Journal of the
Ocean Science Foundation

2025, Volume 43

Morphological variation and worldwide distribution of the lightfish genus *Woodsia* Grey, 1959 (Teleostei: Stomiiformes: Phosichthyidae)

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Abstract

Morphological variation in the poorly known lightfish genus *Woodsia* Grey, 1959 is evaluated by examination of 13 specimens of *Woodsia nonsuchae* and 28 specimens of *Woodsia meyerwaardeni* from all oceans. Morphological data for both species are documented for the first time from the Indian Ocean. The geographic distribution of *Woodsia* species is reviewed based on new data as well as from literature records and museum databases.

Key words: fishes, biogeography, zoogeography, taxonomy, ichthyology, midwater, deepwater, mesopelagic.

Citation: Prokofiev, A.M., Rajakrishnan, R. & Cubelio, S.S. (2025) Morphological variation and worldwide distribution of the lightfish genus *Woodsia* Grey, 1959 (Teleostei: Stomiiformes: Phosichthyidae). *Journal of the Ocean Science Foundation*, 43, 1–11.

doi: https://doi.org/10.5281/zenodo.15073452

Introduction

The phosichthyid genus *Woodsia* is the least known group in the family, with very scarce literature records. Two species of *Woodsia* have been described: *Woodsia nonsuchae* (Beebe, 1932) from the tropical parts of all oceans and *Woodsia meyerwaardeni* Krefft, 1973 from the fauna of the Subtropical Convergence Zone. Beebe (1932) described *Photichthys nonsuchae* based on a single specimen from off Bermuda. Grey (1959, 1964) erected the new genus *Woodsia* for *P. nonsuchae* and presented a supplementary description of the species based on a single additional specimen from the tropical eastern Pacific in the Gulf of Panama off Colombia. Krefft (1973) described the second species, *W. meyerwaardeni*, from the South Atlantic. Pavlov & Andrianov (1986) subsequently reported a specimen of *W. meyerwaardeni* from the Tasman Sea; they did not detail the morphology of their specimen, but reported the wavy arrangement of lateral ventroanal photophores diagnostic of the species. Aizawa (1990) described two specimens of *W. nonsuchae* collected from the Chatham Rise, but the data presented suggest a misidentification of *W. meyerwaardeni*. A number of guides cite meristic data and/or morphological characters for distinguishing the species, however there is no indication that voucher specimens were examined (Fujii 1985, Schaefer et al. 1986, Paulin et al. 1989, Aizawa 2002, Kenaley & Stewart 2015, Mostarda et al. 2023). Almost all other literature sources (see the species synonymy below) present species names without detail or provenance. The scarcity and fragmentary nature of published information on *Woodsia* species prompted us to review the genus based on available specimens, literature sources and various databases on the internet.

Materials and Methods

Measurements and counts follow Hubbs & Lagler (1958) except interorbital width, which was measured in two ways, with io-1 for the narrowest width belonging to the anterior third of the orbit and io-2 at mid-orbit. Dorsal-adipose length was measured from the base of the last dorsal-fin ray to the adipose-fin origin; pectoral-ventral and ventral-anal distance were measured between the origins of the pectoral and pelvic fins and the pelvic and anal fins, respectively. Not all measurements were obtained for each specimen studied because of damage. Tooth counts are not presented since most specimens had teeth missing making any exact count doubtful. The standard photophore nomenclature follows Morrow & Gibbs (1964).

The distribution map for the two species of *Woodsia* is based on our studied specimens (see material examined), literature sources (see synonymic list for each species), and records obtained from the open-access biodiversity databases, i.e. Global Biodiversity Information Facility (https://www.gbif.org), Ocean Biodiversity Information System (https://obis.org) and the online museum databases of BMNH, MCZ, MNHN, NMV, SIO, and USNM.

Abbreviations used include IKT, Isaacs-Kidd midwater trawl; IKTM, Isaacs-Kidd trawl, Samyshev-Aseev modification; RMT, ring midwater trawl; R/V and FRV, research vessel and fishery research vessel, respectively; SL, standard length; sta., oceanographic station. Institutional abbreviations follow Sabaj (2025), except for the IO/SS/FIS, which is the Indian Ocean Sagar Sampada Fish Collection in the Centre for Marine Living Resources and Ecology (CMLRE), Kochi, India.

Woodsia Grey, 1959

Type species. *Photichthys nonsuchae* Beebe, 1932 (by original designation and monotypy).

Diagnosis. *Woodsia* can be distinguished from other phosichthyids by their moderately elongate body with anal fin originating well behind end of dorsal-fin base; anal fin with 14–16 rays; pelvic fins inserted in front of dorsal-fin origin; eyes normal (non-tubular), bearing a conspicuous crescent-shaped segment of luminous tissue along ventral and posterior margins; photophores 29–33 in lateral series and 46–53 in ventral series; two orbital photophores; premaxilla more than half as long as toothed portion of maxilla, entering into mouth gape; jaw teeth

needle-like, those on premaxilla and dentary unequal in size; lower-jaw teeth biserial anteriorly; palatine teeth numerous, uniserial; some gill-rakers on first arch replaced by short spines, often clustered by 2 or 3; sagittal otolith relatively deep, with moderately long rostrum, similarly convex dorsal and ventral rims and relatively pronounced postventral lobe.

Included species. *Woodsia nonsuchae* (Beebe, 1932) and *Woodsia meyerwaardeni* Krefft, 1973. Fossil otolith-based taxon: *Woodsia emi* Brzobohaty & Nolf, 2002.

Key to the *Woodsia* species

1a. First gill arch with three developed rakers; pseudobranch absent; VAV 11 or 12; preanal part of OA series linear; body depth 5.0–7.4 times in SL ..... *W. nonsuchae*

1b. First gill arch with 6–8 developed rakers (rarely 5 or 9); pseudobranch present; VAV 14–16; preanal part of OA series with some photophores more raised than others; body depth 4.0–4.9 times in SL ..... *W. meyerwaardeni*

Woodsia nonsuchae (Beebe, 1932)

Photichthys nonsuchae Beebe 1932: 61, fig. 11 [original description: 7 miles SSW of Nonsuch I., 600 ft]; Mead 1958: 134 [type catalog].
Photichthys nonsuchi [misspelling]: Beebe 1937: 201.
Woodsia nonsuchae: Grey 1959: 175, fig. 1 [new combination, new Pacific record]; Grey 1964: 150, fig. 35 [description based on the holotype and a specimen from the Gulf of Panama]; Krefft 1973: 131 [in key];

Figure 1. *Woodsia* species: A) *W. nonsuchae*, IORAS 03652, 108 mm SL; B) *W. meyerwaardeni*, MNHN-IC-2001-0663, 81 mm SL; both from the Indian Ocean.

Clarke 1974: 342 [Hawaii, diurnal vertical migrations]; Ahlstrom et al. 1984: 191, tab. 55, fig. 99c [larval characters]; Fujii 1984: 45, pl. 48-J [short description, near Ogasawara Is.]; Paxton et al. 1989: 189 [listed]; Parin et al. 1990: 198 [listed, southeastern Pacific]; Rivaton et al. 1990: 42 [New Caledonia, first record]; Boehlert & Mundy 1992: 13, table 2 [Hancock Seamount; record, abundance]; Harold & Weitzman 1996: 343, fig. 11. [phylogenetic relationships]; Watson 1996: 292, 293 fgd [larval description]; Okiyama 1998: 98, 99, 101 [larval characters]; Harold 1999: 1904 [listed]; Rivaton & Bourret 1999: 204, pl. 93, figs. 7–12 [New Caledonia; sagitta figured]; Aizawa 2002: 319 [in key; meristics; distribution]; Love et al. 2005: 37 [listed, North Pacific distribution]; Mundy 2005: 173 [listed; regional and general distribution]; Castellanos-Galindo et al. 2006: 251 [listed, Colombian Pacific]; Bonilla et al. 2010: 201, Table 1 [listed]; Fricke et al. 2011: 357 [listed, New Caledonia]; Harold 2016: 1791 [listed]; Wang et al. 2019: 135, Table 1 [listed]; Love et al. 2021: 58 [listed, north-eastern Pacific]; Olivar & Beckley 2022: Table 1 [listed]; Mostarda et al. 2023: 74 [in key; regional distribution map].

Woodsia sp. nov.: Craddock & Haedrich 1973: 287–288, fig. 2 [Indian Ocean, distribution]; Loeb 1979: 176, table 2 [larvae, North Pacific Central Gyre; distribution, bathymetric records, abundance, larva size

Material examined. Indian Ocean (10 specimens): IO/SS/FIS/00520, 107 mm SL, 07˚45.6' N, 70˚52.6' E, 304–600 m, R/V *Sagar Sampada*, cruise 344, sta. leg I 04, cosmos trawl, 09:45, 09.09.2015; IO/SS/FIS/00521, 101 mm SL, 8˚05.2' N, 71˚52.6' E, 200–400 m, R/V *Sagar Sampada*, cruise 344, sta. leg I 03, cosmos trawl, 18:00, 08.09.2015; IO/SS/FIS/00522, 91 mm SL, 07˚45.2' S, 59˚11' E, 300 m, R/V *Sagar Sampada*, cruise 344, sta. leg II 04, cosmos trawl, 17:25, 08.10.2015; IO/SS/FIS/00659, 3 specimens, 100–113 mm SL, 02˚31.5' S, 67˚34.3' E, 220–400 m, R/V *Sagar Sampada*, cruise 344, sta. leg I 09, 45m midwater trawl, 05:57, 15.09.2015; IORAS 03650, 58 mm SL, 5˚01.5'–5˚03.3' S, 74˚58.6'–75˚14.3' E, 1200–0 m, R/V *Vityaz*, cruise 55, sta. 6886, conical net, 24.01.1974; IORAS 03651, 95 mm SL, 13˚03' S, 78˚59' E, 460 m, R/V *Akademik M. Keldysh*, cruise 11, sta. 1351, IKTM, 22:35–23:35, 04.03.1986; IORAS 03652, 108 mm SL, 13˚14' S, 78˚18' E, 500 m, R/V *Akademik M. Keldysh*, cruise 11, sta. 1356, IKTM, 23:15–00:15, 18–19.03.1986; MCZ 49082, 44.5 mm SL, 7˚56' S, 65˚14' E, 0–504m, R/V *Anton Bruun*, cruise 6, sta. 341B, 10-m IKT, 22:00–03:00, 01.06.1964. **Pacific Ocean** (3 specimens): MCZ 97801, 52 mm SL, 7˚14' S, 150˚40' E, 0–1180 m, R/V *Lady Basten*, 10-m RMT, 00:20–05:48, 16.05.1981; IORAS 03653, 44.5 mm SL, 11˚22'–11˚18' S, 163˚26'–163˚40' W, 500–0 m, R/V *Dmitry Mendeleev*, cruise 20, sta. 1666, IKT, 2:52–3:52, 21.04.1978; MNHN-IC-1992-0342, 65 mm SL, 22˚10' S, 165˚49' E, 600 m, R/V Coriolis, Pelagia 1 sta. 1/17, 29.04.1971.

Specimens examined as photographic records: BMNH 2015.6.8.676, SL not specified, Somali Basin, 2.4366667 N, 58.0216667 E, 267.5 m (https://www.gbif.org/occurrence/1825759659); NMV A26724-013, 2 specimens, 75–78 mm SL, Coral Sea north of New Caledonia, 19°29′59–19°29′08 S, 162°00′28–162°05′05 E, 482–0 m.

Diagnosis. A species of *Woodsia* with an elongate body (greatest depth 13.5–20.2% SL), smaller eye (8.5–11.2, mean 10% SL), three developed rakers on first arch, no pseudobranch, 11 or 12 VAV photophores, and linear OA photophores.

Description. (Fig. 1A & Tables 1 & 2) Body moderately elongate, slender, greatest depth 5.0–7.4 times in SL. Head 3.4–3.9 times in SL. Snout pointed, eye moderately large, 8.9–11.8 in SL. Mouth gape large, maxilla reaching past rear margin of orbit. One to five small teeth in interspace between longer ones on premaxilla and dentary. Pelvic fins inserted in front of dorsal-fin origin; anal-fin short-based, origin well behind vertical at end of dorsal-fin base; adipose fin inserted over mid-base of anal fin. About 40–43 longitudinal scale rows on body (counted by scale pockets, IORAS 03651 and 03652). Photophores conspicuous. Vertebrae 40–45, modally 42 (Watson, 1996; present study), 20 pairs of pleural ribs. Top of head blackish; suborbital area, cheek, and opercle silvery with fine melanophore speckling; scale pockets dark; subdermal pigmentation between photophore series uniformly dark, otherwise pale with melanophore dotting; adipose fin weakly pigmented at base; mouth dark except pale oral sides of jaws and ventral base of tongue; gill cavity dark; gill arches unpigmented. Largest specimen known 113 mm SL.

Distribution. Tropical and subtropical parts of all oceans, but uncertain for the eastern and southern Atlantic

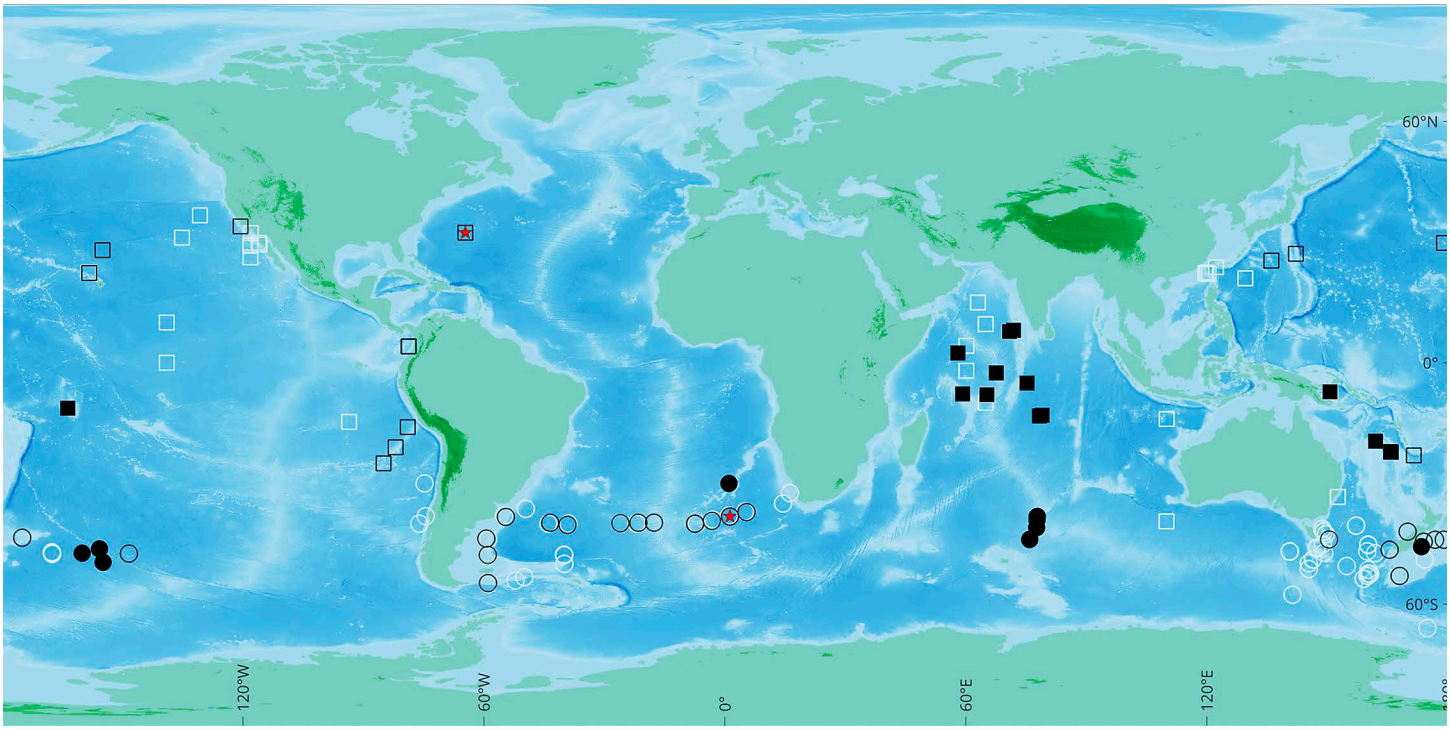

Figure 2. Distribution of *Woodsia nonsuchae* (squares) and *W. meyerwaardeni* (circles). Closed symbols represent our data; open symbols with black borders are based on literature records, those with white borders represent records from web databases. Red stars show holotype localities. A single symbol may indicate more than one capture.

(Fig. 2).

Woodsia meyerwaardeni Krefft, 1973

Woodsia meyerwaardeni Krefft 1973: 130, figs. 1–2 [original description: South Atlantic]; Krefft 1978: 9 [type catalog]; Spanovskaya & Grigorash 1978: 134 [listed]; Menni et al. 1984: 113, 274, fig. 65 [listed]; Pavlov & Andrianov 1986: 553 [47°27′ S, 148°26′ E, 73 mm SL, wavy OA photophores indicated]; Schaefer et al. 1986: 247 [brief description, South Atlantic]; Roberts 1991: 16, appendix 1 [listed; Chatham area, Kaikoura-Banks Peninsula]; Nión et al. 2002: 19 [listed, off Uruguay]; Hoese et al. 2006: 432 [listed]; Kenaley & Stewart 2015: 445 [description; New Zealand region]; Mostarda et al. 2023: 74 [in key; regional distribution map].

Woodsia mayerwaardeni [misspelling]: Paulin et al. 1989: 97 [New Zealand].

Woodsia nonsuchae (*non* Beebe) [misidentification]; Aizawa 1990: 112, fgd [brief description, Chatham Rise]; (?) Young et al. 1996: 575 [listed, off eastern Tasmania].

Material examined. Atlantic Ocean (2 specimens): IORAS 03654, 88 mm SL, off Patagonia (exact coordinates and depth data missing), FRV *Professor Mesyatsev*, cruise 2, bottom trawl Hek-M no. 77, 18.08.1974; IORAS 03655, 100 mm SL, Walvis Ridge at about 30° S, 1° E, large refrigerator trawler *Salekhard*, trawl 52, sample 32, no other data. **Indian Ocean** (13 specimens): MNHN-IC-2000-5023, 2 specimens, 58.5–89 mm SL, 38°16' S, 77°43' E, 370 m, R/V *Curieuse*, Kerams sta. e1, 10.04.2000; MNHN-IC-2000-5026, 54 mm SL, 38°13' S, 77°48' E, 310 m, R/V *Curieuse*, Kerams sta. e2, 10.04.2000; MNHN-IC-2001-0662, 58 mm SL, 43°58' S, 75°52' E, 205 m, R/V *Curieuse*, Kerams sta. a2, 06.04.2000; MNHN-IC-2001-0663, 4 specimens, 61–81 mm SL, 43°55' S, 75°55' E, 320 m, R/V *Curieuse*, Kerams sta. a1, 05.04.2000; MNHN-IC-2001-0664, 4 specimens, 54–63 mm SL, 39°9' S, 77°46' E, 375 m, R/V *Curieuse*, Kerams sta. d1, 09.04.2000; MNHN-IC-2001-0665, 62 mm SL, 41° S, 77°37' E, 340 m, R/V *Curieuse*, Kerams sta. c1, 07.04.2000. **Pacific Ocean** (13 specimens):

IORAS 03656, 2 specimens, 62–64 mm SL, 45˚49.9'–45˚43.9' S, 173˚33'–173˚26.4' E, 500 m, R/V *Dmitry Mendeleev*, cruise 16, sta. 1273, IKT no. 22, 03:06–04:10, 13.01.1976; IORAS 03657, 2 specimens, 97–102 mm SL, 49˚37.2' S, 154˚52.4' W, 600 m, FRV *Mys Tikhii*, pelagic trawl 77.4 m no. 23, 23.09.1977; IORAS 03658, 5 specimens, 80–105 mm SL, 46˚18.5'–46˚18.6' S, 155˚49.1'–155˚47'W, 570 m, FRV *Mys Babushkina*, pelagic trawl 77.4 m, 02.06.1980; IORAS 03659, 3 specimens, 72–105 mm SL, 46˚17.5' S, 155˚46' W, 580–590 m, FRV *Mys Babushkina*, pelagic trawl 77.4 m over bottom, 03:30, 01.06.1980; ZIN 40232, "paratype" of "*Woodsia resima* McGinnis & Lavenberg, 1971" (unpublished name), 32 mm SL, 47˚21' S, 160˚05' W, gear not indicated, 4700 m wire out, R/V *Ob*, sta. 394, 10.04.1958.

Diagnosis. A species of *Woodsia* with a deeper body (greatest depth 20.5–25.0% SL), larger eye (10.1–13.7, mean 12% SL), 5–9 (usually 6–8) developed rakers on first arch, pseudobranch present, 14–16 VAV photophores, and wavy preanal OA photophores.

Description. (Fig. 1B & Tables 1 & 3) Body moderately elongate and robust, greatest depth 4.0–4.9 times in SL. Head 3.0–4.1 times in SL. Snout pointed, eye large, 7.3–9.9 times in SL. Mouth gape large, maxilla reaching past rear margin of orbit. Three to five small teeth in interspace between longer ones on premaxilla and dentary. Pelvic fins inserted in front of dorsal-fin origin; anal-fin short-based, origin well behind vertical of end of dorsal-fin base; adipose fin inserted over mid-base of anal fin. Photophores conspicuous. Vertebrae 43–46, modally 44–45, 20 or 21 pairs of pleural ribs. External coloration uncertain, skin of all specimens examined abraded;

TABLE 1

Meristic data for *Woodsia nonsuchae* and *W. meyerwaardeni*

	Woodsia nonsuchae			*Woodsia meyerwaardeni*			
	Indian Ocean	Pacific Ocean	Literature	Atlantic Ocean	Indian Ocean	Pacific Ocean	Literature
Dorsal-fin rays	11–13	10–12	12	10–11	11–12	10–11	10–11
Anal-fin rays	15–17	15–16	14–15	15–16	15–16	14–16	14–16
Pectoral-fin rays	8–10	8–9	9–11	9–10	9–11	9–11	10
Pelvic-fin rays	7	7	7–8	7	7	7	7
Developed gill rakers	3	3	3	7–8	5–8	5–9	7–9
Pseudobranchs	0	0	0	6–10	5–8	5–15	N/A
Vertebrae	40–42	42	42–45	44–45	N/A	44–46	43–45
Photophore counts							
SO	1	1	1	1	1	1	1
BR	14–15	14–15	14–15	14	14–15	14–15	14–16
IP	11	11	11	11	11	11	10–12
PV	14	14	14–15	14	14	14	13–14
VAV	11–12	11	11–12	16	15–16	15–16	(12)* 14–15
AC	10–12	11–12	12	11–12	12	11–13	11–14
IC	46–48	47–48	48–49	52–53	52–53	52–53	(48)* 51–53
OV	11–13	12	12–13	9–10	10	9–11	10–12
VAL	17–19	18–19	19	21	20	20–22	(17)* 20–23
OA	29–31	30–31	29–32	30–31	30	29–32	29–33

W. nonsuchae literature is Beebe 1932, Grey 1959, 1964, Ahlstrom et al. 1984, Watson 1996, and Aizawa 2002.
W. meyerwaardeni literature is Krefft 1973, Schaefer et al. 1986, Aizawa 1990, and Kenaley & Stewart 2015.
* from Aizawa (1990), photograph indicates the lower counts of VAV and VAL are due to loss in damaged specimen.

TABLE 2

Morphometric data for *Woodsia nonsuchae*

	Atlantic Ocean	Indian Ocean			Pacific Ocean			
	Beebe 1932	our data			our data			Grey 1959 & 1964
		Range (mean±SD)	SE	n	Range (Mean±SD)	SE	n	
SL (mm)	89	44–113 (N/A)	N/A	10	44.5–65.0 (N/A)	N/A	3	76.5
measurements %SL								
Head length	29.8	26.0–29.2 (27.3±0.99)	0.33	9	26.2–28.0 (27.1±1.36)	0.96	2	30.1
Body depth	20.2	15.7–19.0 (17.6±1.11)	0.37	9	13.5–16.8 (15.4±1.79)	1.03	3	20.3
Caudal peduncle length	-	6.7–12.1 (10.5±1.6)	0.53	9	5.8–10.6 (8.3±2.45)	1.41	3	-
Caudal peduncle depth	8.4	7.8–10.1 (8.4±0.71)	0.23	9	7.3–11.5 (8.9±2.29)	1.32	3	9.2
Snout to dorsal-fin origin	-	52.8–57.1 (54.8±1.45)	0.48	9	50–56.9 (54.3±3.8)	2.19	3	56.9
Snout to anal-fin origin	-	73.0–80.5 (76.3±2.02)	0.67	9	74.0–76.4 (75.2±1.18)	0.68	3	73.2
Snout to pelvic-fin origin	-	49.5–52.7 (50.7±1.08)	0.36	9	48.1–52.8 (50.5±2.37)	1.37	3	51.6
Snout to adipose-fin origin	-	78.9–83.5 (81.2±1.54)	0.51	9	82.2–83.8 (82.9±1.28)	0.91	2	-
Dorsal-adipose distance	-	14.0–18.0 (15.9±1.27)	0.44	8	15.4–16.2 (15.7±0.38)	0.22	3	14.4
Pectoral-ventral distance	-	21.4–28.7 (25.4±2.16)	0.72	9	24.7–26.2 (25.2±0.76)	0.43	3	-
Ventral-anal distance	-	22.3–28.7 (25.5±1.87)	0.62	9	23.1–24.6 (23.7±0.78)	0.45	3	22.2
Snout length	7.3	4.9–9.0 (6.1±1.13)	0.37	9	6.7–6.9 (6.7±0.1)	0.06	3	7.2
Eye diameter	9.0	9.2–11.2 (10.2±0.66)	0.22	9	8.5–11.2 (9.7±1.39)	0.80	3	9.8
Interorbital width, io-1	5.1	2.2–4.9 (4.4±0.89)	0.29	9	4.5		1	6.5
Interorbital width, io-2	-	6.0–6.3 (6.1±0.21)	0.14	2	4.9		1	-
Upper-jaw length	-	18.4–24.7 (19.5±1.98)	0.66	9	21.4		1	-

TABLE 3

Morphometric data for *Woodsia meyerwaardeni*

	Atlantic Ocean		Indian Ocean			Pacific Ocean		
	Krefft 1973	our data	our data			our data		
			Range (mean±SD)	SE	n	Range (Mean±SD)	SE	n
SL (mm)	46.0–102.3	88, 100	54–89 (N/A)	N/A	10	32–105 (N/A)	N/A	13
measurements %SL								
Head length	30.5–32.1 (31.5)	31.0, 31.8	31.8–33.3 (32.4±0.5)	0.20	6	27.4–32.5 (31.0±1.39)	0.40	12
Body depth	21.6–24.1 (22.8)	21.6, 21.0	20.6–24.1 (22.8±1.3)	0.53	6	20.5–25.0 (23.0±1.26)	0.36	12
Caudal peduncle length	-	7.9, 9.0	7.7–11.1 (9.2±1.36)	0.60	5	7.5–11.1 (8.7±1.04)	0.31	11
Caudal peduncle depth	9.8–12.7 (11.8)	11.3, 11.5	10.2–12.0 (11.3±0.65)	0.26	6	9.8–12.3 (11.3±0.85)	0.24	12
Snout to dorsal-fin origin	56.0–58.1 (56.9)	52.3, 55.0	52.5–56.8 (54.7±1.64)	0.73	5	52.3–57.1 (54.7±1.49)	0.43	12
Snout to anal-fin origin	74.7–78.3 (76.8)	76.1, 74.0	73.5–77.7 (76.2±2.37)	1.36	3	73.3–80.0 (76.3±2.16)	0.62	12
Snout to pelvic-fin origin	47.1–50.8 (49)	43.0, 47.0	46.2–51.6 (49.7±2.08)	0.93	5	47.0–52.3 (49.3±1.54)	0.44	12
Snout to adipose-fin origin	-	-	80.3–83.8 (82.4±1.86)	1.07	3	79.0–84.7 (81.7±1.77)	0.67	7
Dorsal-adipose distance	15.1–17.4 (16.5)	-	13.4–16.1 (14.4±1.47)	0.85	5	14.0–21.8 (15.8±2.78)	1.05	7
Pectoral-ventral distance	-	23.8, 22.0	22.2–24.6 (22.9±1.15)	0.57	4	19.0–23.4 (20.8±1.42)	0.41	12
Ventral-anal distance	26.2–29.9 (28.3)	26.1, 27.0	23.9–27.1 (25.1±1.33)	0.59	5	25.0–28.5 (27.0±1.38)	0.39	12
Snout length	6.1–6.6 (6.4)	6.0, 6.25	5.6–7.4 (6.6±0.71)	0.29	6	6.2–8.8 (7.1±0.72)	0.20	12
Eye diameter	11.9–13.3 (12.6)	12.8, 12.5	10.1–13.7 (12.4±1.33)	0.54	6	11.1–12.9 (12.3±0.5)	0.14	12
Interorbital width, io-1	-	7.15, 5.3	3.7–5.5 (4.7±0.74)	0.33	5	4.7–7.6 (6.0±0.98)	0.31	10
Interorbital width, io-2	-	8.2, 7.5	6.1–7.7 (6.7±0.84)	0.48	3	6.3–9.2 (8.1±1.09)	0.41	7
Upper-jaw length	22.8–24.4 (23.5)	23.8, 25.0	23.5–26.8 (24.5±1.17)	0.47	6	20.9–32.1 (24.4±2.69)	0.77	12

Indian Ocean specimens with blackish pigmentation on dorsal procurrent caudal-fin rays and adjacent epidermis; epidermal pigmentation around them are blackish in the Indian Ocean specimens; mouth dark except pale oral sides of jaws and ventral base of tongue; gill cavity dark; gill arches unpigmented. Largest specimen known 105 mm SL.

Distribution. Circumglobal in the Southern Hemisphere between 30° and 60° S, mainly in the Subtropical Convergence Zone (Fig. 2).

Discussion. The two species of *Woodsia* can be readily distinguished by the arrangement of the photophores in the preanal portion of the lateral series, number of VAV and VAL photophores (Table 1), the degree of reduction of the gill-rakers and by the presence or absence of the pseudobranch (Krefft 1973, Mostarda et al. 2023). In addition, *W. nonsuchae* is less deep-bodied than *W. meyerwaardeni* (13.5–20.2% vs. 20.5–25.0% SL) and has a slightly smaller eye (8.5–11.2, mean 10% vs. 10.1–13.7, mean 12% SL). The modal vertebral count may distinguish the two species, with 43–46 reported for *W. meyerwaardeni* vs. our specimens of *W. nonsuchae* with 40–42; however, Watson (1996) listed a wider range for *W. nonsuchae* (42–45), with a mode of 42. Potential geographic or population variation may account for some variability and the distinction remains to be confirmed. In general, meristic features are similar for the two species, with little geographic variation other than in dorsal-fin rays. Both species collected from the Indian Ocean show a slightly higher dorsal fin-ray count compared to the Atlantic and Pacific (Table 1).

Morphometrics vary little among specimens of *W. nonsuchae* (Table 2). The body depth is greater in Indian Ocean specimens, but this character is usually growth-dependent in teleosts, and our Pacific specimens are smaller than those from the Indian Ocean (up to 65 mm vs. 113 mm SL). The snout to adipose fin distance is somewhat greater in the Pacific specimens, but the limited number of the specimens makes this distinction uncertain. Additional limitations include measurements of io-2, for which only a single Pacific specimen could be measured as the supraorbitals of the others were damaged.

The geographic variation in morphometrics in *W. meyerwaardeni* is somewhat more pronounced and may reflect true population differences. The Indian Ocean specimens have a slightly longer head, narrower interorbital space, smaller dorsal to adipose and ventral-anal distances, and greater pectoral-ventral distances than Atlantic and Pacific specimens (Table 3). The Atlantic and Pacific populations are more similar to each other, except for snout length, which is greater in Pacific specimens than those from the Atlantic and Indian Oceans (Table 3). However, it should be noted that all of our Indian Ocean specimens were collected from the same location, i.e. the Amsterdam Plateau. This species is expected to occur throughout the subtropical southern Indian Ocean, and additional specimens from different areas may reduce putative interoceanic differences.

The species of *Woodsia* are generally allopatric, with *W. nonsuchae* ranging over a broad tropical distribution between 40° N and 40° S, while *W. meyerwaardeni* appears mostly restricted to the Subtropical Convergence Zone waters with few records at the northern (to about 30° S) or southern limits (to 60° S) (Fig. 2). The northernmost record of *W. meyerwaardeni* in the Atlantic, on the Walvis Ridge at 30° S, may be due to penetration of convergence waters into the Benguela Current. All of the records of *W. meyerwaardeni* in the southeastern Pacific are from the Transitional Zone, between the Subtropical Front and the Eastern South Pacific Central Water Mass. Two tropical records of *W. meyerwaardeni*, from the equatorial western Indian Ocean (BMNH 2015.6.8.676) and the southwestern Pacific at the northernmost part of the Norfolk Ridge (NMV A26724-13), are misidentifications of *W. nonsuchae* according to our examination of the photographs of these specimens.

The distribution of *W. nonsuchae* likely varies among oceans, and, surprisingly, we found only a single documented record from the Atlantic Ocean: the holotype collected from the Gulf Stream portion of the North Atlantic Central Water Mass (Fig. 2). The species is probably absent in the eastern Atlantic, where the only mention is Harold (2016), who lists the species without presenting evidence. The species was not reported in the region by either Blache et al. (1970) or Quéro et al. (1990). Most collections in the Indian Ocean are from the Arabian Sea and the western-central region northward of 20° S (Fig. 2), although a few records are known for the Australasian Mediterranean Water Mass and off southwestern Australia (Olivar & Beckley 2022). In the Pacific Ocean, collections come from the North Pacific Central Gyre and the Californian Transitional Zone and southward to the South Pacific Equatorial and Western South Pacific Central Water Masses. There are very few records from the tropical eastern Pacific, primarily from the Gulf of Panama and off of Colombia (Grey 1959,

1964, Castellanos-Galindo et al. 2006), although we cannot exclude a collection bias. Nevertheless, this species is common in both central and equatorial water masses in the Indo-Pacific and can be considered to be a broadly tropical species here. However, in the Atlantic it may be restricted to the American Mediterranean and the Gulf Stream waters. *Woodsia nonsuchae* may have invaded the American Mediterranean through the Panama Strait during the Miocene-Pliocene and up to the present may have a restricted distribution in the area.

The fossil record of *Woodsia* is particularly scarce. A single otolith-based taxon, *Woodsia emi*, was described from the early Badenian and Tarkhanian regiostages of the Central and Eastern Parathetys (Burdigalian-Serralvian, uppermost early-middle Miocene) (Nolf & Brzobohaty 2002, Schwarzhans 2017). It is similar to the recent species in the general shape of the sagitta, but can be distinguished by the inclined posterior rim and exceptionally protruding postventral lobe. Occurrence of *Woodsia* in the Central and Eastern Paratethys might be explained by prochoresis of Indo-Pacific waters to the Eastern Parathetys during the early Miocene, which has been documented in various other fossil records (Bannikov 1990, Prokofiev 2001, Akhmetiev et al. 2004).

Woodsia specimens have been sampled mainly by pelagic gear and the fish are often collected in mid-water over abyssal depths, although they do tend to concentrate over slopes and seamounts (Fig. 2). The specimens sampled at the South Pacific Rise by FRV *Mys Babushkina* and *Mys Tikhii* (IORAS 03657–03659) were collected by pelagic trawls operated close to the bottom. It is possible that *Woodsia* belong to the so-called "pelagic community of the pseudoceanic zone" of Hulley (1981). Vertical migration has not been documented and most specimens have been collected by non-closed gear, but it is likely that the depth range of both species is above 1000 m, typically 200–600 m.

Acknowledgements

We are sincerely indebted to Guy Duhamel, Jonathan Pfliger, Zora Gabsi (MNHN), and Mikhail Nazarkin (ZIN) for access to the specimens of *Woodsia* under their care, to Andrew Williston and Ichthyology Collection staff at MCZ for the loan of some specimens, and to Martin Gomon (NMV) for the photographs and additional data for the specimens NMV A26724-13. Andrew Stewart and Matthias Stehmann kindly provided useful references. The manuscript was reviewed by two reviewers.

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