unusually dense and thickened bone. *Eocetus schweinfurthi* is the largest species, with elongated vertebrae approaching those of *Basilosaurus* itself in size and proportions. Further collecting at Gueran focused on recovering associated skeletons of protocetids and basilosaurids promises to clarify the important evolutionary transition from foot-powered swimming in Protocetidae to the tail-powered swimming of Basilosauridae and all later Cetacea.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jafrearsci.2015.08.006>

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