

FIRST RECORD OF *MEGANTHIAS NATALENSIS* (ACTINOPTERYGII: SERRANIDAE: ANTHIADINAE) FROM THE SOCOTRA ARCHIPELAGO (NORTH-WESTERN INDIAN OCEAN), WITH NOTES ON *ODONTANTHIAS* AND *SACURA*

Uwe ZAJONZ^{*1}, Sergey V. BOGORODSKY^{1,2}, and Benjamin C. VICTOR³

¹ *Senckenberg Research Institute and Museum of Nature (SMF), Section Ichthyology and Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Biogeography, Frankfurt am Main, Germany*

² *Station of Naturalists, Omsk, Russia*

³ *Ocean Science Foundation, Glenwood, Irvine, California, USA and Guy Harvey Research Institute, Nova Southeastern University, Dania Beach, Florida, USA*

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Abstract. The anthiadine fish *Meganthias natalensis* (Fowler, 1925) is reported for the first time from the Socotra Archipelago based on a single female specimen of 27.5 cm standard length taken by hook-and-line off Abd al-Kuri Island at a depth of 100–120 m. The voucher specimen represents a substantial northern extension of the distributional range for the species and the first record for the Arabian region. A description of the specimen is provided and the distribution of the species in the Western Indian Ocean is summarized. The mitochondrial COI sequence matched vouchered *Meganthias natalensis* sequences from South Africa, confirming the species identification. A phenetic tree of COI sequences of available species of the genera *Meganthias*, *Odontanthias*, and *Sacura* is presented. It shows that the species form well-separated monophyletic lineages and the tree implies that the nominal genera *Odontanthias* and *Sacura* are paraphyletic and in need of a comprehensive phylogenetic analysis.

Keywords: taxonomy, biogeography, phenetic tree, Arabian Sea, Perciformes

INTRODUCTION

The family Serranidae is a large and diverse group of percoid fishes widespread in tropical and temperate seas. The majority of serranid species inhabit shallow waters but some species can be found in deeper waters, down to about 400–500 m depth. Anderson (2018) presented a revised checklist of the valid species of the subfamily Anthiadinae. Parenti and Randall (2020) subsequently published an annotated checklist of the Serranidae, dividing it into three subfamilies: Anthiadinae, Epinephelinae, and Serraninae, considering 231 species in 29 genera. Given four additional species described as new to science since then, the Anthiadinae presently includes 235 species in 29 genera of small- to medium-sized fishes that are found throughout the tropical and temperate Atlantic and Indo-Pacific Oceans, usually on coral reefs or in association with rocky bottoms. These fishes are usually brightly colored, predominantly red.

The species of the family Serranidae in the Arabian region have been critically reviewed by Manilo and Bogorodsky (2003) and Golani and Fricke (2018). Based

on long-term studies, including literature and extensive surveys, Zajonz et al. (2019) documented 682 bony fish species on the Socotra Archipelago and a working list of additional 51 ODU (Operational Diversity Units; see Zajonz et al. 2019, p. 104, Annex 2). Their account included six anthiadine species, five of *Pseudanthias* Bleeker, 1871, and one of *Plectranthias* Bleeker, 1873. Subsequently, during fieldwork in 2019, a single anthiadine fish was taken by hook-and-line from the Socotra Archipelago off the north-western part of Abd al-Kuri Island at a depth of 100–120 m. The specimen was identified as a species of *Meganthias*, a new genus described by Randall and Heemstra (2006) for two species: *Meganthias natalensis* (Fowler, 1925) as the type species (originally *Sacura natalensis*), from the western Indian Ocean, and *Meganthias kingyo* (Kon, Yoshino et Sakurai, 2000) (originally *Holanthias kingyo* from the Ryukyu Islands, Japan, and the Philippines. Two additional species have since been added to the genus: *Meganthias carpenteri* Anderson, 2006 described from

* Correspondence: Dipl.-Biol. Uwe Zajonz, Forschungsinstitut und Naturmuseum Senckenberg, Marine Zoologie, Ichthyologie, Senckenberganlage 25, 60325 Frankfurt am Main, Germany, email: (UZ) uzajonz@senckenberg.de, eco-coasts@web.de, (SVB) ic187196@yandex.ru, (BCV) ben@coralreeffish.com.

the eastern Atlantic Ocean off Nigeria and *Meganthias filiferus* Randall et Heemstra, 2008 from the Arabian Sea off south-western coast of India and the Andaman Sea off the south-western coast of Thailand. Members of the genus are medium-sized fishes, reaching about 20–40 cm standard length, living solitary in moderately deep waters in association with hard substrata. They are notably rare in collections. The Socotra specimen fits the morphology and coloration described for *M. natalensis*. Its mtDNA sequence was compared with sequences of this and related anthiadine species from available databases and matched to vouchered *M. natalensis* sequences.

MATERIALS AND METHODS

The *Meganthias* specimen was collected during fieldwork on the Socotra Archipelago conducted from 21 March 2019 to 23 April 2019 for the project ‘Support to the Integrated Programme for the Conservation and Sustainable Development of the Socotra Archipelago, Yemen’, co-executed by the Senckenberg Biodiversity and Climate Research Centre (SBiK-F) and the Environment Protection Authority of Yemen (EPA) for the United Nations Environment Programme (UNEP), funded by the Global Environment Facility (GEF #5347). The Yemen EPA issued the research and export permit. A tissue sample was obtained when fresh and the specimen was subsequently preserved in 5% formalin and examined by the authors at the Senckenberg Field Research Station and the project center in Hadibo, Socotra. The specimen could not yet be sent to or cataloged at the Senckenberg Research Institute and Museum of Nature, Frankfurt am Main, Germany (SMF) due to the severe logistical constraints posed by the war in Yemen and the global SARS Cov-2/Covid-19 pandemic.

Methods of counts and measurements follow Randall and Heemstra (2006). Standard length (SL) is measured from the median tip of the upper lip to the base of the caudal fin (end of hypural plate). Proportional measurements are rounded to the nearest 0.1. References and genus and species classification follow Eschmeyer’s Catalogue of Fishes (Fricke 2020, Fricke et al. 2020, Van der Laan et al. 2020).

The DNA sequence of a 652-bp segment of the mitochondrial cytochrome c oxidase (COI) gene (the “barcode” marker) was obtained for the Socotra specimen and compared to sequences for anthiadine relatives available on the BOLD database (www.boldsystems.org), including those on GenBank. The DNA procedure used a variety of primers (Ivanova et al. 2007). DNA extractions were performed with the NucleoSpin96 (Machery-Nagel) kit under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. PCR amplifications were performed in 12.5 μ L volume including 6.25 μ L of 10% trehalose, 2 μ L of ultra-pure water, 1.25 μ L of 10 \times PCR buffer (10 mM KCl, 10 mM (NH₄)₂SO₄, 20 mM Tris-HCl (pH 8.8), 2 mM MgSO₄, 0.1% Triton X-100), 0.625 μ L of MgCl₂ (50 mM), 0.125 μ L of each primer (0.01 mM), 0.0625 μ L of each dNTP (10 mM), 0.0625 μ L of Taq DNA polymerase (New England Biolabs), and 2 μ L of template DNA. The PCR conditions consisted of 94°C for 2 min, 35 cycles

of 94°C for 30 sec, 52°C for 40 sec, and 72°C for 1 min, with a final extension at 72°C for 10 min. Sequences were compiled and analyzed using the Barcode of Life Data Systems (Ratnasingham and Hebert 2007, Ward et al. 2009) and the Kimura 2-parameter (K2P) model used by BOLD generated a mid-point rooted neighbor-joining (NJ) phenogram to provide a graphic representation of the species’ sequence divergences.

RESULTS

Family SERRANIDAE

Subfamily ANTHIADINAE

Meganthias natalensis (Fowler, 1925)

Gorgeous swallowtail

Fig. 1, Table 1

Sacura natalensis Fowler, 1925; Fowler 1925: 226; holotype: ANSP 93154; type locality: KwaZulu-Natal, South Africa.

Material examined. SMF uncatalogued [tissue sample ID SOC19-319], female, 27.5 cm SL, Socotra Archipelago, Abd al-Kuri Island, 100–120 m depth, 25 March 2019.

Specimen description. (based on 27.5 cm Socotra female) Dorsal-fin spines and rays X,18; anal-fin spines and rays III,8; dorsal- and anal-fin rays branched, last to base; pectoral-fin rays 17, upper two unbranched; pelvic-fin spine and rays I,5; lateral line arched, becoming straight on caudal peduncle; lateral-line scales 50/49; scales between middle of spinous portion of dorsal fin and lateral line 3; scales between anal-fin origin and lateral line 18; gill rakers 12 + 27. Body deep and compressed, depth 2.1 in SL, width 2.5 in body depth; head moderately large, 2.8 in SL; orbit diameter 4.5 in head length; snout very short, 5.3 in head length; interorbital space slightly convex, least width 3.0 in head length; depth of caudal peduncle 2.8 in head length; length of caudal peduncle 2.1 in head length. Mouth moderately large, distinctly oblique, maxilla reaching to below center of pupil, lower jaw projecting; nostrils before middle of eye, posterior nostril slightly oval opening, close to margin of orbit, anterior nostril ventroanterior to posterior nostril; upper and lower jaws with bands of villiform teeth, small conical teeth in outer row on anterior half of each jaw, and small canine teeth in front of jaws; vomer with chevron-shaped patch of villiform teeth; palatines with slender, slightly curved band of villiform teeth. Opercle with three flat spines, middle spine much closer to lower than to upper spine; posterior margin of preopercle finely serrate, without spine at angle; corner of preopercle somewhat angular, ventral edge finely serrate; margin of subopercle with minute serrae. Scales ctenoid, small accessory scales present on body, more dense on head and nape; scales dorsally on snout reaching upper lip; preorbital, suborbital and jaws covered with very small scales; small scales at base of posterior four dorsal-fin spines, soft portion of fin with broad band of scales on about basal fourth of fin, progressively smaller distally; soft portion of anal fin with small scales basally. Dorsal-fin origin slightly behind vertical through posterior preopercular margin, predorsal length 3.0 in SL, third spine only slightly longer

than remaining spines, its length 2.8 in head length; third dorsal-fin ray longest, but not filamentous, its length 3.5 in SL; anal-fin origin below second dorsal-fin soft ray, third spine longest, its length 3.0 in head length; soft portion of anal fin rounded posteriorly, fourth to sixth rays longest; caudal fin lunate with slightly elongate lobes, length of fin 2.1 in SL; pectoral fin just reaching to above anus, its length 1.2 in head length, tenth ray longest; pelvic fins not reaching anus, length of fin 1.3 in head length.

Coloration: Head and body deep pink, shading to whitish ventrally, with series of irregular yellow spots subequal to orbit diameter just above opercle; head with short, interrupted, yellow stripe behind orbit, yellow posterior preopercular margin, curved yellow band between eye and maxilla, and yellow stripe along ventral margin of lower lip; spinous portion of dorsal fin mostly yellowish, anterior five soft rays yellowish distally; anal fin pinkish basally, with yellowish spinous portion and outer half of soft portion; caudal fin orange-yellow with pinkish hue on middle rays; pectoral fins yellow, seventh to twelfth rays dark brown distally; spine and outer rays of pelvic fins yellow, inner rays whitish.

Distribution. Reported from the western Indian Ocean with records only from the Socotra Archipelago, Kenya, Mauritius, Reunion, Seychelles, Madagascar, Mozambique, and South Africa (Fig. 2) (Randall and Heemstra 2006, Schneider and Janke 2013, Fricke et al. 2018, presently reported study).

DISCUSSION

The Socotra specimen largely matches the description of *M. natalensis* given by Randall and Heemstra (2006) and the mtDNA COI sequence of the specimen matches sequences of *M. natalensis* from the type location in South Africa (Fig. 3). *Meganthias natalensis* is described as having a moderately deep and compressed body, its depth 2.0–2.2 in SL; scales ctenoid, with small accessory scales present on head and body; moderately large mouth, with maxilla distinctly oblique; posterior margin of preopercle finely serrate, without a spine at an angle, preopercular corner rounded; opercle with three flat spines, middle spine much closer to the lower than to the upper spine; first to fifth soft dorsal-fin rays prolonged, greatly elongate in males; caudal fin distinctly lunate, upper and lower lobes greatly prolonged in large adults; dorsal-fin spines and rays X, 17–19; anal-fin spines and rays III, 8–9; lateral-line scales 43–51; gill rakers 11–13 + 24–28. The largest specimen was collected off Kenya and measured approximately 40 cm SL (Schneider and Janke 2013).

The female Socotra specimen essentially fits that description, differing only by a shorter snout (5.3 in SL vs. 3.3–4.1 in SL) and a slightly angular (vs. rounded) preopercular corner. Anderson (2006) discussed sexual dimorphism in *Meganthias carpenteri*, noting that the second to fifth dorsal-fin rays are produced into a long lobe in males whereas in females only the second and third rays are slightly elongated. Males and females of *M. natalensis* apparently exhibit similar sexual dimorphism. In addition, males have a large yellow caudal fin with greatly prolonged

lobes in contrast to females which have an orange-yellow caudal fin, with moderately prolonged lobes.

A male specimen of *M. natalensis* from Kenya (Schneider and Janke 2013) and one of six of the South African specimens in BOLD (<https://doi.org/10.5883/BOLD:AAE9109>) have a broad yellow band along the lateral line, whereas five of the six photographs of South African males do not show that feature. It is likely subject to intraspecific variation unrelated to sex.

Meganthias filiferus is a very similar species known to date only from the holotype from the Andaman Sea (Randall and Heemstra 2008) and one putative specimen from the southeastern Arabian Sea identified as this species by Akhilesh et al. (2009). According to those publications, the species differs from *M. natalensis* by a larger head (2.4–2.5 in SL vs. 2.7–2.9 in SL), an angular corner of the preopercle (vs. rounded), and the dorsoposterior corner of the maxilla somewhat angular (vs. the posterior end of the maxilla broadly rounded). However, two putative *M. natalensis* specimens, one from Walters Shoal (Fig. 1B) and another from the type location at KwaZulu-Natal, South Africa, a photograph of which is deposited in FishBase (Froese and Pauly 2019), appear almost identical to *M. filiferus*. Both specimens differ from *M. filiferus* by having an entirely yellow caudal fin (vs. reddish pink with yellowish lobes), tips of the dorsal-fin spines not red (vs. fifth to tenth spines with red tips), and in lacking spots in the soft portion of the dorsal fin (vs. fifth to eleventh soft rays with yellow-edged red spots distally). The specimen from Walters Shoal (Fig. 1B) has the slightly angled dorsoposterior edge of the maxilla putatively characteristic of *M. filiferus*, as does one specimen from South Africa (ADC2013 166.12 #8, BOLD process ID DSFSG864-13) and another one illustrated in Anderson (2006; Fig. 3D). Additional specimens and some mtDNA sequences of *M. filiferus* are clearly needed to validate the entity and identify diagnostic characters that clearly separate it i.e., from *M. natalensis*.

Although *Meganthias natalensis* is a medium-sized fish, it is rarely documented and known from relatively few localities in the Western Indian Ocean. The species occurs in moderately deep waters in association with rocky substrata on steep slopes at depths of 88–219 m (Randall and Heemstra 2006; the 219 m depth record is from the metadata of the specimen in Fig. 1B). While the predilection for deep habitats certainly contributes to its perceived rarity, little is known about its occupancy and abundance. No species of the group of related genera *Meganthias*, *Odontanthias*, or *Sacura* had hitherto been reported from Socotra (Zajonz et al. 2019). This record adds another species to their list and represents an additional exploited fishery species for the archipelago (Bogorodsky et al. 2020). Three other species from this group have been reported from the wider Arabian Sea and may occur at Socotra: *Odontanthias perumali* (Talwar, 1976) from off the southeastern coast of India (Talwar 1976), *Odontanthias rhodopeplus* (Günther, 1872) from Somalia, the southern coast of Yemen off Mukallah (Attalah et al., in preparation), and off the southwestern

coast of India (Randall and Heemstra 2006); and *Sacura boulengeri* (Heemstra, 1973) from the Gulf of Oman and western coast of India (Heemstra and Randall 1979, Bineesh et al. 2012).

The genus *Odontanthias* Bleeker, 1873 was revised by Randall and Heemstra (2006) who recognized 13 valid species. Four more species have since been added: *Odontanthias cauoh* Carvalho-Filho, Macena et Nunes, 2016; *O. perumali*; *Odontanthias randalli* White, 2011; and *Odontanthias xanthomaculatus* (Fourmanoir et

Rivaton, 1979). *Odontanthias cauoh* was described from the equatorial Atlantic and its placement in the genus is provisional since the species lacks elongate spines and rays in the dorsal fin. Talwar (1976) described *O. perumali* in *Holanthias* based on specimens from the Arabian Sea; the species was considered valid by Manilo and Bogorodsky (2003) but placed in synonymy with the sympatric *O. rhodopeplus* by Randall and Heemstra (2006). According to K.V. Akhilesh (personal communication), *Odontanthias perumali* differs

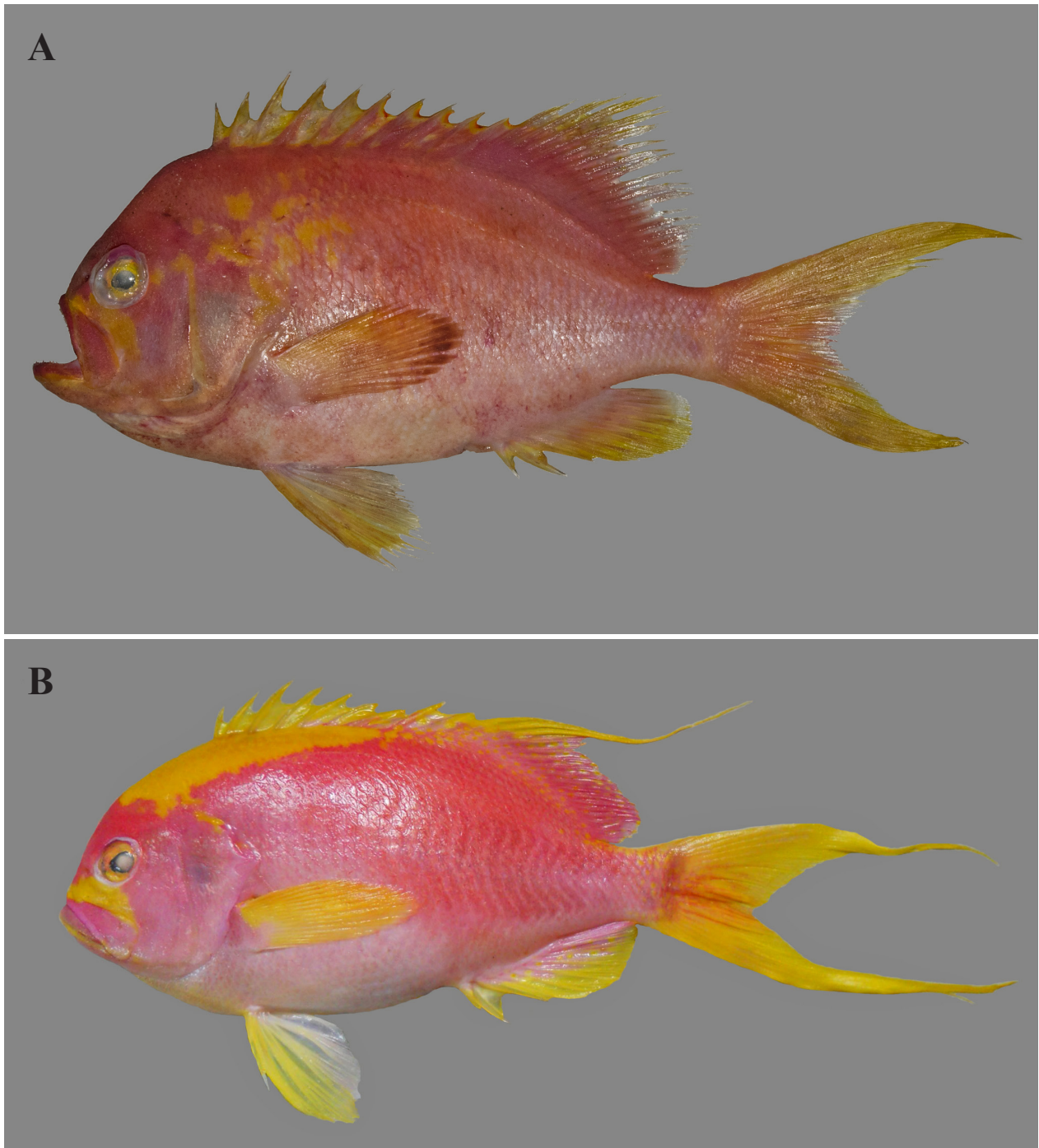


Fig. 1. *Meganthias natalensis*, fresh female, SMF uncatalogued, 27.5 cm SL, Abd al-Kuri Island, Socotra Archipelago, photograph by S.V. Bogorodsky (A); fresh male, Walters Shoal, South Africa, 219 m depth, field number ADC11 166.12 #7, photograph by Allan D. Connell (B)

sufficiently in morphology and coloration and should be resurrected from this synonymy. The barcode sequence data presented here support the validity of *O. perumali* since the two species form divergent monophyletic lineages (Fig. 3). *Odontanthias xanthomaculatus* was originally described in *Anthias* Bloch, 1792, subsequently placed in *Pseudanthias* by Heemstra and Randall (1999) and kept there by Anderson (2018), but Gill and Russell (2019) placed it in *Odontanthias*.

The related genus *Sacura* Jordan et Richardson, 1910 was revised by Heemstra and Randall (1979), who included four valid species: *Sacura boulengeri*; *Sacura margaritacea* (Hilgendorf, 1879); *Sacura parva* Heemstra et Randall, 1979; and *Sacura speciosa* Heemstra et Randall, 1979. Since then, *Sacura sanguinea* Motomura, Yoshida et Vilasri, 2017 has been described from the Andaman Sea. Distinguishing characters between *Odontanthias* and *Sacura* were not defined in the authoritative revisions of both genera (Heemstra and Randall 1979, Randall and Heemstra 2006). Carvalho-Filho et al. (2016, fig. 3) illustrated a double teeth row extending posteriorly to the vomerine patch and uniting to one row, which they considered as a generic character of *Odontanthias* but had compared it with *Holanthias* only. Motomura et al. (2017) suggested that the absence of a median teeth row posterior to the vomerine patch distinguishes *Sacura* from *Odontanthias*. Gill and Russell (2019), however, found that feature is variable (*Odontanthias grahami* Randall et Heemstra, 2006 lacks a median row posterior to the vomerine patch) and hence considered it not useful to separate the genera.

Meganthias is diagnosed in Randall and Heemstra (2006) by having 8–9 soft anal-fin rays, rugose lips, a weakly serrate posterior preopercular margin, and no spine or enlarged serrae at the angle of the preopercle, as well as the middle opercular spine closer to the lower

spine than the upper. In contrast, *Odontanthias* and *Sacura* have 7 soft anal-fin rays, smooth lips, a moderately serrated posterior preopercular margin, and enlarged serrae or a prominent spine at the angle of the preopercle. Furthermore, the middle opercular spine is equidistant to the upper and lower spines in all species of *Odontanthias* and *Sacura boulengeri* and *S. parva*, although closer to the lower spine in *S. speciosa* and *S. sanguinea*, with the condition unknown for *S. margaritacea*.

Randall and Heemstra (2006), and later White (2011), in their keys to the species of *Odontanthias* divide the genus into two groups based on the count of soft dorsal-fin rays and body depth. Species of the first group have 12–14 dorsal-fin rays and body depth 2.4–2.9 in SL. It is composed of *Odontanthias caudicinctus* (Heemstra et Randall, 1986), *Odontanthias dorsomaculatus* (Katayama et Yamamoto, 1986), *Odontanthias elizabethae* Fowler, 1923, *O. grahami*, *O. perumali*, *O. rhodopeplus*, *Odontanthias unimaculatus* (Tanaka, 1917), and *O. xanthomaculatus*. Since *Sacura boulengeri* has 14 dorsal-fin rays and a body depth of 2.4–2.6 in SL it would belong to this group; which is consistent with its placement in the phenetic COI tree (Fig. 3). In addition, all species of the group possess a naked lower jaw. The second group, composed of *Meganthias* and the remaining species of *Odontanthias* and *Sacura*, are morphologically quite similar species with 15–19 dorsal-fin rays, a deeper body with body depth 1.9–2.4 in SL, and the lower jaw mostly or at least partly scaled.

All three genera share the elongation of the second to fifth dorsal-fin soft rays, often into filament or filaments, and a lunate caudal fin, usually with prolonged lobes (except *Odontanthias flagris* Yoshino et Araga, 1975). Many species of *Odontanthias* are characterized by having an elongate, sometimes filamentous, third dorsal-

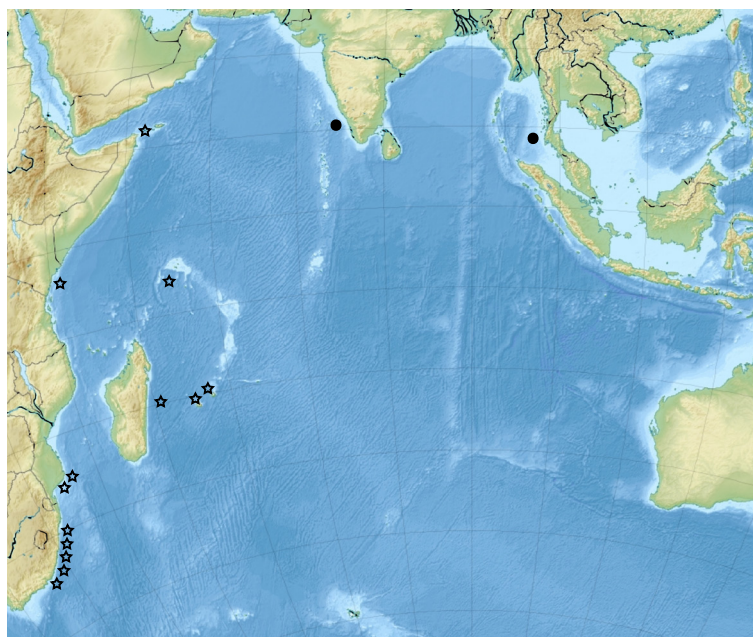


Fig. 2. Distribution map of *Meganthias filiferus* (black circle) and *M. natalensis* (hollow star) (Indian Ocean relief map sourced from Wikimedia Commons)

Table 1

List of samples included in the molecular genetic (COD) analysis of *Meganthias*, *Odontanthias*, and *Sacura* species

| Species identification | BOLD | GenBank | Sample Identifier | Museum registration number | Locality |
|-----------------------------------|----------------|----------|-------------------|----------------------------|---|
| <i>Meganthias kingyo</i> | PHILA1330-15 | MT889102 | PHI-238 | USNM 423593 | Philippines, Cebu |
| <i>Meganthias kingyo</i> | PHILA1086-15 | MT889106 | PIL-147 | USNM 431647 | Philippines, Luzon Island, Batangas |
| <i>Meganthias natalensis</i> | DSFSE916-08 | JF493876 | ADC08-166.12.2 | n/a | South Africa, Pumula |
| <i>Meganthias natalensis</i> | DSFSG1023-13 | KU176438 | ADC13-166.12.9 | n/a | South Africa, St Lucia |
| <i>Meganthias natalensis</i> | DSFSG864-13 | KU176331 | ADC13-166.12.8 | n/a | South Africa, St Lucia |
| <i>Meganthias natalensis</i> | DSFSF438-09 | GU805020 | ADC09-166.12.4 | n/a | South Africa, Pumula |
| <i>Meganthias natalensis</i> | DSFSE945-08 | JF493877 | ADC08-166.12.3.1 | n/a | South Africa, Pumula |
| <i>Meganthias natalensis</i> | DSFSF671-09 | JF493875 | ADC09-166.12.6 | n/a | South Africa, Pumula |
| <i>Meganthias natalensis</i> | LIDMA3193-20 | MT887640 | SOC19-319 | SMF uncatalogued | Yemen, Socotra Archipelago, Abd al-Kuri |
| <i>Odontanthias borbonius</i> | FOAM710-10 | JN311685 | BW-A10673 | CSIRO H 7221-02 | Indonesia, Lombok |
| <i>Odontanthias borbonius</i> | DSFSG340-10 | HQ945924 | ADC10_166.10.2 | n/a | Mozambique, Maputo |
| <i>Odontanthias borbonius</i> | DSFSG335-10 | HQ945920 | ADC10_166.10.1 | n/a | Mozambique, Maputo |
| <i>Odontanthias borbonius</i> | ANGBF39707-19 | KT718580 | n/a | AZISP 0078802 | Taiwan |
| <i>Odontanthias caudicinctus</i> | DSFSG1017-13 | KU176448 | ADC2013_166.11.1 | n/a | South Africa, St Lucia |
| <i>Odontanthias chrysoctictus</i> | ZOSKT2169-16 | KU943457 | n/a | AZISP 0800719 | Taiwan |
| <i>Odontanthias chrysoctictus</i> | ZOSKT493-16 | KU943530 | n/a | AZISP 0806528 | Taiwan |
| <i>Odontanthias chrysoctictus</i> | ZOSKT2168-16 | KU943456 | n/a | AZISP 0800718 | Taiwan |
| <i>Odontanthias chrysoctictus</i> | ZOSKT2167-16 | KU943455 | n/a | AZISP 0800717 | Taiwan |
| <i>Odontanthias chrysoctictus</i> | ZOSKT2170-16 | KU943458 | n/a | AZISP 0800720 | Taiwan |
| <i>Odontanthias elizabethae</i> | GBGC1429-06 | DQ521008 | n/a | BPBM FR353 | Hawaiian Islands |
| <i>Odontanthias perumali</i> | GBMIN124013-17 | KR105806 | n/a | NBFGR:CHN:KN72 | India, Kerala |
| <i>Odontanthias perumali</i> | GBMIN124012-17 | KR105805 | n/a | NBFGR:CHN:VAI34 | India, Kerala |
| <i>Odontanthias perumali</i> | GBMIN119108-17 | KR105808 | n/a | NBFGR:CHN:VAI36 | India, Kerala |
| <i>Odontanthias perumali</i> | GBMIN128996-17 | KR105809 | n/a | NBFGR:CHN:VAI38 | India, Kerala |
| <i>Odontanthias perumali</i> | GBMIN29013-19 | KR105807 | n/a | NBFGR:CHN:KN73 | India, Kerala |
| <i>Odontanthias randalli</i> | FOAM648-10 | JN311680 | BW-A10611 | CSIRO H 7220-01 | Indonesia, Lombok |
| <i>Odontanthias randalli</i> | FOAM708-10 | JN311683 | BW-A10671 | CSIRO H 7221-01 | Indonesia, Lombok |
| <i>Odontanthias randalli</i> | FOAM612-10 | JN311676 | BW-A10575 | CSIRO H 7219-02 | Indonesia, Lombok |
| <i>Odontanthias randalli</i> | FOAM709-10 | JN311684 | BW-A10672 | MZB 20013 | Indonesia, Lombok |
| <i>Odontanthias randalli</i> | FOAN431-11 | JN311692 | BW-A11224 | CSIRO H 7218-01 | Indonesia, Lombok |
| <i>Odontanthias rhodopeplus</i> | GBGCA12439-15 | KJ129022 | n/a | CIFEFGB-OR-001 | India, Kerala |
| <i>Odontanthias rhodopeplus</i> | GBGCA12440-15 | KJ129023 | n/a | CIFEFGB-OR-002 | India, Kerala |
| <i>Odontanthias tapui</i> | MBFA867-07 | JQ431934 | MBIO1470.4 | MNHN 2008-1022 | French Polynesia, Society Islands, Moorea |
| <i>Odontanthias tapui</i> | MBFA866-07 | JQ431935 | MBIO1469.4 | MNHN 2008-1021 | French Polynesia, Society Islands, Moorea |

Table continues on next page.

Table 1 cont.

| Species identification | BOLD | GenBank | Sample Identifier | Museum registration number | Locality |
|---------------------------------------|----------------|----------|-------------------|----------------------------|-----------------------------------|
| <i>Odontanthias unimaculatus</i> | ZOSKT1611-16 | KU892842 | n/a | AZISP 0800912 | Taiwan |
| <i>Sacura boulengeri</i> ¹ | ANGBF39706-19 | KF268191 | n/a | CIFE:FGB-MN-001 | India, Mumbai |
| <i>Sacura boulengeri</i> | GBMIN124019-17 | KR105844 | n/a | NBFGR:CHN:VA135 | India, Kerala |
| <i>Sacura boulengeri</i> | GBMIN124018-17 | KR105842 | n/a | NBFGR:CHN:VA127 | India, Kerala |
| <i>Sacura boulengeri</i> | GBMIN129002-17 | KR105845 | n/a | NBFGR:CHN:VA137 | India, Kerala |
| <i>Sacura boulengeri</i> | GBMIN39779-19 | KR105843 | n/a | NBFGR:CHN:VA133 | India, Kerala |
| <i>Sacura margaritacea</i> | ZOSKT2177-16 | KU943465 | n/a | AZISP 0800911 | Taiwan |
| <i>Sacura margaritacea</i> | ZOSKT2178-16 | KU943466 | n/a | AZISP 0800999 | Taiwan |
| <i>Sacura parva</i> | FOAM649-10 | MT887638 | BW-A10612 | CSIRO unreg | Indonesia, Lombok |
| <i>Sacura speciosa</i> | PHILU065-18 | MT889103 | LUZ-065 | USNM 445282 | Philippines, Luzon Island, Quezon |
| <i>Sacura speciosa</i> | PHILU061-18 | MT889104 | LUZ-061 | USNM 445278 | Philippines, Luzon Island, Quezon |
| <i>Sacura speciosa</i> | PHILU063-18 | MT889105 | LUZ-063 | USNM 445280 | Philippines, Luzon Island, Quezon |

¹ Original identification is *Meganthias natalensis*, reidentified by the presently reported study as *Sacura boulengeri*. Full species authority provided in the text, except for *Odontanthias chrysostrictus* (Günther, 1872) and *Odontanthias tapui* (Randall, Mauge et Plessis, 1979).

fin spine, and all species of *Sacura* have a filamentous third spine. Gill and Russell (2019) argued that the main character uniting the three genera is the presence of two closely spaced predorsal supraneurals, a useful character for the taxonomy of the Anthiadinae.

A phenetic tree of mtDNA COI sequences can be used to compare an individual sequence of a specimen of uncertain identity to those of putative relatives. If the related species resolve into distinct and separate genetic lineages, the unknown sequence can be identified by which lineage it matches. In the present case (Fig. 3), all surveyed species of the genera *Meganthias*, *Odontanthias*, and *Sacura* are well-separated by the COI marker and the specimen from Socotra is confidently assigned to *M. natalensis*.

Another application of the phenetic tree of mtDNA COI sequences is to assess relations between taxa. The phenetic tree is not a phylogenetic tree (which requires multiple markers and an analysis of the statistical support for branches), but it suggests potential relations. In the present tree, both nominal genera, *Odontanthias* and *Sacura* appear as paraphyletic, with species falling within multiple major branches of the tree. The placement of *Sacura margaritacea* (the type species of that genus) and *Odontanthias borbonius* (the type species of that genus) in the same subclade suggests that *Sacura* may be a junior synonym of *Odontanthias*. The two species of *Meganthias* are monophyletic but *Sacura speciosa* shares the branch. Another branch containing five species of *Odontanthias* forms a monophyletic group of lineages, with *S. boulengeri* as a sister lineage. However, the branching pattern is not tested in this tree and in the absence of clear diagnostic features to separate the genera, the presently reported results suggest that a comprehensive phylogenetic analysis is necessary to resolve the status of these genera.

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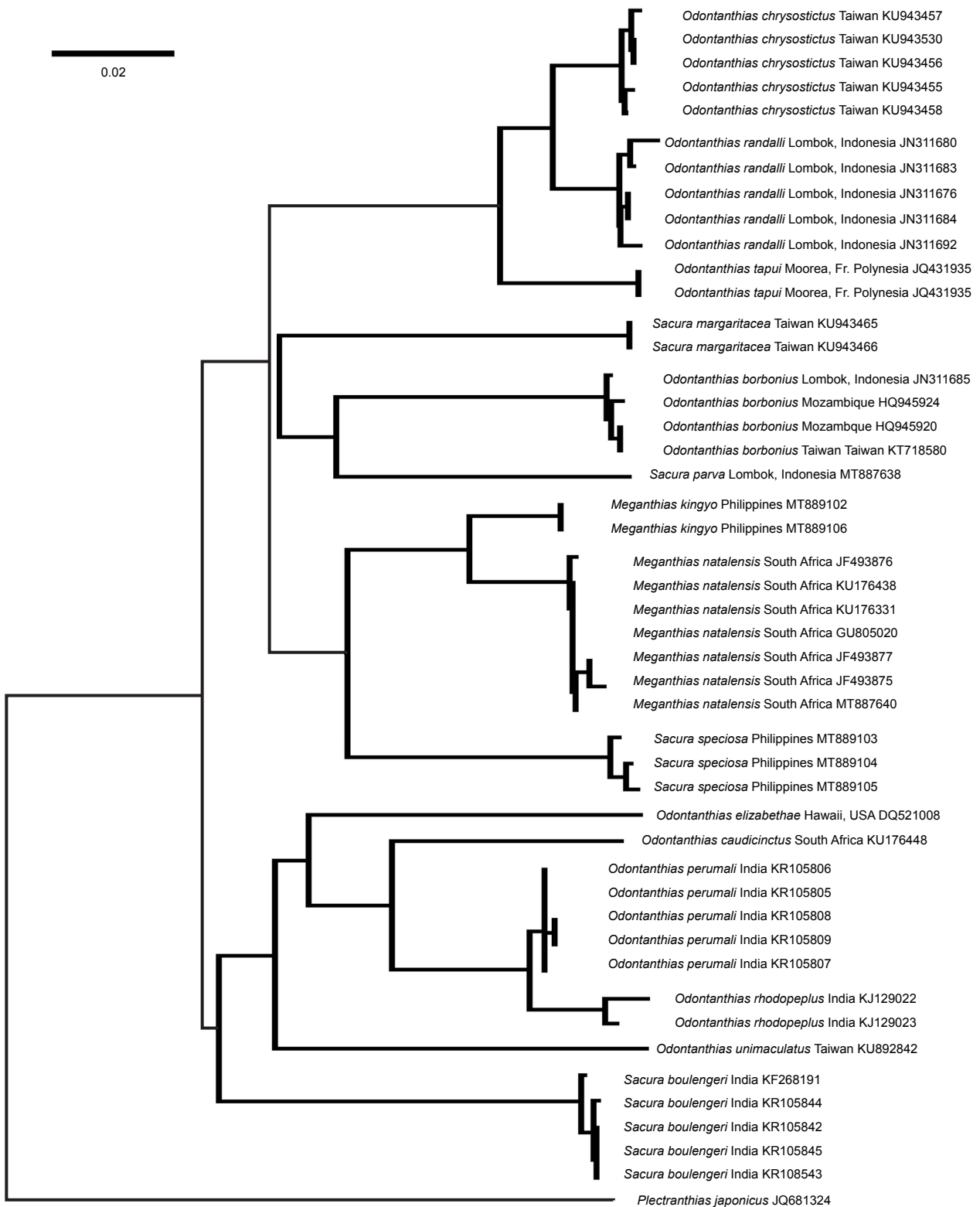


Fig. 3. The neighbor-joining phenetic tree of COI mtDNA sequences of *Meganthias*, *Odontanthias*, and *Sacura* species following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database, <http://www.boldsystems.org>), with *Plectranthias japonicus* as the outgroup; the scale bar at left represents a 2% sequence difference

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