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A delphinid mandible from the Lower Pliocene of Morocco: further fossil evidence of high dietary niche partitioning in true dolphins

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KEY WORDS - Cetacea, Globicephalinae, Pliocene, North Africa, paleoecology.

ABSTRACT - We describe a left mandible of Delphinidae (Cetacea, Odontoceti) from the Lower Pliocene of the Asilah Basin, northwestern Morocco. Despite its fragmentary nature, the specimen reveals key morphological features that support affinities with extant Globicephalinae, i.e., a short mandibular symphysis; a reduced alveolar portion; and a posteroalveolar portion characterized, laterally, by a nearly straight dorsal margin and a ventral margin that sharply curves posteroventrally. However, the Asilah mandible differs from all known extant and fossil globicephalines in its unique character combination, and therefore is here referred to Globicephalinae gen. and sp. indet. pending the discovery of more complete materials. The overall morphology of the reconstructed Asilah mandibles implies a feeding strategy intermediate between suction and grasping. Therefore, this fossil seemingly provides further evidence of a Pliocene generalist delphinid lacking specialized features towards either suction or macropredation, which in turn would have evolved independently multiple times across the family. More generally, this record further supports a high disparity within Delphinidae as early as in Pliocene times, which may correlate with high dietary niche partitioning.

INTRODUCTION

Delphinidae Gray, 1821 (true or oceanic dolphins) constitutes the most diverse family within the suborder Odontoceti Flower, 1867 (toothed whales), with over 35 extant species exhibiting a remarkable range of morphological, ecological and behavioral adaptations. Their evolutionary success is reflected in their global distribution –ocean dolphins inhabit pelagic, coastal and even riverine environments– as well as in their specialization for varied feeding strategies, ranging from macroraptoriality to suction feeding (Jefferson & LeDuc, 2018; Galatius et al., 2020; McGowen et al., 2020).

Molecular phylogenies estimate the origin of crown Delphinidae to have occurred during the Late Miocene, between 12 and 9 million years ago (Steeman et al., 2009; McGowen et al., 2020), a period marked by widespread cetacean diversification. Despite this relatively recent radiation, unambiguous delphinid fossils from pre-Pliocene deposits remain exceptionally rare (Barnes,1976; Murakami et al., 2014; Kimura & Hasegawa, 2020). In contrast, Pliocene deposits have yielded abundant delphinid fossils, providing key insights into the early stages of this group's radiation. However, the spatial distribution of these finds is highly uneven, with most discoveries originating from Italy (Bianucci, 1996, 1997, 2005, 2013; Bianucci et al., 2009) and, subordinately, from eastern and western North Atlantic coasts (Post & Bosselaers, 2005; Whitmore & Kaltenbach, 2008; Post & Kompanje, 2010; Bakker & Post, 2020; Belluzzo & Lambert, 2021). More punctual but significant Pliocene delphinid records come from Mexico (Aguirre-Fernández et al., 2009), East Antarctica (Fordyce et al., 2002) and Peru (Pilleri & Siber, 1989).

Undoubtedly, fossil remains of Delphinidae are very rare in North Africa and are all based on fragmentary remains (e.g., isolated periotics), some of which have no diagnostic value (e.g., isolated teeth) and/or have been only briefly mentioned in faunal lists with no accompanying illustrations and descriptions (Fourtau, 1920; Whitmore, 1987; Geraads et al., 1998; Geraad, 2006; Gingerich, 2010).

In particular, the only known fossil remains referred to Delphinidae to have been discovered in Morocco consist of some periotics and mandibular fragments referred to *Delphinus* sp. or *Stenella* sp. from the earliest Pleistocene (ca 2.5 Ma) paleontological site of Ahl al-Oughlam, located just outside Casablanca (Geraads et al., 1998; Geraads, 2006). To date, these finds have not been described, nor figured.

The aim of this study is to describe an isolated delphinid mandible from the Lower Pliocene of the Asilah Basin, northwestern Morocco. The peculiar morphology of this almost complete mandible provides the opportunity to make detailed comparisons with the wide variety of delphinid mandible morphologies, both extant and fossil, and consequently to formulate considerations on the trophic role of the Asilah dolphin.

MATERIALS AND METHODS

Fossil mandible from Asilah

The dolphin mandible described herein is stored within the paleontological collections of the Department of Geology of the Faculty of Sciences Aïn Chock, Hassan II University of Casablanca, Morocco. Its catalogue number is FSAC As-0.

Institutional abbreviations

AMNH: American Museum of Natural History, USA; FCR: Fondazione Cetacea onlus, Riccione, Italy; FSAC:

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Faculty of Sciences Aïn Chock, Hassan II University of Casablanca, Morocco; IGF: Museo di Geologia e Paleontologia, Università di Firenze, Italy; IRSNB: Institut Royal des Sciences Naturelles de Belgique, Belgium; MCSNC: Museo Civico di Storia Naturale di Comiso, Italy; MGGC: Collezione di Geologia "Museo Giovanni Capellini", Università di Bologna, Italy; MHNP: Museum National d'Histoire Naturelle, France; MMPS: Stamatiadis Museum of Mineralogy and Paleontology, Rhodes, Greece; MPST: Museo paleontologico "Il Mare Antico", Salsomaggiore Terme, Italy; MPTAM: Museo Paleontologico Territoriale dell'Astigiano e del Monferrato, Asti, Italy; MRSNT: Museo Regionale di Storia Naturale di Torino, Italy; MSNUP: Museo di Storia Naturale, Università di Pisa, Italy; MZUF: Museo di Zoologia, Università degli Studi di Firenze, Italy; NNML: Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; USNM: National Museum of Natural History, USA; ZMA: Zoölogisch Museum Amsterdam, Amsterdam, The Netherlands (collections now at NNML).

Anatomical terminology

The anatomical terminology follows Mead & Fordyce (2009).

Measurements

Measurements were taken with a caliper to the nearest 0.1 mm.

Specimens directly observed for systematic comparison

Arimidelphis sorbinii Bianucci, 2005 (MSNV SAE 39756); *Astadelphis gastaldii* (Brandt, 1874) (MGGC 8572; MRSNT PU13883; PU13884); *Cephalorhynchus commersonii* (Lacépède, 1804) (IRSNB 21143, 395353, 550449; ZMA 24934); *Cephalorhynchus heavisidii* (Gray, 1828) (NNML 24759, 24760, 24761); *Cephalorhynchus hectori* (Van Beneden, 1881) (MSNUP C292ZMA 15210); *Delphinapterus leucas* (Pallas, 1776) (MSNUP C276, C277); *Delphinus delphis* Linnaeus, 1758 (IRSNB 1519, 33388; MHNP A3072, A3078; MSNUP C286, C289; NNML 31199; MZUF 12484, 1338); *Etruridelphis giulii* (Lawley, 1876) (IGF 1541V, 8736V; MSNUP I15458); *Feresa attenuata* Gray, 1874 (USNM 484995, 550389, 571268; ZMA 22687); *Globicephala macrorhynchus* Gray, 1846b (MZF 9747; USNM 500247, 504396, 571006, 571933; ZMA 1908, 8871, 8872, 8873, 8875); *Globicephala melas* (Traill, 1809) (IRSNB 1514, 1514B, 1514Y; MHNP 1977-29; MSNUP C302; MZUF 12030, 12510; NNML 31214, 34692, 34692; ZMA 1888, 8055); "*Globicephala*" *etruriae* Pilleri, 1987 (IGV 1675V); *Grampus griseus* (Cuvier, 1812) (MSNUP C294, C295, C296, C297; NNML 31212; USNM 572313, 572921); *Hemisyntrachelus cortesii* (Fischer, 1829) (MGGC 8548, 8547, 8566; MGPT PU 13874, PU 13882; MPST 24059, 240510); *Hemisyntrachelus pisanus* Bianucci, 1996 (MGGC 8560); *Lagenodelphis hosei* Fraser, 1956 (USNM 550022; ZMA 22680); *Lagenorhynchus albirostris* Gray, 1846a (IRSNB 22334, 32196, 35446, 39002, 39141; MSNUP C291); *Lagenorhynchus harmatuki* Whitmore & Kaltenbach, 2008 (USNM 163062, 182914, 183062, 206098, 244317); *Leucopleurus acutus* (Gray, 1828) (IRSNB 1527, 34514; MHNP A3042; NNML 31211; USNM 14312, 14313, 14314, 14315, 200342); *Lissodelphis borealis* (Peale, 1848) (USNM 550027, 550188; ZMA 24439, 84259); *Lissodelphis peronii* (Lacépède, 1804) (MHNP BII-67); *Monodon monoceros* Linnaeus, 1758 (MSUP C274, C275); *Neophocaena phocaenoides* (Cuvier, 1829) (MSUP C279); *Orcaella brevirostris* (Owen in Gray, 1866a) (IRSNB 1512; MSNUP C293; USNM 199743); *Orcinus citoniensis* (Capellini, 1883) (MGGC 8560); *Orcinus orca* (Linnaeus, 1758) (MHNP A3231, A3234; MSNUP C298, C301; NNML 169, 6974, 31219, 31220, 31221; ZMA 13489); *Phocena phocoena* (Linnaeus, 1758) (MSNUP C278); *Peponocephala electra* (Gray, 1846b) (USNM 504948, 550399; ZMA1179, 15956, 15960, 15961, 15962); *Pseudorca crassidens* (Owen, 1846) (MHNP1993-66; MSNUP C300; NNML 2236, 2393; USNM 219325; ZMA 12897, 12898, 21897, 25223); *Rododelphis stamatiadisi* Bianucci et al., 2022 (MMPS 544); *Sagmatias australis* (Peale, 1848) (MHNP A3041); *Sagmatias obliquidens* (Gill, 1865) (USNM 550834, 550913, 550914); *Sagmatias obscurus* (Gray, 1828) (IRSNB 1525, 21371, 21372; NNML 24764); *Septidelphis morii* Bianucci, 2013 (MPTAM 216.1330); *Sotalia* spp. (IRSNB 1516, 20137; MHNP 1888-791, 1888-793, 1928-211; NNML 21756; USNM 571558; ZMA 19780); *Sousa* spp. (MHNP 1993-88; NNML 40059; USNM 258859, 550941; ZMA 13323, 20725); *Stenella attenuata* (Gray, 1846a) (MHNP A3029, A3029, A3030, 1977-26; NNML 21634); *Stenella coeruleoalba* (Meyen, 1833) (MSNUP C288); *Stenella frontalis* (Cuvier, 1829) (IRSNB 1524; MHNP A3031, 1882-94; NNML 24765; ZMA 22963); *Stenella longirostris* (Gray, 1828) (MHNP 1981-159; NNML 24575; ZMA 19462); "*Stenella*" *rayi* Whitmore & Kaltenbach, 2008 (USNM 182930); *Steno bredanensis* (Cuvier in Lesson, 1828) (MCSNC 3404, 3405; IRSNB 1515B, 1515C; MHNP A-3047, A-3048, A-3050, A-3052, 1866-150, 1921-297, 1965-209, 31175, 31177, 31178; ZMA 7889); *Tursiops aduncus* (Ehrenberg in Hemprich & Ehrenberg, 1832) (NNML 12715); *Tursiops truncatus* (Montagu, 1821) (FCR ER01, ER05, ER07, ER09, ER10, MA01, VE01; MSNUP C280, C281, C284, C285; MZF 17833); "*Tursiops*" *osennae* Simonelli, 1911 (MGGC 8561-8562).

GEOLOGICAL AND STRATIGRAPHIC SETTING

The delphinid mandible described herein was discovered during construction works along the high-speed train line connecting Tangier to Casablanca. The specimen was found at a site located approximately 2 kilometers northeast of Asilah (N 35°29'43.77" - W 5°58'51.04") (Fig. 1). The latter town lies about 46 kilometers south of Tangier, on the Atlantic coast of the Tangier Peninsula, northwestern Morocco.

The small Asilah Basin belongs in the "External Rif" Unit. Generally speaking, Neogene deposits in the western region of northern Morocco are mainly situated along the periphery of the Rif Chain. These deposits are particularly well developed within the South Rifian Trough, which separates the Rif Chain from the Meseta and Middle Atlas. Here, various Neogene units can be distinguished, first and foremost by their sedimentological characteristics and paleontological content (Fig. 1a).

South of Tangier, Neogene deposits are exposed in two main basins: 1) the Charf el Akab Basin, which excavates the marls of the Tangier Unit, and 2) the smaller Asilah Basin, located just south of the aforementioned. The Charf el Akab Basin, about 20 kilometers south of Tangier, contains Upper Miocene detrital sediments and fine-grained Pliocene deposits overlain by calcarenites. This area has yielded a relatively abundant, though low-diversity, invertebrate macrofauna (Lamarti-Sefiane et al., 1997).

The Asilah Basin lyes south of Charf el Akab and extends toward the northern edge of the Rharb Basin. It is mostly filled with Lower Pliocene fine sands with lateral transitions into marls. These deposits can be distinguished from those of Charf el Akab by their richer and more diverse paleontological content (Ben Moussa, 1994). In the Asilah Basin, the Lower Pliocene deposits are mainly known from drilling, and represent a complete sedimentary cycle (Nachite, 1993).

The basin fill begins with yellowish to reddish sands, rich in pebbles and devoid of fossils, which unconformably overlie the substrate, outcropping along the eastern margin of the basin. The thickness of these basal sands does not exceed 10 meters. Toward the center of the basin, at depths of about 30 meters, these strata transition into gray, clayey sands. These are still pebble-rich, but containing very few fossils, indicating a shallow-marine environment. Above these are gray clays, which deposited in an outer sublittoral setting during a maximum transgression, reaching up to 20 meters in thickness in the central portion of the basin (Fig. 1b). The succession ends with yellow, fossil-rich, sandy clays, up to 10 meters thick, which deposited in an inner

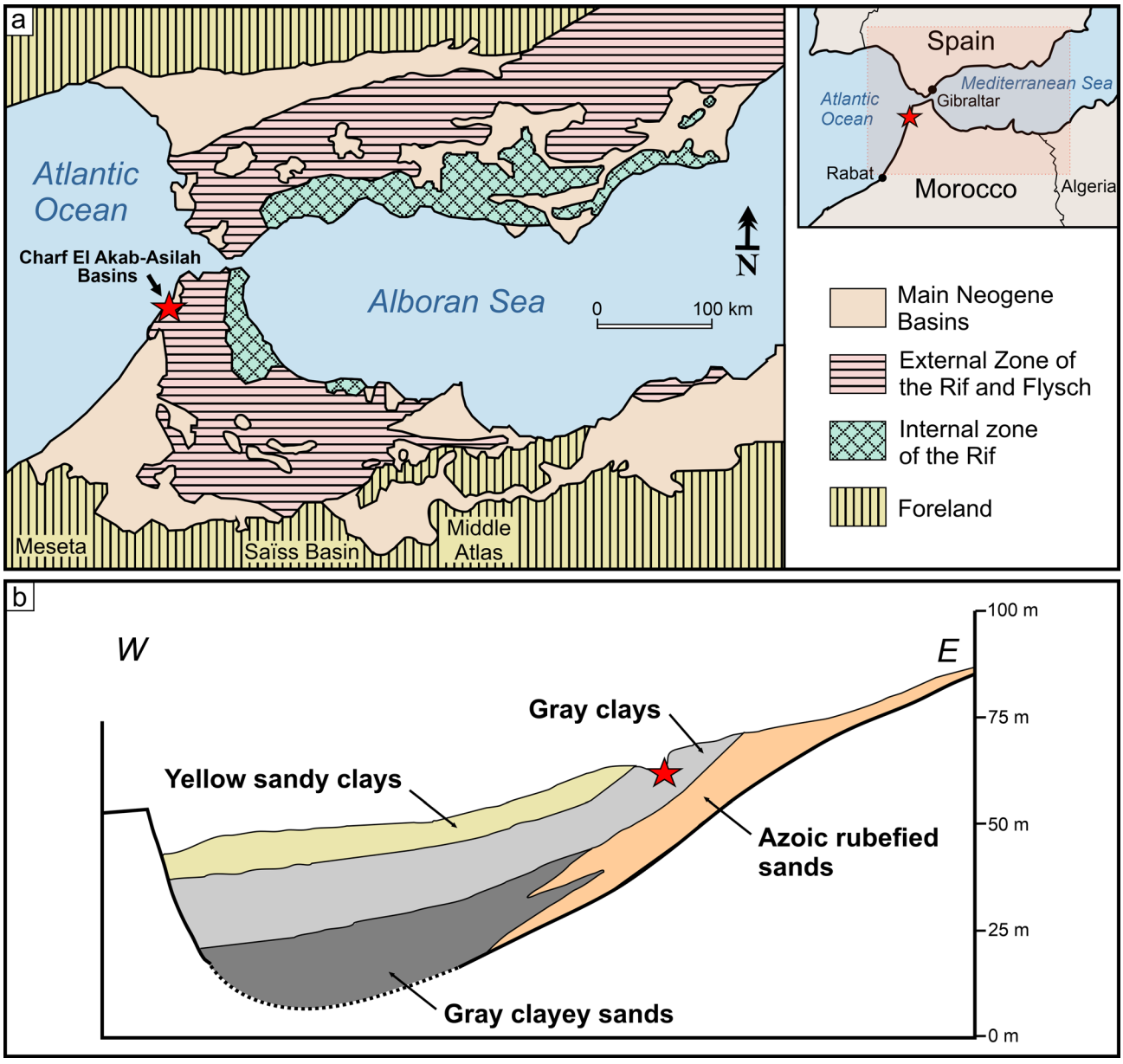

Fig. 1 - (color online) a) Schematic geological map of the Atlantic-Mediterranean area around the Strait of Gibraltar, showing the location (red star) of the Asilah Basin where the FSAC As-01delphinid mandible was found. b) Stratigraphy of the upper Neogene deposits of the Asilah Basin, showing the location of FSAC As-01. Modified and redrawn from Nachite & Bekkali (2010: fig. 2).

sublittoral environment. A diverse ostracod assemblage, including more than fifty identified species, supports the attribution of the Asilah Basin deposits to the Lower Pliocene (Nachite & Bekkali, 2010).

The mandible dealt with herein was recovered from highly fossiliferous, slightly sandy, gray to bluish clays exposed on both sides of the national road P2 (Fig. 1b). East of the road and the railway line, the deposit reaches a thickness of about 10 meters, beginning with a few meters of clayey sands that grade into gray, sandy clays. These fossil-rich layers contain pectinids, ostreids, barnacles, bryozoans, cetacean bones, and a relatively diverse assemblage of benthic foraminifera (*Ammonia*, *Elphidium*, *Lobatula*, *Nonion*, etc.) (Nachite & Bekkali, 2010).

SYSTEMATIC PALEONTOLOGY

Cetacea Brisson, 1762
Odontoceti Flower, 1867
Delphinidae Gray, 1821
Globicephalinae Gray, 1866 sensu McGowen et al., 2020

Genus and species indet.
(Fig. 2; Tab. 1)

Referred specimen - FSAC As-01, a nearly complete left mandible (Fig. 2). The proximal portion, including the coronoid process and mandibular condyle, is missing. Additionally, the medial wall of the posterior part of the mandibular canal is largely missing, with only a small posterior portion of both the dorsal and ventral margins of the mandibular foramen being preserved. The posteroalveolar portion of the mandible exhibits significant post-mortem lateromedial compression, which caused extensive fracturing, particularly with respect to the lateral wall of the mandibular fossa.

Shape reconstruction and size estimation - To reconstruct the missing portions of FSAC As-01, we compared its outlines in dorsal and ventral views with those of morphologically similar extant delphinids (e.g., *Feresa attenuata*, *Globicephala* spp. and *Orcaella* spp.). The posterodorsal region was reconstructed based on the preserved dorsal margin of the mandibular foramen, which indicates that the coronoid process was entirely absent, as this margin typically does not extend beneath the coronoid process. Due to the absence of the mandibular condyle, we cannot exclude the possibility that it was more posteriorly prominent than reconstructed; if so, our estimate of mandibular length may be slightly underestimated. Based on this reconstruction, the total estimated mandibular length is approximately 400 mm.

In ventral view, the medial margin of the mandibular foramen was reconstructed using the inclination of the preserved dorsal and ventral tracts, as well as the posterior extent of the partially preserved medial mandibular wall.

Using a dorsal view photograph, we digitally reconstructed the articulated mandibles, correcting for post-mortem deformation in the posteroalveolar region, and mirroring the left mandible to approximate the right (Fig. 2a4). This reconstruction indicates that the mandibular rami form a symphyseal angle of 38 degrees, suggesting that the rostrum of the cranium was likely short and broad at its base. The estimated distance between the lateral margins of the reconstructed mandibular condyles (i.e., the mandibular width) is 298 mm, a value intermediate between *Grampus griseus* and *Feresa attenua* among extant short-mandibled delphinids. Given that the mandibular width closely approximates the bizygomatic width of the skull, which in turn provides a reliable proxy for body size, we infer that the Asilah dolphin was intermediate between the modern species *G. griseus* and *F. attenuata* in terms of body size, thus likely measuring around 2.5-3 meters in total length.

Description - FSAC As-01 represents a short, relatively robust delphinid mandible (Fig. 2a1). The mandibular symphysis is notably short, comprising approximately 11% of the estimated total mandibular length (Fig. 2a2). In occlusal view, the symphysis is rhomboidal in outline, with its dorsoventral and anteroposterior dimensions being approximately equal to each other (Fig. 2a3). Its surface is marked by deep and irregular sulci. The symphyseal region is strongly compressed mediolaterally, with the gnathion (i.e., the most ventral point of the symphysis) forming a distinct ventral projection that is clearly visible in lateral view.

Posterior to the symphysis, two closely spaced mental foramina pierce the lateral surface of the mandible, each being followed by a shallow posterior groove (Fig. 2a1). A longitudinal fracture running along the foramina and their associated grooves precludes a more precise description of the morphology and dimensions of these anatomical features. The mandibular height at the posterior end of the symphysis, corresponding to the minimum height of the mandible, represents approximately 11% of the estimated mandibular length.

Fifteen alveoli are preserved in occlusal view, ranging from ~7 to 12 mm in transverse diameter, with the largest alveolus accounting for 4% of the total estimated mandibular width (Fig. 2a2, a5). Although the anterior alveoli are partially eroded, the preserved portions suggest that the teeth became progressively more laterally oriented anteriorly, which in turn reflects a slight clockwise torsion of the anterior alveolar portion relative to the main axis of the mandible. The anteriormost well-preserved alveolus, measuring 10 mm in transverse diameter, is close to the symphysis, and appears to have housed an anterodorsally directed tooth. The alveolar portion comprises approximately 41.5% of the total estimated mandibular length.

The dorsal margin of the posteroalveolar portion is nearly straight, forming an angle of 174 degrees with the line connecting the first and last alveoli (Fig. 2a1). The precoronoid crest is very low (i.e., barely discernible) in lateral view and formed by a thin lamina. It is followed posteriorly by a coronoid crest that rises slightly dorsally toward the missing coronoid process. A second parallel crest, located ~1 cm lateral to the coronoid crest, likely represents an attachment site for the musculus temporalis. This lateral crest becomes more pronounced posteriorly, but is interrupted near the broken margin anterior to the missing coronoid process.

The lateral wall of the posteroalveolar portion is thin and convex laterally, delimiting the lateral margin of the

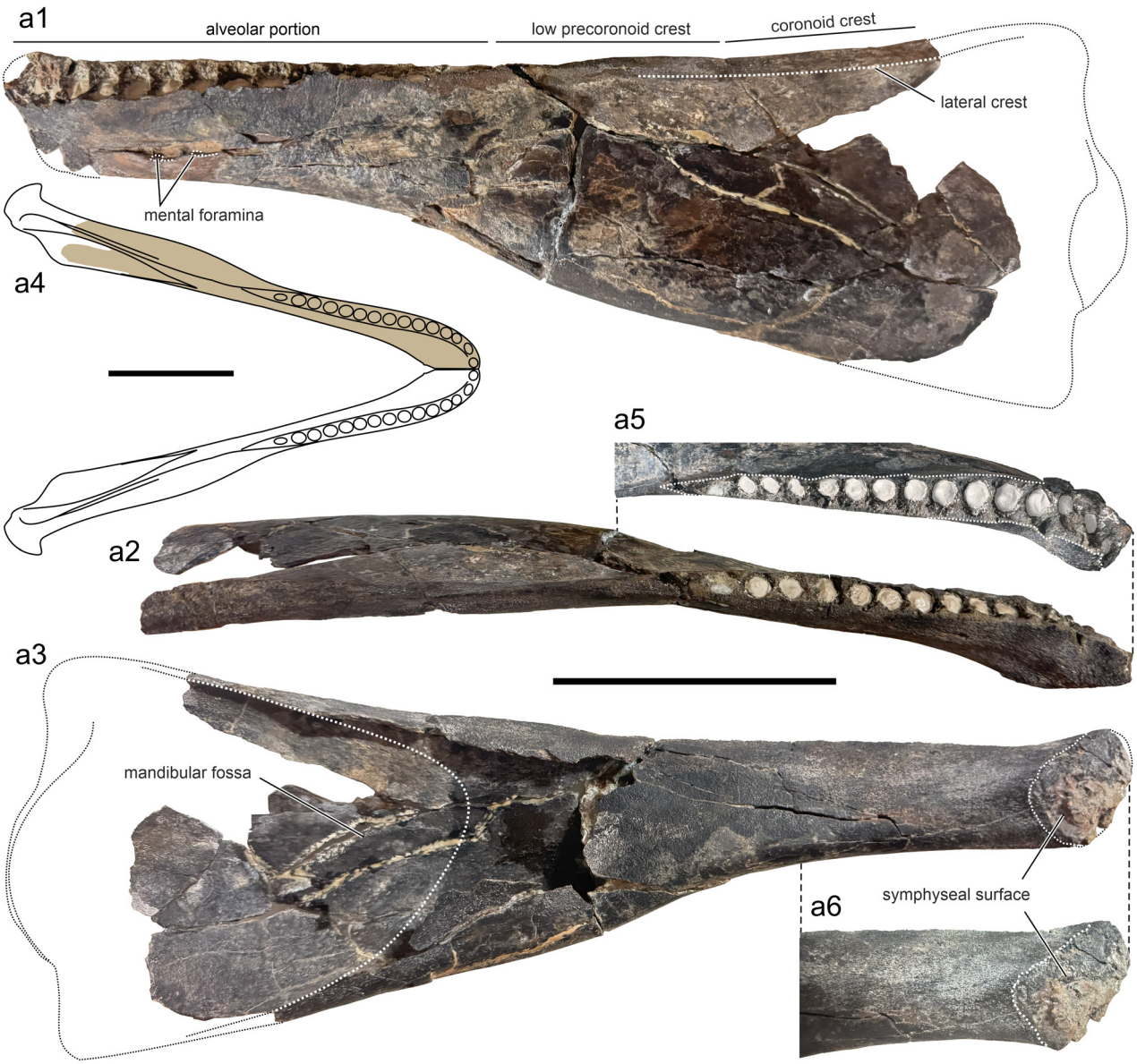

Fig. 2 - (color online) Left delphinid mandible (FSAC As-01) of Globicephalinae genus and species indet. from the Lower Pliocene of the Asilah Basin, Morocco in lateral (a1), occlusal (a2) and medial (a3) views. a4) Interpretive reconstruction of the articulated right and left mandibles in occlusal view. a5) Close-up of the alveolar row in dorsolateral view. a6) Close-up of the symphyseal region in medial view. Dashed lines indicate interpretative outlines of missing or poorly defined areas. Scale bars equal 5 cm.

mandibular fossa. The partially reconstructed medial margin of the mandibular foramen defines a fossa that does not extend far anteriorly (Fig. 2a3). Indeed, the preserved ventral half of the medial margin does abruptly bend anterodorsally, thus preventing a significant anterior extension of the mandibular fossa.

Unlike the nearly straight dorsal margin, the ventral margin of the posteroalveolar portion sharply curves posteroventrally, thus producing an overall strongly concave ventral profile.

Comparisons - FSAC As-01 shares several morphological features with most members of the delphinid subfamily Globicephalinae (sensu McGowen et al., 2020) as well as with certain brevirostrine members of Phocoenidae (e.g., *Phocoena* spp.) and Monodontidae (e.g., *Haborodelphis japonicus* Ichishima et al., 2019), including a markedly short mandibular symphysis, a reduced alveolar portion, and a posteroalveolar portion that is characterized by a nearly straight dorsal margin as well as by a ventral margin that sharply curves posteroventrally in lateral view. However, all known phocoenids possess significantly smaller teeth, and therefore alveoli, than FSAC As-01, and all known both phocoenids and monodontids have anterolaterally oriented anterior teeth. The latter difference reflects the fact that the mandibles of phocoenids and monodontids lack the clear anticlockwise torsion of the alveolar portion that in turn characterizes the mandibles of Delphinidae, and Globicephalinae in particular.

Measurements	mm
Total length as preserved	362
Total length estimated	400
Length of symphyseal portion	43
Height of mandible at the posterior end of symphysis	43
Length of alveolar row	166
Height of mandible at posterior end of alveolar row	66

Tab. 1 - Measurements (in mm) of the left delphinid mandible (FSAC As-01) from the Lower Pliocene of the Asilah Basin, Morocco.

Among extant globicephalines, *Feresa attenuata*, *Globicephala macrorhynchus*, *G. melas*, *Grampus griseus*, *Orcaella brevirostris*, *O. heinsohni* Beasley et al., 2005 and *Peponocephala electra* share the same general mandibular morphology as FSAC As-01 (Fig. 3). Nevertheless, FSAC As-01 differs from all of these taxa in exhibiting a proportionally greater mandibular height at the posterior end of the symphysis. It also differs from all of the aforementioned species but *Orcaella* spp. in possessing a mandibular fossa that extends less anteriorly and is bordered anteromedially by a more rounded margin of the mandibular foramen. Additionally, in most observed mandibles of *G. macrorhynchus*, *G. melas*, *G. griseus* and *P. electra*, the coronoid crest rises more weakly, often remaining nearly horizontal, thus contrasting with the condition observed in FSAC As-01, where it ascends more steeply.

Other differences between FSAC As-01 and these extant globicephalines are reported below, being also quantified in the box-plots of Fig. 4, which illustrate key measurement ratios.

1. *Feresa attenuata* (Fig. 3b) - This species differs from FSAC As-01 in its smaller overall size (maximum mandibular length slightly over 300 mm), lower tooth count, relatively longer alveolar portion and larger alveoli. That said, the relative symphyseal length of FSAC As-01 lies at the lower end of the range observed in *F. attenuata*.

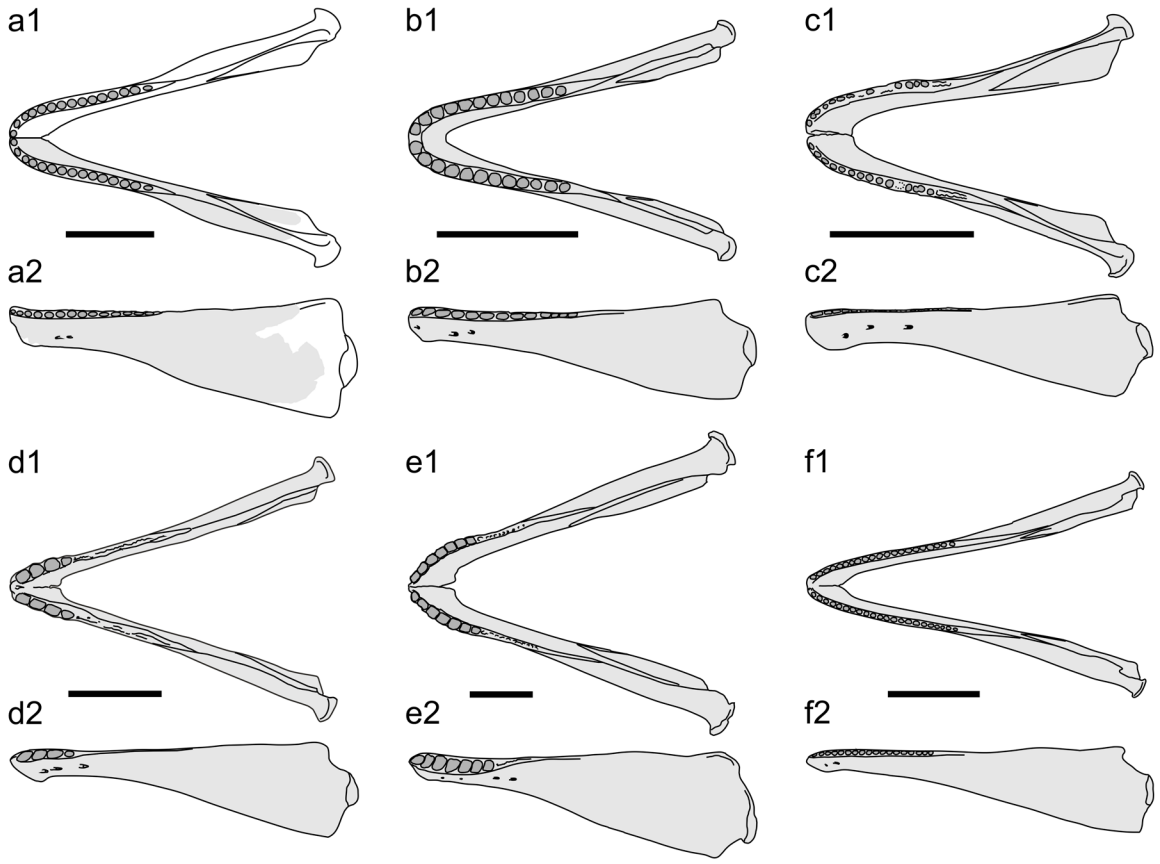

Fig. 3 - Comparisons between the articulated mandibles in dorsal (1) and lateral (2) views of the delphinid from the Lower Pliocene of the Asilah Basin, Morocco, and some roughly similar extant Globicephalinae. a) Globicephalinae genus and sp. indet. (FSAC As-01), white areas correspond to reconstructed parts. b) *Feresa attenuata* (USNM 484995). c) *Orcaella brevirostris* (USNM 199743). d) *Grampus griseus* (USNM 572313). e) *Globicephala macrorhynchus* (USNM 571933). f) *Peponocephala electra* (USNM 550399). Scale bars equal 10 cm.

2. *Globicephala macrorhynchus* (Fig. 3e) and *G. melas* - These species are larger (mandibular length ~500 mm) and exhibit a more elongate symphysis, shorter alveolar portion, lower tooth count and proportionally smaller alveoli than FSAC As-01.

3. *Grampus griseus* (Fig. 3d) - The mandible of this species differs from FSAC As-01 in its longer symphysis, shorter alveolar portion, proportionally larger alveoli, and much lower tooth count.

4. *Orcaella brevirostris* (Fig. 3c) and *O. heinsohni* - These species have smaller mandibles (230-260 mm in length), a relatively longer symphysis, more extended alveolar portion, and smaller alveoli than FSAC As-01. However, their tooth count ranges overlap with that of FSAC As-01.

5. *Peponocephala electra* (Fig. 3f) - The mandible of *P. electra* is more gracile and elongated than that of FSAC As-01 and further differs from the latter in its smaller size (~350 mm), higher tooth count and lower symphyseal angle (28-33°). Although the relative symphyseal length of *P. electra* overlaps with that of FSAC As-01, its symphyseal surface is distinctly elongated anteroposteriorly, in contrast to the broader rhomboidal morphology seen in FSAC As-01.

Among the fossil delphinids from the Mediterranean Basin, where the fossil record of this cetacean group is

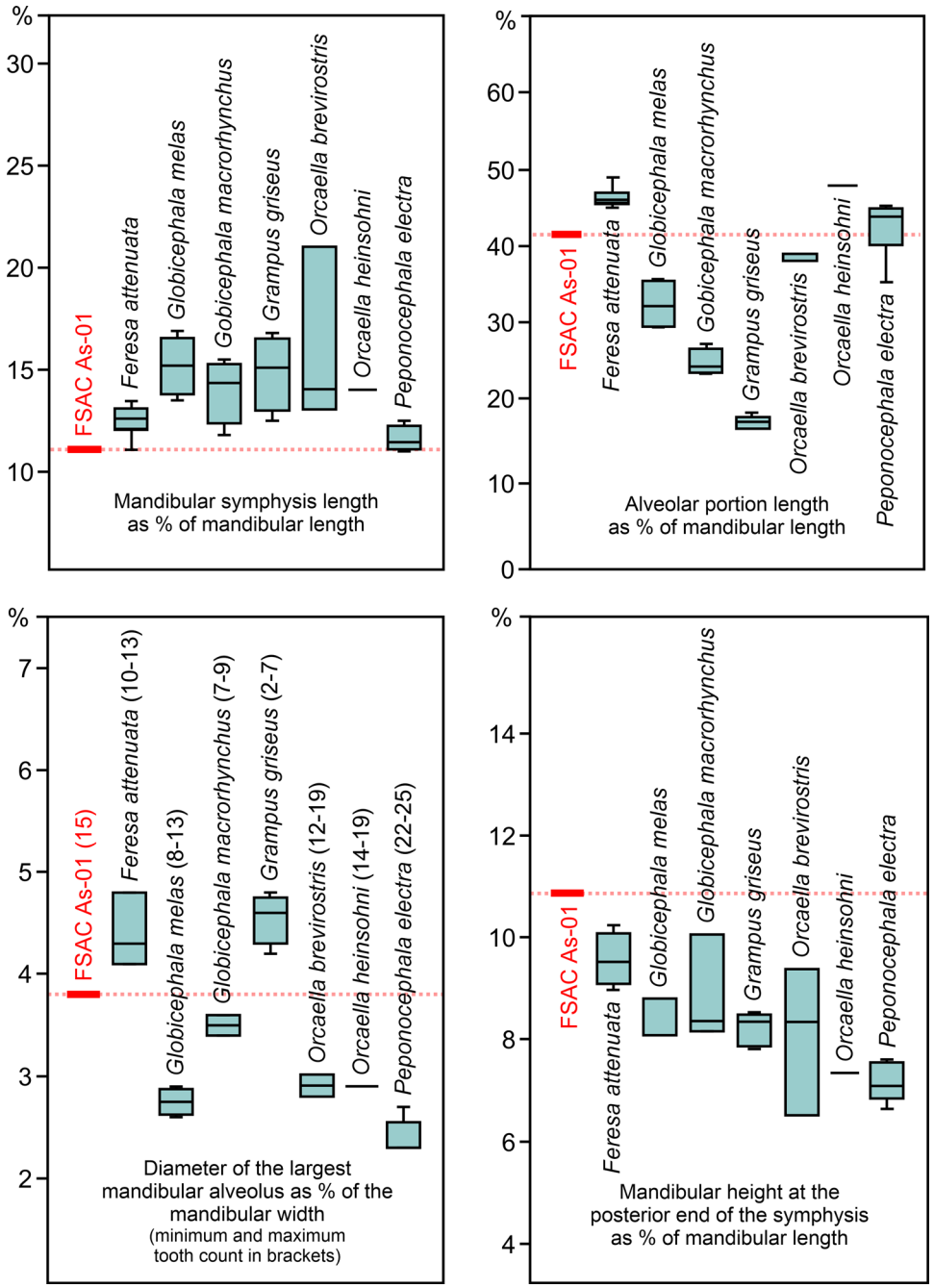

Fig. 4 - (color online) Box-plots comparing some ratios of mandibular measurements in FSAC As-01 and selected extant globicephaline delphinids.

particularly abundant, materials useful for comparisons include the well-preserved mandibles of *Astadelphis gastaldii*, *Etruridelphis giulii*, *Hemisyntrachelus cortesii*, *H. pisanus*, *Orcinus citoniensis* and *Septidelphis morii* from the Pliocene of Italy. None of these delphinid species show the combination of characters observed in FSAC As-01 as well as in the aforementioned globicephaline taxa, i.e., a markedly short mandibular symphysis, a low symphyseal angle, a reduced alveolar portion and a posteroalveolar portion characterized by a nearly straight dorsal margin as well as by a ventral margin that sharply curves posteroventrally in lateral view (Bianucci, 1996, 1997, 2005, 2013; Bianucci et al., 2009; Citron et al., 2022).

The mandibles of the fossil globicephaline *Rododelphis stamatiadisi* from the Pleistocene of Rhodes (Greece) differ from FSAC As-01 by having a larger size (mandibular length ~480-500 mm), lower tooth count (11) and slightly longer mandibular symphysis (accounting for 13% of the estimated mandibular length) (Bianucci et al., 2022).

More fragmentary fossil delphinid mandibles from the Mediterranean Basin are those belonging to the holotypes and only known specimens of *Arimidelphis sorbini* and "*Tursiops*" *osennae* from Italian deposits of Pleistocene and Pliocene age, respectively. The mandible of *A. sorbini* clearly differs from FSAC As-01 in exhibiting a sharp posterior rise of the dorsal margin in the posteroalveolar region (Bianucci, 2005). The mandible fragment of "*Tursiops*" *osennae* exhibits significantly smaller alveoli and a rostral outline that implies a narrower transverse mandibular width compared to FSAC As-01 (Bianucci, 1996). The fragmentary mandible that comprises the holotype of "*Globicephala*" *etruriae* from the Pliocene of Italy is readily distinguishable from FSAC As-01 by its lesser robustness, smaller size, and more abundant, smaller teeth (Bianucci, 1996).

Beyond the Mediterranean, our comparisons may be extended to the putative globicephalines *Protoglobicephala mexicana* Aguirre-Fernández et al., 2009 and *Platalearostrum hoekmani* Post & Kompanje, 2010. While the mandibles of these two species are unknown, the relatively elongate rostrum of *P. mexicana* suggests a lower symphyseal angle than observed in FSAC As-01 (Aguirre-Fernández et al., 2009). Conversely, *P. hoekmani* may have had dorsally broader mandibles with larger teeth (as suggested by a fragmentary mandible tentatively attributed to this species; Post & Kompanje, 2010) and a lower tooth count (as suggested by the occurrence of as few as six teeth in the right upper quadrant, preserved on the holotype rostrum).

Two other delphinids from the Upper Miocene of Japan –namely, *Eodelphinus kabatensis* (Murakami et al., 2014) and *Norisdelphis annakaensis* Kimura & Hasegawa, 2020– also deserve comparisons. When viewed laterally, the posteroalveolar portion of the left mandible of the holotype of *E. kabatensis* shares a roughly similar dorsal profile as observed in FSAC As-01, but the ventral margin descends less steeply and the overall size is smaller (Murakami et al., 2014). No mandibles are known for *N. annakaensis*, but the long rostrum of the holotype suggests a low symphyseal angle (Kimura & Hasegawa, 2020), arguing against a close affinity with FSAC As-01.

The fragmentary, articulated mandibles of the beaked whale-like delphinid *Australodelphis mirus* Fordyce et al., 2002 from the Pliocene of Antarctica are distinctly narrower dorsally (i.e., they display a lower symphyseal angle) and feature a much longer symphysis compared to FSAC As-01 (Fordyce et al., 2002).

The well-preserved mandibles of "*Tursiops*" *oligodon* Pilleri & Siber, 1989 from the uppermost Miocene of Peru share with FSAC As-01 a roughly straight dorsal profile in lateral view. However, they differ from FSAC As-01 in being more gracile and having a lower mandibular angle as well as a lower tooth count (11) (Pilleri & Siber, 1989).

Finally, *Pliodelphis doelensis* Belluzzo & Lambert, 2021 from the Pliocene of Belgium, along with *Lagenorhynchus harmatuki* and *Stenella rayi* from the Pliocene of North Carolina (USA), are only known from their type specimens, none of which preserve any part of the mandibles, but just the crania. Nevertheless, their relatively small cranial dimensions are suggestive of significantly smaller mandibles compared to FSAC As-01 (Whitmore & Kaltenbach, 2008; Belluzzo & Lambert, 2021).

In summary, FSAC As-01 exhibits key morphological features consistent with Globicephalinae. At the same time, it displays a unique combination of traits that distinguish it from all known extant and extinct species, and likely also from any currently recognized genus. Given the fragmentary nature of the specimen, we refrain from erecting a new taxon and instead assign FSAC As-01 to Globicephalinae genus and species indeterminate, pending the discovery of more complete materials.

DISCUSSION

The morphology of the Asilah dolphin provides valuable insights into the trophic adaptations of extinct Delphinidae.

A recent morphometric analysis (Vicari et al., 2024) has shown that the mandibular shape of extant delphinids correlates strongly with feeding strategy. In particular, suction feeders tend to exhibit reduced dentitions and a low coronoid process combined with blunt, shortened, articulated mandibles, all of which are features that define the "amblygnathous" condition, which in turn favors the formation of a circular oral aperture, enhancing suction efficiency (Werth, 2006). FSAC As-01 matches well this condition, even though it retains a greater number of teeth per mandible (15) compared to the extant, highly specialized, suction feeding globicephalines, *Globicephala* spp. and *Grampus griseus*. All things considered, FSAC As-01 likely employed a feeding mode that combined suction-assisted intake with moderate grasping capabilities, especially when dealing with large prey items. Notably, the extant globicephaline *Feresa attenuata* occasionally preys upon small odontocetes, thus demonstrating a remarkable behavioral flexibility (Baird, 2018). This suggests that the slightly larger-bodied FSAC As-01 may have exhibited a similar opportunistic feeding strategy, preying upon a variety of animals, including fish, cephalopods and possibly small tetrapods.

The Lower Pleistocene globicephaline *Rododelphis stamatiadisi* and the Pliocene diminutive killer whale *Orcinus citoniensis* offer roughly analogous ecological models. With fewer and larger teeth and higher coronoid crest than FSAC As-01, *R. stamatiadisi* and *O. citoniensis*

are thought to have pursued a generalist diet dominated by large fish. This may represent an intermediate stage toward the evolution of the more specialized macropredators, the extant *Pseudorca crassidens* and *Orcinus orca* (Bianucci et al., 2022; Citron et al., 2022).

The extinct *Hemisyntrachelus* spp., the most common delphinids of the Italian Pliocene, were also likely generalist predators. *Hemisyntrachelus* shares with FSAC As-01 a similar tooth size and a reduced number of teeth (14-16), but displays a significantly lower mandibular angle (Bianucci, 1996, 1997).

Overall, together with the previously mentioned extinct delphinids, the Asilah dolphin mandible lends support to the hypothesis that various delphinid lineages once occupied a broadly unspecialized trophic niche centered on medium-sized prey. Nowadays, this niche appears to be fully represented only by *Feresa attenuata*, although little is known about the feeding behavior of this extant species (Baird, 2018).

CONCLUSION

The discovery of FSAC As-01 in the Lower Pliocene deposits of the Asilah Basin of Morocco represents a significant addition to the poor Delphinidae record of North Africa.

Despite its fragmentary nature, this specimen displays a unique combination of morphological traits that supports its attribution to an as-yet undescribed genus and species of Globicephalinae.

FSAC As-01 contributes to the emerging picture of Neogene delphinids as ecologically versatile and morphologically experimental. Its unique mandibular configuration underscores the diversity of feeding adaptations within Globicephalinae and highlights a trophic niche –one that is intermediate between raptorial and suction feeding– that is poorly represented among the extant oceanic dolphins.

FSAC As-01 also provides further evidence for high dietary niche partitioning among the Pliocene delphinids, supporting the idea that ecological diversification in this group was well underway by the Early Pliocene.

This discovery underscores the importance of underexplored regions, such as the Moroccan Atlantic margin, in filling geographic and ecological gaps in the fossil record of marine mammals.

Additional finds from this area are likely to further refine our understanding of the evolutionary pathways and ecological dynamics that shaped the diversification of true dolphins during the Neogene.

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