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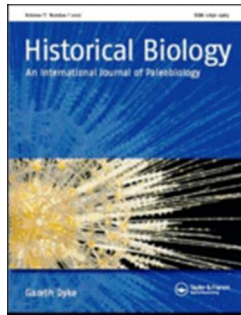
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Teeth, fossil record and evolutionary history of the cowtail stingray *Pastinachus Rüppell 1829*

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3 **Teeth, fossil record and evolutionary history of the cowtail stingray**
4 ***Pastinachus Rüppell 1829***
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Teeth, fossil record and evolutionary history of the cowtail stingray *Pastinachus* Rüppell 1829

Hypolophin ‘dasyatids’ are a common group of large stingrays today frequenting the Indo-Pacific inshores. Being often harvested in their restricted area, few are known about their biology and their evolutionary history despite a very peculiar dental pattern making it easy to track their fossil record. An abundant material consisting of isolated teeth from Late Bartonian (38-40 Ma) lagoonal deposits of Djebel el Kébar, Tunisia, allows to describe a new stingray, *Pastinachus kebarensis* nov. sp. This taxon represents the oldest occurrence for this genus but also the oldest fossil record for hypolophins. A dental comparison of these fossils with 3D rendered models of fresh specimens testifies that early hypolophin representatives had already a strongly arcuate and bulbous upper jaw, interlocking with a broad and elongated tooth plate on the lower jaw. This new fossil and its fossil relatives (here updated), indicate a pre-Bartonian origination for hypolophins in western Neotethys, and reveal a rapid and widespread colonization of the proto-Mediterranean Sea, western Atlantic and Indo-Pacific coasts during the late Paleogene–early Neogene. Finally, it is worth noting that early hypolophin representatives seemingly entered freshwater habitats occasionally as modern cowtail stingrays do.

Keywords: Hypolophin, fossil record, new species, Tunisia, evolutionary history.

INTRODUCTION

The Dasyatidae (Jordan 1888) is a large stingray family represented by 19 genera and at least 86 living species (Last et al. 2016a-c). Excluding the pelagic stingray *Pteroplatytrygon violacea* (Bonaparte 1832), most are marine, demersal, living inshore on continental and insular shelves (rarely found deeper than 400 m). Some stingrays can live in freshwater, occurring in rivers more than 240 km from the coast (Last et al. 2016). Among it, Hypolophinae (Stromer 1910), and its junior synonym Pastinachinae (Roberts 2006) is a subfamily including six Indo-Pacific stingrays belonging to

1
2
3 *Makarraraja* Roberts 2006 and *Pastinachus* Rüppell 1829 (posteriorly named
4
5 *Hypolophus* by Müller and Henle 1837). Anatomically, both are partly characterized
6
7 among Dasyatidae by their strongly arcuate and bulbous upper jaw interlocking with a
8
9 broad and elongated tooth plate on the lower jaw (Last et al. 2005, 2010a-b, 2016a-c ;
10
11 Roberts 2006). Teeth are grinding type, quincuncial and hexagonal or rhomboid,
12
13 varying in size and shape depending the files. Other anatomical features corroborate this
14
15 clade as a caudal sting inserted posteriorly on tail, supporting a well-developed ventral
16
17 skin fold (cowtail). The genus *Makarraraja* differs in having a nearly round disc, very
18
19 fine dermal denticles and four oral papillae, contrary to *Pastinachus*, in which the disc
20
21 is rhombic, with a well-developed denticle band including pearl-shaped midscapular
22
23 thorns, and five oral papillae (Roberts 2006).
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25

26
27 Compared to the unique freshwater *Makarraraja chindwinensis* Roberts 2006,
28
29 which has been described from only one specimen collected in the Chindwin River,
30
31 Irrawaddy basin, in northern Myanmar (Roberts 2006), *Pastinachus* was thought to
32
33 consist of a single species widely distributed around the Indo-Pacific coasts: *P. sephen*
34
35 Forsskål 1775. However, recent advances in molecular phylogenies have demonstrated
36
37 that this species includes today at least five amphidromous species: *P. ater* Macleay
38
39 1883, *P. gracilicaudus* Last and Manjaji-Matsumoto 2010, *P. sephen*, *P. solocirostris*
40
41 Last et al. 2005, and *P. stellurostris* Last et al. 2010. Most of them live on marine soft
42
43 substrates of Indo-Malay Archipelago, except for *P. sephen* which is exclusively
44
45 restricted from Red Sea to Pakistan area. *Pastinachus ater* is the largest and the most
46
47 widespread species, inhabiting all the Indo-Pacific inshores, from Madagascar to North
48
49 Australia coasts, and also occurring in estuaries and freshwater (Last et al. 2016c) up to
50
51 several hundreds of kilometres in the Ganges River (Chaudhuri 1911). If observed
52
53 specimens of *Pastinachus* are known to belong to a solitary foraging species that
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2 occasionally groups when resting on shallow sand flats (Semeniuk and Dill 2006), and
3
4 that feeds on small fishes, molluscs, crustaceans and marine worms (Randal and Hoover
5
6 1995), the biology of the subfamily members is still poorly understood.
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10 TOOTH MORPHOLOGY AND FOSSIL RECORD

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12
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14 Despite its unique dental pattern among dasyatids (Last et al. 2016a,c), teeth
15
16 morphology along jaws of *Pastinachus* have long remained elusive. Only some teeth of
17
18 *Pastinachus* have been figured by Herman et al. (1998, plates 10-13) and Cappetta
19
20 (2012, fig. 15 and 413). Recently, we had the opportunity to scan the fresh specimen of
21
22 *Pastinachus ?ater*, a male of 75 cm DW from Java, available in our collections (UM
23
24 REC 818M) and partially figured in Cappetta (2012, fig. 15). The jaws of this specimen
25
26 was subject to a X-ray micro-CT scans (using a SkyScan 1076 Brucker CT scanner,
27
28 MRI, ISE-M facilities) in order to obtain 3D digital models of the upper and lower jaws.
29
30 We extracted the digital surface using the segmentation tools of AVIZO 6.3
31
32 (Visualization Sciences Group) and compiled in 3D rendered models. The segmentation
33
34 process was performed slice-by-slice manually and we segmented the tooth plates and
35
36 cartilaginous jaws in two separate label fields (Fig. 1A-F). Indeed, the anatomy of tooth
37
38 plates is now available with regard to dental variations along both jaws.
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42 The dentition of hypolophins is characteristic of the crushing-grinding type,
43
44 described in batoids (see Cappetta 2012 and references herein). There is a well-marked
45
46 monognathic heterodonty consisting in the presence of teeth exhibiting a grinding type,
47
48 and to a lesser extent in the presence of tooth files characterized by a crushing type
49
50 (e.g., anterior upper teeth). Dignathic heterodonty is marked by the grinding complex
51
52 between teeth of pestles (curved upper lateral teeth) and teeth of crucibles (antero-
53
54 lateral lower teeth). In hypolophins, this mixing between crushing and grinding types is
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2 particularly notable on upper jaw (Fig. 1A-C), the lower jaw exhibiting a tooth plate
3 more uniform (Fig. 1C), as in most batoids. Indeed, each half-upper jaw consists of a
4 strongly convex dental plate made of large hexagonal teeth, which are narrowly
5 imbricated (Fig. 1C). The contact between the right and left dental plates in the
6 symphyseal region is made by 5-6 tooth files (see Fig. 1C for nomenclature) of crushing
7 type, located in a deep labio-lingual depression. Jaw cartilages have a strongly undulate
8 profile (Fig. 1A) and the shape of teeth varies as a result, with both the position relative
9 to high and low points along the jaw and distance between the symphysis and proximal
10 jaw extremities (Underwood et al. 2015). Consequently, the morphological changes in
11 tooth design are gradual along the half-jaw between the lozenge shaped crushing teeth
12 of the labio-lingual depression (symphyseal and anterior tooth files; see Fig. 1C for
13 nomenclature) and the hexagonal elongated grinding teeth of the convex plate (6-7
14 lateral tooth files). The commissural edges of tooth plate are abruptly limited by teeth
15 with pentagonal occlusal face (posterior tooth file). The lower dentition is rather flat
16 (Fig. 1C-D) on the whole with lozenge shaped (or slightly hexagonal in more anterior
17 tooth files) to pentagonal (posterior tooth file) crushing-grinding teeth. Dental pattern
18 along both jaws seems quite homogenous within the subfamily if we consider the rare
19 jaw illustrated for identified species (Roberts 2006: for *Makararaja chindwinensis*; Last
20 and Manjaji-Matsumoto 2010, fig. 3 for *P. gracilicaudus*; Last et al. 2010, fig. 3 for *P.*
21 *solocirostris*; and Last et al. 2010, fig. 5 for *P. stellurostris*, respectively). In addition,
22 sexual heterodonty seems absent according Herman et al. (1998) but the latter
23 observations are based on old systematics (see Introduction), considering that specimens
24 of males and females might not be conspecific and thus, represent distinct species.

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Herman et al. (1998, p. 154) and Cappetta (2012, p. 420-421) have figured
several isolated teeth of lower and upper hypolophin jaws, and have extensively

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2
3 described the tooth morphology of *Pastinachus*, even if we provisionally exclude a
4
5 dubious specimen from Sarawak figured by Herman et al. (1998, fig. 13, as
6
7 “*Pastinachus sephen*”). Indeed, this specimen displays teeth inconsistent in morphology
8
9 to the hypolophin dental pattern (e.g., polyholacorhize root, occlusal surface of crown
10
11 rounded and smooth, lack of posterior bulge on labial face (under the labial visor) in
12
13 lateral teeth, high root compared to the fine crown). As in many dasyatids and
14
15 especially in those where the crushing-grinding pattern is most efficient, the enameloid
16
17 coat and the outer layer of orthodontine are very thin and rapidly removed by wear, the
18
19 remaining root consisting of trabecular dentine (osteodont type). Most of the
20
21 vascularization canals are vertically directed with some interconnections (Fig. 1H).
22
23 However, when not yet functional (teeth renewal before moving forwarding), the entire
24
25 occlusal surface of teeth bears an irregular, pitted enameloid. Even if these
26
27 ornamentations are widely smoothed on the 3D surface rendering, they are visible on
28
29 most of the tooth files located in the back of the mouth, before functional occlusion,
30
31 between upper and lower jaws. The crown of teeth is only slightly elevated compared to
32
33 the root, except in teeth that are subjected to less grinding stresses, as in symphyseal and
34
35 anterior upper tooth files (Fig. 1 A-C). Root is at the holaulacorhize stage (Herman et al.
36
37 1998; Cappetta 2012), with a complete opening of the vascular canal, converted to a
38
39 unique groove with a foramen opening in the middle in all teeth of both jaws (Fig. 1 E-
40
41 G). Inner and outer foramina are absent. The two root lobes are generally displaced
42
43 towards the back and mostly symmetrical to slightly asymmetrical in lateral and
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45 posterior tooth files, especially along the upper jaw (Fig. 1E-F). Sometimes, abnormal
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47 teeth display more than two lobes (Fig. 1F).
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52 Because of a lack of information regarding *Pastinachus*' tooth morphology
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54 before recent illustrated works, fossils of rays belonging to this genus were long
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3 described as belonging to *Dasyatis*. Conversely, and for the same reason, some teeth
4
5 originally described as *Pastinachus* (formerly *Hypolophus*) were considered as
6
7 belonging to another genus. The oldest documented occurrences of *Pastinachus* are
8
9 from the Priabonian (Late Eocene, Paleogene) of North Africa. Firstly attributed to
10
11 *Dasyatis* spp., the genus *Pastinachus* occurs in the southwestern Morocco (Adnet et al.
12
13 2010). Teeth of *Pastinachus* were collected subsequently in several localities of Egypt,
14
15 notably in the Qasr el-Sagha and Birket Qarun formations, Fayum (Murray et al. 2010,
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17 fig. 2, C-D; Underwood et al. 2011, fig.5. DD-FF ; Antar 2011, fig. 30.J), and in Km55,
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19 Bahariya Oasis (Adnet et al. 2011, fig. 4. F-H). Murray et al. (2010) noticed few
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21 differences between teeth they figured from Late Eocene Birket Qarun Formation and
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23 *Hypolophus sylvestris* (White 1931), an early Eocene species based on teeth and thorns
24
25 from Abbey Wood, Beckenham, High Halstow, and Upnor, England (White 1931, p.70-
26
27 73) and attributed posteriorly by Cappetta (1980) to the extinct genus *Hypolophodon*, a
28
29 large early Paleogene dasyatid exhibiting a grinding-type dentition (Cappetta 2012).
30
31 However, given the tooth shape (hexagonal crown with a bilobed root) and the presence
32
33 of imbricated teeth with a posterior bulge on the labial face of crown, it is highly
34
35 probable that the teeth from the Birket Qarun Formation belong to *Pastinachus* and not
36
37 to *Hypolophodon*. In the Neogene, some teeth were reported from the Maradah
38
39 Formation, Early Miocene of Jabal Zaltan, Libya (Argyriou et al. 2015) and identified
40
41 as *Pastinachus*. Sahni & Mehrotra (1981, pl. 3, 5-6, no 7) and more recently Sharma &
42
43 Patnaik (2013, fig. 6. A-D) have figured teeth from the Lower Miocene Baripada Beds
44
45 (Odisha, India) that they assigned to *Dasyatis sylvestris* White 1931. However, the tooth
46
47 morphology strongly reminds those of found in the Late Paleogene, and as such must be
48
49 considered as fossil representatives of *Pastinachus*. A tooth (Darteville and Casier
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51 1959, pl. XXXIV, 11a-d) and a dermal buckle (Darteville and Casier 1959: pl. XXXVI,
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53 1959, pl. XXXIV, 11a-d) and a dermal buckle (Darteville and Casier 1959: pl. XXXVI,
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3 9a, b) from the Miocene of Malembe (Cabinda, Angola) have also been attributed to
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5 *Hypolophus malembeensis* Darteville and Casier 1959. Dated in fact to the early
6
7 Oligocene by the associated mammals (Pickford 1986), Cappetta (2006) assigned this
8
9 species to the genus *Hypolophodon* despite it represented an unexpected occurrence of
10
11 the genus in post Eocene deposits (Cappetta 1980, 2006, 2012). The hexagonal shape of
12
13 the crown (with angular crown extremities) and the presence of a posterior bulge on the
14
15 labial face favouring the interlocking, missing in *Hypolophodon*, suggest that the tooth
16
17 should be reattributed to *Pastinachus*. The validity of the species *P. malembeensis*
18
19 remains challenging because it relies on a unique antero-lateral upper tooth that was
20
21 formerly distinguished from *Hypolophodon sylvestris* on the basis of the labial marginal
22
23 angles that involve more sharpened and stronger tooth imbrication (Darteville and Casier
24
25 1959, p. 331), two features which define the genus *Pastinachus*, not a new species. Only
26
27 a better knowledge of this Oligocene material will allow to confirm this attribution.
28
29 According to Cappetta (2006, 2012), *Pastinachus* also occurs in the Neogene of Taiwan
30
31 (formerly as *Dasyatis* sp., in Uyeno 1978, pl.4, fig. 25A-b), with a unique tooth sampled
32
33 in the river bed of Ts'ai-liao-hsi, Taiwan. Otherwise, the caudal vertebrae from the
34
35 Eocene of Etterbeck (Belgium), attributed to *Hypolophus sephen* by Hasse (1879,
36
37 pl.XIX, Fig 1,3) are seemingly not belonging to a *Pastinachus* species. Indeed, the
38
39 identification based upon only one caudal vertebrae is extremely vague.
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45 NEW FOSSIL *PASTINACHUS* OF TUNISIA

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49 The sedimentology, stratigraphy and dating of the KEB-1 fossil-bearing locality were
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51 detailed in Marivaux et al. (2014b) and Merzeraud et al. (2016). We only report here the
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53 main information from both works devoted to this. Located in central Tunisia, in the
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55 Kasserine area (Fig. 2A), the Djebel el Kébar is an anticlinal structure of Atlasic
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3 direction, which was formed during the Miocene and Lower Pleistocene compressive
4 stages related to the Alpine collision. On the south eastern flank of the djebel, the base
5 of the stratigraphic section (Fig. 2B) was previously described as recording continental
6 deposits. In contrast, the overlying deposits of the section (Fig. 2B-C) are clearly marine
7 in origin, and represent an interval of deposition ranging from the Eocene up to the
8 Miocene. In these marine deposits, two sedimentological units can be identified. The
9 first one is developed above an erosional transgressive surface and is characterized by
10 facies of shallow marine environments, probably formed in subtidal or high intertidal
11 zones (Merzeraud et al. 2016). The proximal facies reflect lagoonal conditions, which
12 were episodically influenced by storms, as indicated by the presence of bioturbated
13 glauconitic clays (Fig. 2C), burrowed limestone pebbles, and carbonated hummocky
14 cross stratifications. In contrast, the distal facies are clearly marked by open marine
15 conditions. The fossil locality (KEB-1; see Marivaux et al. 2014a-b; Merzeraud et al.
16 2016) having yielded the *Pastinachus* teeth was discovered in the proximal facies. The
17 great abundance of glauconite grains, notably in the fossiliferous level, indicates
18 episodes of condensation associated with transgressive stages. The fossiliferous
19 concentration of KEB-1, which includes an association of marine (e.g., elasmobranchs)
20 and continental vertebrates (Marivaux et al. 2014a-b) is then associated with several
21 periods of low sedimentation rate of late Middle Eocene. This time frame is
22 corroborated and specified (i.e., Bartonian) by radiometric K-Ar analyses, which were
23 performed on few grains of glauconite extracted from the glauconitic clays embedding
24 the fossils of KEB-1 (see Yans in Marivaux et al. 2014b). About thousand teeth of new
25 taxa were recovered by in situ wet screening of about 2.3 tons of sediments. Figured
26 specimens, including the holotype, are housed in the paleontological collections of the
27 museum of the “Office National des Mines” of Tunis, Tunisia

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4 Family Dasyatidae Jordan 1888
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6 Subfamily Hypolophinae Stromer 1910
7

8 Genus *Pastinachus* Ruppell 1829
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10 Type-species: *Pastinachus sephen*
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15 *Pastinachus kebarensis* nov. sp.
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17 Fig. 3
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21 Diagnosis: fossil species of *Pastinachus* only known by numerous isolated teeth
22 displaying a large size (up to 6.7mm wide) and particularly thick and robust crowns
23 with presence of posterior bulge on labial face (under the labial visor) in lateral teeth.
24
25 When unworn and unaltered, the occlusal surface of crown of antero-lateral teeth shows
26 a fine and irregularly pitted or alveolate ornamentation of its enameloid. Rhombic to
27 hexagonal in shape, the crown is extremely elongated in the lateral upper teeth (twice
28 broader than long), a peculiar shape reminiscent to that observed in upper teeth of
29 myliobatids and rhinopterids.
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41 *Derivation nominis*: for the name of the locality (Djebel el Kébar) where the new
42 species was discovered.
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45 Holotype: upper lateral tooth (KEB1-080).
46

47 Material: thousand teeth, including the figured teeth (KEB1-076 to KEB1-085).
48

49 Type locality: Kébar 1 (KEB-1), southeastern flank of Djebel el Kébar, Amamria
50 hamlet, near Soug-Jedid village (Sidi Bouzid Township), central Tunisia (after
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52 Marivaux et al. 2014a-b; Merzeraud et al. 2016).
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3 Age: Late middle Eocene (Bartonian). Dated at ~39.5 Ma by radiometric K-Ar analyses
4 performed on grains of glauconite extracted from the glauconitic clays embedding the
5 fossils of KEB-1 (the ages range from 38.76 ± 1.0 to 40.76 ± 1.1 Ma; see Yans in
6
7
8
9 Marivaux et al., 2014b).

10
11 Formation: Souar-Fortuna Formations

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15 Description: In *Pastinachus*, the dentition is monognathic and dignathic heterodont. In
16 occlusal view from symphyseal (Fig. 3 A-E) to commissural tooth files (Fig. 3 AE-AG),
17
18 teeth vary from rhomboid (near symphysis) to hexagonal (lateral tooth files) on the
19
20 upper jaw. The monognathic heterodonty is less noticeable on lower jaw, except with
21
22 the commissural teeth that are, in both jaws, strongly asymmetrical with an angular and
23
24 rounded side (Fig. 3 AE-AG). The crown is high and primarily composed of
25
26 osteodentine as in living species. When they are not worn (e.g., in upper symphyseal
27
28 tooth), crown wears form a sinuous occlusal surface (Fig. 3 A-E) and/or an irregular and
29
30 alveolate enameloid (Fig. 3 AR-AS). The root type is holaulacorhize, except in some
31
32 abnormal teeth. It is always narrower than the crown, and does not widen toward the
33
34 base, except in symphyseal and some anterior upper teeth. Its two lobes are separated by
35
36 a deep and broad groove where nutritive foramens open. In *P. kebarensis* nov. sp., the
37
38 largest tooth observed (from upper lateral tooth file) is 7 mm large (Fig. 3 U-Y). It is
39
40 almost twice the width of lower lateral teeth (Fig. 3 U-Y), and almost five times the size
41
42 of upper symphyseal-anterior teeth (Fig. 3 A-J), as observed in fresh material (Fig. 1).

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44
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46 The holotype is a large upper lateral tooth (Fig. 3 U-Y). It corresponds to the
47
48 more elongated tooth (twice broader than long), which was probably located in the
49
50 middle of the convex upper dental plates (see Fig. 1). Lateral teeth from the upper jaw
51
52 (Fig. 3 K-AD) are the widest of the mouth. The occlusal surface is flat (because often
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3 weathered) to rounded (Fig. 3 P-T), and its contour is hexagonal, asymmetrical in the
4
5 most anterior (Fig. 3 K-O) to virtually symmetrical (Fig. 3 U-Y) in occlusal view. The
6
7 crown thickness decreases from the mesial to the distal side of the tooth (or inversely,
8
9 Fig. 3, R-T, AC-AD) on lateral teeth located on both sides of the longest ones (e.g.,
10
11 Holotype). In worn teeth, the crown is sometimes almost totally weathered (Fig. 3 Z-
12
13 AC) but when it is preserved, its occlusal part is always longest than its base (e.g., Fig.
14
15 3 T, W). Except for the first lateral tooth in contact with the last anterior tooth (Fig. 3
16
17 K-O), the labial and lingual faces are almost straight and vertically sided (Fig. 3 S, Y),
18
19 thereby indicating that lateral teeth are closely juxtaposed. The low lingual minute bulge
20
21 of the lingual face (e.g., Fig 3 T, W) inserts under the neighbour labial visor of
22
23 following tooth, which is shorted. Roots of lateral teeth are particularly low, largely
24
25 narrower than the crowns, with symmetrical pentagonal lobes in basal view (Fig. 3 V),
26
27 while they are asymmetric in first and last lateral tooth files (Fig. 3 N, Q, AA). Lingual
28
29 marginal foramina are absent on the root and only one or two median nutritive foramina
30
31 open in the large hollow (Fig. 3 Q, V, AA). The first lateral tooth (Fig. 3 K-O) displays
32
33 a mixture of characters between the anterior rhombic teeth (e.g., Fig. 3 F-J) and the
34
35 lateral hexagonal teeth (e.g., Fig. 3 P-Y). These teeth are hexagonal in shape but are
36
37 characterized by their asymmetry because they articulate with the smallest teeth
38
39 (anterior tooth) on their mesial side and with the largest lateral tooth on their distal side.
40
41
42 In lateral view (Fig. 3 L), the labial visor is angular, recalling what we observe in more
43
44 anterior teeth (e.g., Fig. 3 H). In occlusal view (Fig. 3 N), the mesial lobe of the root is
45
46 pentagonal (as in more lateral), while the distal lobe is semi-circular (as in anterior
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48 teeth). In proportions, the tooth is wider than high as in lateral teeth.
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53 On the rest of the upper jaw, the symphyseal teeth (Fig. 3 A-E), rhombic in
54
55 shape, are mostly reminiscent of dasyatid tooth pattern. Because they are poorly
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3 subjected to abrasion, the ornamentation is fairly well preserved (Fig. 3 A), and the
4
5 occlusal surface appears sometimes strongly hilly. The crown is high and its labial face
6
7 is strongly concave with a deep median V-shaped furrow between the ornamented flat
8
9 occlusal surface and the labial rounded labial visor (Fig. 3 C-D). The transverse keel has
10
11 a lingual tip, which, although broken, is protruding above the lingual face, appearing
12
13 concave in lateral view (Fig. 3 C). The root is high and bilobed with two diverging
14
15 lobes separated by a deep axial furrow, as observed in modern *Pastinachus*
16
17 representatives (Fig. 1 F). The anterior teeth (Fig. 3 F-J) are quite similar to previous
18
19 ones with dasyatid design, unlike they are slightly subject to wear. According to their
20
21 position along the jaw, the wearing of crowns is more or less pronounced and the
22
23 occlusal surface can be totally flattened and smooth (Fig. 3 G). Root lobes are more
24
25 robust and less divergent compared to symphyseal teeth. In basal view, the root lobes of
26
27 symphyseal and anterior teeth are semi-circular (Fig. 3 E, J).
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31 On the lower jaws, symphyseal and antero-lateral teeth (Fig. 1, U-Y) are
32
33 hexagonal but smaller and less extended labiolingually than in lateral upper teeth. In
34
35 occlusal view (Fig. 3 AH, AM, AR), the labial extremity of the crowns is always
36
37 narrower than the lingual one, forming a hexagon somewhat asymmetric. The occlusal
38
39 surface is slightly convex to flat depending on the degree of wear. Like on the anterior
40
41 and first lateral teeth of upper jaws, the labial visor of lower teeth is angular, but the
42
43 slope is steeper. For each tooth, the root is relatively robust and low, with vertical lobes,
44
45 sub-pentagonal in shape in basal view (Fig. 3 AI, AN).
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48 The posterior tooth files are a succession of strongly asymmetric teeth (e.g., Fig.
49
50 1). The mesial side of the crown, articulating with lateral teeth, is angular, while the
51
52 distal side is round and free (Fig. 3 AE-AG). In lateral view, the crown is antero-
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54 laterally elongated (Fig. 3 AG) and very narrow, following a mesio-distal axis. Lingual
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2 views reveal a thicker crown on the mesial side, was appearing as truncated in its distal
3 side (Fig. 3 AE). The root is oblique and distally oriented. The two lobes, triangular,
4 sub-triangular or sub-pentagonal in shape are elongated as the crown. Their inner
5 outline varies from slightly curved to well linear.
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13 Discussion. Neither ontogenetic nor gynandric heterodonty was observed on the
14 numerous fossil teeth collected. When pristine, the described teeth share an irregularly
15 alveolate ornamentation of the enameloid (Fig. 3 AS), which seems finer than in figured
16 fresh specimen of Herman et al. (1998, fig 10-12) or greater than in figured fresh
17 specimen of Cappetta (2012, fig. 413). However, this is not the case for the upper
18 symphyseal teeth, which can be subject of marked variation. As discussed before,
19 differences between the large upper lateral teeth of *P. kebarensis* nov. sp. (e.g.,
20 holotype) and the other fossil species reattributed to *Pastinachus* (*P. ?malembeensis*)
21 appear tenuous despite their different age and distinct geographic occurrences.
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33 Considering the shape of crown and root lobes (e.g., Fig. 3 U-Y), the unique tooth of *P.*
34 *?malembeensis* is undoubtedly a lateral upper tooth. Despite the presence of wear
35 obscuring a possible (or not) enameloid ornamentation, this tooth differs from those of
36 *P. kebarensis* nov. sp. in having a more massive crown, overhanging larger root lobes.
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41 Considering the largest upper lateral tooth of *P. kebarensis* nov. sp. (6.7 mm in width),
42 the species probably reached a minimum disc wide of 150 cm by comparison with
43 upper lateral teeth of illustrated fresh specimen jaws, two time smaller than largest
44 living representative (*P. ater*) with 300 cm disc wide (Last and Stevens 1994).
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53 GENERAL DISCUSSION AND CONCLUSIONS

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3 Dental and/or morphological convergences are particularly common within rays,
4 notably across the geological times (e.g., sclerorhynchid/pristid). As remarked by
5 Cappetta (2012, p. 21), some other extant dasyatid (e.g., *Dasyatis margarita*) and
6
7 potamotrygonin (e.g., *Potamotrygon motoro*) species possess such a dental pattern with
8
9 a strongly arcuate and bulbous upper jaws interlocking with a broad and elongated tooth
10
11 plate on the lower jaws. However, none have upper lateral teeth with such an elongated
12
13 and hexagonal crown shape, which strongly recalls what is observed in myliobatid or
14
15 rhinopterid tooth plates. Besides, Leriche (1913) grouped fossil myliobatiforms as
16
17 *Rhombodus* Dames 1881 and *Hypolophytes* Stromer 1910, with *Pastinachus* within the
18
19 family Hypolophidae on the basis of tooth morphology, which he considered as
20
21 intermediate between Dasyatidae and Myliobatidae. If all these groups exhibit a similar
22
23 grinding-type dentition with teeth at the holaulacorhize stage, they are not closely
24
25 related. The Late Cretaceous rhombodontids and the Paleocene *Hypolophytes* are also
26
27 myliobatiforms with grinding-type dentition, but tooth files reveal a slighter
28
29 monognathic heterodonty and are composed of rhombic or hexagonal and closely
30
31 juxtaposed teeth, with a high crown marked by a thin wrinkled enameloid. The dental
32
33 pattern of *Pastinachus* reminds also that of *Pseudohypolophus* Cappetta and Case 1975
34
35 and *Hypolophodon* Cappetta 1980. If the first possesses an orthodontin type histology,
36
37 occurring only in rajiforms, the second displays a tooth pattern with a grinding-type
38
39 dentition and osteodontin type histology. Even if the elongated teeth of *Hypolophodon*
40
41 reminds superficially those of upper lateral teeth of *Pastinachus*, the crown shape
42
43 (smoothed polygonal outline), the vascularisation of roots (presence of numerous
44
45 foramina) and the absence of strong tooth imbrication (lack of posterior bulge) allows
46
47 clearly distinguishing both genera. The Danian *Myliodasyatis* Noubhani and Cappetta
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49 1997 also displays a grinding-type dentition with teeth at the holaulacorhize stage that
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3 might suggest affinities with *Pastinachus kebarensis* nov. sp. But its small teeth are
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5 always broader than long, with crowns showing always hexagonal outlines and the
6
7 presence of a moderately salient visor, a suite of anatomical details that led original
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9 authors to discuss its affiliation to dasyatids (Noubhani and Cappetta 1997; Cappetta
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11 2006). However, these authors suggested that one of the oldest dasyatids from Imin
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13 Tanout, Moroccan Meseta (Late Maastrichtian *Dasyatis martini* Noubhani and Cappetta
14
15 1997) have tooth morphology with hexagonal outline, strikingly close to that of the
16
17 Danian *Dasyatis hexagonalis* Arambourg 1952, *Myliodasyatis* or now Bartonian
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19 hypolophins. Notwithstanding some different dental features (e.g., lack of well-marked
20
21 interlocking bulge on labial crown face), *D. martini* provides a reliable morphological
22
23 pattern of what we can expect for the dental morphology of the first hypolophins
24
25 compared to other more recent dasyatids. The minimum divergence estimates from
26
27 fossil data suggests a splitting event with the other dasyatid subfamilies before 38-40
28
29 Myr ago, and possibly before 65 Myr ago if we consider the possible attribution of *D.*
30
31 *martini* to hypolophins, which then would strengthen support to the hypothesis that the
32
33 living Indo-Pacific cowtail stingrays share a plesiomorphic dental morphotype among
34
35 myliobatiforms when compared with other dasyatids. Such an assumption is surprising
36
37 but consistent with the molecular and morphological phylogenetic results of Lim et al.
38
39 (2015), who propose the family Pastinachidae, inasmuch as these approaches failed to
40
41 classify the species of *Pastinachus* within a defined monophyletic Dasyatidae clade.
42
43
44 Indeed, species of Pastinachidae *sensu* Lim et al. (2015) have a position that remains in
45
46 a state of flux, either near the root of myliobatiforms or near the root of some dasyatids
47
48 (Neotrygonidae *sensu* Lim et al. 2015). The recent detailed phylogenetic investigations
49
50 led by Last et al. (2016a), using more marker-rich molecular studies and a more
51
52 comprehensive taxonomic sampling provide new insights into the generic
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3 interrelationships of Dasyatidae, considered as monophyletic. Contrary to Lim et al.
4
5 (2015) who failed to apply for obligatory Zoobank registration of their taxonomic
6
7 names, Last et al. (2016a) resurrected the subfamily Hypolophinae including the two
8
9 genera (*Pastinachus* + *Makararaja*) and considered that Hypolophin emerges from their
10
11 phylogenetic analysis as sister clade of all the other subfamilies of Dasyatidae.
12
13 Whatever the taxonomic issue of debate, hypolophin seems to have a phylogenetic
14
15 position near the root of clades including whole dasyatids (e.g. Naylor et al. 2012; Lim
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17 et al. 2015; Last et al. 2016a). A hypolophin divergence with the other dasyatid
18
19 subfamilies predating the K/T boundary seems in agreement with the more recent
20
21 phylogenetic relationships and higher-level structure of the Myliobatiformes.
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23

24 Today restricted to the Indo-pacific area, the cowtail stingrays are very common
25
26 inshore rays, being sometimes the most common as is the case in Australia (Last and
27
28 Stevens 1994). Conversely, their known fossil record remains rare and sparse (despite
29
30 the relative great size of teeth visible on field), likely indicating a distinct special
31
32 distribution in the past. If Cenozoic batoids and specifically dasyatids are virtually
33
34 unknown in Southwestern Asia (Adnet et al. 2008, fig. 2, *Dasyatis* sp.) and Australia
35
36 (Kemp 1991, Plate 38, *Dasyatis* sp.), until today the rare record of fossil hypolophins in
37
38 Indo-pacific indicated that the evolutionary history of cowtail stingrays extended back
39
40 only to the Miocene, with fossil specimens from Taiwan (Uyeno 1978) and India (Sahni
41
42 and Mehroratra 1981; Sharma and Patnaik 2013). The Cenozoic dynamics of large-scale
43
44 batoid diversity remain poorly understood, especially for the Western Pacific, in part,
45
46 because of the paucity of well-dated fossil records from the tropics. Basically, the fossil
47
48 record of elasmobranchs from the Western Indian Ocean and Eastern Pacific (originally
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50 Tethys) is clearly incomplete, thereby involving a substantial underestimation of the
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52 paleodiversity of that group in these areas. In contrast, the Cenozoic record of
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3 elasmobranchs frequenting the Eastern Indian Ocean area (originally the western part of
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5 Neotethys) is better known (e.g., White 1927; Casier 1971; Thomas et al. 1989; Case
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7 and West 1991; Kumar and Loyal 1987; Bajpai and Tewissen 2002; Rana et al. 2005;
8
9 Adnet et al. 2007; Kumar et al. 2007; Andrianaivalona et al. 2015). However, no modern
10
11 hypolophin (e.g. *Pastinachus*) has been reported from fossiliferous marine/brackish
12
13 deposits dated from the Early Eocene – Early Oligocene epochs, whereas they are
14
15 recorded and sometimes abundant in contemporaneous localities along the south coast
16
17 of the westernmost Neotethys up to the southeastern Atlantic (e.g., Tunisia, Egypt,
18
19 Southwestern Morocco, and Angola). The lack of hypolophin record in eastern marine
20
21 areas suggests that cowtail stingrays were really absent, at least from western Indian
22
23 Ocean before Early Miocene, while they frequented the tropical seawater of North and
24
25 Western Africa coasts. In this context, *Pastinachus kebarensis* nov. sp. from the
26
27 Bartonian of Tunisia represents therefore the oldest members of the group to be know
28
29 thus far. Based on the known hypolophin fossil record (here updated), it seems that
30
31 cowtail stingrays performed a rapid and widespread colonization of African coasts
32
33 flanked by eastern Atlantic and westernmost Neotethys during the warm episodes
34
35 recorded in the late Paleogene. Cowtail stingrays seems to have survived in southeastern
36
37 Proto Mediterranean sea until the Early Miocene (Argyriou et al. 2015) after which
38
39 there is no more record of hypolophin outside the Indo-Pacific area. The distribution
40
41 area of past hypolophins was therefore more widespread than today.
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46 If the spatial distribution of past and present hypolophins has radically changed,
47
48 their ecology, inferred from the fossils, seems to have remained unchanged through
49
50 time. Merzeraud et al. (2016) interpreted the fossil-bearing deposits of Djebel el Kébar
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52 (KEB-1) as belonging to very shallow water-depth carbonate platform (wave dominated
53
54 and influenced by storms and tide), as also suggested by the presence of numerous
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3 terrestrial mammal remains (see chapter 2). As in Tunisia, fossil teeth of *Pastinachus*
4
5 are often recovered elsewhere in Paleogene deposits with forestland mammal bones
6
7 (e.g., Darteville and Casier 1943; Adnet et al. 2010; Murray et al. 2010). With a similar
8
9 fossil association recorded in the Fayum BQ-2 locality (Egypt, early Late Eocene),
10
11 Murray et al. (2010) concluded that fossil *Pastinachus* (formerly *Hoplophodon* aff. *H.*
12
13 *malembeensis* in text) frequented an area representing a near-coastal environment of
14
15 shallow streams that were often stagnant but flooded periodically, possibly seasonally,
16
17 with freshwater runoff. Other fossil evidence (e.g. Adnet et al. 2011; Antar 2011 ;
18
19 Underwood et al. 2011) suggest that coeval *Pastinachus* representatives inhabited also
20
21 the marine inshore, and precisely, in shallow and macrotidal environment, interpreted as
22
23 dune or channel bar sets (Underwood et al. 2011). Nowadays, all *Pastinachus* species
24
25 are considered as amphidromous, resting on shallow-water inshore sand flats and
26
27 frequently venturing far into estuaries and freshwaters. Paleoenvironments of fossil
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29 hypolophins suggest that their habitats and behaviours were alike during the Paleogene.
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References

Adnet S, Antoine P-O, Hassan Baqri SR, Crochet J-Y, Marivaux L, Welcomme J-L., Métais G. 2007. New tropical carcharhinids (chondrichthyes, carcharhiniformes) from the late Eocene–early Oligocene of Balochistan, Pakistan: Paleoenvironmental and paleogeographic implications. *J Asian Earth Sc.* 30: 303–323.

Adnet S, Cappetta H, Beard KC, Marivaux L, Marandat B, Chaimanee Y, Jaeger J-J, Tun ST, Soe AN. 2008. First myliobatiform teeth (Elasmobranchii, Neoselachii) from the Pondaung Formation (late middle Eocene) of Central Myanmar. *Neues Jahrb Geol P-A.* 247: 335–340.

Adnet S, Cappetta H, Tabuce R. 2010. A Middle–Late Eocene vertebrate fauna (marine fish and mammals) from southwestern Morocco; preliminary report: age and palaeobiogeographical implications. *Geol Mag.* 147: 860–870.

Adnet S, Cappetta H, Elnahas S, Strougo A. 2011. A new Priabonian Chondrichthyans assemblage from the Western desert, Egypt: Correlation with the Fayum oasis. *J African Earth Sc.* 61: 27–37.

Andrianavalona TH, Ramihangihajason TN, Rasoamiaramanana A, Ward D., Ali JR, Samonds KE. 2015. Miocene Shark and Batoid Fauna from Nosy Makamby (Mahajanga Basin, Northwestern Madagascar). *Plos One.* 10(6): e0129444.

Antar MS. 2011. Paleo-environments of the exposed Eocene Sediments between Wadi El-Hitan and east Siwa in the Egyptian Western Desert based on their faunal content especially the vertebrates. [PhD Thesis] Zagazig, Egypt. Zagazig University, Faculty of Science, Geology Department.

- 1
2
3 Arambourg C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-
4 Algérie-Tunisie). Notes et Mémoires Serv Géol Maroc. 92 : 1–372.
5
6
7
8 Argyriou T, Cook TD, Muftah AM, Pavlakis P, Boaz NT, Murray AM. 2015. A fish
9 assemblage from an early Miocene horizon from Jabal Zaltan, Libya. *J African Earth*
10 *Sc.* 102: 86–101.
11
12
13
14 Bajpai S, Thewissen JGM. 2002. Vertebrate fauna from Panandhro lignite field (Lower
15 Eocene), District Kachchh, western India. *Current Sc.* 82: 507–509.
16
17
18
19 Bonaparte CL. 1832. Iconografia della fauna italica per le quattro classi degli animali
20 vertebrati. Tomo III. Pesci. Roma: Fasc. 1, Puntata 1–6, 2 pls.
21
22
23
24 Cappetta H, Case GR. 1975. Sélaciens nouveau du Crétacé du Texas. *Géobios.* 8 : 303–
25 307.
26
27
28
29 Cappetta H. 1980. Modification du statut générique de quelques espèces de Sélaciens
30 Crétacés et Tertiaires. *Palaeovertebrata.* 10: 29–42.
31
32
33
34 Cappetta H. 2006. *Elasmobranchii Post-Triadici (Index specierum et generum)*. Leiden:
35 Backhuys Publishers.
36
37
38
39 Cappetta H. 2012. *Chondrichthyes II Mesozoic and Cenozoic Elasmobranchii: Teeth,*
40 *Handbook of Paleoichthyology.* Stuttgart-New York (NY): Verlag Dr Friedrich Pfeil.
41
42
43
44 Case GR, West RM. 1991. Geology and Paleontology of the Eocene Drazinda Shale
45 Member of the Khirthar Formation, central Western Pakistan, Part II Late Eocene
46 fishes. *Tertiary Res.* 12: 105–120.
47
48
49
50 Casier E. 1971. Sur un materiel ichthyologique des “Midra (and Saila) shales” du Qatar
51 (Golfe Persique). *Bull Inst R Sc N B-S.* 47(2): 1–9
52
53
54
55 Chaudhuri BL. 1911: Freshwater sting-rays of the Ganges. *JAS Bengal.* 7: 625-629.
56
57
58
59
60

1
2
3 Dames W. 1881. Über Fischzähne aus der obersten Tuffkreide von Maastricht für
4 welcher den Gattungsnamen *Rhombodus* vorschlug. Sitzungsberichte der Gesellschaft
5 naturforschender Freunde zu Berlin: 1–3
6
7

8
9 Darteville E, Casier E. 1943. Les poissons fossiles du Bas-Congo et des régions
10 voisines. *An Mus R Congo Belge. Sér. A, 3, 2 (1): 1–200.*
11
12

13
14 Darteville E, Casier E. 1959. Les poissons fossiles du Bas-Congo et des régions
15 voisines. *Ann Mus R Congo Belge. Sér. A, 3, 2 (3): 257–568.*
16
17

18
19 Forskål P. 1775. *Descriptiones animalium, avium, amphibiorum, piscium, insectorum,*
20 *vermium / quae in itinere orientali observavit Petrus Forskål. Post mortem auctoris*
21 *edidit Carsten Niebuhr. Adjuncta est materia medica kahirina atque tabula maris Rubri*
22 *geographica. Post mortem auctoris edidit Carsten Niebuhr. Hauniae. Descriptiones*
23 *animalium quae in itinere ad Maris Australis terras per annos 1772 1773 et 1774*
24 *suscepto : 1–20 + i–xxxiv + 1–164.*
25
26
27
28
29

30
31 Hasse C. 1879. *Das natürliche System der Elasmobranchier auf Grundlage des Baues*
32 *und der Entwicklung ihrer Wirbelsäule. Eine morphologische und paläontologische*
33 *Studie. I. Allgemeiner Theil: 1–76*
34
35

36
37 Herman J, Hovestadt-Euleur M, Hovestadt DC, Stehmann M. 1998. Part B:
38 *Batomorphii. N°4a. Order Rajiformes -Suborder Myliobatoidei-Superfamily:*
39 *Dasyatoidea-Family Dasyatidae-Subfamily Dasyatinae-Genera: Amphotistius, Dasyatis,*
40 *Himantura, Pastinachus, Pteroplatytrygon, Taeniura, Urogymnus and Urolophoides*
41 *(inc. supraspecific taxa of uncertain status and validity). Superfamily Myliobatoidea-*
42 *Family Gymnuridae-Genera: Aetoplatea and Gymnura. Superfamily Plesiobatoidea-*
43 *Family Hexatrygonidae-Genus: Hexatrygon. In Contributions to the Study of the*
44 *Comparative Morphology of Teeth and Other Relevant Ichthyodorulites in Living*
45 *Supraspecific Taxa of Chondrichthyan Fishes. Bull Inst R Sc N B-S. 145–197.*
46
47
48
49
50
51

52
53 Jordan DS. 1888. *A manual of the vertebrate animals of the northern United States,*
54 *including the district north and east of the Ozark mountains, south of the Laurentian*
55
56
57
58
59
60

1
2
3 hills, north of the southern boundary of Virginia, and east of the Missouri river,
4 inclusive of marine species. 5th edition. i–iii + 1–375.
5

6
7 Kemp NR. 1991. Chondrichthyans in the Cretaceous and Tertiary of Australia.
8 Vickers-Rich P, Monaghan JM, Baird RF, Rich TH (Eds.), Vertebrate Pale-
9 ontology of Australasia, vol. 15. Melbourne, Australia: Monash University Publications
10 Committee, p. 497-568.
11
12
13

14
15 Kumar K, Rana RS, Singh H. 2007. Fishes of the Khuiala Formation (early Eocene) of
16 the Jaisalmer Basin, Western Rajasthan, India. *Current Sc.* 93: 553–559.
17
18

19
20 Kumar K, Loyal RS. 1987. Eocene Ichthyofauna from the Subathu Formation,
21 Northwestern Himalaya, India. *J Pal Soc India.* 32: 60–84.
22
23

24
25 Last PR, Stevens JD. 1994. *Sharks and Rays of Australia*. CSIRO, Australia: CSIRO
26 Publishing.
27
28

29
30 Last PR, Manjaji BM, Yearsley GK. 2005. *Pastinachus solocirostris* sp. nov., a new
31 species of Stingray (Elasmobranchii: Myliobatiformes) from the Indo-Malay
32 Archipelago. *Zootaxa.* 1040: 1–16.
33
34

35
36 Last PR, Manjaji-Matsumoto BM. 2010. Description of a new stingray, *Pastinachus*
37 *gracilicaudus* sp. nov. (Elasmobranchii: Myliobatiformes), based on material from the
38 Indo–Malay Archipelago. *CSIRO Marine and Atmospheric Research Paper.* 32: 115–
39 128.
40
41
42

43
44 Last PR, Fahmi, Naylor GJP. 2010. *Pastinachus stellurostris* sp. nov., a new stingray
45 (Elasmobranchii: Myliobatiformes) from Indonesian Borneo. *CSIRO Marine and*
46 *Atmospheric Research Paper.* 32: 129–140
47
48
49

50
51 Last PR, Naylor GJP, Manjaji-Matsumoto BM. 2016a. A revised classification of the
52 family Dasyatidae (Chondrichthyes: Myliobatiformes) based on new morphological and
53 molecular insights. *Zootaxa.* 4139: 345-368.
54
55
56

1
2
3 Last PR, De Carvalho MR, Corrigan S, Naylor GJP, Séret B, Yang L. 2016b. The Rays
4 of the World project – an explanation of nomenclatural decisions. In Rays of the World:
5 Supplementary information (Last PR and Yearsley GK, Eds), CSIRO Special
6 Publication. 1–10
7
8

9
10
11 Last PR, White WT, De Carvalho MR, Séret B, Stehmann MFW, Naylor GJP. 2016c.
12 Rays of the World. McEachran JD (Edt) Cornell University Press: CSIRO publishing.
13
14

15
16 Leriche M. 1913. Les poissons paléocènes de Landana (Congo). Les gisements de
17 poissons paléocènes et éocènes de la côte occidentale d'Afrique. Ann Mus Congo Belge.
18 1: 67–91.
19
20

21
22 Lim KC, Lim P-E, Chong VC, Loh K-H. 2015. Molecular and Morphological Analyses
23 Reveal Phylogenetic Relationships of Stingrays Focusing on the Family Dasyatidae
24 (Myliobatiformes). Plos One. 10(4): e0120518.
25
26

27
28 Macleay W. (1883) Contribution to a knowledge of the fishes of New Guinea. No. III.
29 Proc Linn Soc N S W. ser. 1, 7: 585–598
30
31

32
33 Marivaux L, Essid EM, Marzougui W, Khayati Ammar H, Adnet S, Marandat B,
34 Merzeraud G, Tabuce R, Vianey-Liaud M. 2014. A new and primitive species of
35 Protophiomys (Rodentia, Hystricognathi) from the late middle Eocene of Djebel el
36 Kébar, Central Tunisia. Palaeovertebrata. 38: 1–17.
37
38
39

40
41 Marivaux L, Essid EM, Marzougui W, Khayati Ammar H, Adnet S, Marandat B,
42 Merzeraud G, Ramdarshan A, Tabuce R, Vianey-Liaud M, Yans J. 2014. A
43 morphological intermediate between eosimiiform and simiiform primates from the late
44 middle Eocene of Tunisia: Macroevolutionary and paleobiogeographic implications of
45 early anthropoids: An Early Anthropoid Primate from the Eocene of Tunisia. Am J Phys
46 Anthropol. 154: 387–401.
47
48
49
50

51
52
53 Merzeraud G, Essid EM, Marzougui W, Ammar HK, Adnet S, Marivaux L, Tabuce R,
54 Vianey-Liaud M. 2016. Stratigraphie et sédimentologie des dépôts marins et
55
56
57
58
59
60

1
2
3 continentaux d'âge éocène moyen à miocène en Tunisie centrale (région du Djebel el
4 Kébar). *B Sol Geol Fr.* 187: 11–25.

5
6
7 Müller J, Henle FGJ. 1837. Ueber die Gattungen der Plagiostomen. *Arch Naturgesch.* 3:
8 394–401.

9
10
11
12 Murray AM, Cook TD, Attia YS, Chatrath P, Simons EL. 2010. A freshwater
13 ichthyofauna from the late Eocene Birket Qarun Formation, Fayum, Egypt. *J Vertebr*
14 *Paleontol.* 30: 665–680.

15
16
17
18 Naylor GJP, Caira JN, Jensen K, Rosana KAM, White WT, Last PR. 2012. A DNA
19 sequence-based approach to the identification of shark and ray species and its
20 implications for global elasmobranch diversity and parasitology. *B Am Mus Nat Hist.*
21 367: 1–262.

22
23
24
25
26
27 Noubhani A, Cappetta H. 1997. Les Orectolobiformes, Carcharhiniformes et
28 Myliobatiformes (Elasmobranchii, Neoselachii) des bassins à phosphate du Maroc
29 (Maastrichtien-Lutétien basal). *Systématique, biostratigraphie, évolution et dynamique*
30 *des faunes. Palaeo Ichthyologica.* 8: 1–327.

31
32
33
34
35 Pickford M. 1986. Première découverte d'une faune terrestre paléogène d'Afrique sub-
36 saharienne. *Cr Acad Sci II A.* 303: 1251-1254.

37
38
39
40 Rana RS, Kumar K, Singh H, Rose KD. 2005. Lower vertebrates from the Late
41 Palaeocene-Earliest Eocene Akli Formation, Giral Lignite Mine, Barmer District,
42 western India. *Current Sc.* 89: 1609–1613.

43
44
45
46 Randall JE, Hoover JP. 1995. *Coastal Fishes of Oman.* University of Hawaii Press.

47
48
49
50 Roberts TR. 2006. *Makararaja chindwinensis*, a New Genus and Species of Freshwater
51 *Dasyatidid Stingray from Upper Myanmar.* *Nat Hist B Siam Soc.* 54 (2): 285–293

52
53
54
55 Rüppell WPESE. 1828-1830. *Atlas zu der Reise im nördlichen Afrika. Fische des*
56 *Rothen Meers.* Frankfurt am Main (Heinrich Ludwig Brönnner): 1–141 + 3 pp., col. Pls.

1
2
3 1–35. [Part 1 (1828): 1–26, Pls. 1–6; part 2 (1829): 27–94, Pls. 7–24; part 3 (1830): 95–
4 141, Pls. 25–35.]
5

6
7 Sahni A, Mehrotra DK. 1981. The Elasmobranch Fauna of Coastal Miocene sediments
8 of Peninsular India. Biological Memoirs. 5: 83–121.
9

10
11
12 Semeniuk CA, Dill LM. 2006. Anti-predator benefits of mixed-species groups of
13 cowtail stingrays (*Pastinachus sephen*) and whiprays (*Himantura uarnak*) at rest.
14 Ethology. 112: 33–43.
15
16

17
18
19 Sharma KM, Patnaik R. 2013. Additional Fossil Batoids (Skates and Rays) from the
20 Miocene Deposits of Baripada Beds, Mayurbhanj District, Orissa, India. Earth Sc India.
21 6 (4): 160–184
22
23

24
25 Stromer E. 1910. Reptilien und Fischreste aus dem marinen Alttertiär von Südtogo
26 (West Africa). M Dtsch Geol Ges. 62 (7): 478–505.
27
28

29
30 Thomas H, Roger J, Sen S, Bourdillon-de-Grissac C, Al-Sulaimani Z. 1989. Découverte
31 de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultana d'Oman). Cr Acad
32 Sci II A. 22: 101–120.
33
34

35
36
37 Underwood CJ, Ward DJ, King C, Antar SM, Zalmout IS, Gingerich PD. 2011. Shark
38 and ray faunas in the Middle and Late Eocene of the Fayum Area, Egypt. P Geologists
39 Assoc. 122: 47–66.
40
41

42
43 Underwood CJ, Johanson Z, Welten M, Metscher B, Rasch LJ, Fraser GJ, Smith MM.
44 2015. Development and evolution of dentition pattern and tooth Order in the skates and
45 rays (Batoidea; Chondrichthyes). Plos One. 10(4): e0122553.
46
47

48
49 Uyeno T. 1978. A preliminary Report on Fossil Fishes from Ts'o-chen, Tainan. Sci Rep
50 Geo Paleo Taiwan Mus. 1: 5–17.
51
52

53
54 White EI. 1927. Fossil sharks' teeth from the Zanzibar Protectorate. Rep Paleontol
55 Zanzibar Protectorate. 121–123.
56
57

1
2
3
4
5
6
7
8
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41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

White EI. 1931. The vertebrate faunas of the English Eocene. I. From the Thanet Sands to the Basement Bed of the London Clay. Brit Mus (Nat Hist). 1-121.

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3 Figure 1. 3D models of both upper and lower jaws of *Pastinachus ?ater*, male of 75 cm
4 DW from Java (UM REC 818M). A-B: labial and lingual view of jaws; C-G: views of
5 isolated dental plates with C. occlusal view of both dental plates with tooth files
6 explanation, D. lateral view of both dental plates, E-F: basal views of upper tooth plate;
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8 G. labial view of lower tooth plate; H: transversal x-ray scanning of left upper tooth
9 plate. *Abbreviations*: u.s, upper symphyseal tooth; u.a, upper anterior teeth; u.l, upper
10 lateral teeth; u.p, upper posterior tooth; l.s, lower symphyseal tooth; l.al, lower antero-
11 lateral teeth; l.p, lower posterior tooth.
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19 Figure 2. Locality of KEB-1, Djebel el Kébar, Sidi-Bouzid region, Tunisia. A,
20 Simplified map of Tunisia locating the Djebel el Kébar in central Tunisia; B, the
21 *pastinachus* outline indicates the level having yielded the fossil-bearing KEB-1 locality;
22 C, photograph showing the typical badlands of variegated clays from the early Tertiary
23 sequence of Djebel el Kébar. See Merzeraud et al. (2016) for precise details about
24 geological settings.
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32 Figure 3. *Pastinachus kebarensis* nov. sp. A-E: upper symphyseal tooth (KEB1-076) in
33 A, occlusal view; B, lingual view; C, profile; D, labial view; E, basal view. F-J: upper
34 anterior tooth (KEB1-077) in F, occlusal view; G, lingual view; H, profile; I, labial
35 view; J, basal view. K-O: first upper lateral tooth (KEB1-078) in K, occlusal view; L,
36 profile; M, lingual view; N, basal view; O, labial view. P-T: upper lateral tooth (KEB1-
37 079) in P, occlusal view; Q, basal view; R, labial view; S, profile; T, lingual view. U-Y:
38 upper lateral tooth (Holotype KEB1-080) in U, occlusal view; V, basal view; W, lingual
39 view; X, labial view; Y, profile. Z-AD, upper lateral tooth (KEB1-081) in Z, occlusal
40 view; AA, basal view; AB, profile; AC, lingual view; AD, labial view. AE-AG:
41 posterior tooth (KEB1-082) in AE, lingual view; AF, labial view; AG, profile. AH-AL:
42 Lower antero-lateral tooth (KEB1-083) in AH, occlusal view; AI, basal view; AJ,
43 profile; AK, lingual view; AL, labial view. AM-AQ: lower antero-lateral tooth (KEB1-
44 084) in AM, occlusal view; AN, basal view; AO, profile; AP, lingual view; AQ, labial
45 view. AR: lower antero-lateral tooth (KEB1-085) in occlusal view with AS,
46 magnificence of occlusal surface of crown. Scale bar = 1mm except for AS.
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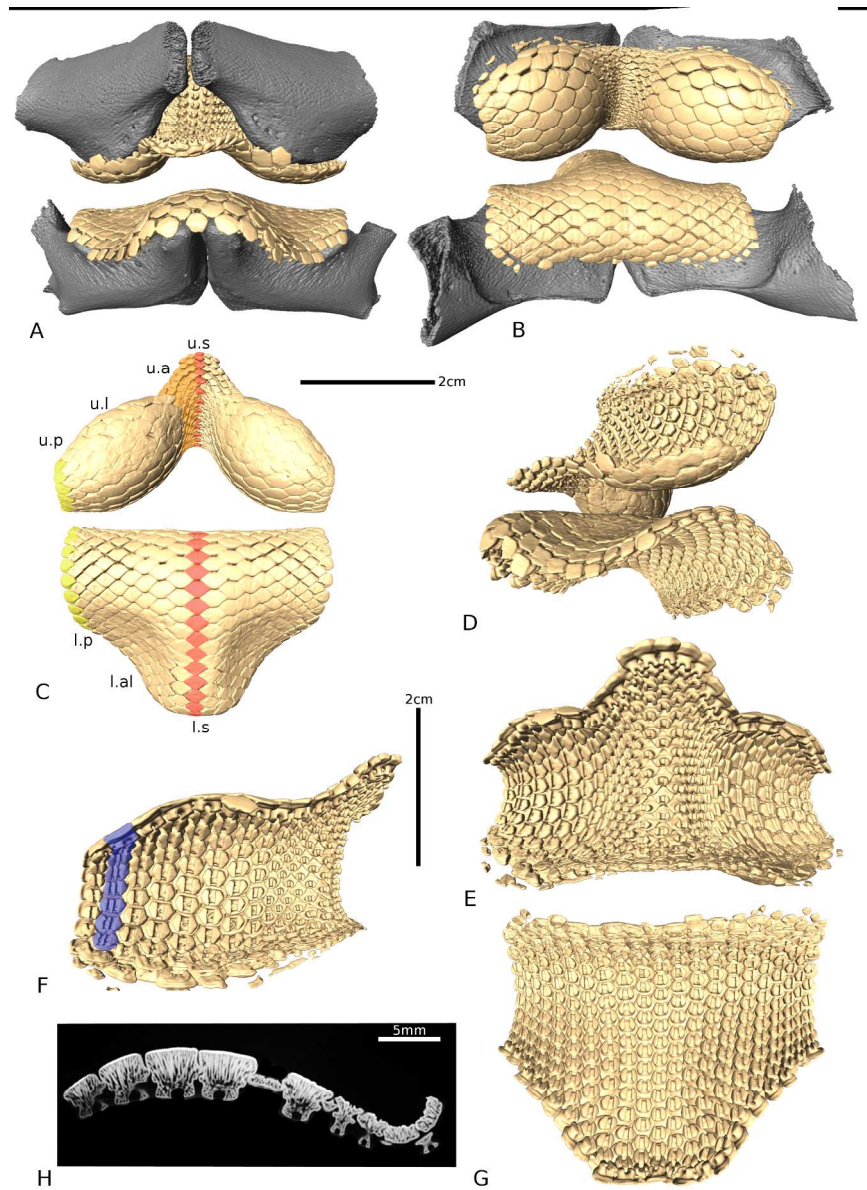


Figure 1. 3D models of both upper and lower jaws of *Pastinachus ater*, male of 75 cm DW from Java (UM REC 818M). A-B: labial and lingual view of jaws; C-G: views of isolated dental plates with C. occlusal view of both dental plates with tooth files explanation, D. lateral view of both dental plates, E-F: basal views of upper tooth plate; G. labial view of lower tooth plate; H: transversal x-ray scanning of left upper tooth plate. Abbreviations: u.s, upper symphyseal tooth; u.a, upper anterior teeth; u.l, upper lateral teeth; u.p, upper posterior tooth; l.s, lower symphyseal tooth; l.al, lower antero-lateral teeth; l.p, lower posterior tooth.

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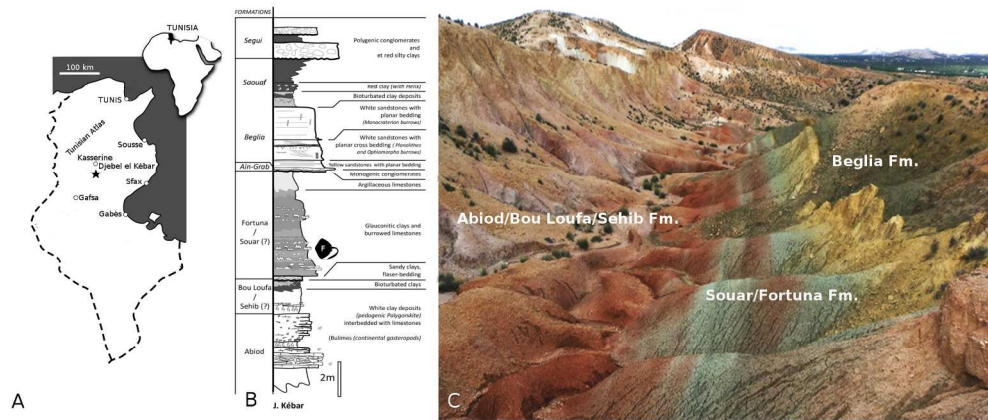


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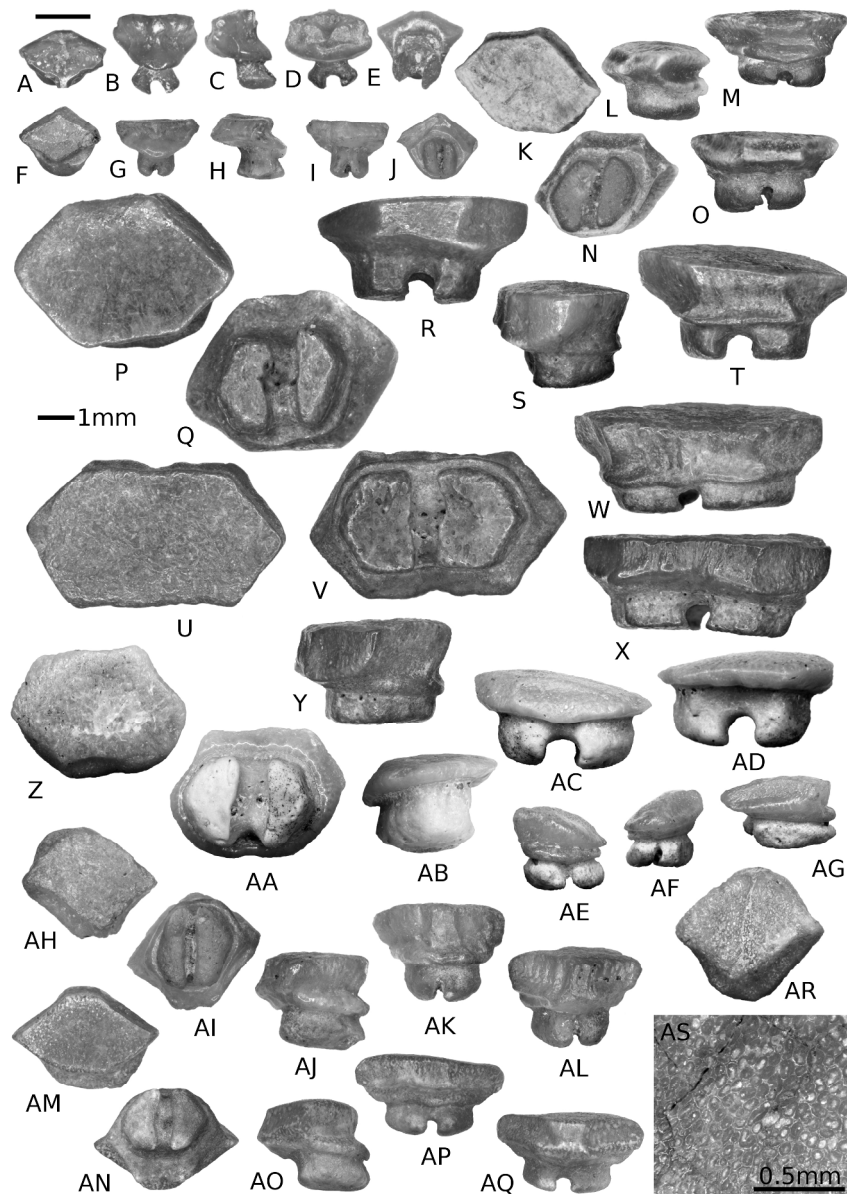


Figure 3. *Pastinachus kebarensis* nov. sp. A-E: upper symphyseal tooth (KEB1-076) in A, occlusal view; B, lingual view; C, profile; D, labial view; E, basal view. F-J: upper anterior tooth (KEB1-077) in F, occlusal view; G, lingual view; H, profile; I, labial view; J, basal view. K-O: first upper lateral tooth (KEB1-078) in K, occlusal view; L, profile; M, lingual view; N, basal view; O, labial view. P-T: upper lateral tooth (KEB1-079) in P, occlusal view; Q, basal view; R, labial view; S, profile; T, lingual view. U-Y: upper lateral tooth (Holotype KEB1-080) in U, occlusal view; V, basal view; W, lingual view; X, labial view; Y, profile. Z-AD, upper lateral tooth (KEB1-081) in Z, occlusal view; AA, basal view; AB, profile; AC, lingual view; AD, labial view. AE-AG: posterior tooth (KEB1-082) in AE, lingual view; AF, labial view; AG, profile. AH-AL: Lower antero-lateral tooth (KEB1-083) in AH, occlusal view; AI, basal view; AJ, profile; AK, lingual view; AL, labial view. AM-AQ: lower antero-lateral tooth (KEB1-084) in AM, occlusal view; AN, basal view; AO, profile; AP, lingual view; AQ, labial view. AR: lower antero-lateral tooth (KEB1-085) in occlusal view with AS, magnification of occlusal surface of crown. Scale bar = 1mm except for AS.