

# Anatomy, relationships and palaeobiogeographic implications of the first Neogene holomorphic stingray (Myliobatiformes: Dasyatidae) from the early Miocene of Sulawesi, Indonesia, SE Asia

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The early Miocene stingray †*Trygon vorstmani* represented by a single specimen collected from the fish-bearing limestones of the Tonasa Formation of SW Sulawesi, Indonesia, is redescribed here in detail. This taxon exhibits a unique combination of features that clearly support the presence of a new genus, †*Protohimantura* **gen. nov.** and its assignment to the whiptail stingrays (Dasyatidae) of the subfamily Urogymninae. The morphological and phylogenetic affinities of †*Protohimantura* **gen. nov.** with the living whipsrays suggest a close association of this taxon with tropical shallow-water habitats hypothesized for the SW Sulawesi palaeoenvironment during early Miocene. Moreover, this occurrence, which also represents the first holomorphic stingray specimen from the Neogene, provides new insights into the role of the Indo-Australian Archipelago for the evolutionary history of fishes associated with reefs in the context of the shift of the marine biodiversity hotspot across the globe during the last 50 million years.

ADDITIONAL KEYWORDS: Batomorphii – Elasmobranchii – hopping hotspots – †*Protohimantura* **gen. nov.** – Urogymninae – whipsrays.

## INTRODUCTION

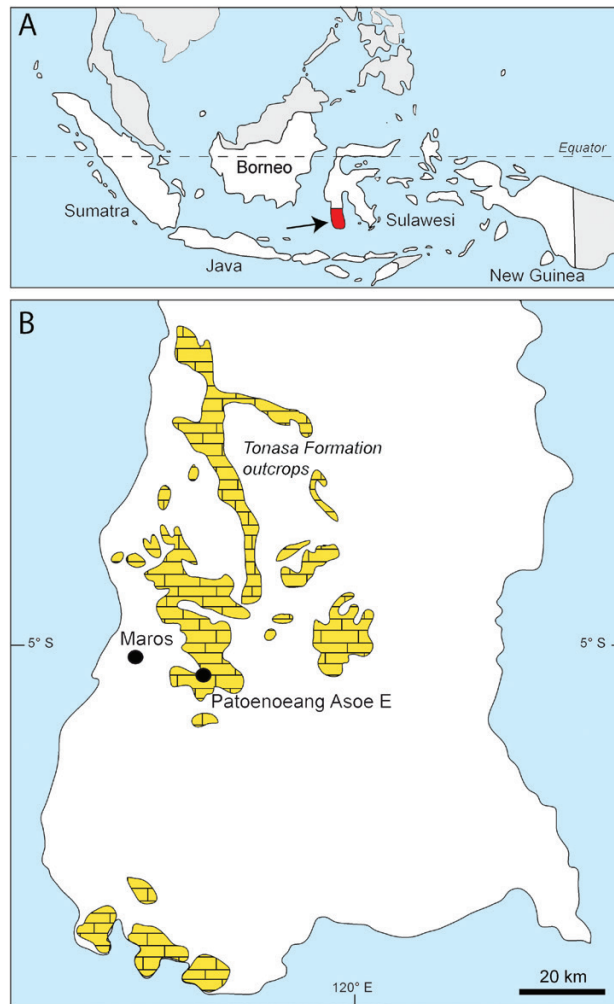
Whiptail stingrays of the family Dasyatidae include small to large rays (up to 2.6 m of disc width and 600 kg) within the batomorph order Myliobatiformes that inhabit demersal inshore habitats of continental and insular shelves up to a depth of 600 m and include about 86 living species in 19 genera with worldwide distributions (Last *et al.*, 2016a; Last, Naylor & Manjaji-Matsumoto, 2016b; Nelson, Grande & Wilson, 2016). Although some morphological and molecular analyses suggest that Dasyatidae might be non-monophyletic (e.g. Lovejoy, 1996; Carvalho *et al.*, 2004; Aschliman, Claeson & McEachran, 2012a), several authors have recognized a set of morphological characters that are used to distinguish whiptail stingrays from all

other myliobatiforms, including variably depressed circular to rhombic discs not more than 1.3 times as broad as long, an angular to obtuse and sometimes very elongated snout, absent caudal and dorsal fins, greatly elongated and slender to whip-like tail with one to four long venomous spines, and a skin ranging from being completely smooth to covered – to varying extents – with small dermal denticles and thorns (Cappetta, 2012; Last *et al.*, 2016a, b; Nelson *et al.*, 2016). However, the most recent molecular and morphological analyses recognized that this family is actually monophyletic (e.g. Aschliman *et al.*, 2012b; Naylor *et al.*, 2012a; Bertozzi, Lee & Donnellan, 2016) and consists of four major subgroups on subfamily level: the Dasyatinae, Neotrygoninae, Hypolophinae and Urogymninae (Last *et al.*, 2016b). The latter subfamily, whose representatives are also known as whipsrays, is a diverse group of stingrays formerly consisting of *Himantura* species and the monotypic genus *Urogymnus*. Recently, Last *et al.* (2016b) recognized at least six morphologically identifiable, monophyletic subdivisions

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for *Himantura*, and the subfamily therefore consists of seven genera: *Brevitrygon*, *Fluvitrygon*, *Fontitrygon*, *Himantura*, *Maculabatis*, *Pateobatis* and *Urogymnus*. On the contrary, the amphi-American '*Himantura*' *schmardae* (Werner, 1904) has been recently included in a different genus, *Styracura*, and recognized as closely related to the freshwater stingray family Potamotrygonidae (Carvalho, Loboda & Da Silva, 2016). The representatives of the subfamily Urogymninae have unique characters within the Dasyatidae, such as the absence of skin folds on the tail, presence of a well-developed band of densely packed heart-shaped denticles on the disc with sharply defined margins and relatively narrow base of the tail with an almost circular cross-section (Last *et al.*, 2016a). Moreover, with the exception of the southern Atlantic *Fontitrygon*, the subfamily appears to be restricted to the Indo-Pacific area (Compagno & Roberts, 1982; Manjaji, 2004; Last *et al.*, 2016a).

Although the fossil record of dasyatids is well-represented, it is heavily biased toward isolated teeth, dermal denticles and caudal spines (Cappetta, 2012). In the Cenozoic, complete and articulated batoids only have been recovered from Palaeogene marine sediments of the Bolca Lagerstätte in Italy, Grube Unterfeld in Germany and freshwater deposits of the Green River Formation, USA (Carvalho *et al.*, 2004; Hovestadt, Hovestadt-Euler & Micklich, 2010; Marramà *et al.*, 2017a, b, c). Furthermore, the fossil record of batoids from SE Asia is very poor and mostly comprises few and isolated teeth from Neogene deposits of Myanmar, Indonesia and New Guinea (Adnet *et al.*, 2008; Cappetta, 2012). The most famous Cenozoic fossil fish sites of SE Asia are those Indonesian of Sumatra (Eocene freshwater) and Sulawesi (Miocene marine), which yielded abundant complete teleosteans (e.g. Brouwer & de Beaufort, 1923; de Beaufort,



**Figure 1.** Location and simplified geological map of the SW Sulawesi, Indonesia. The map, showing the early Miocene outcrops of the Tonasa Formation in which †*Protohimantura vorstmani* (de Beaufort, 1926) has been collected, is adopted and modified from Wilson (2000) and Wilson *et al.* (2000).

1926; Murray *et al.*, 2015). Remains of elasmobranchs, conversely, are absent in Sumatra and only a single, partial skeleton was recovered from shallow-marine limestones from the early Miocene of SW Sulawesi (de Beaufort, 1926). The goal of this paper is to present a morphological and systematic revision of this Neogene stingray, which was only described very cursorily as †*Trygon vorstmani* by de Beaufort (1926). The character combination distinguishes the specimen readily from all other dasyatids, therefore representing a new genus of whiptail stingrays of the subfamily Urogymninae. Palaeogeographic implications, based on the analysis of fossil occurrences of this subfamily, provide new insights into the role of the Indo-Australian Archipelago (IAA) for the evolutionary history of whiptails in the context of the shift of marine biodiversity hotspots across the globe during the last 50 million years.

### GEOLOGICAL SETTING

The specimen that forms the focus of this study was collected by Professor H. A. Brouwer in 1923 in limestone outcrops near the village of Patoenoeang Asoe E, in the Maros District of SW Sulawesi, Indonesia (de Beaufort, 1926) (Fig. 1). The yellowish fossil-bearing, micritic and laminated limestones of this area belong to the uppermost early Miocene strata of the Tonasa Formation from which other remains of bony fishes and terrestrial flora were recovered (see: Brouwer & de Beaufort, 1923; Brouwer, 1924a; Bartstra, 1977; Tyler, 1997). The Tonasa Formation in the Pangkajene area (where Patoenoeang Asoe E is located) consists of an up to 600-m-thick sequence of shallow-water carbonates deposited from the early or middle Eocene to the middle Miocene in a widespread area of carbonate production known as Tonasa Carbonate Platform (Wilson, 1996, 2000; Wilson, Bosence & Limbong, 2000). In SW Sulawesi, the Tonasa Carbonate Platform developed as part of a transgressive sequence to the west of a volcanic arc and is overlain by middle to upper Miocene volcanic rocks of the Camba Formation (Wilson, 2000; Wilson *et al.*, 2000). In the area of Patoenoeang Asoe E, the upper part of the carbonate succession was deposited in a moderate-energy, shallow-water context within the photic zone, as inferred from the presence of larger and small benthic foraminifera, coralline algae, fragmented echinoids, corals and alveolinids (Wilson & Bosence, 1997; Wilson, 2000). The presence of the benthic foraminifer *Flosculinella* sp. suggested an early Miocene age for the strata (Wilson, 2000), as already hypothesized by Brouwer (1924b) who tentatively referred this sequence to the Burdigalian (about 20.4 to 16.0 Mya). Although lithologies, stratigraphy and tectonic evolution of this area have been extensively

documented, mostly in order to study its hydrocarbon resources (see: Wilson, 1996, 2000; Wilson *et al.*, 2000), the palaeontology and evolutionary significance of the fossil organisms (including bony and cartilaginous fishes) have been poorly investigated so far.

### MATERIAL AND METHODS

The single specimen in part and counterpart was collected during a road construction near Patoenoeang Asoe E at the beginning of the 20th century. The specimen, which is housed in the collections of the Naturalis Biodiversity Center Leiden, The Netherlands, and labelled with the repository number RGM 624420, was examined using a stereomicroscope equipped with camera lucida drawing arm. Casts of the embedded teeth and dermal denticles were prepared using silicon compound and epoxy resin, and studied and photographed with a Hitachi S-3500N Scanning Electronic Microscope (SEM) at the University of Bristol. Measurements were taken to the nearest 0.1 mm. Osteological and tooth terminology primarily follows Nishida (1990), Lovejoy (1996), Herman *et al.* (1998, 1999, 2000) and Carvalho *et al.* (2004). Morphometric terminology is adopted and modified from Compagno & Roberts (1982, 1984) and Carvalho *et al.* (2016). Comparative information was derived mainly from the literature. The term 'holomorphic' refers here to being more or less completely (articulated) preserved.

The phylogenetic analysis is based on the morphological dataset of Claeson *et al.* (2010), which in turn is based on the matrix of Carvalho *et al.* (2004). The matrix (see Appendices 1 and 2) was extended with characters provided by Aschliman *et al.* (2012a) and Underwood, Kolmann & Ward (2017), which are useful to better define the relationships within the Myliobatiformes and are not included in the analysis of Claeson *et al.* (2010). Other dental and morphological characters are based on Herman *et al.* (1998, 1999, 2000), Schaefer & Summers (2005), Lim *et al.* (2015) and Last *et al.* (2016a). Characters for all genera considered are coded following Claeson *et al.* (2010), except *Aetomylaeus*, *Pastinachus* and *Neotrygon*, which are not present in Claeson *et al.*'s (2010) study and are, therefore, coded following Aschliman *et al.* (2012a), Carvalho *et al.* (2016) and Underwood *et al.* (2017). The data matrix contains 29 taxa, which represent all living myliobatiform genera analysed by Claeson (2010), Aschliman *et al.* (2012a) and Underwood *et al.* (2017), and includes the two fossil holomorphic stingrays of Carvalho *et al.* (2004) and the new taxon described herein. To our knowledge, this dataset represents the most comprehensive and updated dataset of myliobatiform morphological characters resulting in 102 characters. The character matrix was compiled

in MESQUITE v.3.03 (Maddison & Maddison, 2008). The phylogenetic analysis was performed with TNT v.1.5 using the branch-and-bound method (Goloboff, Farris & Nixon, 2008). All characters are considered unordered and given equal weight. Tree length, consistency (CI) and retention (RI) indices, and Bremer support were subsequently calculated for the two trees retrieved by the analysis.

## SYSTEMATIC PALAEOONTOLOGY

CLASS CHONDRICHTHYES HUXLEY, 1880

SUPERORDER BATOMORPHII CAPPETTA, 1980

ORDER MYLIOBATIFORMES COMPAGNO, 1973

FAMILY DASYATIDAE JORDAN, 1888

SUBFAMILY UROGYMNINAE GRAY, 1851  
(*SENSU*; LAST *ET AL.*, 2016B)

GENUS †*PROTOHIMANTURA* GEN. NOV.

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*Type species*: †*Trygon vorstmani* de Beaufort, 1926.

*Etymology*: From the Ancient Greek word *prōto*, meaning ‘first’, ‘foremost’, ‘earliest form of’, and *Himantura*, one of the living whipray genera, thus indicating a possible close relationship between both taxa.

*Diagnosis*: A whipray characterized by the following combination of characters and body proportions: eye small; interorbital width/eye diameter ratio of 3.5; nasal capsule width/neurocranial length ratio of 0.7; nasal capsule length/neurocranial length ratio of 0.2; anteroposterior fontanelle/neurocranial length ratio of 0.8; scapulocoracoid width/lateral face length ratio of 2.2; 55 propterygial radials; 17 mesopterygial radials; mid-dorsal surface of disc covered by heart-shaped denticles arranged in an antero-posteriorly directed patch having sharply defined outlines; teeth with semi-ovoid or subhexagonal crown with a second transverse keel; lingual and labial crown ornamentation absent.

*Remarks*: The species †*Trygon vorstmani* was created by de Beaufort (1926) who presented a short description (one page long) and figured this single specimen in part and counterpart, which was previously collected by Professor Brouwer at the beginning of the 20th century near Patoenoeang Asoe E in the Maros district of SW Sulawesi, Indonesia. The placement of this taxon in the family Dasyatidae [= Trygonidae of de Beaufort (1926)] was based on the presence of a propterygium that is bent inwards in front to the median line and pectorals of both sides meeting at the snout (de Beaufort, 1926). However, after this first brief

report, no in-depth morphological analysis or identification of characters was provided to distinguish the specimen from other extant or extinct rays, with the exception of a preliminary study by Klug & Kriwet (2012) who recognized its close relationship with the genus *Himantura*. However, at present, *Trygon* is regarded as a junior synonym of *Dasyatis* Rafinesque, 1810, and the Sulawesi species shows several morphological features that distinguish it from *Dasyatis*, *Himantura* and all representatives of the family Dasyatidae (see Description and Discussion). On the contrary, the morphological characters observed in the examined specimen and discussed below corroborate the erection of a new genus to contain †*Trygon vorstmani* and its inclusion in the subfamily Urogyminae.

*Included species*: Type species only.

†*PROTOHIMANTURA VORSTMANI* (DE BEAUFORT, 1926)

(FIGS 2–5, 7)

†*Trygon vorstmani* de Beaufort, 1926: p. 119, pl. 1 (original occurrence of name, photograph and outline reconstruction); de Beaufort, 1931: p. 462.

†*Himantura vorstmani* (de Beaufort, 1926); Klug & Kriwet, 2012: p. 93.

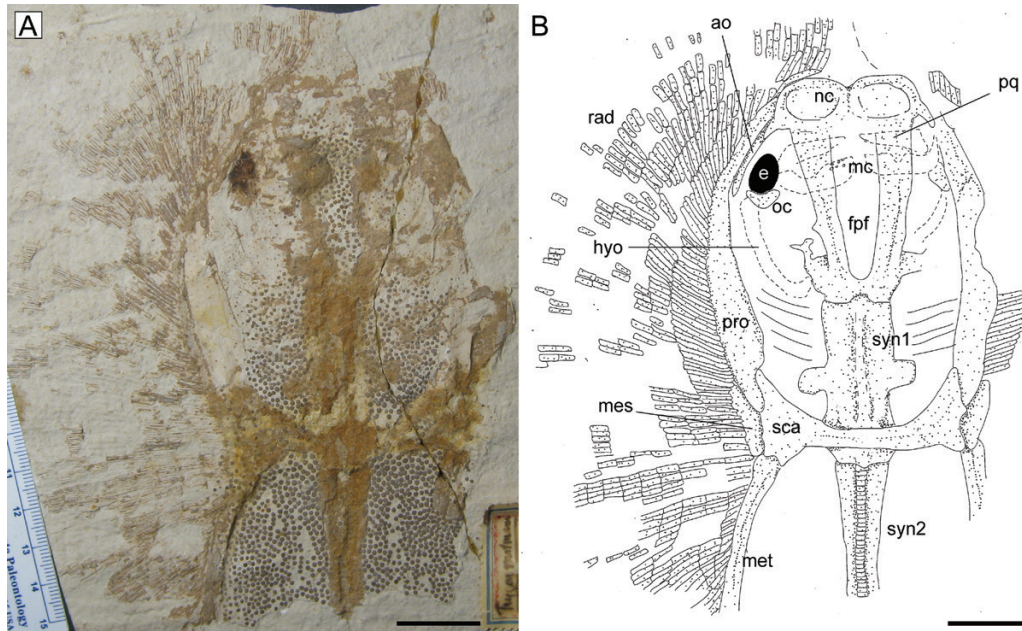
*Holotype*: RGM 624420, single specimen in part and counterpart, lacking the posterior region of body.

*Type locality and horizon*: Patoenoeang Asoe E, Maros District, SW Sulawesi, Indonesia; Tonasa Formation, ?Burdigalian, early Miocene (see: Wilson, 2000; Wilson *et al.*, 2000).

*Diagnosis*: As for the genus.

### Description

The specimen examined is represented by a single partial skeleton lacking part of the external margin of the pectoral disc and the posterior portion of the body, including the tail (Fig. 2). However, the anterior portion of the body is quite complete and preserves several anatomical structures that identify this specimen as a new genus of the family Dasyatidae. Measurements and meristics for †*Protohimantura vorstmani* are summarized in Table 1. The body preserved in the main slab measures 161 mm from the anterior margin of the disc to the last preserved vertebra, just posteriorly to the second synarcual. Comparing this size to that of modern whiprays, it is therefore likely that the individual could have reached a total length of about 50–60 cm, comparable to the size of an adult individual of most living urogyminines (see: Last *et al.*, 2016a). The high calcified bones corroborate the hypothesis of an adult stage for the specimen. In Fig. 2 the specimen is displayed in ventral view, as suggested



**Figure 2.** †*Protohimantura vorstmani* (de Beaufort, 1926) from early Miocene of Sulawesi, Indonesia. A, RGM 624420, holotype; B, reconstruction, dermal denticles omitted. Scale bars 20 mm. Abbreviations: ao, antorbital cartilage; e, eye; fpf, frontoparietal fontanelle; hyo, hyomandibula; mc, Meckel's cartilage; mes, mesopterygium; met, metapterygium; nc, nasal capsules; oc, optic capsule; pq, palatoquadrate; pro, propterygium; rad, radials; sca, scapulocoracoid; ss, suprascapulae; syn1, cervicothoracic synarcual; syn2, thoracolumbar synarcual.

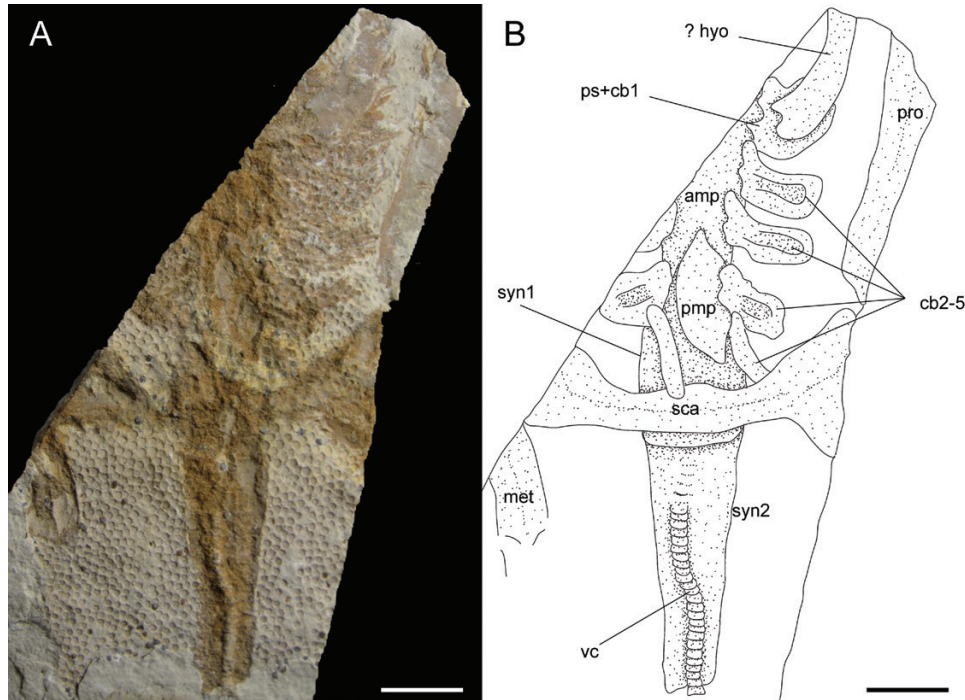
by dermal denticles showing their ventral surface, and by the counterslab showing the gill arch skeleton (Fig. 3). The head is relatively close to the anterior margin of the disc and preserves traces of the eye. The eye is small, with the length of eyeball being 3.5 units in interorbital

width. The central portion of the disc is covered with an antero-posteriorly directed band of denticles.

*Neurocranium:* The neurocranium is antero-posteriorly elongate, longer than wide, with its greatest width at

**Table 1.** Morphometric and meristic data for RGM 624420, †*Protohimantura vorstmani* (de Beaufort, 1926) from the early Miocene of Sulawesi, Indonesia

		mm	% of neurocranial length
Measurements	Anteroposterior fontanelle	45.7	79.9
	Nasal capsule width	39.2	68.6
	Nasal capsule length	13.8	24.1
	Internarial width	17.9	31.3
	Interorbital width	39.0	68.2
	Eyeball length	11.3	19.7
	Mouth width	15.3	26.7
	Synarcual length	51.7	90.4
	Postorbital process length	14.2	24.9
	Postorbital process width	10.8	18.9
	Scapulocoracoid width	53.3	93.2
	Lateral face of scapulocoracoid length	23.8	41.7
	Neurocranial length	57.2	100.0
Count	Propterygial radials	55	
	Mesopterygial radials	17	
	Metapterygial radials	25+?	



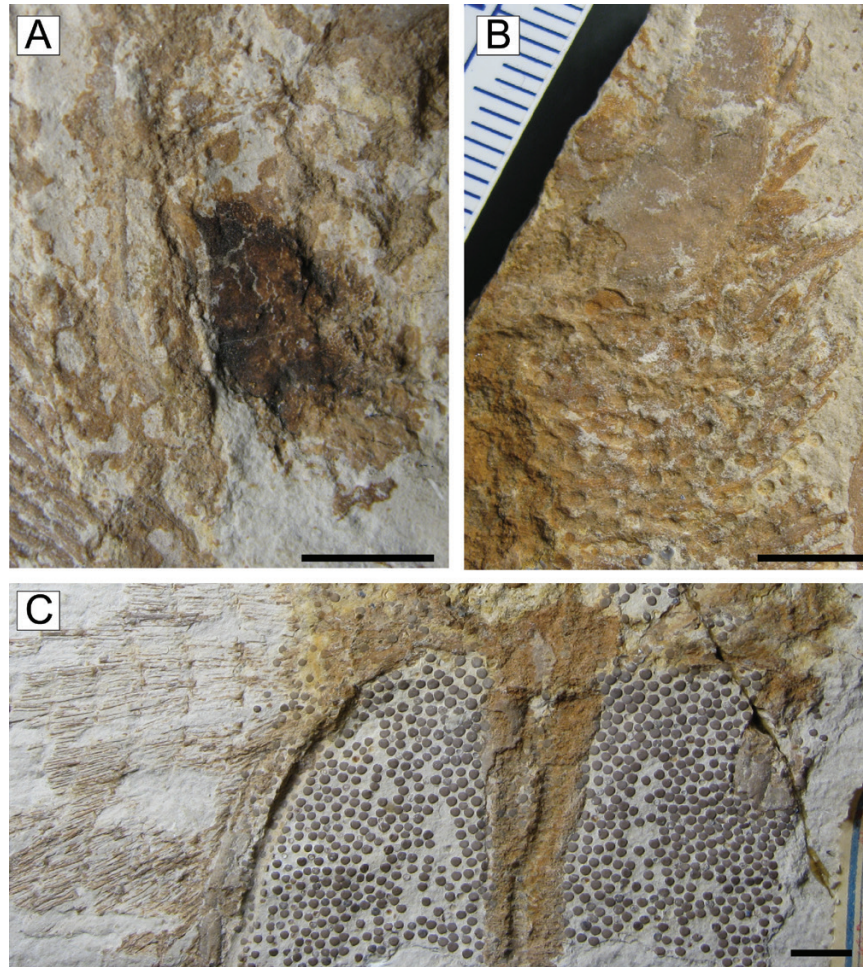
**Figure 3.** †*Protohimantura vorstmani* (de Beaufort, 1926) from early Miocene of Sulawesi, Indonesia. A, RGM 624420, holotype, counterslab. B, reconstruction, dermal denticles omitted. Scale bars 10 mm. Abbreviations: amp, anterior medial plate; cb, ceratobranchial; hyo, hyomandibula; met, metapterygium; pmp, posterior medial plate; pro, propterygium; ps, pseudohyoid; sca, scapulocoracoid; syn1, cervicothoracic synarcual; syn2, thoracolumbar synarcual; vc vertebral centra.

the level of nasal capsules (Fig. 2). The rostral cartilage is absent, resembling the condition of adult stingrays (e.g. Compagno, 1977; Miyake *et al.*, 1992). The nasal capsules are antero-posteriorly short, transversely broad and ovoid in shape. Their anterior margin is rounded and biconvex with a small and triangular anterior median indentation. The nasal capsule width and length are about 70% and 20% of the neurocranial length, respectively. The internasal plate between the two capsules appears antero-posteriorly elongate and extremely narrow. The preorbital processes are small, posteriorly directed, and protrude by the posterolateral aspect of nasal capsules. The supraorbital process is small, triangular in shape and located just anteriorly to the postorbital process. The orbital region is longer than wide. The specimen preserves traces of an eye as a brown-coloured carbon film contoured by its optic capsule (Fig. 4A). The eyeball is ovoid in shape, slightly antero-posteriorly elongated, and possibly consists of an accumulation of melanosome-like microbodies containing molecularly preserved traces of melanin (see: Lindgren *et al.*, 2012; Marramà & Carnevale, 2015). The neurocranium is narrower at the level of the otic region, with its least width being about 30% of the total neurocranial length. The otic capsules are short. Although the specimen shows the ventral side in the main slab, it is possible to recognize (possibly

due to taphonomic compression) the outline of the fronto-parietal fontanelle, which is antero-posteriorly elongated and covers about 75–80% of the neurocranial length; its posterior margin is concave and does not show any indentation. The precerebral fontanelle is difficult to examine. The postorbital processes are broad and shelf-like.

The antorbital cartilage is very long and laterally narrow (Fig. 2). Its maximum width is at the level of the articulation with the postero-lateral aspect of the nasal capsule and extends posteriorly close to the hyomandibula at the level of the jaw joint. The antorbital cartilage is simple, not branched, posteriorly directed and articulates with propterygium.

**Jaws:** Both jaws are poorly preserved and their outline is difficult to describe. However, the palatoquadrate appears labio-lingually compressed, smaller and narrower than the Meckel's cartilage. The Meckel's cartilages are stouter and broader than the palatoquadrate. It is not possible to recognize the medial symphyseal process nor the anterior processes of the Meckel's cartilage, which are present in *Himantura* and *Dasyatis* according to Underwood *et al.* (2017). Wing-like processes, which project laterally from close to the lower jaw symphysis in pelagic stingrays, are absent in †*Protohimantura* **gen. nov.** The lateral oral

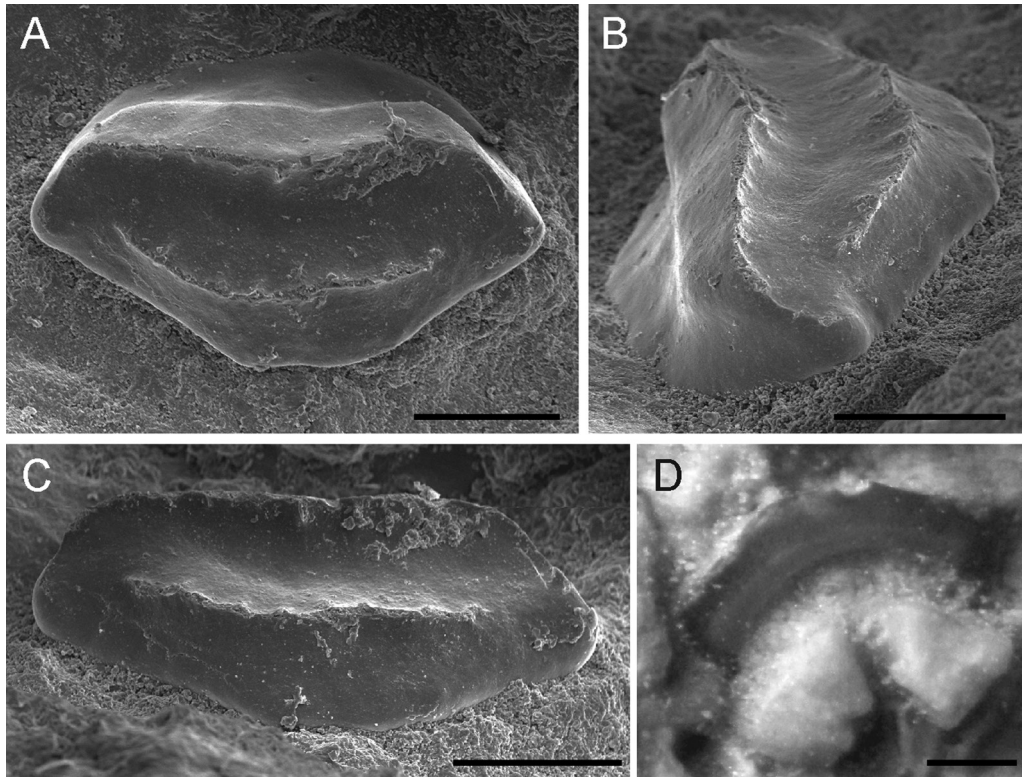


**Figure 4.** †*Protohimantura vorstmani* (de Beaufort, 1926) from early Miocene of Sulawesi, Indonesia; RGM 624420, holotype. Close up of the eye (A), the branchial rays (B), and part of the denticle band (C). Scale bars 5 mm.

diastema appears to be wider than the occlusal width. Antimeres of both upper and lower jaws are narrower and separated at symphysis.

*Hyoid and gill arches:* The hyomandibulae are preserved only as outline in the main slab (Fig. 2). They appear laterally compressed and narrow at about midlength, slightly arched and with a concave inner margin. The distal end of the hyomandibula articulates with the lower jaw through a strong and stout terminal portion. In the counterpart (Fig. 3), the hyomandibula appears strongly calcified and its proximal portion at the articulation with the otic region is enlarged and stouter than its mesial part. There is no trace of the angular cartilages typical of potamotrygonids or secondary hyomandibular cartilages as in *Urolophus* and pelagic stingrays (see: Lovejoy, 1996; Carvalho *et al.*, 2004, 2016; Claeson *et al.*, 2010). The ventral gill arch skeleton of †*Protohimantura* **gen. nov.** is partially well-preserved in the counterslab (Fig. 3)

and its morphology is consistent, at least in part, to that of *Dasyatis* and *Himantura* depicted in Miyake & McEachran (1991, fig. 8). Although the anterior portion is not completely preserved, it is possible to recognize an enlarged central medial plate, which results from the fusion of the basibranchial copula and the basibranchial components (Miyake & McEachran, 1991; Carvalho *et al.*, 2004). The medial plate is composed of an anterior and a posterior portion forming the mid-ventral skeleton of gill arches of stingrays (Miyake & McEachran, 1991). The incomplete anterior portion of the medial plate appears tubular and subrectangular in shape. The posterior portion is ovoid or pseudorhombic in shape, and tapers posteriorly into a small median projection. It is not possible to detect if the basihyal is fused or not to the first hypobranchial. There are five pairs of ceratobranchials. The first one appears to be fused with the pseudohyoid, as in most of the stingrays and *Brevitrygon imbricata* in particular (see: Miyake & McEachran, 1991, fig. 8I), whereas



**Figure 5.** Teeth of †*Protohimantura vorstmani* (de Beaufort, 1926) from early Miocene of Sulawesi, Indonesia, RGM 624420, in lingual (A), lateral (B), occlusal (C) views (cast, SEM pictures). D, basal view (original specimen, Nikon camera attached to binocular). Scale bars 250  $\mu$ m.

all the other ceratobranchials articulate with small rami along the lateral margin of the anterior portion of the medial plate. The last two ceratobranchials appear ankylosed but not fused in their proximal portion. The fifth ceratobranchial articulates with the anterior margin of scapulocoracoid. The preservation of the counterslab is so optimal that it is possible to recognize the filamentous branchial rays associated with the ceratobranchials (Figs 3A, 4B), although their number on each ceratobranchial is difficult to discern. Pharyngobranchials and extrabranchials are not preserved in the available material.

**Synarcuals and vertebral column:** Both anterior (cervicothoracic) and posterior (thoracolumbar) synarcual cartilages are preserved and strongly calcified. Anteriorly, the cervicothoracic synarcual articulates with the occipital condyles of the chondrocranium. Its medial crest, whose exposure in the main slab resulted from taphonomic compression, runs antero-posteriorly along almost its entire length (Fig. 2). The cervicothoracic synarcual possesses lateral stays, which are tab-like, located at about midlength and project perpendicularly laterally, although this might be due to taphonomy, since they should be dorsally directed

forming a U-shape structure, as in all myliobatiforms (e.g. Aschliman *et al.*, 2012a). It is not possible to detect the number of fused vertebrae that constitute the first synarcual, or the foramina. The thoracolumbar synarcual is as long as the cervicothoracic synarcual. It articulates anteriorly with the first synarcual but contrary to this latter, the thoracolumbar synarcual is relatively simpler, triangular in shape and tapers posteriorly. About 30 unfused individual vertebral centra can be seen along its entire length. The vertebral centra are strongly calcified, subrectangular in shape and antero-posteriorly short. However, since the posterior part of the body is not preserved, the number of vertebrae forming the vertebral column of †*Protohimantura* is unknown. Ribs are most likely absent as in all myliobatiforms (McEachran, Dunn & Miyake, 1996; Aschliman *et al.*, 2012a).

**Pectoral fins and girdle:** The scapulocoracoid consists of a single straight and robust transverse structure, located ventral to the synarcual, and between the basibranchial copula and the articulation between the two synarcuals. Its width is about twice the length of its lateral margins. Anteriorly, the scapulocoracoid articulates with the fifth pair of ceratobranchials.



**Table 2.** List of synapomorphies for each node depicted in Figure 8. See the explanation of characters and states in Appendix 1

Node	Clade	Synapomorphies
A	Myliobatiformes	19(1), 22(1), 66(1), 67(1), 69(1), 73(1), 74(1), 75(1), 78(1), 79(1), 80(1)
B	-	12(1), 21(1), 43(1)
C	Myliobatoidea	10(1), 27(1), 28(1), 34(2), 81(3), 100(0), 101(1)
D	Myliobatidae	7(1), 11(1), 15(1), 17(1), 18(1), 19(3), 21(2), 22(0), 23(1), 25(1), 33(1), 35(1), 37(1), 38(1), 44(1), 45(1), 46(1), 48(1), 54(1), 57(1), 60(1), 61(1), 70(3), 71(2), 76(3), 96(1), 97(1), 98(1)
E	-	55(1), 92(2)
F	-	9(1), 24(1), 27(2), 51(1)
G	-	5(1), 6(1), 28(0)
H	-	44(0), 95(1)
I	Dasyatoidea	88(1)
J	Urolophidae	8(1), 29(2), 99(1)
K	-	68(1)
L	-	32(1)
M	-	19(2), 25(1), 69(0), 76(1)
N	Urotrygonidae	1(1), 41(1)
O	-	33(1), 34(2), 81(2), 85(1), 88(2)
P	Potamotrygonidae	3(2), 25(0), 30(1), 39(1), 40(1)
Q	-	3(1), 14(1), 24(1), 26(1), 34(1), 36(2), 71(1)
R	Dasyatidae	87(1), 89(1)
S	Urogymninae	99(1), 102(1)
T	-	34(1), 71(1), 83(0), 84(1)
U	Neotrygoninae	36(1), 92(1)
V	-	82(1), 88(1)
W	-	57(1&2)
X	-	34(1)

The scapular fossa (or foramen) cannot be recognized in the available material, as well as the ball and socket articulation between scapular process and first synarcual. The suprascapulae are not exposed in the available material. Laterally, the scapulocoracoid articulates with the internal skeleton of the pectoral fins. The propterygium is long and arched, and extends to the anterior disc margin. The propterygium gradually tapers distally. It is distally segmented and the first small segment is adjacent to the anterior margin of the nasal capsule, resembling the condition seen in *Dasyatis brevis*, *Hypanus longus* and *Fluvitrygon signifer* (see: Garman, 1913; Lovejoy, 1996; Aschliman et al., 2012a). The proximal portion of the propterygium is enlarged and articulates with the anterior portion of the lateral margin of the scapulocoracoid, and with the anterior mesial margin of the mesopterygium. The mesopterygium is small and subtriangular in shape; it is a single, non-fragmented element and its external margin is more or less straight, not fused to radials. The mesopterygium is shorter than the pro- and metapterygium. The metapterygium is poorly and incompletely preserved, lacking its distal portion in the main slab. However, it appears to be long, arched and tapers posteriorly. It is more slender than propterygium.

The metapterygium appears to be a single element, at least in its proximal part. All pectoral radials articulate directly with the pterygia. Although it is not possible to detect the total number of pterygial radials, there are about 55 propterygial and 17 mesopterygial radials. We also counted 25 metapterygial radials but this number is far from being real, due to the lack of the distal portion of the metapterygium. Each radial is composed of at least nine segments. However, since the external margin of the disc is incompletely preserved, it is possible that the number of segments was much higher. For the same reason, the number of bifurcation of each radial before reaching the edge of the pectoral fin margin is unknown. The distalmost radials of †*Protohimantura* **gen. nov.** are calcified in chain-like patterns, forming the so-called 'catenated calcification', which is typical of batoids with undulatory swimming mode, including all myliobatiforms with the exception of *Plesiobatis*, *Gymnura* and pelagic stingrays (Schaefer & Summers, 2005).

**Dentition:** Teeth of †*Protohimantura* **gen. nov.** are minute and not in pavement-like arrangement, as in myliobatids. The dentition is probably gradient monognathic heterodont with low-crowned teeth,

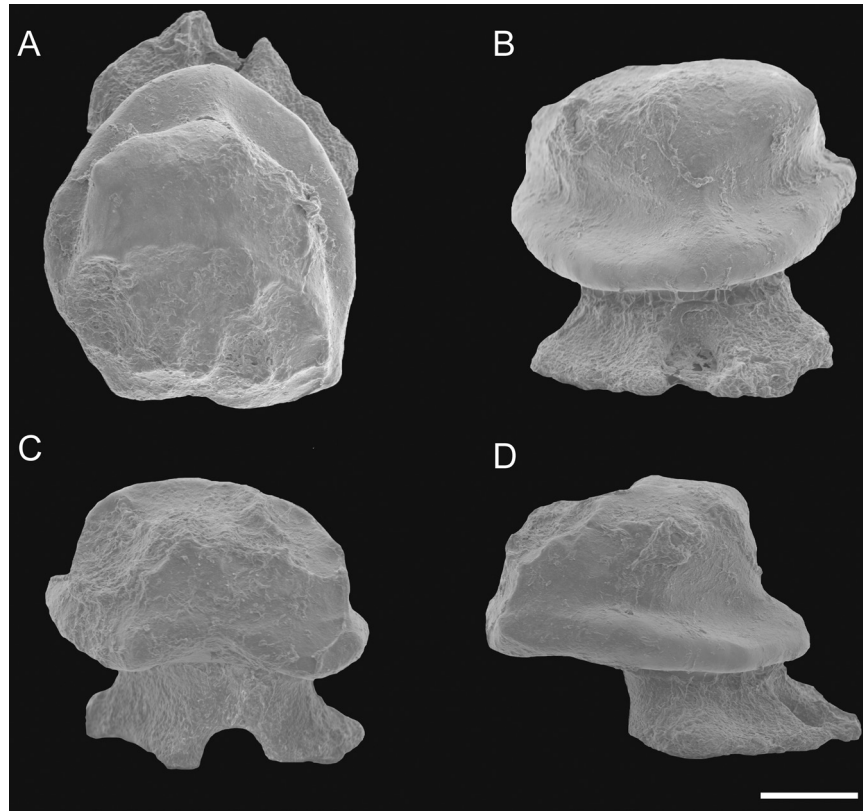
which decrease in size toward the commissure. Sexual and ontogenetic heterodonties are unknown. The tooth morphology is consistent with that of *Himantura uarnak* figured by Herman *et al.* (1998, pls 8–9). In occlusal view (Fig. 5A, C) the crown is semi-oval or subhexagonal in shape, broader than long. The crown has an inwardly bent, low, transverse keel, which divides the crown into distinct labial and lingual parts. A second transverse keel, running more or less parallel to the main keel, is present on teeth of †*P. vorstmani*, resembling the condition seen in *Himantura*, *Trygonoptera*, *Urobatis* and *Urolophus* among myliobatiforms (Herman *et al.*, 1999, 2000), and supports its sister-group relationship with *Himantura* in this study. Lingual and labial ornamentations seemingly are absent, conversely to the condition seen in teeth of the extant *Fluvitrygon signifer* (Fig. 6). The basal view of the crown (Fig. 5D) shows a broad and slightly convex crown rim at the outer part, which gradually narrows to half its width at the inner part. The crown–root junction is located in a shallow depression in the centre of the basal surface of the crown. The root is of holaulacorhizous type with two lobes, which are triangular in shape in basal view (Fig. 5D). The root base has a well-developed and deep median groove that encloses a single large central foramen. There are no inner or outer foramina discernable. The root is lower than the crown. Due to the poor preservation of the specimen, it was not possible to count the number of tooth rows.

**Dermal denticles:** The mid-dorsal surface of the disc is covered by a dermal armour consisting of numerous heart-shaped denticles arranged in an incomplete ovoid, antero-posteriorly directed patch, whose outline is sharply defined (Figs 2A, 4C). Dermal denticles are closely arranged and cover the mid-dorsal part of the disc running from the base of nasal capsules between the eyes up to the posterior-most preserved portion of the body. The denticle morphology is consistent with that of most urogymines (see: Compagno & Roberts, 1982, 1984; Deynat & Fermon, 2001; Manjaji, 2004; Last *et al.*, 2016a; Last, Bogorodsky & Alpermann, 2016c). The denticles are heart-shaped, broadly double-rounded anteriorly and triangular posteriorly (Fig. 7A–C). The crown appears to be flat or slightly globular in appearance. Denticles have a sub-circular basal plate without well-differentiated peduncle. The pectoral fins and the region of the disc anterior to the nasal capsules are sparsely covered with smaller denticles with blunt crowns (Fig. 7D). There are no thorns in the specimen examined, although we do not exclude that thorns, as well as one or more stings, might have been present in the not preserved tail.

#### PHYLOGENETIC ANALYSIS

The analysis of 102 morphological characters coded for 29 taxa produced only two most parsimonious trees with the same length of 214 steps and with the same relatively high consistency index (CI = 0.65) and retention index (RI = 0.79), which are depicted in Fig. 8. A complete list of synapomorphies for each node is listed in Table 2. The two trees are very similar and only differ in the dissimilar position of *Plesiobatis* and the extinct Eocene freshwater stingrays †*Asterotrygon* and †*Heliobatis*. The monophyly of the Myliobatiformes, as recognized by McEachran *et al.* (1996), Carvalho *et al.* (2004), McEachran & Aschliman (2004) and Aschliman *et al.* (2012a), is confirmed and supported herein by 11 synapomorphies: basihyal as a single element, but separate from first hypobranchials (character 19[1], see Appendix 1); presence of a median projection of the basibranchial medial plate (ch. 22[1]); presence of levator and depressor rostri muscles (ch. 66[1]), serrated tail stings (ch. 67[1]); thorns absent (ch. 69[1]); rostral cartilage vestigial or absent (ch. 73[1]); postorbital process very broad and shelf-like (ch. 74[1]); jugal arch absent (ch. 75[1]); presence of ball and socket articulation between scapular process and synarcual (ch. 78[1]) and thoracolumbar synarcual (ch. 79[1]); and absence of ribs (ch. 80[1]). The sixgill stingray *Hexatrygon* is the sister to all other stingrays as detected by Carvalho *et al.* (2004), Claeson *et al.* (2010), Aschliman *et al.* (2012a) and Underwood *et al.* (2017), but not in recent molecular analyses (e.g. Bertozzi *et al.*, 2016).

One of the main results of our phylogeny is the recovery of a dichotomous nature of myliobatiforms (excluding *Hexatrygon*), which is consistent, at least in part, with the hypothesis of Nishida (1990), but never recovered in more recent morphological or molecular analyses. This might be due to the use of a large dataset, including 102 morphological characters taken from different works (Herman *et al.*, 1998, 1999, 2000; Carvalho *et al.*, 2004; Claeson *et al.*, 2010; Aschliman *et al.*, 2012a; Underwood *et al.*, 2017), most of them highly homoplastic in myliobatiforms. The analysis shows two main groups that correspond, at least in part, to the superfamilies Myliobatoidea and Dasyatoidea, as recognized by Nishida (1990) and Cappetta (2012). From a morphological point of view, the dichotomy seems to reflect the different calcifications of radial cartilages, body shapes and swimming modes detected in the two main groups by Schaefer & Summers (2005). The monophyly of the myliobatoids (including *Gymnura* that is sister to pelagic stingrays of the family Myliobatidae *sensu*; Claeson *et al.*, 2010) is supported herein by seven synapomorphies: short orbital region with more anteriorly placed supraorbital and postorbital process (ch. 10[1]); mesopterygium fragmented (ch. 27[1]); lateral expansion of radials in pectoral region (ch. 28[1]); caudal

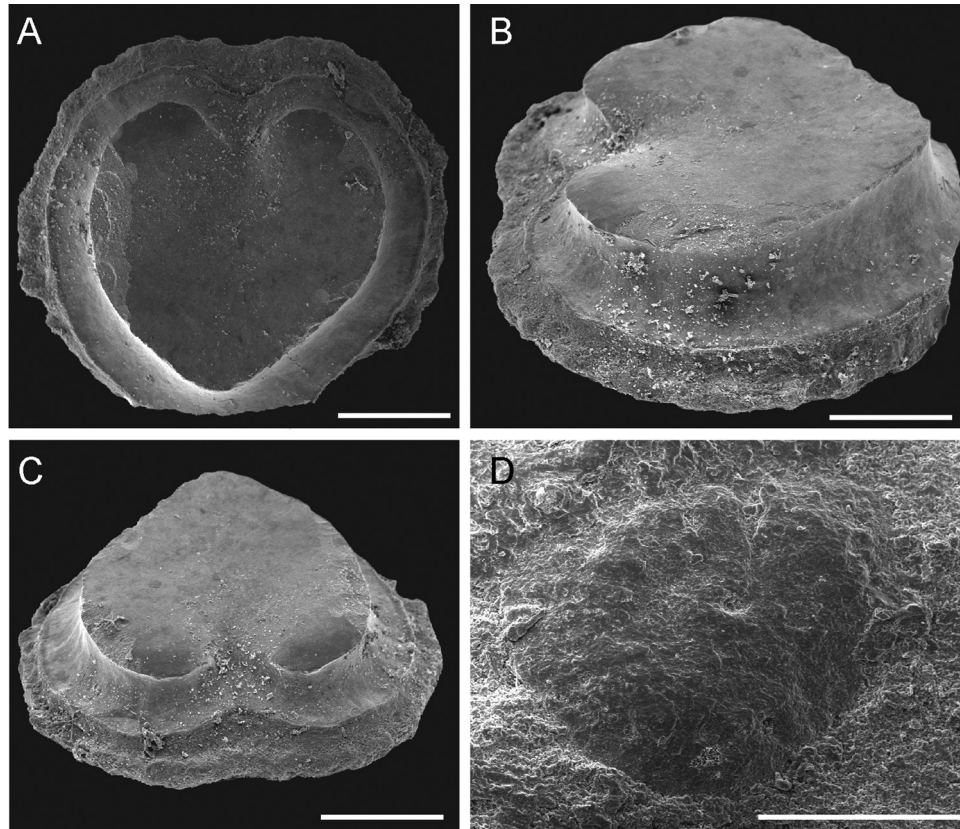


**Figure 6.** Single tooth of the extant freshwater whipray *Fluvitrygon signifer* (Compagno & Roberts, 1982) from SE Asia, IPUW-Chond-T-23, in: A, occlusal; B, labial; C, lingual; and D, lateral views. Scale bar 200  $\mu$ m.

fin absent (ch. 34[2]); first segment of propterygium adjacent to anterior margin of antorbital cartilage or anterior to margin of nasal capsule (ch. 81[3]); ‘crustal’ calcification pattern of radials (ch. 100[0]); and wing-like body shape, with pectoral fins greatly expanded (ch. 101[1]). This group is entirely composed of stingrays having crustal calcification of radials and a wing-like body shape that reflect their unique swimming mode adaptation, which is oscillatory according to Schaefer & Summers (2005). The recovered trees, therefore, present a hypothesis that differs from more recent morphological and molecular analyses (e.g. [Aschliman et al., 2012b](#); [Bertozzi et al., 2016](#)) in resurrecting the *Gymnura*+*Myliobatidae* clade. The sister-group relationship between *Gymnura* and pelagic stingrays in previous studies is only weakly supported according to [Aschliman \(2014\)](#) due to a limited set of taxa and ambiguous character states. Molecular data, conversely, resolved *Gymnura* as sister to *Urolophus* ([Aschliman et al., 2012b](#)), *Hexatrygon* ([Bertozzi et al., 2016](#)) or placed it much closer to the base of all myliobatiforms ([Last et al., 2016a](#)). Consequently, the sister-group relationship recovered here remains debatable. The family *Myliobatidae* was recognized here to be monophyletic, as detected by [Carvalho et al. \(2004\)](#), [Claeson et al. \(2010\)](#)

and [Aschliman et al. \(2012a, b\)](#), and strongly supported by 28 synapomorphies (see [Table 2](#)).

The monophyly of the clade *Dasyatoidea* (including all remaining stingrays except *Hexatrygon*) is supported only by one character, which is the spiracularis split into lateral and medial bundles, with the medial bundle inserting on to the posterior surface of Meckel’s cartilage and the lateral bundle inserting onto the dorsal edge of the hyomandibula (ch. 88[1]). This group is entirely composed by members having the general condition of the disc shape (rhomboidal, quadrangular or oval) and ‘catenated’ calcification of radials, which reflect their undulatory swimming mode and benthic habits ([Schaefer & Summers, 2005](#)). The dasyatoid diversification seems to be achieved by the step-by-step adding of characters. The pair formed by *Urolophus*+*Trygonoptera* (family *Urolophidae*) is sister to all dasyatoid stingrays, and its monophyly as detected by [Carvalho et al. \(2004\)](#), [Claeson et al. \(2010\)](#) and [Bertozzi et al. \(2016\)](#) is confirmed and supported herein by three characters: very enlarged foramen for the optic (II) nerve (ch. 8[1]); external margin of mesopterygium highly sinuous, fused with articulating radial elements (ch. 29[2]); and presence of a second transverse tooth keel (ch. 99[1]).



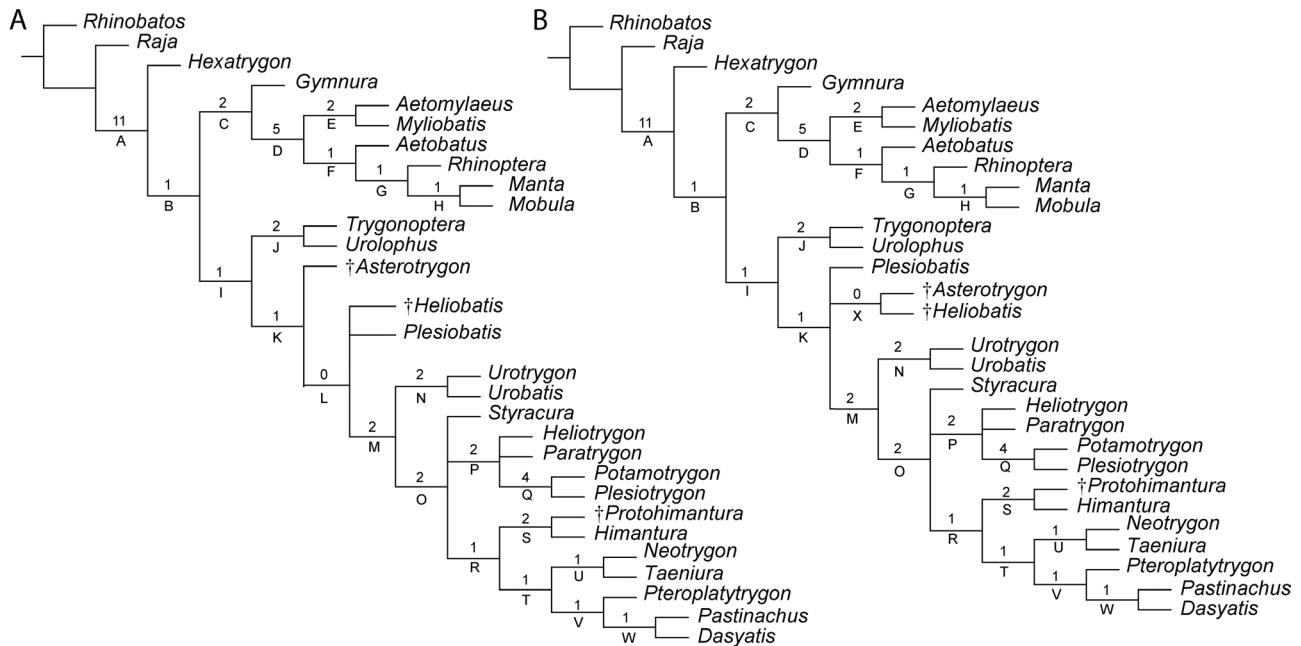
**Figure 7.** Dermal denticles of †*Protohimantura vorstmani* (de Beaufort, 1926) from early Miocene of Sulawesi, Indonesia, RGM 624420. A–C, single dermal denticle from the dorsal band in, A, dorsal, B, dorso-lateral and, C, dorso-lingual view; D, dermal denticle from pectoral fin in dorsal view. Scale bars 250  $\mu$ m.

The two trees retrieved only differ in the different position of *Plesiobatis*, †*Asterotrygon* and †*Heliobatis*, whose relationships are different from those proposed by [Carvalho et al. \(2004\)](#). Of note is that in one of the two trees ([Fig. 8B](#)), the Eocene freshwater stingrays †*Asterotrygon* and †*Heliobatis* form a monophyletic group supported by a single character (caudal fin reduced to tail-folds; ch. 34[1]). Although the relationship is weakly supported (Bremer value = 0), this might suggest that these taxa diverged after their common ancestor invaded the freshwater system of Green River Formation, contrary to the hypothesis of [Carvalho et al. \(2004\)](#), who hypothesized that †*Asterotrygon* and †*Heliobatis* might have invaded independently the Eocene freshwaters of Fossil Lake.

In our phylogeny, the pair formed by *Urotrygon*+*Urobatis* (family Urotrygonidae) is sister to a polytomy that includes *Styracura*, freshwater potamotrygonids and dasyatids. The representatives of this polytomy share the following characters: presence of a cartilaginous rod in tail: (ch. 33[1]); caudal fin absent (ch. 34[2]); first segment of propterygium adjacent to the nasal capsule (ch. 81[2]); cartilage forming component claw in claspers absent (ch. 85[1]); and

spiracularis that extends beyond the hyomandibula and Meckel's cartilage (ch. 88[2]).

Recently, [Carvalho et al. \(2016\)](#) redescribed in detail the morphology of '*Himantura*' *schmardae*, recognizing a set of characters (angular cartilage, presence of spiracularis extending beyond Meckel's cartilage towards the midline, first segmentation of the propterygium at the level of the posterior nasal capsule, etc.) which support the creation of a new genus, *Styracura*, and its placement within the family Potamotrygonidae. The study has, therefore, confirmed previous morphological ([Lovejoy, 1996](#); [Carvalho et al., 2004](#); [Manjaji, 2004](#); [Aschliman et al., 2012a](#)) and molecular-based ([Naylor et al., 2012a, b](#); [Bertozzi et al., 2016](#); [Last et al., 2016a](#)) phylogenetic hypotheses. Although the relationship between freshwater potamotrygonids and *Styracura* is almost certainly true, based on morphological, molecular and chrono/geographic evidence, our phylogeny does not recognize this genus as a genuine member of the family. This can be due to the fact that *Styracura* lacks some characters of the lateral-line, and pectoral and pelvic fin skeleton of potamotrygonids, which on the contrary resemble some dasyatids ([Carvalho et al., 2016](#)). The placement of *Styracura*

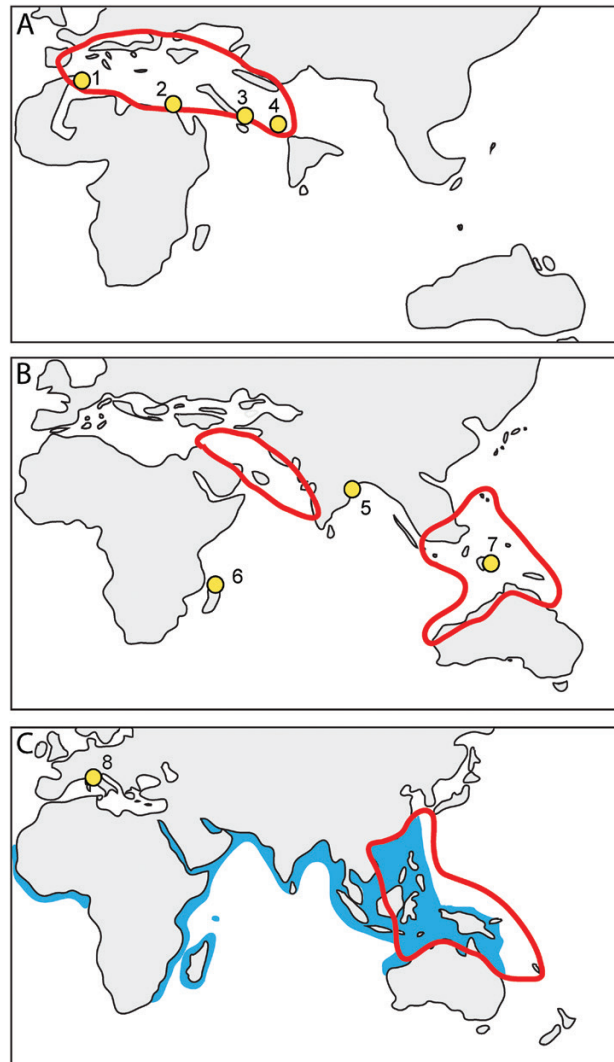


**Figure 8.** The two most parsimonious trees retrieved in TNT v.1.5 based on 102 morphological characters showing the hypothetical relationships of †*Protohimantura vorstmani* (de Beaufort, 1926) within the Myliobatiformes. Please note that characters used for coding *Himantura* are mostly based on [Claeson et al. \(2010\)](#) and [Aschliman et al. \(2012a\)](#) who used several species formerly included within the genus *Himantura*, which are now included in different genera of the subfamily Urogyminae according to [Last et al. \(2016b\)](#). Numbers on nodes indicate the Bremer support. The list of synapomorphies on each node (capital letters) is given in [Table 2](#).

in Potamotrygonidae would, therefore, require more homologous character states. The monophyly of freshwater potamotrygonids *Heliotrygon*, *Paratrygon*, *Potamotrygon* and *Plesiotrygon* is supported herein by five synapomorphies: suborbital components of infraorbital lateral line canals forming a complex web-like pattern on lateral aspects of the anteroventral disc region (ch. 3[2]); absence of fossa on dorsal scapular region (ch. 25[0]); very elongated median prepelvic process (ch. 30[1]); urea excreted in urine (ch. 39[1]); and rectal gland reduced (ch. 40[1]).

Although the monophyly of the Dasyatidae, including *Himantura*, *Neotrygon*, *Taeniura*, *Pteroplatytrygon*, *Pastinachus* and *Dasyatis*, was rejected by some analyses (e.g. [Carvalho et al., 2004](#); [Aschliman et al., 2012a](#); [Lim et al., 2015](#)), its representatives form here a clade recognized as unquestionably monophyletic and supported by two synapomorphies: ventral terminal cartilage free of axial cartilage (ch. 87[1]) and presence of sexual heterodonty (ch. 89[1]). This supports the monophyletic status of Dasyatidae as recognized by [Aschliman et al. \(2012b\)](#), [Naylor et al. \(2012a\)](#), [Bertozzi et al. \(2016\)](#), as well as by the alternative phylogenetic analysis of [Carvalho et al. \(2004, appendix 2\)](#). The presence of tail-folds used to diagnose the family Dasyatidae by [Bigelow & Schroeder \(1953\)](#), [Compagno & Roberts \(1982, 1984\)](#)

and [Nishida \(1990\)](#) is not supportive of the clade because it is present also in *Styracura*, potamotrygonids and †*Heliobatis*, and, therefore, is considered homoplastic. The sister-group relationship between †*Protohimantura* and *Himantura* is supported by two characters, which are the presence of a second transverse tooth keel (ch. 99[1]), and mid-dorsal surface of disc covered by heart-shaped denticles arranged in an antero-posteriorly directed patch having sharply defined outlines (ch. 102[1]). This pair forms the sister-group of all remaining dasyatids, whose monophyly is supported by the presence of a caudal fin reduced to tail-folds (ch. 34[1]), osteodont tooth vascularization (ch. 71[1]), dorsal marginal clasper cartilage lacking a medial flange (ch. 83[0]) and dorsal terminal cartilage with a crenate margin (ch. 84[1]). The placement of *Himantura*+*Protohimantura* as the sister of all other dasyatids is in accordance with molecular analysis presented by [Puckridge et al. \(2013\)](#) but inconsistent with the molecular and morphological phylogenetic results of [Lim et al. \(2015\)](#) or those of [Last et al. \(2016b\)](#). *Neotrygon* is placed sister to *Taeniura* in accordance with the molecular analyses of [Aschliman et al. \(2012b\)](#), [Puckridge et al. \(2013\)](#), [Lim et al. \(2015\)](#) and [Last et al. \(2016b\)](#), whereas the pair *Dasyatis*+*Pastinachus* is recovered here as the most derived clade amongst dasyatoids.



**Figure 9.** Palaeobiogeographical distribution of whiptail stingrays of the subfamily Urogymninae during middle Eocene to early Oligocene (A), Miocene (B), and Pliocene to present day (C). 1, Morocco; 2, Egypt; 3, Pakistan; 4, Oman; 5, India; 6, Madagascar; 7, Indonesia (this paper); 8, Italy. The blue colour marks the main area of the modern representatives of the Urogymninae. Data on fossil occurrences taken from Sahni & Mehrotra (1980), Case & Wiest (1991), Cappetta & Cavallo (2006), Adnet *et al.* (2007, 2010), Underwood *et al.* (2011) and Andrianavalona *et al.* (2015). The enclosed solid red lines delimit the West Tethys, Arabian, and IAA biodiversity hotspots according to Renema *et al.* (2008).

## DISCUSSION

### COMPARISON AND RELATIONSHIPS

Although represented by an incomplete specimen, the morphological analysis of †*Protohimantura vorstmani* has revealed the presence of several characters that support unquestionably its inclusion in the order Myliobatiformes, including the absence of rostral cartilage, the presence of a very broad and shelf-like postorbital process, and a second (thoracolumbar) synarcual (see: Compagno, 1977; Carvalho *et al.*, 2004; Aschliman *et al.*, 2012a). Although it was not possible to detect the absence of ribs, it is most

likely that †*Protohimantura* might have shown this character, as will all other myliobatiforms. The placement of the Sulawesi stingray within the derived monophyletic clade of the Dasyatidae is supported by a combination of several plesiomorphic characters, e.g. absence of angular cartilages (present in potamotrygonids), first segment of propterygium adjacent to anterior margin of antorbital cartilage or anterior to margin of nasal capsule (posterior to mouth, between mouth and antorbital cartilage, or adjacent to the nasal capsule in non-dasyatids dasyatoids), an external margin of the mesopterygium that is more or less straight and which is not fused to radials

**Table 3.** Summary of selected morphometric and meristic features used to discriminate fossil and living genera of the subfamily Urogymninae. Includes new data from the examined material and data from Compagno & Roberts (1982, 1984), Nishida (1990), Deynat & Fermon (2001), Manjaji (2004), Last et al. (2016a, b, c) and Manjaji-Matsumoto & Last (2016)

	<i>Protohimantura</i>	<i>Brevitrygon</i>	<i>Fluvitrygon</i>	<i>Fontitrygon</i>	<i>Himantura</i>	<i>Maculabatis</i>	<i>Pateobatis</i>	<i>Urogymnus</i>
Interorbital width/eye diameter	3.5	1.2–2.1	2.0–3.2	1.2–5.3	1.8–3.6	1.3–4.1	1.3–4.7	1.3–7.1
Nasal capsule width/Neurocranial length	0.7	0.9	0.7–0.8	?	0.8	0.8–1.0	0.8–0.9	0.7–0.9
Nasal capsule length/Neurocranial length	0.2	0.3	0.2–0.3	?	0.2–0.3	0.2–0.3	0.2–0.3	0.3
Anteroposterior fontanelle/Neurocranial length	0.8	0.7	0.7	?	0.7	0.7	0.7	0.6–0.7
Scapulocoracoid width/lateral face length	2.2	2.1	1.8–2.0	?	1.4	?	1.8	?
Propterygial radials	55	45–50	50–56	49–70	57–64	48–53	52–62	64–73
Mesopterygial radials	17	9–17	11–16	15–22	18–25	16–22	18–30	18–20
Metapterygial radials	25+?	42–47	44–50	49–64	65–72	57–67	54–74	62–66

(undulated, not fused to radials in *Gymnura*; highly sinuous, fused with articulating radial elements in Urolophidae; e.g. Carvalho et al., 2004). Moreover, the absence of features characterizing *Gymnura* and pelagic stingrays (short orbital region with more anteriorly placed supraorbital and postorbital process, secondary hyomandibular cartilages, symphyseal fusion of upper and lower jaws, fourth and fifth ceratobranchials fused to each other, lateral expansion of radials in pectoral region, first segment of propterygium adjacent to anterior margin of antorbital cartilage or anterior to margin of nasal capsule, ‘crustal’ calcification pattern of radials, wing-like body shape, with pectoral fins greatly expanded and different arrangement of teeth on jaws; e.g. Carvalho et al., 2004; Claeson et al., 2010; Aschliman et al., 2012a; Lim et al., 2015) supports the exclusion of †*Protohimantura* **gen. nov.** from myliobatoid stingrays. The morphological and phylogenetic analysis detected †*Protohimantura* **gen. nov.** as a genuine member of the family Dasyatidae, sister to *Himantura* (the recovered relationship is only among taxa included in this particular analysis, which omitted the numerous closely related genera erected by Last et al., 2016b), and this latter relationship is supported by the presence of a second transverse tooth keel and mid-dorsal surface of disc covered by heart-shaped denticles arranged in an antero-posteriorly directed patch having sharply defined outlines, characters that are lacking in other dasyatids (see: Herman et al., 1998, 1999, 2000; Last et al., 2016a, b). In fact, Last et al. (2016a, b) recognized two distinct morphological groups within Dasyatidae: the first one is characterized by the absence of skin folds on tail, presence of a well-developed band of densely packed denticles on the disc with sharply defined margins, and base of the tail relatively narrow and almost rounded in cross-section. This group only includes the subfamily Urogymninae (*Brevitrygon*, *Fluvitrygon*, *Fontitrygon*, *Pateobatis*, *Maculabatis*, *Himantura* and *Urogymnus*), which are also characterized by characteristic heart-shaped dermal denticles (Compagno & Roberts, 1982, 1984; Deynat & Fermon, 2001; Manjaji, 2004; Last et al., 2016a, c). Representatives of the second group are characterized by the presence of distinct skin folds on tail, lack of, or poorly developed, denticle band, and base of the tail depressed and oval in cross-section. This group includes all remaining three subfamilies of dasyatids (Dasyatinae, Neotrygoninae, Hypolophinae; Last et al., 2016a). In this perspective, the presence of a well-developed denticle band on the disc formed by heart-shaped placoid scales in †*Protohimantura* **gen. nov.** corroborates its sister-group relationship with *Himantura* and its inclusion in the almost entirely Indo-Pacific subfamily Urogymninae.

†*Protohimantura* **gen. nov.** differs from the other urogymnine genera by having a unique combination of

morphometric and meristic features (Table 3). It can be easily separated from *Brevitrygon* and *Fluivtrygon* for the different interorbital width/eye diameter ratio (3.5 vs. 1.2–3.2), from *Brevitrygon*, *Himantura*, *Maculabatis* and *Pateobatis* for the different nasal capsule width/neurocranial length ratio (0.7 vs. 0.9–0.9) and from all genera for the different anteroposterior fontanelle/neurocranial length ratio (0.8 vs. 0.6–0.7). †*Protohimantura* **gen. nov.** differs from *Brevitrygon* and *Urogymnus* for the different nasal capsule length/neurocranial length ratio (0.2 vs. 0.3) and from *Brevitrygon*, *Fluivtrygon*, *Himantura* and *Pateobatis* for the different scapulocoracoid width/lateral face length (2.2 vs. 1.4–2.1). Moreover, the number of propterygial radials in †*Protohimantura* **gen. nov.** (55) is useful to separate it from *Brevitrygon* and *Maculabatis* (45–53), and from *Himantura* and *Urogymnus* (57–73), whereas the number of mesopterygial radials distinguish the new fossil genus (17) from *Fluivtrygon* (11–16) and from *Pateobatis*, *Himantura* and *Urogymnus* (18–30). Comparing with other fossil specimens, teeth of †*Protohimantura* **gen. nov.** differ from those figured by [Andrianaivalona et al. \(2015\)](#), fig. 5) and referred to *Himantura* sp. from the Miocene of NW Madagascar in lacking the crown ornamentation consisting of longitudinal and equally spaced wrinkles. The absence of the same character allows separation of †*P. vorstmani* from *Himantura menoni* from the late Miocene of India ([Sahni & Mehrotra, 1980](#)). Teeth figured by [Cappetta & Cavallo \(2006, pl. 10, figs 1, 2\)](#) and referred to *Himantura* sp. from the Pliocene of Italy do not possess a median ridge with strong concavity and the crown is strongly ornamented, which support their exclusion from the species described here. No other comparisons with other fossil teeth of *Himantura* can be performed since no additional material has been described or figured.

#### PALAEOBIOGEOGRAPHY AND EVOLUTIONARY SIGNIFICANCE

Extant stingrays of the subfamily Urogymninae are typically benthic marine demersal batoids occurring on inner continental or insular shelves on sandy or muddy bottoms, although some species are exclusively brackish or freshwater ([Last et al., 2016a; Nelson et al., 2016](#)). The subfamily today mainly inhabits warm-temperate to tropical waters down to 70–80 m, often associated with mangroves and coral reefs of the Indo-Australian Archipelago, with the exception of the genus *Fontitrygon*, which mainly occurs in demersal habitats on continental shelves of the western and eastern Atlantic ([Last et al., 2016a](#)). In this perspective, the presence of †*Protohimantura* **gen. nov.** in the early Miocene limestones of Sulawesi might suggest a close affinity

of this taxon with the tropical shallow-water habitats associated with corals, as hypothesized for the uppermost sequence of the Tonasa Formation ([Wilson, 1996, 2000; Wilson et al., 2000](#)).

The fossil record of whiptail stingrays of the family Dasyatidae is extensive and well documented. The earliest putative known fossil dates back to the Hauterivian, early Cretaceous, and was included in the genus *Dasyatis* by [Underwood et al. \(1999\)](#). However, [Cappetta \(2012\)](#) hypothesized that it might represent a different genus, since the simpler morphology of these teeth is quite different from *Dasyatis*, which has been often used as basket/repository genus for many early fossil teeth with ‘dasyatoid’ morphology ([Underwood et al., 1999; Cappetta, 2012](#)). Except for †*Protohimantura vorstmani*, the fossil record of whiprays of the subfamily Urogymninae is only represented by isolated teeth that have been all included in the genus *Himantura* (Fig. 9). However, the paucity of fossil whiprays probably represents an artefact, since the teeth of ‘*Himantura*’ are very similar to those of *Dasyatis* rendering the identification and assignment of fossil teeth quite difficult. Indeed, [Cappetta \(2012\)](#) supposed that most of the Miocene and possibly older taxa included in *Dasyatis* might actually belong to *Himantura*. The oldest record referring to *Himantura* dates back to the middle–late Eocene (Lutetian to Priabonian) of Egypt ([Underwood et al., 2011](#)), Morocco and Pakistan ([Case & West, 1991; Adnet et al., 2007; Adnet, Cappetta & Tabuce, 2010](#)). Oligocene occurrences of *Himantura* sp. are reported from the Rupelian of Pakistan and Oman ([Thomas et al., 1989; Adnet et al., 2007](#)), whereas †*Protohimantura* **gen. nov.**, along with *Himantura menoni* from India ([Sahni & Mehrotra, 1980](#)) and *H.* sp. from NW Madagascar ([Andrianaivalona et al., 2015](#)), mark the Miocene occurrences of urogymnines. Finally, the youngest fossil occurrence was reported from the Pliocene of Italy ([Cappetta & Cavallo, 2006](#)). Although the presence of sampling biases must be considered, it seems evident that the spatial and temporal dynamics of Urogymninae identifies an eastward movement of the fossil occurrences from the Tethys during the Eocene, to the Arabian Peninsula and IAA in the Miocene, and almost all species occurring mostly in IAA today (Fig. 9). A very similar pattern was highlighted for another dasyatid subfamily, the Hypolophinae, whose fossil occurrences indicate a pre-Bartonian origination for the group in western Neotethys, followed by a rapid and widespread colonization of the proto-Mediterranean Sea, western Atlantic and Indo-Pacific during the late Paleogene–early Neogene ([Adnet et al., 2018](#)). Spatial and temporal dynamics of Urogymninae and Hypolophinae appear to be consistent, at least in part, with the ‘hopping-hotspots’ model hypothesized



by Renema *et al.* (2008), who evidenced that the location of the main marine centre of palaeobiodiversity has moved across the globe during the last 50 million years, triggered by plate tectonics from the Tethys during the Eocene, to the Arabian Peninsula and IAA during the Miocene, before leaving a single hotspot in the IAA in the present days (Renema *et al.*, 2008; Leprieur *et al.*, 2016). In fact, it has been also suggested that the IAA acted as a region of accumulation and survival from the Palaeocene to the Oligocene, before acting as a centre of origin during the Miocene and, most recently, as a centre of expansion and export from the Pliocene onward (Cowman & Bellwood, 2013; Evans *et al.*, 2016). Comprehensive and robust divergence time estimates (Bertozzi *et al.*, 2016) predicted that myliobatiforms diverged from their sister-group (panrays) around 147 Mya, although their diversification (possibly including the origin of dasyatids) only occurred around the end-Cretaceous extinction event. In this perspective, one can suppose a Palaeocene or Eocene Tethyan origin for the Urogyminae based on fossil occurrences. Fossils from the celebrated Eocene Tethyan Bolca Lagerstätte (see Marramà *et al.*, 2016a) also yielded several dasyatid specimens but apparently no representatives of Urogyminae (Marramà *et al.*, 2017c). However, this Konservat-Lagerstätte marks indeed the earliest record of many extant tropical fish lineages, which suddenly filled the ecological niches left vacant by the end-Cretaceous extinction event through the expansion and rise of new feeding modes (Bellwood, 2003; Goatley, Bellwood & Bellwood, 2010; Schmitz & Wainwright, 2011; Bellwood *et al.*, 2014; Frédéricich *et al.*, 2016; Marramà, Garbelli & Carnevale, 2016b, c; Marramà & Carnevale, 2017; Marramà *et al.*, 2017a). In this perspective, after their Tethyan origin, the IAA may have acted as a refuge area for whiptail stingrays of the subfamily Urogyminae from the early Miocene, whose representatives later disappeared at least from Tethys. Subsequently, from the late Miocene, the IAA might have acted as a centre of speciation and then, starting in the Pliocene, as a centre of export toward the Mediterranean (with the Pliocene *Himantura* sp. from northern Italy) and Atlantic realms (with the living genus *Fontitrygon*) (see: Cappetta & Cavallo, 2006; Last *et al.*, 2016a).

## CONCLUSIONS

Although the early Miocene stingray from Sulawesi lacks portions of the posterior body, including the tail and the characteristic spines, several features are preserved and allow identification as a new representative of the family Dasyatidae, subfamily Urogyminae, and the creation of a new genus, †*Prothimantura*. A monophyletic family Dasyatidae is recovered based

on the parsimony analyses. The phylogenetic analysis recovered a dichotomous nature of the relationships of the Myliobatiformes, which might reflect a phylogenetic signal in the nature of calcification of their pectoral radials, in their body shape and, consequently, in their swimming style. The analysis of the fossil record of the Urogyminae seems to suggest that the modern distribution of whiptays is the final result of their spatial dynamics across the Palaeogene and consistent, at least in part, with the eastward shift of the marine centre of palaeobiodiversity across the globe during the last 50 million years.

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## APPENDIX 1

### LIST OF MORPHOLOGICAL CHARACTERS USED FOR THE PHYLOGENETIC ANALYSIS

Data are based on characters of [Claeson et al. \(2010\)](#) (from 1 to 65), [Aschliman et al. \(2012a\)](#) (from 66 to 85), [Underwood et al. \(2017\)](#) (from 88 to 96). Characters 97 to 102 are based on [Herman et al. \(1998, 1999, 2000\)](#), [Schaefer & Summers \(2005\)](#), [Lim et al. \(2015\)](#), [Last et al. \(2016a, b\)](#). Characters for all genera are coded following [Claeson et al. \(2010\)](#), except *Aetomylaeus*, *Pastinachus* and *Neotrygon*, which are not present in [Claeson et al. \(2010\)](#) and are therefore coded following [Carvalho et al. \(2016\)](#) and [Underwood et al. \(2017\)](#). Some states have been re-coded to exclude those states not present in our myliobatiform or outgroup taxa, or to follow previous or more recent and updated anatomical descriptions (see Remarks below).

Characters 1–65 are from [Claeson et al. \(2010\)](#), which in turn are based on those of [Carvalho et al. \(2004\)](#) (CMG). Dental character information for *Aetomylaeus* and *Pastinachus* is taken from [Herman et al. \(1998, 2000\)](#).

1. (01 of CMG) Tubules of subpleural components of hyomandibular lateral line canals: (0) not

branched at extremities; (1) extremities dichotomously branched.

2. (02 of CMG) Subpleural components of the hyomandibular lateral line canals: (0) posterior branch extends caudally more or less parallel to longitudinal body axis; (1) posterior branch inflects towards midline to form a lateral hook; (2) posterior branch inflects to continue anteriorly almost parallel to anterior branch, forming a large indentation.
3. (03 of CMG) Suborbital components of infraorbital lateral line canals: (0) projecting posteriorly lateral to mouth; (1) projecting posteriorly lateral to mouth and anteriorly lateral to nasal openings; (2) forming a complex web-like pattern on lateral aspects of the anteroventral disc region.
4. (04 of CMG) Scapular loops formed by scapular components of trunk lateral line canals: (0) absence of loops; (1) presence of scapular loops.
5. (05 of CMG) Anterior process of neurocranium: (0) absent; (1) present.
6. (06 of CMG) Preorbital process: (0) present; (1) absent.
7. (07 of CMG) Preorbital canal for passage of superficial ophthalmic nerve: (0) dorsally located; (1) anteriorly located.
8. (08 of CMG) Foramen for the optic (II) nerve: (0) moderately sized; (1) very enlarged.
9. (09 of CMG) Postorbital process of neurocranium: (0) infraorbital lateral line canal separates postorbital process from small, anterior triangular outgrowth (supraorbital process) of the supraorbital crest; (1) postorbital process with small foramen for passage of infraorbital lateral line canal.
10. (10 of CMG) Extent of orbital region: (0) orbital region of neurocranium long; (1) shortened orbital region with more anteriorly placed supraorbital and postorbital process.
11. (11 of CMG) Postorbital process: (0) without ventrolateral projection; (1) continuing ventrolaterally to form a cylindrical projection.
12. (12 of CMG) Ventrolateral expansion of nasal capsules: (0) nasal capsules laterally expanded; (1) nasal capsules ventrolaterally expanded.
13. (13 of CMG) Articulation between hyomandibula and Meckel's cartilage: (0) hyomandibulae directly attached to lower jaws; (1) hyomandibulae articulating with lower jaws through strong, stout ligament (hyomandibular–Meckelian ligament) at distal tip.
14. (14 of CMG) Angular cartilages: (0) absence of angular cartilages within hyomandibular–Meckelian ligament; (1) presence of angular cartilages within ligament.

15. (15 of CMG) Secondary hyomandibular cartilages: (0) absent; (1) present.
16. (16 of CMG) Symphyseal fusion of upper and lower jaws: (0) antimeres separate at symphysis; (1) both antimeres of jaws symphyseally fused.
17. (17 of CMG) Mandibular width at symphysis: (0) lower jaws slender at symphysis; (1) lower jaws symphyseally thickened.
18. (18 of CMG) Lateral projections of lower jaws: (0) absent; (1) present.
19. (20 of CMG) Basihyal cartilage: (0) basihyal laterally elongated, fused to first hypobranchials; (1) basihyal a single element, but separate from first hypobranchials; (2) basihyal separate from first hypobranchials but fragmented into more than one component; (3) basihyal absent.
20. (21 of CMG) Fusion of ventral pseudohyoid and first ceratobranchial: (0) absent; (1) present.
21. (22 of CMG) Arrangement of posterior ceratobranchials: (0) separate from each other; (1) ankylosis between fourth and fifth ceratobranchials; (2) fourth and fifth ceratobranchials fused to each other.
22. (23 of CMG) Median projection of the basibranchial medial plate: (0) absent; (1) present.
23. (24 of CMG) Articulation between fifth epi- and ceratobranchial elements to scapulocoracoid: (0) close together; (1) widely separated.
24. (25 of CMG) Lateral stay of synarcual: (0) originates ventral to spinal nerve foramina; (1) originates dorsal to spinal nerve foramina; (2) contacting synarcual both dorsally and ventrally to foramina.
25. (26 of CMG) Fossa on dorsal scapular region: (0) absent; (1) present.
26. (27 of CMG, modified) Contact between pro- and mesopterygium in the pectoral fin: (0) present; (1) absent. **Remarks:** this character was originally described by [Lovejoy \(1996\)](#) who recognized the absence of articulation between pro- and mesopterygium as a derived state in *Potamotrygon* and *Plesiomyxus*, unique among myliobatiforms. Subsequent phylogenetic analyses ([Carvalho et al. 2004](#); [Claeson et al. 2010](#)) have considered the presence of this articulation as derived state (1) but coded incorrectly the state for all taxa considered. For this character we, therefore, followed the original description of [Lovejoy \(1996\)](#) and coded the derived state (absence) only for *Potamotrygon* and *Plesiomyxus*.
27. (28 of CMG) Distinct components of the mesopterygium: (0) mesopterygium single element; (1) fragmented; (2) missing altogether.
28. (29 of CMG) Lateral expansion of radials in pectoral region: (0) absent; (1) present.
29. (30 of CMG) External margin of mesopterygium: (0) more or less straight, not fused to radials; (1) undulated, not fused to radials; (2) highly sinuous, appearing to be fused with articulating radial elements.
30. (31 of CMG) Median prepelvic process: (0) absent or weakly developed; (1) very elongated.
31. (32 of CMG) Pelvic girdle shape: (0) not arched or only moderately so; (1) greatly arched.
32. (33 of CMG) Dorsal fin: (0) present; (1) absent.
33. (34 of CMG) Cartilaginous rod in tail: (0) absent; (1) present.
34. (35 of CMG) Caudal fin: (0) present; (1) reduced to tail folds; (2) absent.
35. (36 of CMG) Adductor mandibulae complex: (0) without posteromedial extension; (1) posteromedial extension present.
36. (37 of CMG) Spiracularis muscle: (0) projecting ventrally to insert on either palatoquadrate, Meckel's cartilage, and or hyomandibula; (1) projecting ventrally and posteriorly beyond hyomandibulae and both sets of jaws to insert dorsal to coracomandibularis; (2) projecting ventrally and posteriorly beyond hyomandibulae and both sets of jaws to insert ventral to coracomandibularis.
37. (38 of CMG) Depressor mandibularis muscle: (0) present; (1) absent.
38. (39 of CMG) Coracohyoideus muscle: (0) not connected at midline; (1) connected at midline.
39. (40, CMG) Urea retention: (0) urea retained in blood; (1) urea excreted in urine.
40. (41 of CMG) Rectal gland: (0) present; (1) reduced.
41. (42 of CMG) Spiracular tentacle: (0) absent; (1) present.
42. (43 of CMG) Cephalic lobes: (0) absent; (1) single and continuous; (2) single with an indentation; (3) paired.
43. (44 of CMG) Nasal curtain: (0) not reaching mouth region; (1) extending posteriorly as far as mouth opening.
44. (Modified from 19 of CMG) Tooth type in both upper and lower jaws: (0) minute; (1) broad.
45. (Modified from 19 of CMG) Arrangement of teeth in both upper and lower jaws: (0) arranged in separate diagonal rows or ribbons; (1) horizontal conveyor or pavement-like arrangement.
46. (Modified from 19 of CMG) Tooth shape: (0) square to rounded; (1) hexagonal, six distinct sides; (2) rectangular with posteriorly deflected lateral margins.
47. Lateral teeth: (0) present; (1) absent.
48. Differentiation of median teeth from lateral teeth: (0) median and lateral teeth are similar; (1) median teeth relatively expanded.

49. Differentiation among lateral teeth: (0) lateral teeth unexpanded; (1) some lateral teeth expanded.
50. Relative amount of curvature in expanded lower teeth: (0) straight and uncurved; (1) moderately curved; (2) strongly curved.
51. Upper tooth curvature: (0) uncurved; (1) curved.
52. Direction of tooth curvature: (0) concave; (1) flat; (2) convex.
53. Tooth association: (0) loosely interlocking; (1) sometimes loosely interlocking or tightly interlocking; (2) tightly interlocking.
54. Tooth interlocking mechanism: (0) overlapping; (1) tongue and groove; (2) no direct contact.
55. Shape of interlocking tongue: (0) bulbous; (1) short shelf; (2) long shelf.
56. Crown height: (0) high, the crown height exceeds root depth on unworn teeth; (1) low crown.
57. Occlusal surface: (0) cusped; (1) smooth; (2) depressed.
58. Crown shape in anterior or posterior view: (0) straight; (1) domed; (2) deep.
59. Lateral margins: (0) not pinched; (1) pinched.
60. Root type: (0) holaulacorhizous; (1) polyaulacorhizous.
61. Number of roots: (0) 2 roots; (1) more than 2 roots. **Remarks:** we only included two states instead of the original three of Claeson *et al.* (2010) since their state (1) (3 to 4 roots) is only characteristic of *Brachyrhizodus*, which is not included here. States are, therefore, re-coded consequently. †*Protohimantura* shows the basal condition of myliobatiforms with two roots (state 0).
62. Roots in basal view: (0) triangles; (1) wide blocks; (2) narrow blocks; (3) fine edges. **Remarks:** we only included two states instead of the original three of Claeson *et al.* (2010) since the state (1) (wide blocks) is only characteristic of extinct myliobatids, which is not included here. States are, therefore, re-coded consequently. †*Protohimantura* shows the basal condition of myliobatiforms with root triangular in basal view (state 0).
63. Distance between roots: (0) broad, groove wider than root; (1) narrow.
64. Inclination of roots: (0) no inclination; (1) offset and step-like; (2) long and strongly inclined.
65. Root groove position: (0) regularly spaced between laminae; (1) irregularly spaced between laminae.
- Characters 66–88 are selected characters from Aschliman *et al.* (2012a) (ASC); they are useful to better define the relationships within the Myliobatiformes and were not included in the analysis of Carvalho *et al.* (2004) and Claeson *et al.* (2010). Amongst the 89 characters of Aschliman *et al.* (2012a), only 23 characters were conserved herein since the others are uninformative for myliobatiforms and outgroups selected.
66. (9 of ASC) Levator and depressor rostri muscles: (0) absent; (1) present.
67. (14 of ASC) Serrated tail stings: (0) absent; (1) present.
68. (15 of ASC, modified) Placoid scales: (0) uniformly present; (1) limited; (2) absent. **Remarks:** Aschliman *et al.* (2012a) considered myliobatiforms as largely to totally free of denticles over the entire body surface and, consequently, coded this character as (2) for all myliobatiforms. However, *Raja* and most of the stingrays (*Himantura*, *Plesiobatis*, *Pastinachus*, *Paratrygon*, *Styracura*, *Plesiotrygon*, *Potamotrygon*, *Teniura* and *Pteroplatytrygon*) actually still retain dermal denticles, although they are reduced and not uniformly present (1) (see Last *et al.*, 2016a). Fossil stingrays †*Heliobatis* and †*Asterotrygon* (see Carvalho *et al.*, 2004) and †*Protohimantura* are coded (1) as well. On the contrary, *Hexatrygon*, *Urolophus*, *Trygonoptera*, *Myliobatis*, *Aetobatus*, *Rhinoptera* are totally free of dermal denticles (Last *et al.* 2016) and were coded (2). Depending on the species, the genera *Urobatis*, *Urottrygon*, *Neotrygon*, *Dasyatis*, *Gymnura*, *Aetomylaeus*, and *Mobula* can show both the derived states (1 and 2) (Last *et al.*, 2016a). The limited (1) and absence (2) of dermal denticles are considered derived states.
69. (16 of ASC, modified) Thorns: (0) present; (1) absent. **Remarks:** Although Aschliman *et al.* (2012a) considered the presence of thorns only in Dasyatidae among myliobatiforms, we recoded and modified this character based on the most recent descriptions of Last *et al.* (2016a). Since *Rhinobatos* and *Raja* are our outgroups, we considered the presence of thorns as the basal condition (0). The absence of thorns (1) can be considered as derived condition in *Hexatrygon*, *Plesiobatis*, *Urolophus*, *Trygonoptera*, *Pastinachus*, *Neotrygon*, *Gymnura* and all pelagic stingrays (except *Aetomylaeus*) (Last *et al.*, 2016a) and in fossil †*Heliobatis* and †*Asterotrygon* (Carvalho *et al.*, 2004). This condition is coded as unknown for †*Protohimantura* since we cannot exclude the presence of thorns in the regions of body not preserved.
70. (18 of ASC) Pulp cavities in tooth roots: (0) large; (1) broad and elongated; (2) small; (3) absent
71. (19 of ASC, modified) Tooth vascularization: (0) orthodont; (1) osteodont; (2) modified osteodont. **Remarks:** Aschliman *et al.* (2012a) reported

the presence of osteodentine only in rajids, although osteodentine was not observed in *Raja* (Herman *et al.*, 1995, 1996). Moreover, Herman *et al.* (2000) considered of osteodont type (1) teeth of *Plesiotrygon*, *Potamotrygon*, *Taeniura*, *Pteroplatytrygon*, *Dasyatis* and *Manta*. A distinct type of osteodentine (modified) was observed only in *Aetobatus*, *Aetomylaeus*, *Myliobatis*, *Rhinoptera* and *Pastinachus*. The tooth vascularization is unknown in †*Protohimantura*.

72. (21 of ASC) Infraorbital loop of suborbital and infraorbital canals: (0) absent; (1) present and forming a simple posterolaterally directed loop; (2) present and forming a complex reticular pattern or a number of loops; (3) the loop is directed to the anterior.
73. (26 of ASC, modified) Rostral cartilage: (0) complete; (1) vestigial or absent. **Remarks:** we only include two states instead of the original three of ASC since the state 1 of ASC (rostral cartilage fails to reach the tip of the snout) was only coded for the batoids *Platyrrhina* and *Platyrrhinoidis*, not considered in our analysis. The rostral cartilage is vestigial or absent in all myliobatiforms, including †*Protohimantura*.
74. (36 of ASC, modified) Postorbital process: (0) narrow; (1) very broad and shelf-like. **Remarks:** we only include two states instead of the original three of ASC since the state 1 of ASC (absent) is only characteristic of torpediniforms, which are not included here. †*Protohimantura* shows a broad and shelf-like postorbital process (1).
75. (39 of ASC, modified) Jugal arch: (0) present; (1) absent. **Remarks:** our states are inverted with respect those of Aschliman *et al.* (2012a) since the presence of this character is basal in outgroups that we considered, whereas its absence is a derived condition in myliobatiforms. The character is unknown in †*Protohimantura*.
76. (48 of ASC) Basihyal and first hypobranchial: (0) both present and unsegmented; (1) basihyal is segmented; (2) basihyal is absent; (3) basihyal and first hypobranchial cartilages absent.
77. (50 of ASC) Suprascapulae: (0) articulates with vertebral column; (1) fused medially to synarcual (= pectoral arch); (2) fused medially and laterally to synarcual. **Remarks:** we only include three states instead of the original four of ASC since the state (0) of ASC (free of vertebral column) is only characteristic of torpediniforms, which are not included here. States are, therefore, re-coded consequently. †*Protohimantura* appears to have suprascapulae which are fused medially and laterally to synarcual as in all myliobatiforms (2).
78. (53 of ASC) Ball-and-socket articulation between scapular process and synarcual: (0) absent; (1) present.
79. (54 of ASC) Second (thoracolumbar) synarcual: (0) absent; (1) present.
80. (55 of ASC) Ribs: (0) present; (1) absent.
81. (63 of ASC) Segmentation of propterygium: (0) posterior to mouth, (1) proximal segment of propterygium of pectoral girdle is between mouth and antorbital cartilage; (2) the first segment is adjacent to the nasal capsule; (3) the first segment is adjacent to anterior margin of antorbital cartilage or anterior to margin of nasal capsule.
82. (74 of ASC) Pseudosiphon: (0) present; (1) absent.
83. (75 of ASC) Dorsal marginal clasper cartilage: (0) lacks medial flange; (1) possesses medial flange.
84. (76 of ASC) Dorsal terminal cartilage: (0) smooth margin; (1) crenate margin.
85. (77 of ASC) Cartilage forming component claw: (0) present; (1) absent; (2) cartilage embedded in integument and is not visible externally; (3) cartilage lines the inner ventral margin of the clasper glans and often forms the component shield.
86. (78 of ASC) Ventral terminal cartilage (accessory terminal 1 cartilage in rajids): (0) simple; (1) free distally and forms component sentinel or is fused with ventral marginal cartilage and forms component projection; (2) folded ventrally along its long axis to form a convex flange.
87. (79 of ASC) Ventral terminal cartilage (accessory terminal 1 cartilage in rajids): (0) attached over length to axial cartilage; (1) free of axial cartilage.
88. (85 of ASC, modified) Spiracularis: 0 = undivided; (1) splits into lateral and medial bundles, with the medial bundle inserting onto the posterior surface of Meckel's cartilage and the lateral bundle inserting onto the dorsal edge of the hyomandibula; (2) extends beyond the hyomandibula and Meckel's cartilage; (3) subdivided proximally and inserts separately onto the palatoquadrate and the hyomandibula. **Remarks:** we only include four states instead of the original five of ASC since the state 1 of ASC (spiracularis divided and one bundle enters the dorsal oral membrane underlying the neurocranium) is only characteristic of torpediniforms, which are not included here.

Characters 89–97 are selected from Underwood *et al.* (2017) (UND). Amongst the 77 characters of Underwood *et al.* (2017) only nine characters were conserved herein, since the others are the same of Carvalho *et al.* (2004) and/or Claeson *et al.* (2010) or autapomorphic for single genera.



89. (52 of UND, modified) Sexual heterodonty: (0) absent; (1) present. **Remarks:** Underwood *et al.* (2017) have considered the presence of sexual heterodonty only in some pelagic stingrays (*Aetobatus* and *Mobula*) amongst living myliobatiforms. However, Herman *et al.* (2000) have suggested that this kind of sexual dimorphism is also present in *Urolophus*, *Taeniura*, *Pteroplatytrygon*, *Dasyatis* and *Himantura*. Carvalho *et al.* (2004) recognized sexual heterodonty also in †*Asterotrygon*. The character is coded as unknown for †*Protohimantura*.
90. (63 of UND) Medial symphyseal processes of the Meckel's cartilage: (0) absent; (1) present.
91. (68 of UND) Lateral processes of the palatoquadrate extending far anteriorly: (0) absent; (1) present.
92. (69 of UND) Anterior processes of the Meckel's cartilage: (0) absent; (1) present; (2) extending anterior past jaw joint.
93. (71 of UND) Lateral oral diastema alt: (0) diastema width greater than occlusal width; (1) occlusal width greater than diastema width.
94. (72 of UND) Upper jaw profile: (0) oval in cross-section (most batoids); (1) flat top, convex occlusal surface (myliobatids); (2) strongly flattened (mobulids).
95. (73 of UND) Upper jaw mineralization: (0) all surfaces mineralized; (1) lingual face partly unmineralized (mobulids).
96. (74 of UND) Lower jaw profile: (0) oval in cross-section; (1) strongly linguolabially expanded.
97. (75 and 76 of UND, modified): Upper and lower jaw trabeculae: (0) absent; (1) weakly developed; (2) strongly developed.
- The characters 98–102 pertain to new morphological features detected from literature, but never included in a phylogenetic framework.
98. Mesiodistally enlarged teeth up to one single tooth row: (0) absent; (1) present. **Remarks:** this character is described by Herman *et al.* (2000) who consider it a derived state for *Aetobatus*, *Aetomylaeus*, *Myliobatis*, *Pastinachus*, *Rhinoptera*, *Manta* and *Mobula*. This condition was not observed in †*Protohimantura* or described for other taxa (state 0).
99. Second transverse keel: (0) absent; (1) present. **Remarks:** A second transverse keel is present on teeth of *Himantura*, *Trygonoptera*, *Urobatis* and *Urolophus* according to Herman *et al.* (2000). †*Protohimantura* also shows a second transverse keel similar to the condition of *Himantura*, and this character supports their sister-group relationship in our phylogeny. A second transverse keel was not reported for †*Heliobatis* or †*Asterotrygon* (see Carvalho *et al.*, 2004).
100. Calcification pattern of radials: (0) crustal; (1) catenated. **Remarks:** Schaefer & Summers (2005) have shown that calcification of radials in batoids is strictly related to their swimming mode. Stiffer radials completely covered by mineralized tissue ('crustal calcification') are typical of batoids with axial-undulatory or oscillatory swimming mode, including *Rhinobatos*, *Plesiobatis*, *Gymnura* and all pelagic stingrays. On the contrary, less stiff radials calcified in chain-like patterns ('catenated calcification') are typical of batoids with undulatory swimming mode, including *Raja*, and all myliobatiforms (except pelagic stingrays and *Plesiobatis*). †*Protohimantura*, †*Heliobatis* and †*Asterotrygon* are coded as (1) since they clearly show catenated calcification (see also Carvalho *et al.*, 2004).
101. Body disc shape: (0) rhombus, quadrangular or oval, with pectoral fins not greatly expanded; (1) wing like, with pectoral fins greatly expanded. **Remarks:** this character is modified from Lim *et al.* (2015). Most of batoids have the general condition of a rhomboidal, quadrangular or oval shape of the disc, and pectoral fins are not greatly expanded (0), including outgroups and most of the myliobatiforms. *Gymnura* and all pelagic stingrays have the derived wing-like condition, with pectoral fins greatly expanded (Lim *et al.*, 2015; but see also Last *et al.*, 2016a). †*Protohimantura*, †*Heliobatis* and †*Asterotrygon* are coded as (0), since their disc clearly show the basalmost condition (see also Carvalho *et al.*, 2004).
102. Mid-dorsal surface of disc covered by heart-shaped denticles arranged in an antero-posteriorly directed patch having sharply defined outlines: (0) absent; (1) present. **Remarks:** this condition has been recognized as diagnostic for urogymnines, and distinguishes them from all other members of the family Dasyatidae (Last *et al.*, 2016a, b). In our matrix, this character is present in only *Himantura* and †*Protohimantura* supporting their sister group relationship in the phylogenetic analysis.

APPENDIX 2  
DATA MATRIX USED IN THE PHYLOGENETIC ANALYSIS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40			
<i>Rhinobatos</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Raja</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hexatrygon</i>	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	
<i>Plesiobatis</i>	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Urolophus</i>	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
<i>Trygonoptera</i>	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	?	0	0	0	
<i>Urobatis</i>	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	1	1	0	[01]	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Urotrygon</i>	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	3	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Paratrygon</i>	0	0	2	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	1	0	1	1	2	0	0	0	0	1	1		
<i>Styracura</i>	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	1	1	0	0	1	0	0	0	0	0	0	1	1	2	0	2	0	0	0	0		
<i>Heliotrygon</i>	0	0	2	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0		
<i>Plesiotrygon</i>	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	
<i>Potamotrygon</i>	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	2	0	0	0	0	0	
<i>Taeniura</i>	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	2	0	0	0	0	0	
<i>Pteroplatytrygon</i>	0	1	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	2	0	0	0	0	
<i>Dasyatis</i>	0	1	[01]	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0		
<i>Himantura</i>	0	1	[01]	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	1	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0		
<i>Gymnura</i>	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	1	1	0	2	0	0	0	0	0	0	
<i>Myliobatis</i>	0	2	0	1	0	0	1	0	0	1	1	1	0	1	1	0	1	?	1	1	3	1	2	0	1	0	1	0	1	0	0	0	0	1	2	0	1	0	1	0	0	0	
<i>Aetobatus</i>	0	2	0	1	0	1	1	0	1	1	1	1	0	1	1	0	1	1	1	3	1	2	0	1	?	1	?	2	0	?	0	1	0	1	2	1	0	1	1	0	0	0	
<i>Rhinoptera</i>	0	2	0	1	1	1	1	0	1	1	1	0	0	1	1	0	1	1	3	1	3	1	2	0	1	?	1	?	2	0	?	0	1	0	1	2	1	0	1	1	0	0	
<i>Mobula</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Manta</i>	0	2	0	1	0	0	1	0	0	1	1	0	1	0	1	0	1	?	1	3	1	2	0	1	1	1	1	?	2	1	?	0	1	0	1	2	1	0	1	1	0	0	
<i>Aetomylaeus</i>	0	2	0	1	0	0	1	0	0	1	1	0	1	0	1	0	1	?	1	3	1	2	0	1	0	1	0	1	0	1	0	0	0	1	2	1	0	1	1	0	0	0	
<i>Pastinachus</i>	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	1	0	0	1	0	0	1	0	?	0	0	0	1	1	0	0	1	1	0	0	0	0	0
<i>Neotrygon</i>	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	
† <i>Protohimantura</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
† <i>Heliobatis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
† <i>Asterotrygon</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80		
<i>Rhinobatos</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Raja</i>	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hexatrygon</i>	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Plesiobatis</i>	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Urolophus</i>	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Trygonoptera</i>	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Urobatis</i>	1	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Urotrygon</i>	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Paratrygon</i>	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Styracura</i>	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Heliotrygon</i>	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

