C. R. Palevol 13 (2014) 599–610

Contents lists available at ScienceDirect

Comptes Rendus Palevol

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General palaeontology, systematics and evolution (Vertebrate palaeontology)

New marine mammal faunas (Cetacea and Sirenia) and sea level change in the Samlat Formation, Upper Eocene, near Ad-Dakhla in southwestern Morocco

Nouveaux mammifères marins (Cetacea et Sirenia) et le changement du niveau de la mer dans la formation de Samlat, Éocène supérieur, Ad-Dakhla, Sud-Ouest du Maroc

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ARTICLE INFO

Article history:
Received 1st October 2013
Accepted after revision 1st April 2014
Available online 22 July 2014

Handled by Lars van den Hoek Ostende

Keywords:
Cetacea
Archaeoceti
Sirenia
Dugongidae
Late Eocene
Ad-Dakhla
Morocco

ABSTRACT

The Samlat Formation is well exposed in coastal sections bordering the Atlantic Ocean south of Ad-Dakhla in southwestern Morocco. Here some 22 m of rhythmically-bedded, chert-rich, marine siltstones and marls are overlain by 1–1.5 m of vertebrate-bearing microconglomeratic sandstone, another 4–8 m of rhythmically-bedded siltstone and marl, and finally a second 3–6 m unit of vertebrate-bearing muddy sandstone. The microconglomeratic and muddy sandstones represent low sea stands in what is otherwise a deeper water sequence. Cetacean skeletons are rare but cetacean vertebrae are common in the lower sandstone (bed B1), where many show the effects of reworking. The cetaceans in bed B1represent a minimum of five species, from smallest to largest: cf. *Saghacetus* sp., cf. *Stromerius* sp., *Dorudon atrox*, cf. *Dorudon* sp., and *Basilosaurus isis*. Bed B1 yields rib fragments that may represent sirenians, but sirenians, if present, are rare. The only identifiable cetacean found in the upper sandstone (bed B2) is *Basilosaurus* sp. Dugongid sirenians identified as cf. *Eosiren* sp. are the most common mammal in bed B2. We interpret co-occurrence of the typically Early Priabonian species *Dorudon atrox* and *Basilosaurus isis* with smaller species more like Middle Priabonian genera *Saghacetus osiris* and *Stromerius nidensis* to indicate that bed B1 was deposited during low sea stand Pr-2 between the Early and Middle Priabonian (between the early and middle Late Eocene). Bed B2 is separated from B1 by an interval of deeper water sediment accumulation. Bed B2 could represent a later phase of Pr-2 or a subsequent Priabonian low sea stand (possibly Pr-3).

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http://dx.doi.org/10.1016/j.crpv.2014.04.002
1631-0683/

R É S U M É

La formation Samlat affleure largement dans les falaises longeant la côte atlantique du Sud d'El Argoub, jusqu'au sud de Punta Chica, dans la région d'Ad-Dakhla, dans le Sud-Ouest du Maroc. La séquence d'environ 22 m d'épaisseur est formée d'une alternance régulière de couches de silts et de marnes à chert, surmontées par un niveau de 1 à 1,5 m de sable micro-conglomératique contenant des fossiles de Vertébrés (B1). L'ensemble est recouvert par une nouvelle alternance de silts et de marnes de 4 à 8 m d'épaisseur, elle-même surmontée par un deuxième niveau fossilifère sablo-marneux de couleur ocre (B2) de 3 à 6 m d'épaisseur. Le sable microconglomératique et le sable marneux correspondraient à une baisse du niveau marin, en comparaison avec le reste de la formation. Les squelettes de cétacés sont rares, mais les vertèbres sont nombreuses dans le niveau fossilifère inférieur (B1), où la plupart d'entre elles montrent un impact de remaniement. Les cétacés représentent au minimum cinq espèces différentes, de la plus petite à la plus grande: cf. *Saghacetus* sp., cf. *Stromerius* sp., *Dorudon atrox*, une forme de grande taille « *Dorudon*-like » à vertèbres pentagonales et *Basilosaurus isis*. Le niveau B1 a fourni également des fragments de côtes pouvant représenter des siréniens. Cependant, s'ils sont présents dans B1, les siréniens seraient très rares. Le seul cétacé identifiable dans le niveau fossilifère supérieur (B2) est provisoirement identifié comme *Basilosaurus* sp. Les siréniens Dugongidae, identifiés comme cf. *Eosiren* sp., sont les mammifères marins les plus communs dans le niveau B2. La cooccurrence des deux espèces *Dorudon atrox* et *Basilosaurus isis* typiques du Priabonien inférieur avec celles des genres *Saghacetus* et *Stromerius* du Priabonien moyen indiquerait que le niveau B1 a été déposé sous un faible niveau marin (Pr-2) entre le Priabonien inférieur et moyen (entre l'Éocène supérieur inférieur et moyen). Les niveaux B1 et B2 sont séparés par des dépôts de plus grande profondeur. Le niveau B2 pourrait représenter une deuxième phase de régression (Pr-2), telle qu'elle est documentée en Egypte, ou encore correspondre à un autre épisode régressif de la mer priabonienne (probablement Pr-3).

Mots clés :
Cetacea
Archaeoceti
Sirenea
Dugongidae
Éocène supérieur
Ad-Dakhla
Maroc

1. Introduction

Adnet et al. (2010) reported several new fossiliferous sites yielding Eocene vertebrates, principally selachian teeth, from the Samlat Formation in the middle of the Ad-Dakhla Basin in southwestern Morocco (Fig. 1). The fossils were found in a series of localities along the Moroccan coast, where they came from two sandstone intervals, beds B1 and B2, in a sequence of rhythmically-bedded, chert-rich marine siltstones and marls. Adnet et al. (2010) described a proboscidean tooth (?*Numiditherium* sp.) from bed B1 north of Garitas, and reported seeing remains of many archaeocete whales at different localities (Basilosauridae; one partial tooth was illustrated). The deposits were previously mapped as Mio-Pliocene (Rjimati et al., 2008), but the selachians, the proboscidean, and the archaeocetes indicate that the age is unequivocally Eocene.

Field et al. (2011) reviewed these findings and identified the whales as *Basilosaurus* sp., *Dorudon* sp., and a smaller basilosaurid. Paleobiology Database collection 96686 records the three archaeocete species from sandstone interval B1, and Paleobiology Database collection 96688 records the same three species from sandstone interval B2 (http://paleodb.org/cgi-bin/bridge.pl; entry by Uhen in 2010).

We initiated further field research in 2013 (Fig. 2A) to find more and better archaeocete specimens and to clarify identification of the taxa. We collected most specimens in the field ourselves, but local collectors contributed some vertebrae studied here. The exact provenance of these last vertebrae is uncertain, however, knowing that there are only two fossiliferous levels (B1 and B2). Our results show that a dugongid sirenian is present in addition to the cetaceans, and the distribution of marine mammal remains is more complicated and more interesting than previously recognized.

2. Abbreviations

UHC DAK: Faculté des sciences, Université Hassan-II, Dakhla collection (Casablanca, Morocco); UM: University of Michigan Museum of Paleontology (Ann Arbor, USA).

3. Geological context

The Tarfaya–Laâyoun–Ad-Dakhla Basin (also named Boujdour or Aioun Basin) is one of a series of mature passive margin basins that lie along the Central Atlantic margins of Northwest Africa and North America (Davison and Dailly, 2010, and references therein). It extends for almost 1000 km along the African margin from the Cap Blanc Fracture Zone in northern Mauritania, north through southern Morocco to the intersection of the North Canary Island Fracture Zone and the South Atlas Fault (Fig. 1A, insert). The Tarfaya–Laâyoun–Ad-Dakhla Basin comprises two discrete sub-basins separated by the Dakhla Fracture Zone (Fig. 1A). The northern is the Boujdour sub-basin, and the southern is the Ad-Dakhla sub-basin. The latter is characterized among other things by the absence of Cenomanian-Paleocene sediments onshore (Fig. 1B; von Rad et al., 1979, 1982).

Nevertheless, almost in the middle of Ad-Dakhla Basin along the Atlantic coast, the Paleogene Samlat Formation overlies Cretaceous outcrops (Ratschiller, 1967; von

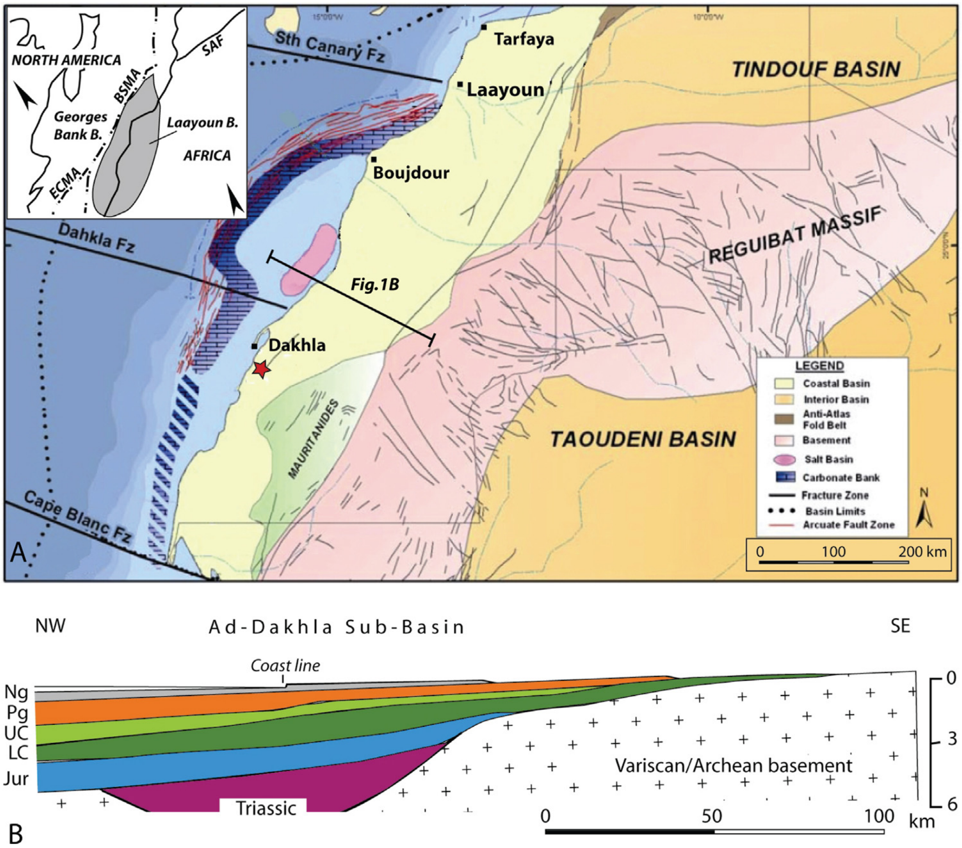

Fig. 1. (Color online.) Geological setting of Ad-Dakhla area, **A.** Sketch map of the Saharan Provinces of Morocco, after Davison and Dailly (2010), modified. **Star**: location of the studied outcrops. Insert: Location of the Tarfaya–Laayoun–Dakhla Basin in the restored Central Atlantic Domain. BSM/ECMA: Black Spur/East Coast Magnetic Anomaly. SAF: South Atlas Fault. **B.** Generalized NW-SE cross-section of the internal Ad-Dakhla sub-basin after the geological map of Morocco, scale 1:1,000,000 (onshore) and Davison and Dailly (2010), offshore (Courtesy A. Michard). Vertical scale approximate. Jur: Jurassic. LC/UC: Lower/Upper Cretaceous. Pg: Paleogene. Ng: Neogene.

Fig. 1. (Couleur en ligne.) Contexte géologique de la région d'Ad-Dakhla, **A.** Carte géologique simplifiée des provinces sahariennes du Maroc, d'après Davison et Dailly (2010), modifié. Étoile : emplacement des affleurements étudiés. Encart : localisation du bassin de Tarfaya–Laâyoune–Ad-Dakhla dans le domaine de l'Atlantique central. BSM/ECMA : Black Spur/East Coast Magnetic Anomaly. SAF : South Atlas Fault (accident sud-atlasique). **B.** Coupe NW–SE dans le Nord du bassin d'Ad-Dakhla d'après la carte géologique du Maroc au 1:1 000 000 (onshore) et Davison et Dailly (2010), offshore (avec l'aimable autorisation d'André Michard). Échelle verticale approximative. Jur : Jurassique. LC/UC : Crétacé inférieur/Crétacé supérieur. PG : Paléogène. Ng : Néogène.

Rad et al., 1979). The Samlat Formation includes three members:

- a Paleocene Itgui Member with well-preserved foraminifera;
- an Eocene Guerran Member that is white earthy siliceous carbonates interbedded with silty coarse sandstones and conglomerate;
- a younger Moreba Member (Ratschiller, 1967).

The Eocene Guerran Member of the Samlat Formation of interest here is primarily marine siliceous chalk, becoming more clastic farther onshore (Davison, 2005; Ratschiller, 1967). In the vicinity of Ad-Dakhla the Eocene part of the Samlat Formation is exposed in cliffs along the Atlantic coast from south of El Argoub village to the military position commonly named "Garitas", but it is more easily accessible on the flat outcrops south of "Garitas" (Fig. 2).

This sequence of strata (Fig. 3), all part of the Guerran Member, was described in detail by Adnet et al. (2010), who divided it into three units. The lower unit, Unit 1 of Adnet et al. (2010), includes some 22 m of rhythmically-bedded, chert-rich marine siltstones and marls. These are overlain by 1–1.5 m of vertebrate-bearing conglomeratic sandstone, another 4–8 m of rhythmically-bedded siltstone and marl, and a second 3–6-m unit of vertebrate-bearing muddy sandstone (Unit 2 of Adnet et al., 2010). Bonebeds B1 and B2 are both located in Unit 2. The highest unit, Unit 3 of Adnet et al. (2010), is a 2–3-m interval of sandy to bioclastic limestone of Neogene age.

Rhythmically-bedded, chert-rich marine siltstones and marls like those in Unit 1 and Unit 2 of the Samlat Formation are generally interpreted to reflect Milankovitch-periodic variation in the production and accumulation of siliceous plankton, diluted by fine-grained, wind-blown, terrigenous clastics and by carbonate ooze in an offshore deep-water environment (Decker, 1991). More massive, coarser-clastic sandstones with abundant shark teeth and vertebrate bone, like those of bonebeds B1 and B2 at the bottom and top of Unit 2, are conspicuously different and represent a higher-energy nearshore environment. Alternation of such different environments can only be

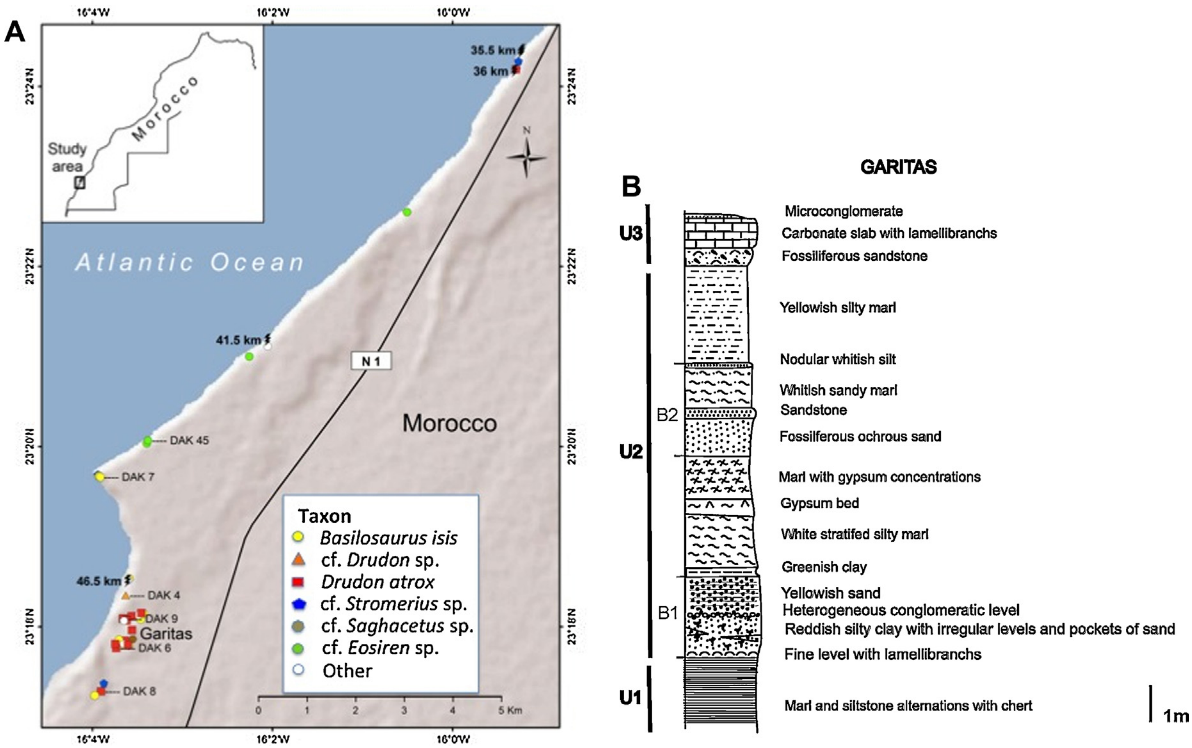

Fig. 2. A. (Color online.) Map showing the distribution of Ad-Dakhla fossil localities studied in 2013. All are actively exploited by commercial collectors. The distances (in kilometers) indicate the locations of stratigraphic sections of Adnet et al. (2010; distance given is 'as a crow flies' south from Ad Dakhla); Inset shows the location of the El Argoub-Garitas map here relative to Ad-Dakhla itself, and the location of Ad-Dakhla relative to the rest of Morocco. **B.** Stratigraphic section at Garitas south of Ad-Dakhla. Gypsum in this section is primary, representing evaporitic deposition during the transition from a deeper-water environment with accumulation of stratified marl to a shallow nearshore environment with ochrous sands of bone bed B2. White stratified silty marl here is thicker and includes rhythmically-bedded, chert-rich siltstones and marls in stratigraphic sections north of Garitas.

Fig. 2. A. (Couleur en ligne.) Localisation des sites fossilifères de la région d'Ad-Dakhla étudiés en 2013. Tous sont activement exploités par les collectionneurs à but commercial. Les distances, en kilomètres, indiquent les emplacements des coupes stratigraphiques d'Adnet et al. (2010) ; elles sont données à vol d'oiseau d'Ad-Dakhla. L'encart montre l'emplacement des localités fossilifères étudiées par rapport à Ad-Dakhla et la situation d'Ad-Dakhla par rapport au reste du Maroc. **B.** Séquence stratigraphique relevée à Garitas, au sud d'Ad-Dakhla. Le banc de gypse dans cette section est d'origine primaire. Il correspond à une sédimentation évaporitique mise en place lors de la transition d'un environnement d'eau profonde avec des dépôts de marnes à un milieu côtier peu profond avec des dépôts de sables ocre renfermant le *bedbone* B2. Les dépôts marno-silteux de couleur blanche sont plus épais et comprennent une alternance de couches silteuses riches et cherts et de marnes au nord de la localité de « Garitas ».

explained by changing sea level. The conglomeratic and muddy sandstones of B1 and B2 represent low sea stands in what is otherwise a deeper water sequence.

Adnet et al. (2010) assigned a Late Eocene age to Unit 2 with bonebeds B1 and B2 based on the selachian fauna. Bonebed B1 has provided a large number of vertebrae of cetaceans belonging at least to five different species, with possible rib fragments of sirenians and also some remains of crocodiles, turtles, sea snakes and birds. Upper bonebed B2 yielded cetacean remains attributed to *Basilosaurus* sp. and common remains of a dugongid.

4. Systematic paleontology

CETACEA Brisson, 1762
ARCHAEOCETI Flower, 1883
Basilosauridae Cope, 1868
Saghacetus Gingerich, 1992
cf. *Saghacetus* sp.
(Fig. 4A–D, G)
Referred specimens and measurements: Table 1.

Provenance: All specimens for which the provenance is known come from bed B1 of Adnet et al. (2010).

Description: The most interesting specimen is DAK-1 (Fig. 4A–B), a well-preserved juvenile right maxilla with dP^{2-4} representing a very small basilosaurid. The teeth are all long, narrow, and low-crowned relative to adult teeth at the same position. Deciduous dP^2 is simple with anterior and posterior but no accessory roots; dP^3 has anterior and posterior roots, but also a small medial root visible on the buccal side of the tooth and a prominent protocone swelling of the crown and root visible on the lingual side; dP^4 lacks the medial root but has a prominent protocone swelling and root like that on dP^3. There are deep embrasure pits located posteromedial to all three teeth (the latter to receive the apical cusp of M^1). The midline suture joining the maxillae is preserved, indicating that the rostrum was narrow. A suture for the premaxilla is preserved along the dorsal margin of the maxilla, and an infraorbital canal opens in via a 9 mm maxillary foramen above the anterior root of dP^3.

The best preserved thoracic element is a simple centrum, DAK-20, that is 'D-shaped' in transverse section, with

Fig. 3. (Color online.) Exposure of fossiliferous bed B1 in a sea-cliff section of the Samlat Formation. Partial skeleton of *Dorudon atrox* was found at this site. Note thin planar bedding through most of deeper-water marine stratigraphic unit 1, which is chert-rich in the lower part, with thicker bedding of marl near the top. Note too that bed B1 is overlain by rhythmically-bedded, chert-rich, deeper-water siltstones and marls in stratigraphic unit 2. Stratigraphic nomenclature follows Adnet et al. (2010).

Fig. 3. (Couleur en ligne.) Emplacement du « bedbones » B1 dans la séquence stratigraphique de la formation Samlat dans une falaise au bord de l'océan Atlantique. Un squelette partiel de *Dorudon atrox* a été trouvé dans ce site. Notez la faible épaisseur des strates de la plupart de l'unité 1, riche en silex dans sa partie inférieure et les couches relativement plus épaisses près de son sommet. Notez également que le « bedbones » B1 est recouvert par une couche de marnes dans l'unité stratigraphique 2. Nomenclature stratigraphique d'après Adnet et al. (2010).

the flat part of the D, the dorsal surface, flooring a broad neural canal. Facets for rib capitula are small and high on the centrum, indicating an anterior thoracic. The best preserved lumbar centrum is DAK-7 (Fig. 4C–D), which is elliptical in transverse section. Left and right pedicles of the neural arch are well separated, indicating that this is an anterior lumbar. The better of the two distal humeri is DAK-31 (Fig. 4G). This has a prominent deltopectoral crest on the anterior margin of the diaphysis, rising 45 mm above the distal end of the bone. The curved distal articular surface is 24 mm in diameter, but the articular surface itself is damaged, as are the lateral and posterior surfaces of what remains of the diaphysis.

Discussion: Archaeocete teeth form in the jaws before they erupt, and these teeth do not continue to grow after eruption. The definitive lengths of deciduous and permanent cheek teeth (premolars and molars) in juvenile and adult *Zygorhiza* and *Dorudon* (Kellogg, 1936; Uhen, 2004) can be used to enable prediction of M^1 length in DAK-1: four specimens with dP^3 and M^1 yield a prediction of 15.0 mm, and three specimens with dP^4 and M^1 yield a prediction of 18.5 mm for M^1 length in DAK-1. These predicted M^1 lengths indicate that DAK-1 represents an archaeocete the size of *Saghacetus osiris* from the Middle Priabonian, Late Eocene of Egypt, which is distinctly small for a basilosaurid. There are no dental characters on deciduous teeth that enable one basilosaurid to be distinguished from another, but the sizes of deciduous and permanent teeth limit possible identifications. We identify the taxon represented here as cf. *Saghacetus* sp. based on size, pending recovery of more complete specimens. No other basilosaurid known is this small.

The vertebrae and humeri included in cf. *Saghacetus* sp. are considered to represent the same taxon as the maxilla because they are similar in size, but none of the elements described here were found associated and more than one taxon may be represented.

Stromerius Gingerich, 2007
cf. *Stromerius* sp.
(Fig. 4E–F, H–J)

Referred specimens and measurements: Table 2.

Provenance: All specimens for which the provenance is known come from bed B1 of Adnet et al. (2010).

Description: Specimens described here are distinctly larger than those included in cf. *Saghacetus* sp. They are referred to cf. *Stromerius* sp. on the basis of size. DAK-10 (Fig. 4E–F) is an anterior lumbar with a centrum more circular in transverse section than is typical for *Stromerius*. DAK 21 is a posterior lumbar vertebra, and DAK 35 (Fig. 4I–J) is a posterior lumbar or anterior caudal vertebra. Both are more elongated anteroposteriorly than is typical for *Stromerius*. The vertebral centra of cf. *Stromerius* sp. described here are comparable in length to those of *Dorudon* cf. *D. atrox*, but they are conspicuously smaller and more similar to *Stromerius* in width and height.

DAK-36 (Fig. 4H) is a left humerus of an adult that is complete except for a missing proximal epiphysis, with a large bite mark perforating the lateral surface of the mid-shaft. There is no cancellous bone that would indicate this to be immature or subadult. The curved distal articular surface is 33 mm in diameter. The distal end of DAK-36 is about 30% wider than that of humeri here attributed to cf. *Saghacetus* sp., and it is about 33% narrower than the distal ends of humeri of *Dorudon atrox* from Egypt, making it likely that DAK-36 belongs with other specimens grouped here as cf. *Stromerius* sp. DAK-36 is smaller but has a very prominent deltopectoral crest like that of *Dorudon atrox* from Egypt (Uhen, 2004).

Discussion: cf. *Stromerius* sp. almost certainly represents a genus and species new to science, but known specimens are inadequate to justify naming a new taxon.

Stromerius nidensis is known from Middle Priabonian, Late Eocene, strata in Egypt, as is *Saghacetus osiris*. Identification of Dakhla specimens from bed B1 as cf. *Saghacetus* sp. and cf. *Stromerius* sp. is consistent with a Priabonian age for the bed. Basilosaurids are rare before the Priabonian and not known after the Priabonian.

Dorudon Gibbes, 1845
cf. *Dorudon atrox* (Andrews, 1906)
(Fig. 5A–E)

Referred specimens and measurements: Table 3.

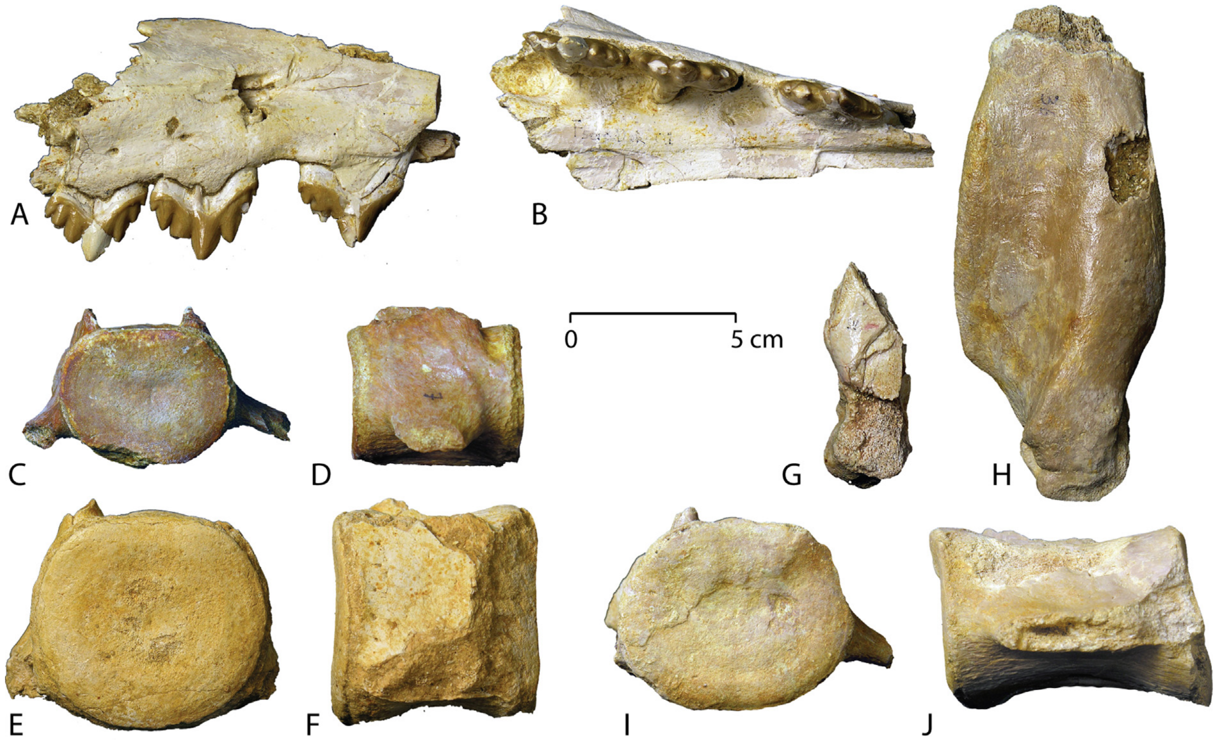

Fig. 4. (Color online.) Specimens of the archaeocetes cf. *Saghacetus* sp. and cf. *Stromerius* sp. from Ad-Dakhla. **A–B**. Right maxilla of cf. *Saghacetus* sp. with dP^{2-4} in right lateral and occlusal view (UHC DAK-1); **C–D**. Centrum of anterior lumbar vertebra of cf. *Saghacetus* sp. in anterior and left lateral view (UHC DAK-7); **E–F**. Centrum of anterior lumbar of cf. *Stromerius* sp. in anterior and left lateral view (UHC DAK-10); **G**. Distal portion of left humerus of cf. *Saghacetus* sp. in lateral view (UHC DAK-31); **H**. Distal portion of left humerus of cf. *Stromerius* sp. in lateral view (UHC DAK-36); **I–J**. Centrum of posterior lumbar or anterior caudal of cf. *Stromerius* sp. in anterior and left lateral view (UHC DAK-35). See Tables 1 and 2 for measurements. Note small narrow deciduous teeth of cf. *Saghacetus* sp., and differences in sizes of the humeri and lumbar vertebrae of the two species.

Fig. 4. (Couleur en ligne.) Les archaeocètes cf. *Saghacetus* sp. et cf. *Stromerius* sp. d'Ad-Dakhla. **A–B.** Maxillaire droit avec dP^{2-4} (UHC DAK-1) attribué à cf. *Saghacetus* sp. en vue latérale droite et occlusale ; **C–D.** *Centrum* de vertèbre lombaire antérieure de cf. *Saghacetus* sp. en vue antérieure et latérale gauche (UHC DAK-7) ; **E–F.** *Centrum* de lombaire antérieure de cf. *Stromerius* sp. en vues antérieure et latérale gauche (UHC DAK-10) ; **G.** Extrémité distale d'humérus gauche de cf. *Saghacetus* sp. en vue latérale (UHC DAK-31) ; **H.** Humérus gauche de cf. *Stromerius* sp. en vue latérale (UHC DAK-36) ; **I–J.** *Centrum* de vertèbre lombaire postérieure ou de vertèbre caudale antérieure de cf *Stromerius* sp. en vue antérieure et latérale gauche (UHC DAK-35). Voir les Tableaux 1 et 2 pour les mesures. Notez les petites et étroites dents lactéales de cf. *Saghacetus* sp., ainsi que les différences de dimensions des vertèbres lombaires et des humérus des deux espèces (*Saghacetus* sp. et cf. *Stromerius* sp.).

Provenance: All specimens for which the provenance is known come from bed B1 of Adnet et al. (2010). Some specimens received from local collectors may have come from bed B2.

Description: Cranial fragments are known, but none is complete enough to describe here. The most informative elements are vertebrae. These include DAK-37 with pieces of cervicals C1 (atlas), C2 (axis), and C7, and the

Table 1
Measurements (mm) for specimens of cf. *Saghacetus* sp. All are UHC DAK specimens, and adult unless otherwise indicated.
Tableau 1
Dimensions (mm) des spécimens de cf. *Saghacetus* sp. Tous les spécimens (UHC DAK) appartiennent à des individus adultes, sauf indication contraire. L'astérisque indique les mesures estimées.

DAK	Description	Length	Width	Height
1.	Right maxilla with dP^{2-4} (juvenile)	32.2	8.2	19.9
	¨	33.0	14.1	22.2
	¨	31.3	11.7	20.2*
7.	Anterior lumbar vertebral centrum	52.6	56.9	44.2
12.	Posterior lumbar or anterior caudal centrum	57.5	50.9	45.0
13.	Anterior thoracic centrum (ant. epiphysis missing)	49.5*	60.2	42.6
15.	Anterior thoracic centrum (ant. epiphysis missing)	47.2	53.0	43.2
20.	Anterior thoracic centrum	37.9	46.2	35.4
24.	Anterior thoracic centrum (juv.)	29.5*	38.6*	25.7*
25.	Posterior lumbar or anterior caudal centrum (juv.)	40.3*	47.5*	40.3*
30.	Distal left humerus (subadult)	–	26.2*	–
31.	Distal left humerus	–	26.0*	–

Asterisks in this and following tables indicate that the length, width, or height reported is a measured estimate on an imperfectly preserved specimen.

Table 2
Measurements (mm) for specimens of cf. *Stromerius* sp. All are UHC DAK specimens, and adult unless otherwise indicated. Length for axis UHC DAK-19 is functional length without the dens. Height for humerus UHC DAK-36 is maximum anteroposterior length over the deltopectoral crest.
Tableau 2
Dimensions (mm) des spécimens attribués à cf. *Stromerius* sp. Tous les spécimens (UHC DAK) appartiennent à des individus adultes, sauf indication contraire. La longueur de l'axis (UHC DAK-19) est une longueur fonctionnelle. La hauteur de l'humérus UHC DAK-36 est la longueur antéro-postérieure maximale de la crête deltopectorale. L'astérisque indique les mesures estimées.

DAK	Description	Length	Width	Height
3.	Neural spine of an anterior thoracic vertebra	–	–	–
10.	Anterior lumbar vertebral centrum	60.8	68.7	63.0
19.	Second cervical (axis) centrum	33.6	48.2	41.7
21.	Posterior lumbar (both epiphyses missing)	80.9*	74.1	61.1
35.	Posterior lumbar or anterior caudal centrum	85.5	72.0	61.7
36.	Left humerus lacking the proximal epiphysis	180.0*	34.2	67.3

Asterisks indicate estimates.

capitular process of thoracic T1 or T2. DAK-18 is the centrum of a middle cervical, probably C4; DAK-16 is the centrum of cervical C7; and DAK-17 is the centrum of a first thoracic T1. DAK-14 is the centrum of a middle thoracic vertebra, and DAK-28 is the centrum of a posterior thoracic with the capitular facets on short but massive transverse processes.

DAK-2 (Fig. 5A–E) is an associated series of nearly identical posterior lumbar or anterior caudal vertebrae. One vertebra has the anterior epiphysis fused to the centrum, showing that the series came from an adult specimen even though epiphyses are missing on the other vertebrae. These we excavated from sand in bed B1, where they were found associated within a few centimeters of each other but not articulated (meaning we do not know their sequence in life). The centra are large for their length, cylindrical, and match the size and form of *Dorudon atrox*. Each includes at least one of its two transverse processes. These are broad anteroposteriorly, flat dorsoventrally, and angled slightly downward and slightly anteriorly relative to the centrum axis. The neural arch is well preserved on one lumbar in the series (Fig. 5A–B), and this specimen has a neural spine that is elongated anteroposteriorly and compressed bilaterally. It rises to a moderate height dorsally above the centrum.

The other lumbar and anterior caudal centra listed in Table 3 are a little smaller or larger than the centra of DAK-2, but lie within the range of variation expected for *Dorudon atrox*. DAK-23 is a relatively small near-terminal posterior caudal with a centrum tapering posteriorly. This too is similar to terminal caudals found in *D. atrox* in being compressed dorsoventrally relative to its width, indicating that it was in the caudal fluke in life.

Finally, DAK-37 includes the distal end of a rib R1 measuring 26.2 × 35.9 mm in anteroposterior and transverse diameter, respectively, that is the right size to belong to *Dorudon atrox*.

Discussion: Each of the elements described here is indistinguishable in size and shape from the homologous element in a sample of *Dorudon atrox* (Uhen, 2004). We identify the Ad-Dakhla specimens as African *D. atrox* (Andrews) rather than North American *D. serratus* Gibbes because of their provenance and because *D. atrox* is much better known anatomically. The two species *D. atrox* and *D. serratus* are the same size and only questionably distinguishable.

Dorudon atrox is abundant through all Early Priabonian strata in Egypt, and identification of Ad-Dakhla specimens from bed B1 as cf. *D. atrox* is consistent with an Early

Table 3
Measurements (mm) for specimens of cf. *Dorudon atrox*. All are UHC DAK specimens, and adults unless otherwise indicated.
Tableau 3
Dimensions (mm) des spécimens de cf. *Dorudon atrox*. Tous les spécimens (UHC DAK) appartiennent à des individus adultes, sauf indication contraire. L'astérisque indique les mesures estimées.

DAK	Description	Length	Width	Height
2.	Four post. lumbar or ant. caudal vertebral centra	72.5*	84.7	82.3
	(most epiphyses missing)	74.4*	84.8	78.6
	..	74.0*	75.9	78.6
	..	75.0*	81.7	78.4
6.	Post. lumbar or ant. caudal centrum (epiph. missing)	92.3*	87.1*	94.2*
8.	Post. lumbar or ant. caudal centrum (epiph. missing)	80.4*	77.9	73.7
9.	Post. lumbar or ant. caudal centrum (epiph. missing)	77.5*	83.7	72.8
11.	Posterior lumbar centrum (epiphyses missing)	76.4*	95.0	85.1
14.	Middle thoracic centrum (ant. epiphysis missing)	59.3	79.8	60.2
16.	Cervical C7 centrum	40.7	61.6	48.4
17.	Thoracic T1 centrum	41.5	65.6*	45.1
18.	Cervical C3 or C4 centrum	27.0	59.4	53.8
23.	Posterior caudal centrum	26.9	45.5	38.6
26.	Posterior caudal partial centrum	–	–	76.9*
27.	Anterior lumbar partial centrum (epiphyses missing)	68.4*	–	–
28.	Posterior thoracic (epiphyses missing)	60.1	91.5*	71.4
29.	Anterior lumbar	70.6	84.1	67.8
37.	Cervical C7 partial centrum	29.1	–	50.1

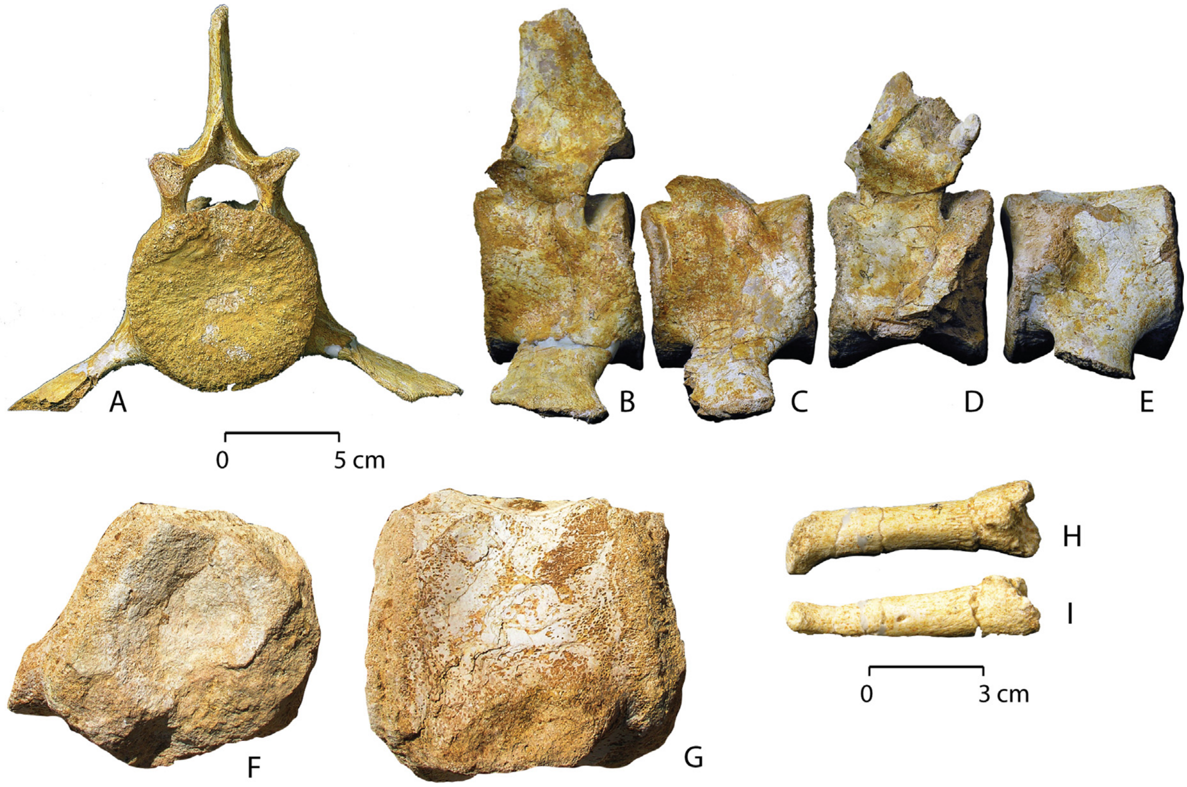

Fig. 5. (Color online.) Specimens of the archaeocetes cf. *Dorudon atrox* and cf. *Dorudon* sp. from Ad-Dakhla. **A–B**. Centrum of posterior lumbar or anterior caudal vertebra of cf. *Dorudon atrox* in anterior and left lateral views (UHC DAK-2); **C–E**. Adjacent posterior lumbar or anterior caudal of the same specimen in left lateral view (UHC DAK-2); **F–G.** Centrum of posterior lumbar or anterior caudal of cf. *Dorudon* sp. in anterior and left lateral view (UHC DAK-42); **H–I**. Proximal phalanx of left digit II (II-1) of cf. *Dorudon* sp. in dorsal and medial view (UHC DAK-4). Note difference in size of the posterior lumbar or anterior caudal vertebrae of the two species. See Tables 3 and 4 for measurements. Proximal phalanx referred to cf. *Dorudon* sp. is similar to *Dorudon atrox* in length but similar to *Basilosaurus isis* in robustness.

Fig. 5. (Couleur en ligne.) Spécimens d'archaeocètes cf. *Dorudon atrox* et cf. *Dorudon* sp. d'Ad-Dakhla. **A–B.** *Centrum* de vertèbre lombaire postérieure ou caudale antérieure de cf. *Dorudon atrox* en vues antérieure et latérale gauche (UHC DAK-2); **C–E.** Vertèbres lombaires postérieures ou caudales antérieures adjacentes du même individu en vue latérale gauche (UHC DAK-2); **F–G.** *Centrum* de vertèbre lombaire postérieure ou caudale antérieure cf. *Dorudon* sp. en vues antérieure et latérale gauche (UHC DAK-42); **H–I.** Phalange proximale du doigt II gauche (Phal. II-1) de cf. *Dorudon* sp. en vues dorsale et médiale (UHC DAK-4). Notez la différence de dimensions des vertèbres lombaires postérieures ou caudales antérieures des deux espèces. Voir les Tableaux 3 et 4 pour les mesures. La phalange rapportée à cf. *Dorudon* sp. a une longueur similaire à celles de *Dorudon atrox*, mais semblable à *Basilosaurus isis* en robustesse.

Priabonian age for the bed. The type specimen of *D. serratus* is also Early Priabonian in age (Uhen, 2013).

cf. *Dorudon* sp.
(Fig. 5F–I)

Referred specimens and measurements: Table 4.

Provenance: Both specimens were found in bed B1 of Adnet et al. (2010).

Description: DAK-42 (Fig. 5F-G) is the centrum of a lumbar vertebra similar in proportion to those of *Dorudon* but substantially larger. The centrum is massive and distinctly amphicoelous in having slightly concave anterior and posterior epiphyses, but little more can be said due to its poor preservation.

DAK-4 (Fig. 5H–I) is the diaphysis of the proximal phalanx of digit II of a left manus. Proximal epiphysis is missing, but the distal end is well formed with an angled distal articular surface very much like that of *D. atrox* illustrated by Uhen (2004: p. 118). The phalanx is here referred to cf. *Dorudon* sp. because the diaphysis is much larger in diameter than its homolog in *Dorudon atrox* (19.8 and 16.7 mm compared to 14.0 and 14.0 mm), and distinctly shorter than its homolog in *Basilosaurus isis* (68.0 mm compared to 83.0 mm).

Discussion: Specimens of cf. *Dorudon* sp. are not very informative, but they do indicate presence of a large *Dorudon*-like species at Dakhla that is intermediate in size between *Dorudon atrox* and *Basilosaurus isis*.

Basilosaurus Harlan, 1834
Basilosaurus isis (Beadnell, in Andrews, 1904)
(Fig. 6)

Referred specimens and measurements: Table 4. Additional specimens were mapped in the field.

Provenance: Both specimens described here came from bed B1 of Adnet et al. (2010), but this or a similar species is also known from bed B2.

Description: DAK-43 is part of an articulated skeleton excavated by commercial collectors. Eight vertebrae representing the posterior lumbar or anterior caudal portion of

Table 4
Measurements (mm) for specimens of cf. *Dorudon* sp. (UHC DAK-4 and 42) and *Basilosaurus isis* (UHC DAK-43and 44). All are adult unless otherwise indicated. UHC DAK-4 is missing the proximal epiphysis. UHC DAK-43 was modified diagenetically during burial in a way that may have affected all of the centrum lengths: these average 320 mm in length (width and height were unmeasureable).
Tableau 4
Dimensions (mm) des spécimens de cf. *Dorudon* sp. (UHC DAK-4 et 42) et *Basilosaurus isis* (UHC DAK-43 et 44). Tous les spécimens appartiennent à des individus adultes, sauf indication contraire. UHC DAK-4 n'a pas d'épiphyse proximale. UHC DAK-43 a été modifié diagénétiquement au cours de l'enfouissement de manière qui pourrait avoir affecté la longueur du *centrum* : sa longueur moyenne est de 320 mm (largeur et hauteur ne sont pas mesurables). L'astérisque indique les mesures estimées.

DAK	Description	Length	Width	Height
4.	Proximal phalanx of digit II (II-1) of the left manus	68.0*	19.8*	16.7*
42.	Posterior lumbar or anterior caudal centrum	136.0	120.0	120.0
43.	Eight posterior lumbar or anterior caudal centra	–	–	–
	"	330.0*	–	–
	"	250.0*	–	–
	"	325.0*	–	–
	"	375.0*	–	–
	"	345.0*	–	–
	"	325.0*	–	–
	"	285.0*	–	–
44.	Two posterior lumbar or anterior caudal centra	320.0	195.0	–
	"	330.0		—

Asterisks indicate estimates.

Fig. 6. (Color online.) Lumbar vertebrae of the archaeocete *Basilosaurus isis* from Ad-Dakhla (UHC DAK-43). Six vertebrae are shown here in a sequence of eight observed in the field. See Table 4 for measurements. Note the large size, the anteroposteriorly short neural spines, and the relatively short prezygapophyses characteristic of *Basilosaurus isis*.
Fig. 6. (Couleur en ligne.) Vertèbres lombaires d'archaeocète *Basilosaurus isis* d'Ad-Dakhla (UHC DAK-43). Six vertèbres sont présentées ici à partir d'une séquence de huit observées sur le terrain. Voir le Tableau 4 pour les mesures. Notez la grande taille des vertèbres, les épines neurales courtes antéropostérieurement et les prézygapophyses relativement courtes caractéristiques de *Basilosaurus isis*.

the skeleton were left in the field. These average 320 mm in centrum length, the neural spine is relatively short anteroposteriorly, and the prezygapophyses end well short of the anterior margin of the centrum.

DAK-44 included several vertebrae that were associated but not articulated. These are similar in size and form to those of DAK-43.

Discussion: Vertebrae of *Basilosaurus* described here match corresponding elements of *Basilosaurus isis* from Egypt in size, neural spine length, and prezygapophysis length. The size of DAK-43 and 44 is an important difference from lumbar and anterior caudal vertebrae of the larger species *Basilosaurus cetoides* (Owen, 1841). The relatively short neural spine (short anteroposteriorly) and the relatively short prezygapophyses ending well short of the anterior margin of the centrum are both important differences from Bartonian *Basilosaurus drazindai* (Gingerich et al., 1997).

Basilosaurus isis is abundant through all Early Priabonian strata in Egypt and Jordan (Zalmout et al., 2000), but it is not known from Bartonian nor from Middle and Late Priabonian strata. Identification of Dakhla specimens from bed B1 as *B. isis* is consistent with an Early Priabonian age for the bed.

SIRENIA Illiger, 1811
Family Dugongidae Gray, 1821
Eosiren Andrews, 1902
cf. *Eosiren* sp.
(Fig. 7)

Referred specimen: UHC DAK-45, a partial skeleton. Additional specimens identifiable as sirenian were mapped in the field.

Provenance: All specimens for which the provenance and identification are known come from bed B2 of Adnet et al. (2010; Fig. 7A), but rib fragments that may be sirenian were also found, rarely, in bed B1.

Description: The best specimen of cf. *Eosiren* sp. known from Ad-Dakhla is DAK-45, which is illustrated in Fig. 7B. This is an association of left and right ribs. Most are moderate in size and osteosclerotic, but several are also pachyostotic like the anteriormost ribs of *Eosiren*. The largest of these measure 38 × 34 mm and 40 × 35 mm in transverse diameter. None of the ribs is complete, so it is not possible to give a length for these.

Discussion: DAK-45 is an association of left and right ribs similar in size and form to those of *Eosiren libyca* from Middle Priabonian deposits of Egypt (Zalmout and Gingerich, 2012). The preserved pieces are insufficient to be certain of their identification.

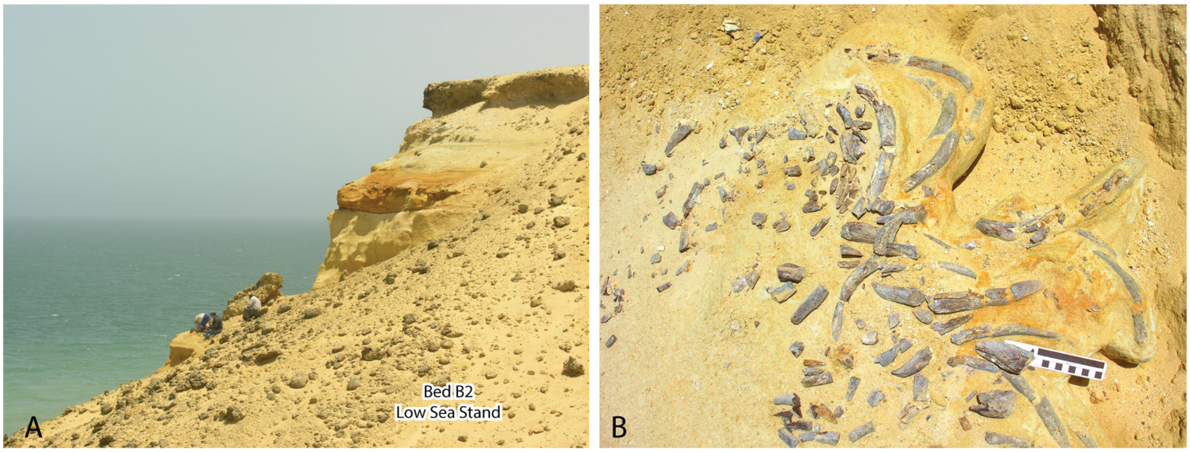

Fig. 7. (Color online.) Ribs of the dugongid cf. *Eosiren* sp. from Ad-Dakhla (UHC DAK-45). **A.** Location of specimen where collectors are working in bed B2 on a cliff above the Atlantic Ocean; **B.** specimen as found in the field, with left and right ribs mixed together. Measurements are given in the text. Note thick rib ends typically found on the most anterior vertebrae of *Eosiren*.

Fig. 7. (Couleur en ligne.) Côtes de dugongidé cf. *Eosiren* sp. d'Ad-Dakhla (UHC DAK-45). **A.** Emplacement de l'échantillon dans le niveau fossilifère B2 dans une falaise surplombant l'océan Atlantique; **B.** Le même échantillon tel qu'il a été trouvé sur le site, avec des côtes gauches et droites mélangées. Les mesures sont indiquées dans le texte. Notez la grande épaisseur des extrémités des côtes caractéristiques des vertèbres les plus antérieures du genre *Eosiren*.

The ribs of DKA-45 are osteosclerotic throughout, meaning that they fragment into pieces when exposed by erosion. One neural spine was found embedded in sand with the ribs, suggesting that vertebrae may have been part of the specimen when it was buried. If so, then these have either been destroyed by erosion or removed by commercial collectors.

5. Discussion

Measurements for Ad-Dakhla archaeocete lumbar and anterior caudal vertebrae given in Tables 1–4 are plotted on natural logarithmic axes in Fig. 8, where the vertebrae form clusters. Ellipses approximate a 95% confidence range for each cluster. These ellipses span 0.6 units on the length axis and 0.4 units on the width axis, reflecting the scatter observed in 75 posterior thoracic, lumbar, and anterior caudal vertebrae in five specimens of *Dorudon atrox* from Egypt (measurements in Uhen, 2004). Ellipses represent the scatter to be expected in archaeocete species of any size when represented on logarithmic axes. There are clearly a minimum of five species represented: cf. *Saghacetus* sp., cf. *Stromerius* sp., cf. *Dorudon* sp., and *Basilosaurus isis* do not overlap at all, and the range of variation in the overlapping cf. *Stromerius* sp. and cf. *Dorudon atrox* clusters is too great to represent a single species. All five of these species were found in bed B1, and *Basilosaurus isis* was found in bed B2 as well.

The basilosaurid partial tooth illustrated by Adnet et al. (2010) is similar in size to P^3or P^4 of *Saghacetus osiris*, but it is conspicuously lower crowned. It is probably a dP^3 or dP^4 of cf. *Stromerius* sp. Identification of three basilosaurid species from the Samlat Formation, *Basilosaurus* sp., *Dorudon* sp., and a small basilosaurid (Field et al., 2011), is confirmed, with the addition of a fourth small basilosaurid species, a fifth intermediate basilosaurid species, and a sirenian. It is not clear, contrary to Uhen's

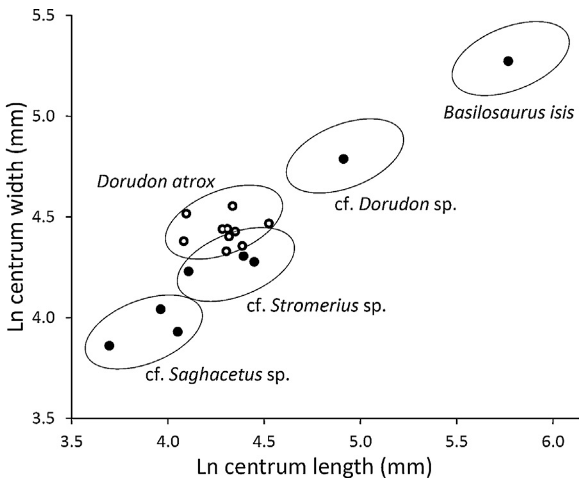

Fig. 8. Relative sizes of vertebrae representing five species of archaeocete cetaceans from Dakhla. Measurements of centrum length (abscissa) and centrum width (ordinate) are plotted for lumbar and anterior caudal vertebrae (Tables 1–4). Ellipses approximate expected 95% confidence intervals (see text). Length is more variable than width because within a species length changes more than width from centrum to centrum along the vertebral column. Note the clear separation of cf. *Saghacetus* sp., cf. *Stromerius* sp., cf. *Dorudon* sp., and *Basilosaurus isis* (filled circles). Note too the overlapping variability of cf. *Stromerius* sp. and cf. *Dorudon atrox* (open circles).

Fig. 8. Dimensions relatives des vertèbres de cinq espèces d'archéocètes de Dakhla. Diagramme des longueurs (abscisses) et largeurs du *centrum* (ordonnées) des vertèbres lombaires et caudales antérieures (Tableaux 1–4). Les ellipses montrent les intervalles de confiance à 95 %. La longueur est plus variable que la largeur parce qu'au sein d'une même espèce, la longueur varie plus que la largeur d'un centrum à l'autre le long de la colonne vertébrale. Notez la séparation claire des différents taxons : cf. *Saghacetus* sp., cf. *Stromerius* sp., cf. *Dorudon* sp. et *Basilosaurus isis* (cercles pleins). Notez aussi le chevauchement de la variabilité des deux taxons cf. *Stromerius* sp. et cf. *Dorudon atrox* (cercles ouverts).

2010 entries in the Paleobiology database that the three species of Field et al. (2011) come from bed B1 and from bed B2. The dugongid sirenian cf. *Eosiren* is known with certainty only in bed B2.

The depositional environment at Ad-Dakhla parallels that near the base of the Qasr el-Sagha Formation in Egypt (Peters et al., 2009) in the sense that a marine sequence (units 1 and 2 of Adnet et al., 2010) is interrupted by a coarser clastic unit (bed B1) that is rich in bones that are abraded and reworked in some cases, but fresh and intact in others. The difference is that the rhythmically bedded siltstone with gray chert and marl of the Samlat Formation on the Dakhla coast was deposited in deeper water (Decker, 1991), but in both cases the coarser clastic unit represents a temporally-condensed interval related to substantial lowering of sea level. Bones that are reworked and broken were eroded from an earlier nearshore shelf environment higher on the shoreline, and bones that are fresh and intact were deposited locally where a nearshore shelf environment replaced deeper water sediment accumulation.

This is important because there are relatively few low sea stands in the Priabonian. Peters et al. (2009) concluded that the low sea stand in Egypt mixing larger and older *Dorudon* and *Basilosaurus* archaeocetes with smaller and younger *Saghacetus* and *Stromerius* archaeocetes is Pr-2, which separates the Early and the Middle Priabonian (see also Gingerich et al., 2012). Adnet et al. (2010) regarded the interval, unit 2, spanning fossiliferous beds B1 and B2, as probably Late Eocene in age. Here we go farther and, on the basis of the archaeocete association, correlate bed B1 with the Pr-2 low sea stand in Egypt. We cannot prove that two or more marine mammal faunas are mixed in Ad-Dakhla bed B1 but we suspect this from similarity to the taxonomically mixed fauna in Pr-2 in Egypt; from similarity to the taphonomically mixed collection of abraded and reworked vertebrae in Pr-2 in Egypt, with fresher material including partially articulated and associated skeletons; and from the mixture of reworked early Middle Eocene and Late Eocene sharks at Ad-Dakhla reported by Adnet et al. (2010).

Adnet et al. (2010) reported that Ad-Dakhla beds B1 and B2 yield the same species assemblages of sharks. These beds are separated by 2-5 meters of rhythmically-bedded siltstone with gray chert and marl, indicating a return to deeper water deposition farther offshore (Decker, 1991). The rhythmically-bedded unit required a substantial amount of time to accumulate. Gypsum in the Garitas section (Fig. 2B) suggests a lagoonal environment with evaporates. Gypsum is found in the transition from offshore marine strata overlying bone bed B1 to the nearshore sands of bone bed B2. We cannot estimate the time difference between bone beds B1 and B2, but the mammalian fauna of bed B2 is conspicuously different from that of bed B1, being dominated by dugongid sirenians rather than archaeocete cetaceans. Bone bed B2 probably represents a second low sea stand, either a later phase of Pr-2 in the Middle Priabonian, or possibly Pr-3 separating the Middle and the Late Priabonian. Bed B2 does not have the taxonomic mixture of archaeocetes seen in bed B1, nor does it have the same taphonomic mixture of abraded and fresher specimens.

Acknowledgments

We thank G. Bianucci and an anonymous referee for careful reviews of the manuscript. Mr. Amer and Mr. Mohamed helped in the field. W. Sanders provided help cleaning fossils and B. Miljour provided help in assembling figures. This research was supported by grant 9202-12 from the National Geographic Society and by grant EAR-0920972 from the U.S. National Science Foundation.

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