
Neotype designation and re-description of Forsskal's reticulate whipray *Himantura uarnak*

Borsa Philippe ^{1,*}, Williams Collin Taylor ², McIvor Ashlie Jane ^{2,3}, Hoareau Thierry B. ⁴,
Berumen Michael L. ²

¹ Institut de recherche pour le développement, IRD-UMR 250 'Écologie marine tropicale des océans Pacifique et Indien', 34394, Montpellier, France

² Division of Biological and Environmental Science and Engineering, Red Sea Research Center, King Abdullah University of Science and Technology (KAUST), Thuwal, 23955-6900, Saudi Arabia

³ MARE - Marine and Environmental Sciences Centre, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (ARDITI), Edifício Madeira Tecnopolo, Caminho da Penteada, 9020-105, Funchal, Madeira, Portugal

⁴ Department of Biochemistry, Genetics and Microbiology, University of Pretoria, X20, Hatfield, 0028, Pretoria, South Africa

* Corresponding author : Philippe Borsa, email address : philippe.borsa@ird.fr

Abstract :

A continuing impediment to the taxonomy of the reticulate whipray *Himantura* spp. species complex is the absence of a type specimen for *H. uarnak* (Gmelin [ex Forsskal], 1789). Here, reticulate whipray specimens were sampled from the Jeddah region in the Red Sea, the assumed type locality of *H. uarnak*, and characterized genetically at the cytochrome-oxidase subunit 1 (CO1) locus. One of these specimens now in the fish collection of the California Academy of Sciences was designated as neotype. The maximum-likelihood phylogeny of all available CO1 gene sequences from the genus *Himantura* had the following topology: ((*H. leoparda*, *H. uarnak*), (*H. undulata*, (*Himantura* sp. 2, (*H. australis* + *Himantura* sp. 1))), *H. tutul*), where *H. uarnak* haplotypes formed a distinct lineage sister to *H. leoparda*. Based on these CO1 gene sequences, the geographic distribution of *H. uarnak* includes the eastern Mediterranean, the Red Sea, the East African coast, and the Arabian Sea. At least one lineage in the reticulate whipray species complex remains to be named.

Keywords : Taxonomy, Dasyatidae, Neotype, Redescription, Nucleotide sequence

Introduction

Among the marine fishes listed from P. Forsskål's expedition to the Red Sea were three stingrays, namely the cowtail stingray *Pastinachus sephen* (Forsskål, 1775), the reticulate whipray *Himantura uarnak* (Gmelin, 1789) and the blue-spotted ribbontail ray *Taeniura lymma* (Forsskål, 1775). All three species have long been believed to have a wide Indo-Pacific distribution (e.g., Last & Compagno 1999) but this view has recently been challenged by molecular phylogenetics (Naylor et al. 2012; Arlyza et al. 2013). While the first written mention of the name 'Uárnak' rests with Forsskål (1775), the first author to have used it as an epithet in a formal Linnean binomen ('*Raja uarnak*') was Gmelin (1789), who is therefore considered as the author of *H. uarnak* (Fricke 2008). We here follow Fricke (2008) in referring to 'P. Forsskål's *H. uarnak*'. Although Gmelin (1789) hastily stated that the distribution of *R. uarnak* included the European seas, the Red Sea and the Indian Ocean ('*omni mari europaeo, rubro, indico*'), Fricke (2008) indicates 'Red Sea' as the type locality for *H. uarnak*. The designation by Klausewitz (1960) of a specimen used by Rüppell (1837) as lectotype is not considered valid (Fricke et al. 2021). Thus, no type is available yet for this species.

H. uarnak belongs to a species complex that comprises at least six distinct lineages also including *Himantura undulata* Bleeker, 1852, *Himantura leoparda* Manjaji-Matsumoto and Last, 2008, *Himantura tutul* Borsa, Durand, Shen, Arlyza, Solihin and Berrebi, 2013, *Himantura australis* Last, White and Naylor, 2016, and one lineage, '*uarnak* 4' that still has to be named formally (Naylor et al. 2012; Last et al. 2016b; Borsa 2017). All species in this complex possess spots all over hence could potentially correspond to Gmelin's [1789, ex-Forsskål's (1775)] brief description. Authors who recently described new *Himantura* species formerly under *H. uarnak* (Manjaji-Matsumoto and Last 2008; Last et al. 2016c) did not provide diagnoses of their new species against typical *H. uarnak*. Neither did Borsa et al. (2013) in their description of *H. tutul* as this species was discovered as a cryptic lineage under Manjaji-Matsumoto and Last's (2008) *H. leoparda* (Arlyza et al. 2013; Borsa 2017). *Himantura tutul* was declared a synonym of *H. uarnak* without justification other than 'morphological resemblance' (Weigmann 2016), but was subsequently maintained as a valid species by other authors (Miesen et al. 2016; Fernando et al. 2019; Kumar et al. 2020). Several of these lineages have wide, overlapping Indo-West Pacific distributions (Naylor et al. 2012; Arlyza et al. 2013).

No material from the Red Sea has yet been analyzed genetically. However, two whipray specimens from the eastern Mediterranean Sea and sub-sampled for DNA were identified as *H. leoparda* based on the proximity of the nucleotide sequence of the *CO1* gene with this species (Yucel et al. 2017). In the absence of accepted type material, it is unclear which of the foregoing *Himantura* spp. lineages – or eventually another lineage – corresponds to P. Forsskål's *H. uarnak*. Under these circumstances, it is advisable to designate a neotype for *H. uarnak* and to provide a diagnostic description of it, so as to identify the lineage that corresponds to this species, stabilize the nomenclature of species in the genus *Himantura* [International Commission on Zoological Nomenclature (ICZN) 1999] and enable unambiguous identification to species of any individual in this genus. The purpose of the present note is to characterize reticulate whipray material collected recently from the Red Sea, to designate a neotype for *H. uarnak*, and to attempt to clarify the intricate taxonomy of the reticulate whipray species complex based on the universal *CO1* barcode.

Materials and methods

Thirteen reticulate whipray individuals were captured on shallow-water sand flats of the eastern shore of the central Red Sea between 2016 and 2019: eight were captured near the coastal town of Thuwal, Saudi Arabia (22.313°N 39.090°E); the other five were captured approximately 15 km offshore on Sirrayn Island (19.616°N 40.647°E) in the Farasan Banks region of Saudi Arabia (Fig. 1). Specimen identification numbers and sampling details are provided in Supplementary Table S1. All live specimens were photographed, measured, and a small section of the pelvic fin was excised

as genetic material. One individual [no. KAUST-RSRC-H006 (H006)] was retained whole as voucher specimen to be deposited in a museum collection; it was euthanized by immersion in ice-refrigerated seawater; so was another specimen (H009) whose jaws and tissue sample were preserved. The other individuals were released at their capture site within minutes after their capture. An additional tissue sample was obtained from an individual on sale at the Jeddah (Saudi Arabia) fish market. The total length, disc width (DW), and length from snout to origin of cloaca were measured on live specimens. Additional measurements were made on the voucher specimen using the indications of Manjaji (2004). Pigmentation was described using the following parameters: (i) number of spots counted in a rectangular band drawn between spiracles; (ii) number of spots crossed along a line running from mid-scapular point to extremity of pectoral fin, as shown in figure 1 of Borsa et al. (2013); (iii) dorsal-spot diameter; (iv) thickness of paler outer disc margin at extremity of pectoral fin on the dorsal side; and (v) thickness of pigmented outer disc margin at extremity of pectoral fin on the ventral side. Tissue samples ($N = 14$) were placed in ~95% ethanol and stored at -20°C until further processing.

Genomic DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) following the manufacturer's recommendations. The *FishF1/FishR1* primer pair (Ward et al. 2005) was used to target a 655-bp portion of the *COI* gene located between homologous nucleotide sites no. 5571 and no. 6225 of the mitochondrial DNA in *H. leoparda* (NC_028325; Shen et al. 2016) for amplification by polymerase chain reaction (PCR). PCR was run in individual wells loaded with 12 μL reaction mixture composed of 2 μL DNA extract, 5.4 μL Multiplex PCR Master Mix (Qiagen), 0.4 μL of each primer (10 μM), and 3.7 μL H_2O . The PCR program included a denaturing step at 95°C for 15 min, followed by 35 cycles of denaturing at 94°C for 30 s, annealing at 50°C for 60 s, and extension at 72°C for 45 s, ending with by a final extension step at 72°C for 10 min. The PCR products were analyzed with the QIAxcel DNA Screening Kit (Qiagen) to confirm successful amplification. Amplified DNA was purified by adding 1.2 μL of ExoProStar (GE Healthcare, Piscataway, USA) to each well before a single thermal cycle of 37°C for 60 min, 85°C for 15 min, and a hold at 4°C until sequencing. PCR samples were then sent for Sanger sequencing at the KAUST Bioscience Core Lab. The sequencing reaction was done in each direction, using either *Fish F1* or *Fish R1* as the sequencing primer. Sanger sequencing of purified target DNA was conducted using the 3730xl DNA Analyzer (Applied Biosystems, Foster City, USA).

Reticulate whipray *COI* gene sequences from the Red Sea were compared to all homologous *Himantura* spp. sequences available including 201 sequences downloaded from the GenBank (www.ncbi.nlm.nih.gov/genbank/; Clark et al. 2016) and BOLD (<http://www.boldsystems.org/>; Ratnasingham and Hebert 2007) public repositories, and two unpublished sequences (Supplementary Table S2). Reticulate whipray, *Himantura* spp. *COI* gene sequences from GenBank and BOLD were labelled '*H. astra*' ($N = 1$), '*H. australis*' ($N = 1$), '*H. fava*' ($N = 1$), '*H. leoparda*' ($N = 85$), '*H. tutul*' ($N = 30$), '*H. uarnak*' ($N = 62$), '*H. uarnak* i' ($N = 2$), '*H. uarnak* ii' ($N = 3$), '*H. uarnak* iii' ($N = 3$), '*H. undulata*' ($N = 11$), "*Himantura* sp.'" ($N = 1$) and "*Urogymnus asperimus*" ($N = 1$) (Supplementary Table S2). Partial nucleotide sequences of the *COI* gene were aligned and trimmed to a core length of 613 bp using the BioEdit sequence editing software (Hall 1999). The nucleotide sequences were sorted by species and nucleotide synapomorphies were then assessed visually.

A maximum-likelihood (ML; Felsenstein 1981) tree of partial *COI* gene sequences was constructed using the MEGA X package (Kumar et al. 2018). All three codon positions were included. Of all models tested under MEGA X, the HKY model (Hasegawa et al. 1985) had the lowest Bayesian information score. A discrete Gamma distribution was used to model evolutionary rate differences among sites ($G = 1.19$) and some sites were allowed to be evolutionarily invariable. GenBank sequences nos. EU398838, EU398867, EU398869, JF493649, KF899470, KF899491, KM073002, KM073006 and KP641389 (*Maculabatis* spp.), EU398849, KF899499, KM072993, KM073009 and KM073010 (*Pateobatis* spp.), EU398860, FJ384709, KF899521, KF899528, KM072995 and KR003772 (*Brevitrygon* spp.) and KF965292 were included as an outgroup to root

the tree. Mean nucleotide distances between and within lineages were estimated using the Maximum Composite Likelihood model under MEGA X.

The Assemble Species by Automatic Partitioning (ASAP; Puillandre et al. 2021) algorithm was used to partition the DNA sequence dataset into species hypotheses. The alignment of ingroup sequences ($N = 216$) in FASTA format was uploaded to the ASAP website at the Museum national d'histoire naturelle, Paris (<https://bioinfo.mnhn.fr/abi/public/asap/>; accessed 06 February 2021). We used the default options of ASAP and the genetic distances were estimated using the Kimura-2-parameter substitution model. The general mixed Yule coalescent (GMYC) algorithm (Pons et al. 2006) was also used to the same purpose. The GMYC algorithm implemented in the program SPLITS under R (R Development Core Team 2011; Fujisawa & Barraclough 2013) compares the branching patterns that are consistent with coalescent and speciation processes. We used BEAST v. 2.6.1 (Bouckaert et al. 2019) to construct an ultrametric tree, assuming a non-calibrated relaxed lognormal clock, a Yule tree prior, and the HKY model of nucleotide substitution. The run included a total of 10^6 Markov chain-Monte Carlo generations, which were sampled to obtain 10,000 genealogies and model parameter values. Inspection of the output in TRACER v. 1.5 (Drummond and Rambaut 2007) helped confirm that the sampling scheme was correct. The sampled trees were then summarised using TREEANNOTATOR v. 2.6.1 (Bouckaert et al. 2019) to produce the final ultrametric tree, based on maximum clade credibility and mean node height. The SPLITS program was then run to obtain genetic assignment of each sequence to a cluster.

Results

Disc width ranged between 284 mm and 748 mm. The claspers of the one of the five male specimens (HC256) were calcified. Reticulate whipray specimen no. H006 is presented in Fig. 2a-d. The colour of the dorsal side of all individuals sampled was beige and the ventral side was creamy white. The dorsal side was covered with numerous brown spots, which generally were evenly distributed and had a circular, or slightly elongated, or dumbbell shape. In a proportion of individuals, circular spots were often associated as pairs. Colour tones and spot patterns on the dorsal side were similar to those encountered in the reticulate whipray's mangrove habitat in the central Red Sea (Fig. 2e). The ventral side was either immaculate or with few dark-grey spots, apart from the outer margin of the posterior half of the disk which had a pale greyish hue with densely distributed small, dark-grey spots. A summary of the measurements used to describe spot patterns on all twelve specimens is reported in Table 1. Dorsal-spot diameter was correlated with disk width (Pearson's $r = 0.66$; $P < 0.05$) and so was dorsal-spot density estimated from transects ($r = 0.82$, $r = 0.56$; Fisher's combined $P < 0.01$), indicating that both the size and number of dorsal spots increase with age.

The ML tree of *Himantura* spp. sequences (Fig. 3) showed the four main lineages (I-IV) previously uncovered by Arlyza et al. (2013) with strong statistical support. Lineage I comprised haplotypes sampled from off eastern Africa, including the holotype of *H. tutul*, to the Sulu Sea. Lineage-I haplotypes have been previously identified as either '*H. leoparda*' (Lim et al. 2015; Bineesh et al. 2017; Mohd-Arshaad & Jamaludin 2018), '*H. tutul*' (Arlyza et al. 2013; Borsa et al. 2013), '*H. uarnak*', '*H. uarnak* i', '*H. uarnak* ii', '*H. uarnak* iii' (Bineesh et al. 2017; Gouws 2020; Hanner 2020), '*Himantura* sp.' (Hanner 2020), or '*Urogymnus asperrimus*' (Priyanga et al. 2013). Lineage II comprised haplotypes sampled from the Arabian Sea to the Sulu Sea, all identified as either '*H. fava*' (Ward et al. 2005) or '*H. undulata*' (Arlyza et al. 2013; Lim et al. 2015; Bineesh et al. 2017; Mohd-Arshaad & Jamaludin 2018; Segura-Garcia & Yain Tun 2018; Ahmed et al. 2019; present work). Further partitions were distinguished within lineage III. Lineage III₁ included two sequences sampled from the Sulu Sea so far labelled '*H. uarnak*' and '*H. uarnak* ii', respectively (Lim et al. 2015; Hanner 2020) while lineage III₂ included haplotypes sampled from tropical Australia exclusively and so far referred to as either '*H. astra*' (Cerutti-Pereyra et al. 2012), '*H. australis*' (Appleyard 2020), '*H. leoparda*'

(Cerutti-Pereyra et al. 2012), or '*H. uarnak*' (Cerutti-Pereyra et al. 2012 ; Appleyard 2020 ; McGrouther 2020). Haplogroup III_3 , which in the ML tree was paraphyletic with III_2 , exclusively comprised haplotypes sampled from the Coral Triangle and labelled either '*H. uarnak*' (Arlyza et al. 2013; Santos et al. 2014; Lim et al. 2015; Mohd Arshaad & Jamaludin 2018; Appleyard 2020; Hanner 2020; Mohd Arshaad 2020) or '*H. uarnak* i' (Hanner 2020). All *Himantura* spp. *CO1* gene sequences sampled from the Red Sea clustered into a single, highly distinctive and statistically strongly supported lineage IV_2 , also including haplotypes from the eastern Mediterranean Sea, Natal (South Africa) and the Arabian Sea. These were initially assigned to either '*H. leoparda*' (Bineesh et al. 2017; Yucel et al. 2017) or '*H. uarnak*' (Steinke et al. 2011). Lineage IV_1 which was sister to IV_2 exclusively comprised haplotypes from a geographic region spanning from India to the Coral Triangle. These were initially identified as either '*H. leoparda*' (Arlyza et al. 2013; Shen et al. 2016; Appleyard 2017; Ravi et al. 2019) or '*H. undulata*' (Appleyard 2020). Lineage IV_2 specific to the Red Sea and adjacent localities was separated from lineage IV_1 by 1.8% nucleotide distance at the *CO1* locus. The mean nucleotide distance was 0.3% within sub-clade IV_1 and 0.4% within sub-clade IV_2 .

The ASAP species delineation algorithm distinguished either three, four, six, seven, or eight hypothetical species in the genus *Himantura*. All five partitions coincided with partitions derived from the ML phylogeny (Fig. 3). Further ASAP partitions (i.e. from 12 up to 25 distinct species) were less probable. The three- and four-species hypotheses were deemed too conservative as they failed to recognize *H. australis* as a distinct species. Therefore, the six-, seven- and eight-species partitions, which had approximately equally high probabilities, were the only three hypotheses retained (Fig. 3c-e). Lineage IV_2 was identified as a distinct species in all three hypotheses. Of the three, the seven-species hypothesis was the one that scored best; a convenient threshold genetic distance (> 0.01) was associated with it. The most likely outcome of GMYC clustering was the nine-species partition represented in Fig. 3f, with a confidence interval of six to 11 species. A consensual partition based on the ML tree topology, the geographic distribution of lineages, the seven-species hypothesis resulting from ASAP partitioning and a conservative interpretation of the GMYC partition was eventually retained (Fig. 3g).

Discussion

The taxonomic value of mitochondrial DNA sequences has been demonstrated in morphologically intractable species complexes in Elasmobranchs such as those of the long-tailed butterfly ray *Gymnura poecilura* (Naylor et al. 2012 ; Muktha et al. 2018), the whitespotted whiptail *Maculabatis gerrardi* (Ward et al. 2008; Naylor et al. 2012) or the blue-spotted maskray *Neotrygon kublii* (Naylor et al. 2012; Puckridge et al. 2013; Borsa et al. 2018; Pavan-Kumar et al. 2018). The reticulate whiptail *Himantura* spp. species complex is another example in which morphological overlap among species has led to considerable confusion (Naylor et al. 2012; Borsa 2017), as confirmed by the plethora of names assigned to mitochondrial DNA haplotypes that cluster within a given lineage (present survey). For example, the name '*H. uarnak*' is currently assigned to no less than five distinct *Himantura* lineages in the GenBank and BOLD sequence databases.

For the present study, we collated the largest *CO1* gene sequence dataset to date in the genus *Himantura*. A total of seven distinct lineages or haplogroups were identified from the phylogenetic tree of the reticulate whiptail species complex (Fig. 3). The strongly-supported, highly distinctive lineage IV_2 was the only one that included haplotypes from the Red Sea (from at least two separate locations north and south of Jeddah), including that of a specimen preserved whole and here chosen as *H. uarnak*'s neotype (see next section). As a consequence, lineage IV_2 is here designated as P. Forsskål's *H. uarnak*. This lineage was distinct from lineage (IV_1) which included all leopard whiptail *H. leoparda* specimens from the Coral Triangle and adjacent regions. *Himantura leoparda*, whose type locality is the Gulf of Carpentaria turns out to be the sister-species of *H. uarnak*. The other lineages were identified as *H. australis* (III_2), *H. tutul* (I) and *H. undulata* (II) based on this and

previous genetic work employing nuclear, *cyt b*, and *CO1* markers (Arlyza et al. 2013; Borsa et al. 2013; Borsa 2017; Appleyard 2020) and on geographic consistency with the type locality of *H. australis* (southern New Guinea; Last et al. 2016c). Under the present seven-species hypothesis, two lineages here labelled *Himantura* sp. 1 (*III*₂) and *Himantura* sp. 2 (*III*₁) may represent undescribed species. Thus, the fixation of a neotype for *H. uarnak* strengthens the current nomenclature for species in the genus *Himantura*, clarifies the identity of over 200 specimens whose *CO1* gene sequences have been deposited in public databases and opens the way to the possible description or re-description of up to two other yet-unnamed species in the genus *Himantura*.

Despite the brevity of its original description, P. Forsskål's *H. uarnak* has been universally treated as a single, valid taxon in the subsequent literature (Rüppell 1837; Bleeker 1852; Duméril 1865; Last and Compagno 1999; Manjaji 2004). Multiple lineages that qualify as distinct species have since been assigned to *H. uarnak* (Naylor et al. 2012; Last et al. 2016c; Borsa 2017; present study) demonstrating taxonomic confusion up to this day. For clarifying past and future research dealing with the reticulate whipray species complex we elected to designate a neotype, a nomenclatural act that leads to unambiguously identifying *H. uarnak*.

Spot patterns may change with age, may vary among individuals within a species and may overlap with other species, therefore, this character should be considered as insufficiently reliable for species diagnoses in the genus *Himantura*, compared to mitochondrial DNA sequences (Naylor et al. 2012; Arlyza et al. 2013; Borsa et al. 2013). Neither are morphological measurements helpful as illustrated by Supplementary Table S3, where no single morphological character used in species 'diagnoses' in the *Himantura* literature was clearly diagnostic, save two characters that may single out *H. undulata*. In the following section, we provide the necessary morphological details on the neotype and we re-describe P. Forsskål's *H. uarnak* based on mitochondrial DNA sequences. For a justification of species descriptions based on DNA sequences, see Cook et al. (2010).

Neotype designation and re-description of *Himantura uarnak*

Genus *Himantura* Müller & Henle, 1837; species *H. uarnak* [Gmelin (ex-Forsskål), 1789], type species of the genus. The authorship of the species has been discussed extensively by Fricke (2008).

Both Forsskål's (1775) initial description and Gmelin's (1789) formal description mentioned a whipray ('*cauda, quae apterygia*') with spots all over ('*tota maculata*'). Reticulate whipray specimen KAUST-RSRC-H006 (male, 369 mm DW, collected on April 25, 2019 by AJM and CTW) has the foregoing attributes and it was captured off the Saudi Arabian shore of the central Red Sea ca. 80 km north of Jeddah. This specimen, which was allocated collection no. CAS-ICH 247241 in the fish collections of the California Academy of Sciences, San Francisco, USA, is here designated as *Himantura uarnak*'s neotype. This designation thus satisfies the conditions expressed in the International Code of Zoological Nomenclature (ICZN 1999: Articles nos. 8 and 75).

Neotype locality is Thuwal, Saudi Arabia (22°18'40"N 39°05'26"E); habitat is shallow sand flat ~50 cm deep adjacent to mangroves dominated by *Avicennia marina*.

Morphological description of neotype (see also Table 1 and Fig. 2a-d): disc rhomboidal, length 94.6% DW; snout with distinct apical lobe; anterior margins of disc slightly concave, lateral apices narrowly rounded; posterior margin convex, free rear tip rounded. Pelvic fins moderately elongate, length 17.4% DW; width across base 14.5% DW. Two remarkably large, heart-shaped thorns in mid-scapular region in posterior part of a line of 24 consecutive, slightly enlarged thorns, but no other enlarged thorns extending along mid-line of disc and tail. Nasal curtain skirt-shaped, broad and short with finely fringed posterior margin. Tail whip-like, tapering gently toward sting, length 230.8% DW. Small sharp thorns on dorsal side of tail beyond caudal sting. Additional morphological measurements taken on neotype after it was fixed in formalin were the following (in mm): disc width 351, total length 1089, snout to pectoral-fin insertion 299, end of orbit to pectoral insertion 214, snout to maximum width 135, snout to origin of cloaca 284, cloaca origin to sting 129,

pectoral insertion to sting origin 138, disc thickness 48, snout to preorbital (direct) 77, snout to preorbital (horizontal) 68, orbit diameter 16, eye diameter 19, spiracle length 14, orbit+spiracle length 36, interorbital width 51, inter-eye width 77, distance between spiracles 82, head length (direct) 165, preoral length (to lower jaw) 77, snout (prenasal) 58, nostril length 20, nasal curtain length 23, nasal curtain width 41, distance between nostrils 34, mouth width 38, distance between 1st gill slits 74, distance between 5th gill slits 51, width of 1st gill slit 10, width of 3rd gill slit 10, width of 5th gill slit 7, tail width at axil of pelvic fins 21, tail width at base of sting 11, tail height at axil of pelvic fins 17, tail height base of caudal sting 8, sting length 79, cloaca length 2, greatest width across pelvic fins 88 (resting) or 102 (spread), clasper length 31 (post-cloaca) or 13 (from pelvic axil).

Re-description of *H. uarnak*. A species in the genus *Himantura*, as re-defined by Last et al. (2016a). *CO1* gene sequences cluster into a distinct lineage in the phylogenetic tree of the genus *Himantura* (Fig. 3). Nucleotide sequence of partial *CO1* gene of neotype, comprised between homologous nucleotide sites no. 69 and no. 699 of the *CO1* gene in *H. leoparda* (GenBank accession no. NC_028325; Shen et al. 2016) is 5'- C G G T G C G T G A G C A C G G A T A G T G G G T A C T G G C C T T A G C C T G C T T A T T C G G A C A G A G C T A A G C C A A C C A G G C G C A T T A C T G G G T G A T G A T C A A A A A T A T A A T G T A A T T G T T A C C G C C C A T G C C T T C G T A A T A A T C T T T T T C A T G G T A A T A C C T A T T A T A A T T G G G G G C T T T G G T A A T T G A C T C G T C C C C C T A A T A A T C G G T G C T C C A G A T A T A G C C T T T C C T C G A A T A A A C A A C A T G A G T T T T T G A C T T C T T C C A C C A T C C T T T C T A C T A C T T T T G G C C T C T G C T G G A G T A G A G G C T G G C G C T G G A A C A G G C T G A A C A G T C T A T C C C C C A C T A G C T G G T A A T C T A G C A C A T G C A G G G G C T T C A G T A G A C T T A G C A A T C T T T T C C C T A C A C C T G G C C G G T G T A T C T T C T A T C C T A G C C T C T A T T A A T T T T A T C A C C C A C A A T C A T T A A C A T A A A A C C A C C A G C A A T T T C G C A G T A T C A A A C A C C C T C T T T G T C T G A T C A A T C C T T A T C A C A G C C G T A C T C C T C T T G T T A T C T C T T C C T G T C C T A G C A G C A G G T A T T A C G A T A C T T C T A A C A G A T C G T A A C C T C A A T A C A A C C T T C T T T G A T C C T G C A G G A G G A G G T G A C C C A A T T C T T T A T C A A -3'. The four diagnostic nucleotides here underlined (T, C, A, G in respective positions 270, 478, 480, 624 of the *CO1* gene sequence) distinguish *H. uarnak* from all other species in the genus *Himantura*.

Geographic distribution: *H. uarnak* specimens whose identity was here ascertained from their partial *CO1* gene sequences (Supplementary Table S2) were previously reported as '*H. leoparda*' (Arlyza et al. 2013; Borsa et al. 2013; Yucel et al. 2017; Bineesh et al. 2017) or '*H. uarnak*' (Steinke et al. 2011). Conversely, the identity of specimens previously assigned to '*H. uarnak*' are now correctly assigned to *H. australis*, *H. tukul*, and two yet-unnamed *Himantura* spp. (see Supplementary Table S2). Based on these genetically validated records, the distribution of *H. uarnak* outside the Red Sea includes the eastern Mediterranean Sea (Yucel et al. 2017), Natal (Steinke et al. 2011), and the Arabian Sea (Bineesh et al. 2017).

Notice

The present article in portable document (.pdf) format is a published work in the sense of the International Code of Zoological Nomenclature (ICZN 1999). It has been registered in ZooBank (<http://zoobank.org/>), the online registration system for the ICZN. The ZooBank life science identifier for this publication is [urn:lsid:zoobank.org:pub:B2113697-5EBF-4364-B50C-63019A1A076A](http://zoobank.org/urn:lsid:zoobank.org:pub:B2113697-5EBF-4364-B50C-63019A1A076A). The online version of this work is archived and available from the *Marine Biodiversity* website (<https://www.springer.com/journal/12526>), and from the hal-IRD (<https://hal.ird.fr>) repository.

Acknowledgements Foremost, thanks are due to M. Tietbohl for donating tissue samples, assisting in field collections, and providing laboratory assistance. Additionally, we are grateful to J. Spaet and members of KAUST's Reef Ecology Lab for their support at various stages of this project; to D. Catania and L.A. Rocha for allocating a CAS collection number to the neotype of *H. uarnak*; to X. Chen for sharing reticulate whipray sequences; to M. Bennett-Smith for sharing excellent photographs; to S. Bogorodsky, H. Debelius and R. Fricke for insightful discussions about the taxonomy and nomenclature of reticulate whiprays; to G. Lim (ICZN) for confirming the validity of the present neotype designation. Useful taxonomic literature was communicated to us by C.-W. Chang, K.-N. Shen, and an anonymous reviewer. Several books including P. Forsskål's *Descriptiones animalium*, J.F. Gmelin's *Systema naturae* and Rüppell's *Fische des rothen Meeres* were accessed from the Biodiversity Heritage Library website (<http://www.biodiversitylibrary.org/>).

Funding information Support to this study was provided by the King Abdullah University of Science and Technology (KAUST) through baseline funding to MLB and Institut de recherche pour le développement, Marseille to PB.

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Reticulate whipray specimens were captured in accordance with KAUST's institutional animal care and use committee (IACUC) under animal study proposal # 18IACUC14.

Data availability All data generated during this study are included in this published article or in the appended Supplementary Tables. Sequences produced through the present study have been deposited in GenBank (<https://www.ncbi.nlm.nih.gov/nucleotide/>) under accession nos. MW178184-MW178196. Photographs of all specimens are available from the authors upon request.

Author contributions AJM and CTW participated in the design of the study, collected and measured specimens, did the molecular analyses and participated in the writing. MLB contributed funding and laboratory facilities and supervised the study. PB designed the study, provided directions, compiled and analyzed the data and led the writing. TBH ran additional data analyses. All authors read, edited and approved the final version of the manuscript.

References

- Ahmed M.S., Zhilik A.A., Chowdhury N.Z., Ahmed S. (2019) DNA barcoding of marine fishes of Bangladesh. <https://www.ncbi.nlm.nih.gov/nuccore/MN013427>
- Appleyard SA (2017) http://www.boldsystems.org/index.php/Public_RecordView?processid=FOAO1113-18, FOAO1135-18, FOAO1142-18
- Appleyard SA (2020) http://www.boldsystems.org/index.php/Public_RecordView?processid=FOAG126-07, FOAJ878-09, FOAO1107-18
- Arlyza IS, Shen K-N, Solihin DD, Soedharma D, Berrebi P, Borsa P (2013) Species boundaries in the *Himantura uarnak* species complex (Myliobatiformes: Dasyatidae). *Mol Phyl Evol* 66:429-435
- Bineesh KK, Gopalakrishnan A, Akhilesh KV, Sajeela KA, Abdussamad EM, Pillai NGK, Basheer VS, Jena JK, Ward RD (2017) DNA barcoding reveals species composition of sharks and rays in the Indian commercial fishery. *Mitoch DNA Pt A* 28:458-472
- Bleeker P (1852) Bijdrage tot de kennis der Plagiostomen van den Indischen archipel. *Verhandel Batav Genoot Kunst Wetensch* 24:1-92, pls 1-4

- Borsa P (2017) Comments on ‘Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity’ (Weigmann, 2016). *J Fish Biol* 90:1170-1175
- Borsa P, Arlyza IS, Hoareau TB and Shen K-N (2018) Diagnostic description and geographic distribution of four new cryptic species of the blue-spotted maskray species complex (Myliobatoidei: Dasyatidae; *Neotrygon* spp.) based on DNA sequences. *J Oceanol Limnol* 36:827-841
- Borsa P, Durand J-D, Shen K-N, Arlyza IS, Solihin DD, Berrebi P (2013) *Himantura tutul* sp. nov. (Myliobatoidei: Dasyatidae), a new ocellated whipray from the tropical Indo-West Pacific, described from its cytochrome-oxidase I gene sequence. *C R Biol* 336:82-92
- Bouckaert R, Vaughan TG, Barido-Sottani J, Duchene S, Fourment M, Gavryushkina A, Heled J, Jones G, Kuhnert D, De Maio N, Matschiner M, Mendes FK, Muller NF, Ogilvie HA, du Plessis L, Poppinga A, Rambaut A, Rasmussen D, Siveroni I, Suchard MA, Wu CH, Xie D, Zhang C, Stadler T, Drummond AJ (2019) BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *Plos Comput Biol* 15:28
- Cerutti-Pereyra F, Meekan MG, Wei N-WV, O’Shea O, Bradshaw CJA, Austin CM (2012) Identification of rays through DNA barcoding: an application for ecologists. *PLoS One* 7:e36479
- Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW (2016) GenBank. *Nucl Acids Res* 44:D67-D72
- Cook LG, Edwards RD, Crisp M, Hardy NB (2010) Need morphology always be required for new species descriptions? *Invert Systematics* 24:322–326
- Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol Biol* 7:214
- Duméril A (1865) Histoire naturelle des poissons ou ichthyologie générale. Tome premier Elasmobranches. Librairie encyclopédique du Roret, Paris, 720 p
- Felsenstein J (1981) Evolutionary trees from DNA sequences: A maximum likelihood approach. *J Mol Evol* 17:368–376
- Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791
- Fernando D, Brown RMK, Tanna A, Gobiraj R, Ralicki H, Jockusch EL, Ebert DA, Jensen K, Caira JN (2019) New insights into the identities of the elasmobranch fauna of Sri Lanka. *Zoo-taxa* 4585:201-238
- Forsskål P (1775) *Descriptiones animalium, avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forsskål (post mortem auctoris edidit Carsten Niebuhr). Adjuncta est materia medica kahirina atque tabula maris Rubri geographica.* Mölleri, Hauniae, xxxiv+164 p
- Fricke R (2008) Authorship, availability and validity of fish names described by Peter (Pehr) Simon Forsskål and Johann Christian Fabricius in the ‘*Descriptiones animalium*’ by Carsten Niebuhr in 1775 (Pisces). *Stuttg Beitr Naturk A Neue Ser* 1:1–76
- Fricke R, Eschmeyer WN, van der Laan R (eds) (2021) Eschmeyer’s catalog of fishes: genera, species, references (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>; accessed 22 Feb. 2021)
- Fujisawa T, Barraclough TG (2013) Delimiting species using single-locus data and the generalized mixed Yule coalescent approach: A revised method and evaluation on simulated data sets. *Syst Biol* 62:707-724
- Gmelin JF (1789) *Caroli a Linné [...] Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species; cum characteribus, differentiis, synonymis, locis. Editio decimo tertia, aucta, reformata, vol 1, pars III.* G.E. Beer, Lipsiae, pp 1033–1516
- Gouws G (2020) http://www.boldsystems.org/index.php/Public_RecordView?processid=SAIAB712-08,SAIAB713-08,SAIAB714-08,SAIAB715-08

- Hall TA (1999) BIOEDIT: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl Acids Symp Ser 41:95-98
- Hanner R (2020) http://www.boldsystems.org/index.php/Public_RecordView?processid=IRREK171-08, IRREK193-08, IRREK662-08, IRREK678-08, IRREK679-08, IRREK687-08, IRREK741-08, IRREK752-08, IRREK829-08
- Hasegawa M., Kishino H., Yano T. (1985) Dating the human-ape split by a molecular clock of mitochondrial DNA. J Mol Evol 22:160-174.
- ICZN (1999) International code of zoological nomenclature, 4th edn. International Trust for Zoological Nomenclature, London, 306 p
- Klausewitz W (1960) Die Typen und Typoide des Naturmuseums Senckenberg, 23: Pisces, Chondrichthyes, Elasmobranchii. Senckenbergiana Biol 41:289-296
- Kumar A, Adhavan D, Vinuganesh A, Prakash S (2020) DNA barcoding revealed first record of the ‘fine spotted whipray’ *Himantura tutul* (Myliobatoidei: Dasyatidae) in the Indian coastal waters. J Appl Ichthyol 36:515–518
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35:1547-1549.
- Last PR, Compagno LJV (1999) Dasyatidae - Stingrays. In Carpenter KE, Niem VH (eds) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae). FAO, Rome, 1479-1505.
- Last PR, Naylor GJP, Manjaji-Matsumoto BM (2016a) A revised classification of the family Dasyatidae (Chondrichthyes: Myliobatiformes) based on new morphological and molecular insights. Zootaxa 4139:345-368
- Last PR, White WT, de Carvalho MR, Séret B, Stehmann MFW, Naylor GJP (eds.) (2016b) Rays of the World. CSIRO Publishing, Melbourne, 790 p
- Last PR, White WT, Naylor G (2016c) Three new stingrays (Myliobatiformes: Dasyatidae) from the Indo-West Pacific. Zootaxa 4147:377-402
- Lim KC, Lim PE, Chong VC, Loh KH (2015) Molecular and morphological analyses reveal phylogenetic relationships of stingrays focusing on the family Dasyatidae (Myliobatiformes). PLoS One 10:e0120518
- Manjaji BM (2004) Taxonomy and phylogenetic systematics of the Indo-Pacific whip-tailed stingray genus *Himantura* Müller and Henle 1837 (Chondrichthyes: Myliobatiformes: Dasyatidae). PhD Thesis, University of Tasmania, xxii+607 p
- Manjaji-Matsumoto BM, Last PR (2008) *Himantura leoparda* sp. nov., a new whipray (Myliobatoidei: Dasyatidae) from the Indo-Pacific. CSIRO Mar Atmosph Res Pap 22:292-301
- McGrouther M.A. (2020) http://www.boldsystems.org/index.php/Public_RecordView?processid=AMS045-06
- Miesen FW, Droppelmann F, Hüllen S, Hadiaty RK, Herder F (2016) An annotated checklist of the inland fishes of Sulawesi. Bonn Zool Bull 64:77–106
- Mohd Arshaad W (2020) http://www.boldsystems.org/index.php/Public_RecordView?processid=JTFR099-17, JTFR112-17
- Mohd Arshaad W, Jamaludin N-A (2018) DNA barcoding of rays in Malaysia. <https://www.ncbi.nlm.nih.gov/nuccore/MG774902>, MG774903, MG774913, MG774915, MG774922, MG792078, MG792101, MG792110, MG792112, MG792113, MG792123, MG792124, MG792125
- Muktha M, Akhilesh KV, Sandhya S, Jasmin F, Jishnudev MA, Kizhakudan SJ (2018) Re-description of the longtail butterfly ray, *Gymnura poecilura* (Shaw, 1804) (Gymnuridae: Myliobatiformes) from Bay of Bengal with a neotype designation. Mar Biodiv 48:1085-1096

- Naylor GJP, Caira JN, Jensen K, Rosana KAM, White WT, Last PR (2012) A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. *Bull Am Mus Nat Hist* 367:1-262
- Pavan-Kumar A, Kumar R, Pitale P, Shen K-N, Borsa P (2018) *Neotrygon indica* sp. nov., the Indian-Ocean blue spotted maskray (Myliobatoidei, Dasyatidae). *C R Biol* 341:120-130
- Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP (2006) Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Syst Biol* 55:595–609
- Priyanga K, Thangaraj M, Singh R (2013) Molecular identification of *Urogymnus asperrimus* (family: Dasyatidae) using cytochrome oxidase I (*COI*) as a molecular marker. <https://www.ncbi.nlm.nih.gov/nuccore/KC508509>
- Puckridge M, Last PR, White WT, Andreakis N (2013) Phylogeography of the Indo-West Pacific maskrays (Dasyatidae, *Neotrygon*): A complex example of chondrichthyan radiation in the Cenozoic. *Ecol Evol* 3:217-232
- Puillandre N, Brouillet S, Achaz G (2021) ASAP: assemble species by automatic partitioning. *Mol Ecol Resour* 21:609-620
- Ratnasingham S, Hebert PD (2007) BOLD: the barcode of life data system (<http://www.barcodinglife.org>). *Mol Ecol Notes* 7:55–364
- Ravi RK, Venu S, Bineesh KK, Akhilesh KV, Sajeela KA, Basheer VS, Gopalakrishnan A (2019) <https://www.ncbi.nlm.nih.gov/nuccore/MK422130>
- R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (<http://www.R-project.org/>).
- Rüppell E (1837) *Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des rothen Meeres.* Siegmund Schmerber, Frankfurt am Mein, ii+148 p, 33 pl
- Santos MD, Asis AMM, Lacsamana JKM (2014) Illegal trade of regulated and protected aquatic species in the Philippines detected by DNA barcoding. <https://www.ncbi.nlm.nih.gov/nuccore/KC970332>
- Segura-Garcia I, Yain Tun T (2018) Unscrambling Myanmar marine fishery biodiversity using DNA barcoding. <https://www.ncbi.nlm.nih.gov/nuccore/MH235646>, MH235647
- Shen K-N, Chang C-W, Tsai S-Y, Wu S-C, Lin Z-H, Chan Y-F, Chen C-H, Hsiao C-D, Borsa P (2016) Next generation sequencing yields the complete mitogenomes of leopard whipray (*Himantura leoparda*) and blue-spotted maskray (*Neotrygon kuhlii*) (Chondrichthyes: Dasyatidae). *Mitoch DNA Pt A* 27:2613-2614
- Steinke D, Zemplak TS, Connell AD, Heemstra PC, Hebert PDN (2011) <https://www.ncbi.nlm.nih.gov/nuccore/JF493651>, JF493652
- Ward RD, Holmes BH, White WT, Last PR (2008) DNA barcoding Australasian chondrichthyans: results and potential uses in conservation. *Mar Freshw Res* 59:57–71
- Ward RD, Zemplak TS, Innes BH, Last PR, Hebert PDN (2005) DNA barcoding Australia's fish species. *Phil Trans Roy Soc Lond B* 360:1847–1857
- Weigmann S (2016) Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *J Fish Biol* 88:837-1037
- Yucel N, Sakalli A, Karahan A (2017) First record of the honeycomb stingray *Himantura leoparda* (Manjaji-Matsumoto & Last, 2008) (Myliobatoidei: Dasyatidae) in the Mediterranean Sea, confirmed by DNA barcoding. *J Appl Ichthyol* 33:530–532

Table 1 *Himantura uarnak*. Pigmentation patterns in 12 DNA-barcoded specimens from the Jeddah region in the central Red Sea. *DW* disk width; *na* no data

Specimen no.	DW (mm)	Dorsal side				Ventral side			
		Spot density between spiracles ^b	Spot density on pectoral fin ^c		Spot diameter (mm) ^d	Outer margin (% DW) ^e		Outer margin (% DW) ^f	
			Left	Right		Left	Right	Left	Right
H001	319	35	14	18	3.1 ± 0.4	15.4	14.9	na	na
H002	346	13	7	13	4.0 ± 0.6	18.7	20.0	na	na
H003	284	2	4	7	4.6 ± 0.5	25.8	25.3	na	na
H004	326	19	7	9	3.3 ± 0.3	11.8	9.8	na	na
H005	317	19	5	5	3.2 ± 0.6	29.1	25.0	na	na
H006 ^a	369	33	13	12	4.9 ± 0.6	2.9	3.1	31.3	25.6
H009	531	28	11	9	5.5 ± 1.1	9.1	6.8	na	na
HC127	278	15	8	11	3.3 ± 0.5	11.3	11.3	na	na
HC131	310	15	10	5	5.2 ± 0.6	9.6	14.1	na	na
HC150	288	21	11	12	4.0 ± 0.6	7.0	8.1	na	na
HC256	748	34	26	25	5.2 ± 0.7	4.1	5.6	12.5	na
HC289	580	16	15	9	6.6 ± 1.2	2.3	2.4	na	na

^a Neotype

^b Number of spots counted in band between spiracles

^c Number of spots crossed along line running from mid-scapular point to extremity of pectoral fin (see figure 1 of Borsa et al. 2013)

^d Average ± SD, from 30-36 randomly-chosen dorsal spots in central area of pectoral fin

^e Thickness of paler outer disc margin at extremity of pectoral fin

^f Thickness of pigmented outer disc margin at extremity of pectoral fin

Fig. 1 Reticulate whipray sampling localities in the central Red Sea

Fig. 2 Reticulate whipray *Himantura uarnak* (Gmelin [ex Forsskål], 1789). **a** Dorsal view of neotype, no. CAS-ICH 247241 deposited at the fish collections of the California Academy of Sciences, San Francisco (formerly at the Red Sea Research Center, Thuwal as no. KAUST-RSRC-H006); scale bar: 5 cm. **b** Neotype, ventral view; scale bar: 5 cm. **c** Neotype, spine details in median dorsal region; scale bar: 1cm. **d** Neotype, mouth details; scale bar: 1cm. **e** Sandy mangrove habitat of *H. uarnak* off Thuwal, Red Sea, 22.313°N 39.090°E (credit: M. Bennett-Smith / KAUST)

Fig. 3 Reticulate whipray *Himantura* spp. species complex. Maximum-likelihood tree of *CO1* gene haplotypes based on the HKY+G+I model. Tree with highest log likelihood (-16139.6) is shown. Tree is drawn to scale, with branch length measured in the number of substitutions per site. Haplotype sequences are listed using their GenBank or BOLD accession number. Score at a node is percentage of pseudo-trees in which the associated taxa clustered together (from 500 iterations of bootstrap resampling; Felsenstein 1985). The first four main partitions are designated by roman numbers *I-IV* following Arlyza et al. (2013); numbers in subscript indicate further partition. Arrow indicates placement of *H. uarnak* neotype. **a** Partition into main lineages according to ML tree topology. **b** Geographic origin of specimens: a colour-blind friendly colour palette was chosen (<https://venngage.com/blog/color-blind-friendly-palette/>; accessed 05 Feb. 2021): *red*, Red Sea (including eastern Mediterranean); *orange*, western Indian Ocean, including Arabian Sea; *paler blue*, eastern Indian Ocean, including western Australia; *darker blue*, Coral Triangle, including northern Australia. **c** Outcome of species delineation analysis using the ASAP algorithm, six-species hypothesis. **d** Idem, seven-species hypothesis. **e** Idem, eight-species hypothesis. **f** Most likely GMYC clustering. **g** Species names assigned to lineages defined consensually by ML, ASAP and GMYC analyses

Supplementary Table S1 Sampling details for reticulate whipray *Himantura uarnak* specimens from the Red Sea including specimen no. KAUST-RSRC-H006 / CAS-ICH 247241 chosen as neotype (highlighted red)

Supplementary Table S2 Reticulate whipray *Himantura uarnak* species complex. List of nucleotide sequences at the *CO1* locus used for the present work, with GenBank and BOLD identification nos. and other details including sampling locations and references. Sequences were retrieved on 23 March 2020 from the GenBank and BOLD public databases ($N = 201$) or donated by X. Chen (Wenzhou Medical College, China) ($N = 2$) or produced through the present survey ($N = 13$). Sequences are arranged by species and presented in alphabetical order

Supplementary Table S3 Main morphological characters used in the diagnoses of the four *Himantura* spp. species considered valid by Last et al. (2016b, 2016c) and Weigmann (2016). *Diagnosticity*: utility of character to diagnose at least one (*One sp.*) or all four species (*All spp.*); *N*, sample size; *NA* not specified

Fig. 1 - Borsa et al.

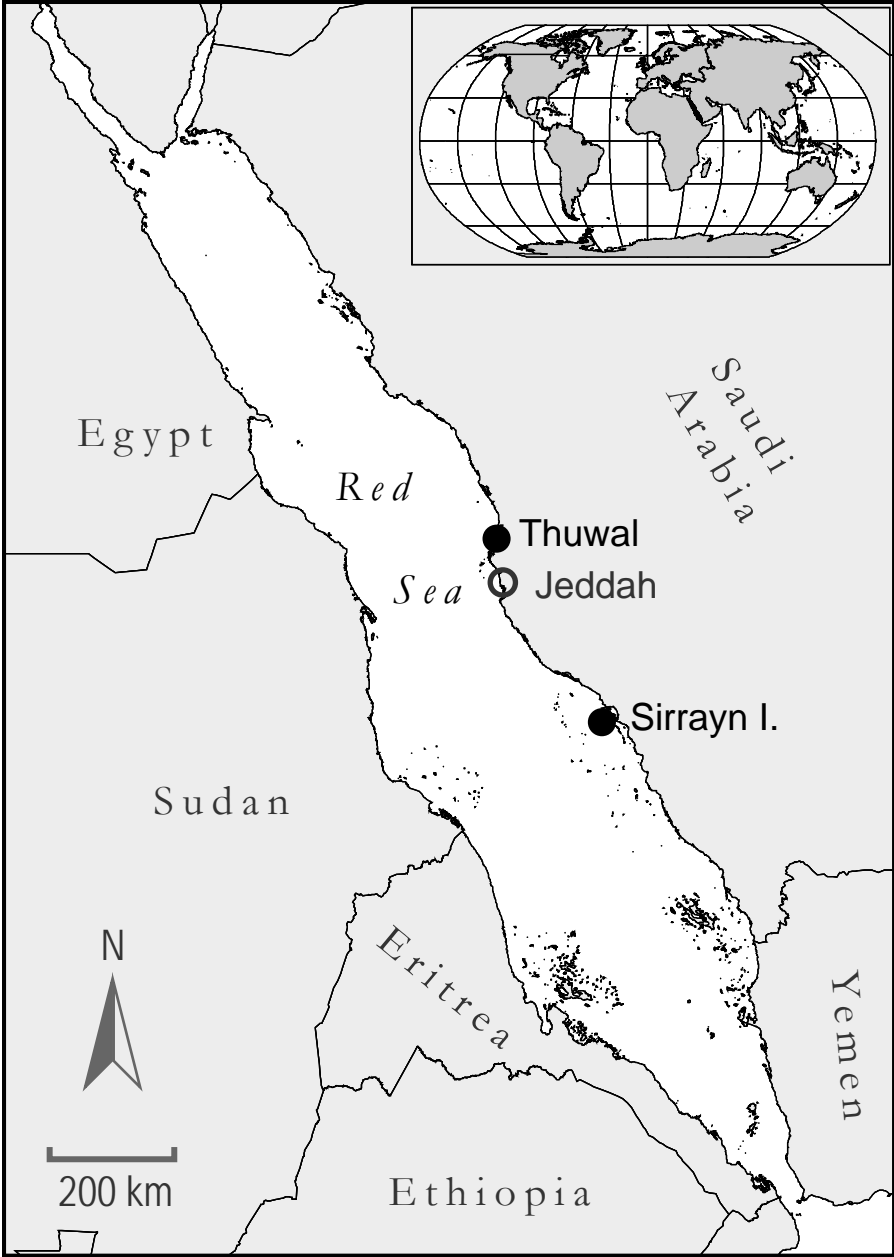


Fig. 2 - Borsa et al.

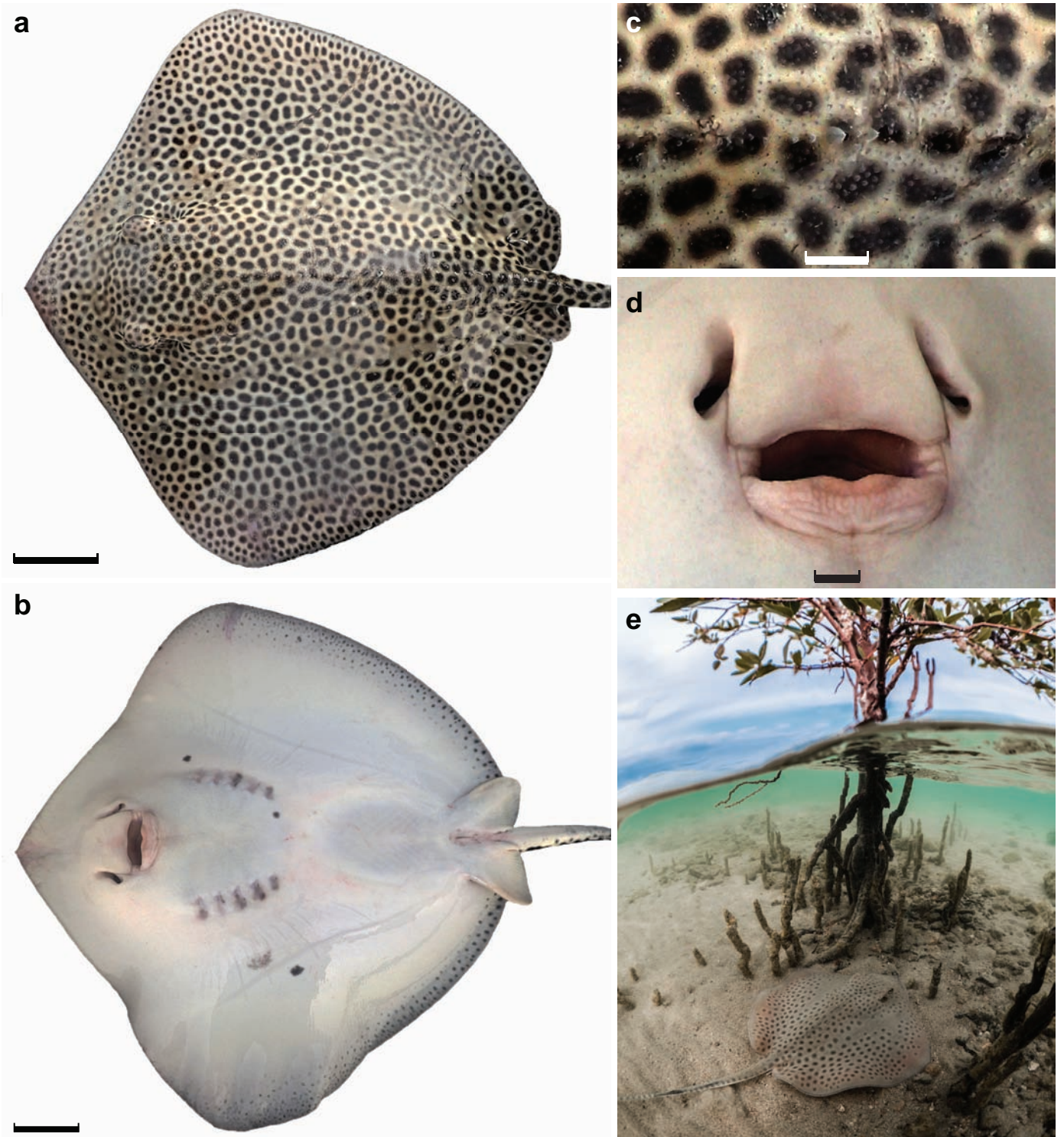
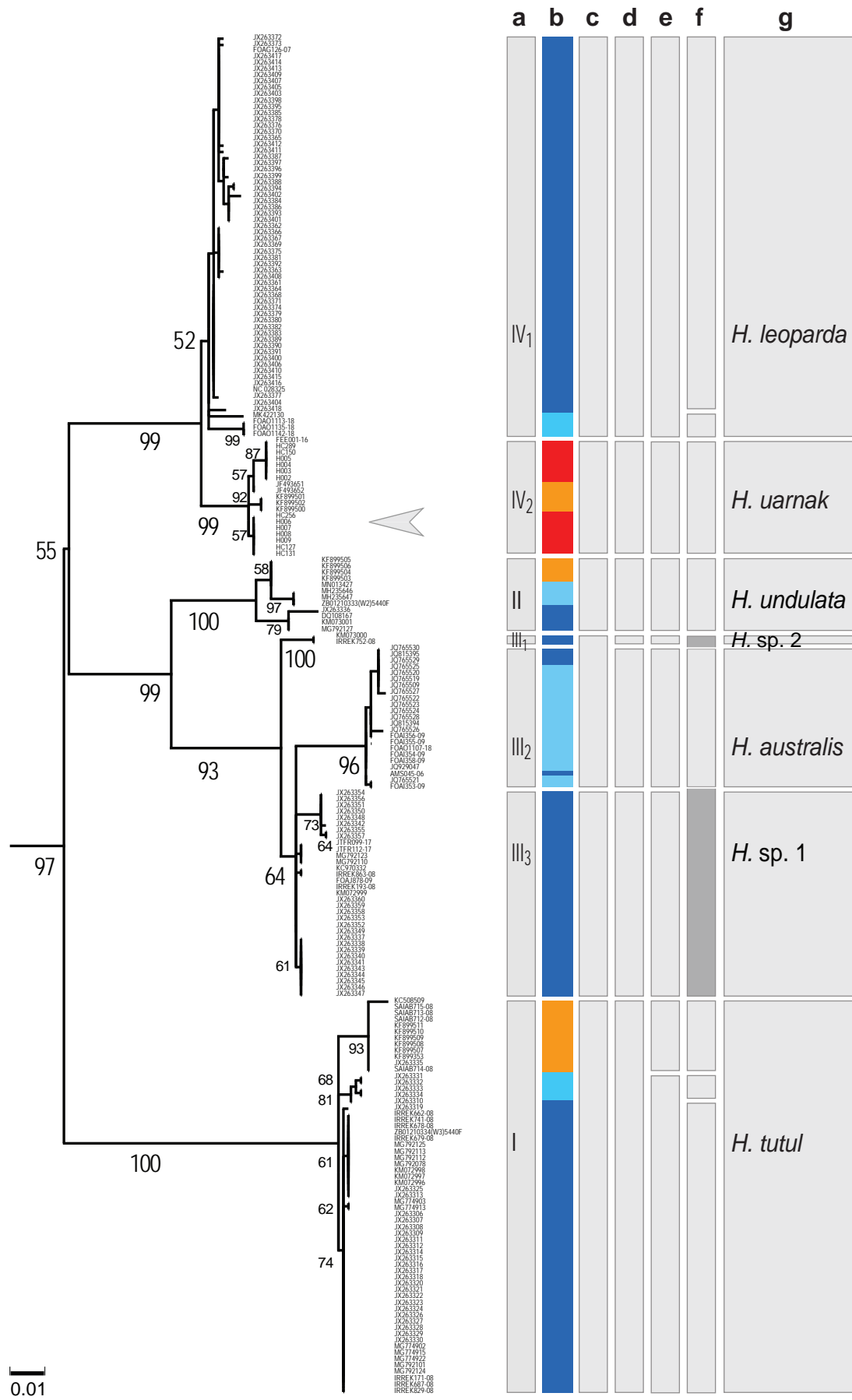


Fig. 3 - Borsa et al.



Supplementary Table S1 Sampling details for reticulate whipray *Himantura uarnak* specimens from the Red Sea including specimen no. KAUST-RSRC-H006 / CAS-ICH 247241 chosen as neotype (highlighted red)

Specimen ID	Location	Date	Approximate depth	Collector	Method of capture	Sex	No.	Total length (cm)	Disk width (cm)	Snout-to-cloaca length (cm)
H001	Sirrayn south	14 Feb. 2019	15 cm	AJM, CTW	15-m seine net	F	1	113.2	31.9	23.8
H002	Sirrayn south	14 Feb. 2019	15 cm	AJM, CTW	15-m seine net	F	1	121.8	34.6	26.5
H003	Sirrayn south	14 Feb. 2019	15 cm	AJM, CTW	15-m seine net	M	na	103.2	28.4	22.8
H004	Sirrayn south	14 Feb. 2019	15 cm	AJM, CTW	15-m seine net	F	1	120.2	32.6	25.0
H005	Sirrayn south	15 Feb. 2019	20 cm	AJM, CTW	15-m seine net	M	1	100.2	31.7	24.7
H006	KAUST north beach	25 Apr. 2019	50 cm	AJM, CTW	15-m seine net	M	1	109.9	36.9	28.9
H007	Jeddah fish market	29 Apr. 2019	na	AJM, CTW	Chunk of pectoral fin purchased	na	na	na	na	na
H008	KAUST north beach	22 May 2019	20 cm	AJM, CTW	Handline baited with shrimp	M	1	103.4	27.2	22.1
H009	KAUST harbor	Dec. 2016	na	M. Tietbohl	15-m seine net	F	2	na	53.1	na
HC127	KAUST pier	01 Feb. 2019	39 cm	AJM, CTW	15-m seine net	F	na	102.0	27.8	29.0
HC131	KAUST pier	23 Mar. 2019	30 cm	AJM, CTW	Dip net	F	2	113.4	31.0	24.6
HC150	KAUST north beach	30 Apr. 2019	10 cm	AJM, CTW	15-m seine net	F	1	96.7	28.8	23.2
HC256	KAUST north beach	25 Apr. 2019	80 cm	AJM, CTW	15-m seine net	M	1	197.0	74.8	54.8
HC289	KAUST pier	01 Feb. 2019	74 cm	AJM, CTW	15-m seine net	F	2	184.0	58.0	48.0

Supplementary Table S2 Reticulate whipray *Himantura uarnak* species complex. List of nucleotide sequences at the CO1 locus used for the present work, with GenBank and BOLD identification nos. and other details including sampling locations and references. Sequences were retrieved on 23 March 2020 from the GenBank and BOLD public databases ($N = 201$) or donated by X. Chen (Wenzhou Medical College, China) ($N = 2$) or produced through the present survey ($N = 13$). Sequences are arranged by species and presented in alphabetical order. Type material highlighted red

GenBank no.	BOLD no.	Other identifier	Initial identification	Sampling locality	Reference	BIN	Species*
<i>H. australis</i>							
JQ765509	GBGC11930-13	FCP-HUNR08	<i>H. astra</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765519	GBGC11920-13	FCP-HUNR22	<i>H. leoparda</i>	Ranger Bay, Ningaloo, 21°54'S 113°59'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765520	GBGC11919-13	FCP-HUNR23	<i>H. leoparda</i>	Ranger Bay, Ningaloo, 21°54'S 113°59'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765521	GBGC11918-13	FCP-HUNR25	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765522	GBGC11917-13	FCP-HUNR26	<i>H. uarnak</i>	Mangrove Bay, Ningaloo Marine Park, -21.97 113.93	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765523	GBGC11916-13	FCP-HUNR27	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765524	GBGC11915-13	FCP-HUNR28	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765525	GBGC11914-13	FCP-HUNR29	<i>H. uarnak</i>	Point Cloates, Ningaloo, 22°42'S 113°40'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765526	GBGC11913-13	FCP-HUNR30	<i>H. uarnak</i>	Point Cloates, Ningaloo, 22°42'S 113°40'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765527	GBGC11912-13	FCP-HUNR31	<i>H. uarnak</i>	Stanley's Pool, Ningaloo, 22°59'S 113°48'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765528	GBGC11911-13	FCP-HUNR32	<i>H. uarnak</i>	Mangrove Bay, Ningaloo Marine Park, -21.97 113.93	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765529	GBGC11910-13	FCP-HUNT34	<i>H. uarnak</i>	Shoal Bay, NT, 12°21'S 131°01'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ765530	GBGC11909-13	FCP-HUNT35	<i>H. uarnak</i>	Shoal Bay, NT, 12°21'S 131°01'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ815394	GBGC11830-13	isolate 24	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ815395	GBGC11829-13	isolate 36	<i>H. uarnak</i>	Meckets Creek, NT, 12°20'S 130°57'E	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
JQ929047	GBGC11827-13	isolate 21	<i>H. leoparda</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Cerutti-Pereyra et al. 2012	BOLD:ABZ0063	<i>H. australis</i>
-	AMS045-06	AMS I.39533-003	<i>H. uarnak</i>	Cairns area, Queensland, -16.92 145.77	McGrouther 2020	BOLD:ABZ0063	<i>H. australis</i>
-	FOAI353-09	BW-A6280, GT 4012 #2	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Appleyard 2020	BOLD:ABZ0063	<i>H. australis</i>
-	FOAI354-09	BW-A6281, GT 4013 #21	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Appleyard 2020	BOLD:ABZ0063	<i>H. australis</i>
-	FOAI355-09	BW-A6282, GT 4014 #55	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Appleyard 2020	BOLD:ABZ0063	<i>H. australis</i>
-	FOAI356-09	BW-A6283, GT 4015 #60	<i>H. uarnak</i>	Skeleton Bay, Coral Bay, -23.12 113.77	Appleyard 2020	BOLD:ABZ0063	<i>H. australis</i>
-	FOAI358-09	BW-A6285, GT 4017 #40	<i>H. uarnak</i>	Mangrove Bay, Ningaloo Marine Park, -21.97 113.93	Appleyard 2020	BOLD:ABZ0063	<i>H. australis</i>
-	FOAO1107-18	BW-A14305, GT 10444	<i>H. australis</i>	Western Australia, -19.35 118.12	Appleyard 2020	BOLD:ABZ0063	<i>H. australis</i>
<i>H. leoparda</i>							
JX263361	GBGC12896-13	IR003	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263362	GBGC12895-13	IR004	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263363	GBGC12894-13	IR008	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263364	GBGC12893-13	IR009	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263365	GBGC12892-13	IR010	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263366	GBGC12891-13	IR011	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263367	GBGC12890-13	IR012	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263368	GBGC12889-13	IR013	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>
JX263369	GBGC12888-13	IR014	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830	<i>H. leoparda</i>

JX263370	GBGC12887-13	IR015	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263371	GBGC12886-13	IR016	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263372	GBGC12885-13	IR017	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263373	GBGC12884-13	IR018	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263374	GBGC12883-13	IR019	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263375	GBGC12882-13	IR020	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263376	GBGC12881-13	IR021	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263377	GBGC12880-13	IR022	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263378	GBGC12879-13	IR023	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263379	GBGC12878-13	IR025	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263380	GBGC12877-13	IR027	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263381	GBGC12876-13	IR028	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263382	GBGC12875-13	IR030	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263383	GBGC12874-13	IR031	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263384	GBGC12873-13	IR032	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263385	GBGC12872-13	IR033	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263386	GBGC12871-13	IR034	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263387	GBGC12870-13	IR035	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263388	GBGC12869-13	IR036	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263389	GBGC12868-13	IR039	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263390	GBGC12867-13	IR040	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263391	GBGC12866-13	IR041	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263392	GBGC12865-13	IR042	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263393	GBGC12864-13	IR046	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263394	GBGC12863-13	IR048	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263395	GBGC12862-13	IR050	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263396	GBGC12861-13	IR051	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263397	GBGC12860-13	IR053	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263398	GBGC12859-13	IR054	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263399	GBGC12858-13	IR057	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263400	GBGC12857-13	IR058	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263401	GBGC12856-13	IR059	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263402	GBGC12855-13	IR060	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263403	GBGC12854-13	IR061	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263404	GBGC12853-13	IR062	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263405	GBGC12852-13	IR063	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263406	GBGC12851-13	IR064	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263407	GBGC12850-13	IR065	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263408	GBGC12849-13	IR066	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263409	GBGC12848-13	IR067	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>

JX263410	GBGC12847-13	IR069	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263411	GBGC12846-13	IR070	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263412	GBGC12845-13	IR071	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263413	GBGC12844-13	IR072	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263414	GBGC12843-13	IR074	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263415	GBGC12842-13	IR075	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263416	GBGC12841-13	IR077	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263417	GBGC12840-13	IR078	<i>H. leoparda</i>	Batang	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
JX263418	GBGC12839-13	IR087	<i>H. leoparda</i>	Sunda	Arlyza et al. 2013	BOLD:AAB7830 <i>H. leoparda</i>
MK422130	-	CR03J	<i>H. leoparda</i>	India	Ravi et al. 2019	- <i>H. leoparda</i>
NC_028325	-	wjc329	<i>H. leoparda</i>	Taiwan	Shen et al. 2016	- <i>H. leoparda</i>
-	FOAG126-07	BW-A4003, TWG-58	<i>H. undulata</i>	Tashi fish market, Taiwan	Appleyard 2020	BOLD:AAB7830 <i>H. leoparda</i>
-	FOAO1113-18	BW-A14311	<i>H. leoparda</i>	Western Australia, -19.605 117.292	Appleyard 2017	BOLD:AAB7830 <i>H. leoparda</i>
-	FOAO1135-18	BW-A14335	<i>H. leoparda</i>	Western Australia, -19.724 116.499	Appleyard 2017	BOLD:AAB7830 <i>H. leoparda</i>
-	FOAO1142-18	BW-A14342	<i>H. leoparda</i>	Western Australia, -19.968 116.031	Appleyard 2017	BOLD:AAB7830 <i>H. leoparda</i>
<i>Himantura</i> sp. 1						
JX263337	GBGC12920-13	IR089	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263338	GBGC12919-13	IR090	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263339	GBGC12918-13	IR091	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263340	GBGC12917-13	IR092	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263341	GBGC12916-13	IR093	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263342	GBGC12915-13	IR094	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263343	GBGC12914-13	IR095	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263344	GBGC12913-13	IR096	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263345	GBGC12912-13	IR097	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263346	GBGC12911-13	IR098	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263347	GBGC12910-13	IR099	<i>H. uarnak</i>	Makassar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263348	GBGC12909-13	IR100	<i>H. uarnak</i>	Selayar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263349	GBGC12908-13	IR101	<i>H. uarnak</i>	Selayar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263350	GBGC12907-13	MZB-20875, LIP1 4419, IR102	<i>H. uarnak</i>	Selayar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263351	GBGC12906-13	IR103	<i>H. uarnak</i>	Selayar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263352	GBGC12905-13	IR104	<i>H. uarnak</i>	Selayar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263353	GBGC12904-13	IR105	<i>H. uarnak</i>	Selayar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263354	GBGC12903-13	IR106	<i>H. uarnak</i>	Selayar	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263355	GBGC12902-13	IR107	<i>H. uarnak</i>	Kendari	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263356	GBGC12901-13	IR108	<i>H. uarnak</i>	Kendari	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263357	GBGC12900-13	IR109	<i>H. uarnak</i>	Kendari	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263358	GBGC12899-13	IR110	<i>H. uarnak</i>	Labuan Bajo	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263359	GBGC12898-13	IR111	<i>H. uarnak</i>	Labuan Bajo	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1
JX263360	GBGC12897-13	wjc637	<i>H. uarnak</i>	Taiwan	Arlyza et al. 2013	BOLD:AAB7832 <i>Himantura</i> sp. 1

KC970332	BFPHL067-13	DFBOC I	<i>H. uarnak</i>	Philippines	Santos et al. 2014	BOLD:AAB7832	<i>Himantura</i> sp. 1
KM072999	ANGBF12762-15	HUAR3	<i>H. uarnak</i>	Semporna, Malaysia	Lim et al. 2015	BOLD:AAB7832	<i>Himantura</i> sp. 1
MG792110	ANGBF48003-19	-	<i>H. uarnak</i>	Sandakan, Sabah, 5.84N 118.12E	Mohd Arshaad & Jamaludin 2018	BOLD:AAB7832	<i>Himantura</i> sp. 1
MG792123	ANGBF48002-19	-	<i>H. uarnak</i>	Sandakan, Sabah, 5.84N 118.12E	Mohd Arshaad & Jamaludin 2018	BOLD:AAB7832	<i>Himantura</i> sp. 1
-	FOAJ878-09	BW-A7728, IN01396	<i>H. uarnak</i>	Tanjung Luar, Lombok, 8.75S 116.58E	Appleyard 2020	BOLD:AAB7832	<i>Himantura</i> sp. 1
-	IRREK193-08	GN2238, JPAG 036	<i>H. uarnak</i>	Bacolod City, Philippines	Hanner 2020	BOLD:AAB7832	<i>Himantura</i> sp. 1
-	IRREK863-08	GN3119, BO-82	<i>H. uarnak</i> i	Sarawak, Malaysia	Hanner 2020	BOLD:AAB7832	<i>Himantura</i> sp. 1
-	JTFR099-17	PSK11	<i>H. uarnak</i>	Sandakan, Sabah, 5.84N 118.12E	Mohd Arshaad 2020	BOLD:AAB7832	<i>Himantura</i> sp. 1
-	JTFR112-17	PSK26	<i>H. uarnak</i>	Sandakan, Sabah, 5.84N 118.12E	Mohd Arshaad 2020	BOLD:AAB7832	<i>Himantura</i> sp. 1
<i>Himantura</i> sp. 2							
KM073000	ANGBF12763-15	HUAR 1	<i>H. uarnak</i>	Sandakan, Sabah	Lim et al. 2015	BOLD:ACV9539	<i>Himantura</i> sp. 2
-	IRREK752-08	GN3006, HBO-109	<i>H. uarnak</i> ii	Lahad Datu, Sabah	Hanner 2020	BOLD:ACV9539	<i>Himantura</i> sp. 2
<i>H. tutul</i>							
JX263306	GBGC12950-13	IR001	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263307	GBGC12949-13	IR002	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263308	GBGC12948-13	IR005	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263309	GBGC12947-13	IR006	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263310	GBGC12946-13	IR024	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263311	GBGC12945-13	IR026	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263312	GBGC12944-13	IR029	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263313	GBGC12943-13	IR037	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263314	GBGC12942-13	IR043	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263315	GBGC12941-13	IR044	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263316	GBGC12940-13	IR045	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263317	GBGC12939-13	IR047	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263318	GBGC12938-13	IR049	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263319	GBGC12937-13	IR052	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263320	GBGC12936-13	IR055	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263321	GBGC12935-13	IR056	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263322	GBGC12934-13	IR073	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263323	GBGC12933-13	IR076	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263324	GBGC12932-13	IR079	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263325	GBGC12931-13	IR080	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263326	GBGC12930-13	IR081	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263327	GBGC12929-13	IR082	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263328	GBGC12928-13	IR083	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263329	GBGC12927-13	IR084	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263330	GBGC12926-13	IR085	<i>H. tutul</i>	Batang	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263331	GBGC12925-13	IR086	<i>H. tutul</i>	Sunda	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>
JX263332	GBGC12924-13	IR088	<i>H. tutul</i>	Sunda	Arlyza et al. 2013; Borsa et al. 2013	BOLD:AAB7831	<i>H. tutul</i>

JX263333	GBGC12923-13	IR112	<i>H. tutul</i>	Bali	Arlyza et al. 2013; Borsa et al. 2013 BOLD:AAB7831	<i>H. tutul</i>
JX263334	GBGC12922-13	IR113	<i>H. tutul</i>	Southern central Java	Arlyza et al. 2013; Borsa et al. 2013 BOLD:AAB7831	<i>H. tutul</i>
JX263335	GBGC12832-13	MNHN:ICTI5184 (HOLOTYPE)	<i>H. tutul</i>	Mkoani, Tanzania	Arlyza et al. 2013; Borsa et al. 2013 BOLD:AAB7831	<i>H. tutul</i>
KC508509	GBGC11390-13	CASMBAUTRL16	<i>Urogymnus asperrimus</i>	-	Priyanga et al. 2013	BOLD:AAB7831 <i>H. tutul</i>
KF899353	ANGBF10976-15	NBFGR:CHN:HL49	<i>H. leoparda</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAB7831 <i>H. tutul</i>
KF899507	ANGBF11561-15	NBFGR:CHN:K42	<i>H. uarnak</i>	Kochi, India	Bineesh et al. 2017	BOLD:AAB7831 <i>H. tutul</i>
KF899508	ANGBF11560-15	NBFGR:CHN:K43	<i>H. uarnak</i>	Kochi, India	Bineesh et al. 2017	BOLD:AAB7831 <i>H. tutul</i>
KF899509	ANGBF11559-15	NBFGR:CHN:204	<i>H. uarnak</i>	Kochi, India	Bineesh et al. 2017	BOLD:AAB7831 <i>H. tutul</i>
KF899510	ANGBF11558-15	NBFGR:CHN:K44	<i>H. uarnak</i>	Kochi, India	Bineesh et al. 2017	BOLD:AAB7831 <i>H. tutul</i>
KF899511	ANGBF11557-15	NBFGR:CHN:BM42	<i>H. uarnak</i>	Kochi, India	Bineesh et al. 2017	BOLD:AAB7831 <i>H. tutul</i>
KM072996	ANGBF12752-15	HLEO2	<i>H. leoparda</i>	Sandakan, Malaysia	Lim et al. 2015	BOLD:AAB7831 <i>H. tutul</i>
KM072997	ANGBF12753-15	HLEO1	<i>H. leoparda</i>	Sandakan, Malaysia	Lim et al. 2015	BOLD:AAB7831 <i>H. tutul</i>
KM072998	ANGBF12754-15	HLEO3	<i>H. leoparda</i>	Sandakan, Malaysia	Lim et al. 2015	BOLD:AAB7831 <i>H. tutul</i>
MG774902	JTFR010-17	PDGN04	<i>H. leoparda</i>	Dungun, Malaysia, 4.77 N 103.25 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG774903	JTFR011-17	PDGN05	<i>H. leoparda</i>	Dungun, Malaysia, 4.77 N 103.25 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG774913	JTFR021-17	PKTN102	<i>H. leoparda</i>	Kuantan, Malaysia, 3.47 N 103.19 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG774915	JTFR023-17	PKTN18	<i>H. leoparda</i>	Kuantan, Malaysia, 3.47 N 103.19 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG774922	JTFR030-17	PKTN35	<i>H. leoparda</i>	Kuantan, Malaysia, 3.47 N 103.19 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG792078	ANGBF47998-19, JTFR056-17	PMKH19	<i>H. leoparda</i>	Malaysia, 2.54 N 112.05 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG792101	ANGBF47999-19, JTFR090-17	PSK01	<i>H. leoparda</i>	Sandakan, Malaysia, 5.84 N 118.12 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG792112	ANGBF47994-19, JTFR101-17	PSK14	<i>H. leoparda</i>	Sandakan, Malaysia, 5.84 N 118.12 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG792113	ANGBF47995-19, JTFR102-17	PSK15	<i>H. leoparda</i>	Sandakan, Malaysia, 5.84 N 118.12 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG792124	ANGBF47996-19, JTFR113-17	PSK27	<i>H. leoparda</i>	Sandakan, Malaysia, 5.84 N 118.12 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
MG792125	ANGBF47997-19, JTFR114-17	PSK28	<i>H. leoparda</i>	Sandakan, Malaysia, 5.84 N 118.12 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAB7831 <i>H. tutul</i>
-	IRREK171-08	GN2207	<i>Himantura</i> sp.	Singapore	Hanner 2020	BOLD:AAB7831 <i>H. tutul</i>
-	IRREK662-08	GN2916, BOD-49	<i>H. uarnak</i> iii	Malaysia	Hanner 2020	BOLD:AAB7831 <i>H. tutul</i>
-	IRREK678-08	GN2932, BOD-65	<i>H. uarnak</i> ii	Malaysia	Hanner 2020	BOLD:AAB7831 <i>H. tutul</i>
-	IRREK679-08	GN2933, BOD-66	<i>H. uarnak</i> iii	Malaysia	Hanner 2020	BOLD:AAB7831 <i>H. tutul</i>
-	IRREK687-08	GN2941, BOD-74	<i>H. uarnak</i> iii	Malaysia	Hanner 2020	BOLD:AAB7831 <i>H. tutul</i>
-	IRREK741-08	GN2995, HBO-86	<i>H. uarnak</i> ii	Sandakan, Sabah, Malaysia	Hanner 2020	BOLD:AAB7831 <i>H. tutul</i>
-	IRREK829-08	GN3085, BO-47	<i>H. uarnak</i> i	Sarawak, Malaysia	Hanner 2020	BOLD:AAB7831 <i>H. tutul</i>
-	SAIAB712-08	80368-1, LS07-0449	<i>H. uarnak</i>	Niule Reef, Tanga, 5.08S 39.10 E	Gouws 2020	BOLD:AAB7831 <i>H. tutul</i>
-	SAIAB713-08	80368-2, LS07-0930	<i>H. uarnak</i>	Niule Reef, Tanga, 5.08S 39.10 E	Gouws 2020	BOLD:AAB7831 <i>H. tutul</i>
-	SAIAB714-08	80368-3, LS07-0934	<i>H. uarnak</i>	Niule Reef, Tanga, 5.08S 39.10 E	Gouws 2020	BOLD:AAB7831 <i>H. tutul</i>
-	SAIAB715-08	80368-4, LS07-0750	<i>H. uarnak</i>	Niule Reef, Tanga, 5.08S 39.10 E	Gouws 2020	BOLD:AAB7831 <i>H. tutul</i>
-	-	ZB01210334(W3)5440F	<i>H. tutul</i>	Thailand	X. Chen (pers. comm., 2015)	- <i>H. tutul</i>
<i>H. uarnak</i>						
JF493651	TZMSC474-05	Smith 30.10-2	<i>H. uarnak</i>	Cape Vidal 28.13 S 32.56 E	Steinke et al. 2011	BOLD:AAB7830 <i>H. uarnak</i>
JF493652	TZMSC232-05	ADC30.10-1	<i>H. uarnak</i>	Cape Vidal 28.13 S 32.56 E	Steinke et al. 2011	BOLD:AAB7830 <i>H. uarnak</i>
KF899500	ANGBF10975-15	NBFGR:CHN:PK60	<i>H. leoparda</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAB7830 <i>H. uarnak</i>

KF899501	ANGBF10974-15	NBFGR:CHN:PK61	<i>H. leoparda</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAB7830	<i>H. uarnak</i>
KF899502	ANGBF10973-15	NBFGR:CHN:PK62	<i>H. leoparda</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAB7830	<i>H. uarnak</i>
-	FEE001-16	IMSMETU-HL-01	<i>H. leoparda</i>	off Hatay, Turkey 36°11'N 35°48'E	Yucel et al. 2017	BOLD:AAB7830	<i>H. uarnak</i>
MW178184	-	H002	-	Sirrayn South	Present survey	-	<i>H. uarnak</i>
MW178185	-	H003	-	Sirrayn South	Present survey	-	<i>H. uarnak</i>
MW178186	-	H004	-	Sirrayn South	Present survey	-	<i>H. uarnak</i>
MW178187	-	H005	-	Sirrayn North	Present survey	-	<i>H. uarnak</i>
MW178188	-	CAS-ICH 247241 (NEOTYPE)	<i>H. uarnak</i>	KAUST North Beach, Thuwal, Saudi Arabia	Present survey	-	<i>H. uarnak</i>
MW178189	-	H007	-	Jeddah Fish Market	Present survey	-	<i>H. uarnak</i>
MW178190	-	H008	-	KAUST North Beach	Present survey	-	<i>H. uarnak</i>
MW178191	-	H009	-	KAUST Harbor	Present survey	-	<i>H. uarnak</i>
MW178192	-	HC127	-	KAUST Pier	Present survey	-	<i>H. uarnak</i>
MW178193	-	HC131	-	KAUST Pier	Present survey	-	<i>H. uarnak</i>
MW178194	-	HC150	-	KAUST North Beach	Present survey	-	<i>H. uarnak</i>
MW178195	-	HC256	-	KAUST North Beach	Present survey	-	<i>H. uarnak</i>
MW178196	-	HC289	-	KAUST Pier	Present survey	-	<i>H. uarnak</i>
<i>H. undulata</i>							
DQ108167	FOA221-04	BW-A221	<i>H. fava</i>	Sandakan, Malaysia	Ward et al. 2005	BOLD:AAF0692	<i>H. undulata</i>
JX263336	GBGC12921-13	IR007	<i>H. undulata</i>	Batang fish landing place, Java Sea	Arlyza et al. 2013	BOLD:AAF0692	<i>H. undulata</i>
KF899503	ANGBF11565-15	NBFGR:CHN:BM3	<i>H. undulata</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAF0692	<i>H. undulata</i>
KF899504	ANGBF11564-15	NBFGR:CHN:BM4	<i>H. undulata</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAF0692	<i>H. undulata</i>
KF899505	ANGBF11563-15	NBFGR:CHN:BM48	<i>H. undulata</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAF0692	<i>H. undulata</i>
KF899506	ANGBF11562-15	NBFGR:CHN:BM49	<i>H. undulata</i>	Mumbai, India	Bineesh et al. 2017	BOLD:AAF0692	<i>H. undulata</i>
KM073001	ANGBF12764-15	HUND1	<i>H. undulata</i>	Tawau, Malaysia	Lim et al. 2015	BOLD:AAF0692	<i>H. undulata</i>
MG792127	ANGBF48004-19	JTFR116-17, PSK31	<i>H. undulata</i>	Sandakan, Malaysia, 5.84 N 118.12 E	Mohd-Arshaad & Jamaludin 2018	BOLD:AAF0692	<i>H. undulata</i>
MH235646	-	USNM:444112	<i>H. undulata</i>	Tanintharyi, Myanmar, 12.43N 98.60E	Segura-Garcia & Yain Tun 2018	-	<i>H. undulata</i>
MH235647	-	ISGDG1	<i>H. undulata</i>	Tanintharyi, Myanmar, 12.43N 98.60E	Segura-Garcia & Yain Tun 2018	-	<i>H. undulata</i>
MN013427	GBGC15127-19	DUZM_MF_036B	<i>H. undulata</i>	Cox's Bazar, Bangladesh, 21.28N 91.25E	Ahmed et al. 2019	BOLD:AAF0692	<i>H. undulata</i>
-	-	ZB01210333(W2)5440F	<i>H. undulata</i>	Thailand	X. Chen (pers. comm., 2015)	-	<i>H. undulata</i>

* identification of individual to species based on haplotype placement in CO1 gene phylogeny

Supplementary Table S3 Morphological characters used in the diagnoses of the four *Himantura* spp. species considered valid by Last et al. (2016c, 2016b) and Weigmann (2016). *Diagnosticity*: utility of character to diagnose at least one (*One sp.*) or all four species (*All spp.*); *N*, sample size; *NA* not specified

Character	Species (<i>N</i>)				Diagnosticity	
	<i>H. australis</i> (29 ^a)	<i>H. leoparda</i> (12 ^c)	<i>H. uarnak</i> (NA)	<i>H. undulata</i> (NA)	One sp.	All spp.
Disc width (DW)	‘≥ 113 cm’ ^b	‘≥ 140 cm’ ^b	‘≤ 160 cm’ ^b	‘≥ 130 cm’ ^b	No	No
DW/disc length	‘1.00-1.10’ ^b	‘1.00-1.16’ ^c	‘1.00-1.10’ ^b	‘DW subequal to disc length’ ^b	Yes	No
Disc shape	‘Weakly rhomboidal’ ^a ‘Very broad, weakly rhombic, robust’ ^b	‘Robust, weakly rhombic’ ^b ‘Rhomboidal’ ^c	‘Broad, rhombic, robust’ ^b	‘Robust, suboval’ ^b	Yes	No
Snout shape	‘Moderately short, rather broad, with distinct apical lobe’ ^a ‘broadly triangular, tip pointed’ ^b	‘Broadly triangular (more so in young) with small apical lobe, broadly pointed’ ^b ‘With distinct apical lobe’ ^c	‘Broadly triangular, tip pointed’ ^b	‘Narrowly pointed, triangular, small pointed lobe at tip’ ^b	No	No
Snout length	‘19–22% DW’ ^a	‘Moderately long’ ^c	NA	NA	?	?
Angle at apex	‘117–127°’ ^a	‘101–120°’ ^c	NA	NA	?	No
Anterior margins	‘Straight (rather than concave)’ ^b	‘Straight or weakly concave’ ^b	‘Concave’ ^b	‘Straight to convex’ ^b	No	No
Lateral apices	‘Narrowly rounded’ ^a ‘Narrowly to broadly rounded’ ^b	‘Narrowly rounded (more angular in young)’ ^b ‘Moderately angular to narrowly rounded’ ^c	‘Weakly angular to narrowly rounded’ ^b	‘Broadly rounded’ ^b	No	No
Orbits	‘Moderately large, often strongly protruding (particularly in young)’ ^a	‘Moderately large, protruded slightly’ ^c	NA	NA	?	No
Suprascapular denticles	‘1–2, mostly heart-shaped (not preceded before and after by row of smaller primary denticles)’ ^a ‘usually with 2 small, broadly heartshaped thorns, but no other enlarged thorns extending along mid-line of disc’ ^b	‘Usually 2, broad heart-shaped thorns, preceded by row of up to 13 smaller denticles of similar shape and a row of smaller denticles posteriorly’ ^b ‘2 prominent, broad heart-shaped, 1 row of enlarged widely spaced, narrow, heart-shaped’ ^c	‘1–3 small heart-shaped thorns, but no other enlarged thorns extending along mid-line of disc and tail’ ^b	‘Large pearl thorn, followed by 2–3 slightly smaller similar thorns in adults, no other enlarged thorns extending along mid-line of disc and tail’ ^b	Yes	No
Nasal curtain	‘Skirt-shaped, broad and short, posterior margin finely fringed’ ^b	‘Skirt-shaped, broad and short, posterior margin finely fringed’ ^b	‘Broad and short, posterior margin finely fringed’ ^b	‘Skirt-shaped, broad and short, posterior margin finely fringed’ ^b	No	No
Pectoral-fin radials	‘146–152’ ^a	‘148-158’ ^c	NA	NA	?	No
Vertebral centra (incl. synarcual)	‘123 (124)’ ^a	‘117-123 (120-126)’ ^c	NA	NA	?	No
Tail shape	‘Narrow-based and subcircular in cross-section, tapering evenly toward sting’ ^b	‘Narrow-based, suboval in cross-section, tapering evenly toward caudal sting’ ^b	‘Narrow-based, subcircular in cross-section, tapering evenly toward sting’ ^b	‘Narrow-based, suboval in cross-section, tapering evenly toward caudal sting’ ^b	No	No
Tail squamation	‘Small prickly denticles beyond caudal sting’ ^b	NA. Note: holotype lacks tail	‘Small sharp thorns beyond caudal sting’ ^b	NA	?	?
Caudal sting(s)	‘Usually one’ ^b	‘Usually one’ ^b	‘Usually one’ ^b	‘Usually one’ ^b	No	No

^a From Last et al. (2016c); ^b from Last et al. (2016b); ^c from Manjaji-Matsumoto and Last (2008)