Two new species of parasitic copepods from the genera *Nothobomolochus* and *Unicolax* (Cyclopoida: Bomolochidae) from Australian waters

James P. Bernot[1] and Geoffrey A. Boxshall[2]

[1] Institute for Biomedical Sciences, George Washington University, Washington, DC, United States of America
[2] Department of Life Sciences, The Natural History Museum, London, United Kingdom

Corresponding author
James P. Bernot,
jbernot@gwmail.gwu.edu

ABSTRACT

A 2016 collaborative survey of commercial fish parasites in Moreton Bay, Queensland, Australia led to the discovery of two new species of parasitic copepods belonging to the family Bomolochidae. Females of *Nothobomolochus johndaveorum* n. sp. were found attached to the gill filaments of *Gerres subfasciatus* and *Gerres oyena*. The new species most closely resembles *N. leiognathicola* and *N. quadriceros*. All 3 species possess 3 modified setae on the first antennulary segment that are approximately the same length and have a robust seta on the second antennulary segment adjacent to the 3 modified setae giving a superficial appearance of 4 modified setae on the antennule. The new species can be distinguished from these two species in its possession of longer inner setae on the first two endopodal segments of leg 4: the seta on endopodal segment 1 extends past the midline of the distal segment in the new species vs to the proximal margin of the distal segment in the other two species, and the seta on segment 2 extends well beyond the distal margin of the endopod in the new species vs just to the margin in the other two species. Females and males of *Unicolax longicrus* n. sp. were found in the nasal sinuses of *Sillago maculata* and *Sillago ciliata*. The new species differs from 6 of its 7 congeners in having a leg 4 exopod formula of II, I, 4 rather than II, I, 3 or II, I, 5. The new species resembles *U. anonymous* in this feature, but differs in its possession of a leg 5 that is relatively longer and less wide, and, whereas *U. anonymous* possesses inner and outer distal spines on leg 5 that are approximately the same length, those of the new species are relatively longer and asymmetrical. *Unicolax longicrus* n. sp. is unique among its congeners in its possession of a leg 4 with highly elongated endopodal segments 2 and 3, from which its name is derived. In addition to describing the two new species, host and locality reports for all species of *Nothobomolochus* and *Unicolax* are reviewed.

INTRODUCTION

As part of a concerted effort to survey parasites of commercial fish of Moreton Bay, Queensland, Australia, a diversity of fish species were examined for parasitic copepods. Two new species of copepods belonging to the family Bomolochidae Claus, 1875 collected

from Australian teleosts during this survey are described below: one belonging to the gill-inhabiting genus *Nothobomolochus Vervoort, 1962* and the other the nostril-inhabiting genus *Unicolax Cressey & Cressey, 1980*. In addition to describing these two new species, we review all host and locality reports for each species of *Nothobomolochus* and *Unicolax*.

MATERIALS & METHODS

Fish were collected by tunnel net or rod-and-reel in Moreton Bay, Queensland, Australia in January and June of 2016 under permit 187264 from the Queensland Department of Agriculture, Fisheries, and Forestry following the guidelines of the Animal Welfare Unit at the University of Queensland (approval number SBS/248/15/ABRS/ARC). Fish examined consisted of 4 specimens of *Gerres oyena* (Forsskål, 1775), 4 specimens of *Gerres subfasciatus* Cuvier, 1830, 1 specimen of *Sillago ciliata* Cuvier, 1829, and 1 specimen of *Sillago maculata* Quoy & Gaimard, 1824. The body surface, gill arches, and nasal passages were examined for parasitic copepods using a dissecting microscope. Copepods were preserved in 70% ethanol at the time of collection. Specimens were cleared in lactic acid for at least 3 h prior to examination in glass cavity slides using a Leica dissecting microscope. When necessary, appendages were dissected using tungsten wire needles that had been electrolytically sharpened in saturated potassium hydroxide following standard protocols. Observations and drawings were made on an Olympus BX51 compound microscope equipped with differential interference contrast (DIC) and a drawing tube. Measurements were made on the same microscope using an ocular reticule. Measurements are given in micrometers and are presented as the minimum and maximum, followed in parentheses by the mean, standard deviation, and number of specimens measured. Setation formulae are given from proximal to distal segment, separated by semicolons, with Roman numerals indicating spines and Arabic numerals indicating setae; aesthetasks are indicated with ae. Appendage terminology follows *Huys & Boxshall (1991)*. Fish taxonomy follows *Betancur et al. (2017)* for classification above the family level, and Fishbase (*Froese & Pauly, 2018*) for family level and below. Museum abbreviations used are as follows: QM, Queensland Museum, South Brisbane, Australia; NHMUK, The Natural History Museum, Department of Life Sciences, London, UK; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone (*International Commission on Zoological Nomenclature, 2012*). This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:E8663AB9-EF47-4382-8096-C45B10A879A7. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central, and CLOCKSS.

RESULTS

Family Bomolochidae Claus, 1875
Genus *Nothobomolochus Vervoort, 1962*
Nothobomolochus johndaveorum n. sp.
(Figs. 1–4).

LSID: urn:lsid:zoobank.org:act:D5F768DE-686A-4B00-B241-8BBA061BF4A9
Type-host: *Gerres subfasciatus* Cuvier, 1830 (Gerreiformes: Gerridae).
Other host: *Gerres oyena* (Forsskål, 1775) (Gerreiformes: Gerridae).
Type-locality: Moreton Bay, Queensland, Australia (27°22′S, 153°13′E).
Site: Branchial chamber attached to gill lamellae.
Type-material: Holotype female (QM W29438) and 11 female paratypes (2 paratypes QM W29439; 4 paratypes NHMUK 2018.194–2018.197; 4 paratypes USNM 1532298–1532300), 1 fully dissected female paratype not deposited.
Etymology: This species is named in honor of John Page and Dave Thompson for their generosity in providing us with host specimens.

Adult female.
Body (Fig. 1C) 1,000–1,642 (1,371 $\pm$ 172; $n = 9$) long, measured along midline from frontal margin of rostrum to posterior margin of caudal rami excluding caudal setae; greatest width 602–768 (684 $\pm$ 48; 11) at posterior of dorsal cephalothoracic shield. Prosome 648–994 (815 $\pm$ 101; 10) long by 602–768 (684 $\pm$ 48; 11) wide, comprising broad cephalothorax and 3 free pedigerous somites. Urosome 467–647 (555 $\pm$ 62; 10) long by 196–241 (221 $\pm$ 15; 10) wide, comprising 5th pedigerous somite, genital double-somite, and 3 free abdominal somites. Genital double-somite (Fig. 1E) bearing paired genital apertures dorso-laterally. Abdominal somites unornamented; anal somite with anal slit deeply incised; bearing caudal rami. Caudal rami longer than wide, bearing principal seta and 5 small setae. Egg sacs elongate, multiseriate. Swimming leg armature summarized in Table 1.

Antennule (Fig. 1A) indistinctly 7-segmented; first segment heavily sclerotized at base; second to fourth segments partially fused; 3 distal segments cylindrical. First segment with frontally-directed pedestal bearing 3 modified, spine-like setae (Fig. 1B) plus 2 hirsute setae proximally. Compound segments 2, 3, and 4 bearing in total: 10 hirsute setae arrayed along anterior margin, one proximal claw-like naked seta (Fig. 1B) and 2 conspicuously elongate naked setae on anterior margin, and 2 simple naked setae plus cluster of 4 naked setae on ventral surface; 2 short setae present on dorsal surface of segment. Distal 3 segments with the following setal formula: 4; 2 + 1 ae; 7 + 1 ae.

Antenna (Fig. 1D) uniramous, 3-segmented, comprising elongate coxobasis bearing long naked seta, short first endopodal segment bearing short seta, and heavily armed compound distal segment. Distal segment ornamented with 4 irregular rows of spinules, 2 rows of spinules extending onto elongate distal process; bearing one pectinate process
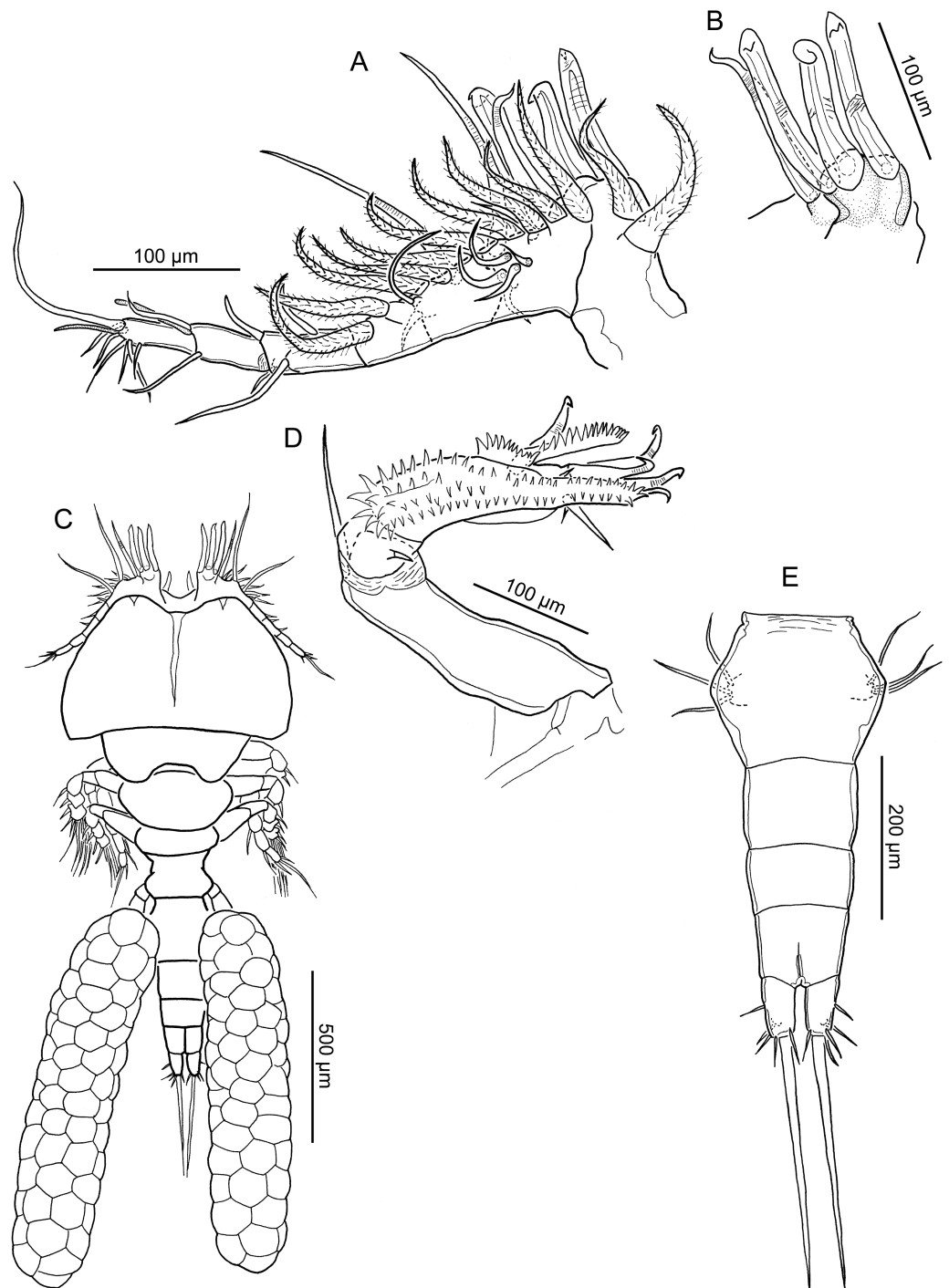
Figure 1 Line drawings of *Nothobomolochus johndaveorum* n. sp. (A) Antennule, ventral view (dissected paratype). (B) Pedestal of first antennulary segment and modified adjacent seta, dorsal view (dissected paratype). (C) Habitus, dorsal view (holotype QM W29438). (D) Antenna, ventral view (dissected paratype). (E) Urosome, ventral view (holotype QM W29438). Drawing credit: James P. Bernot.
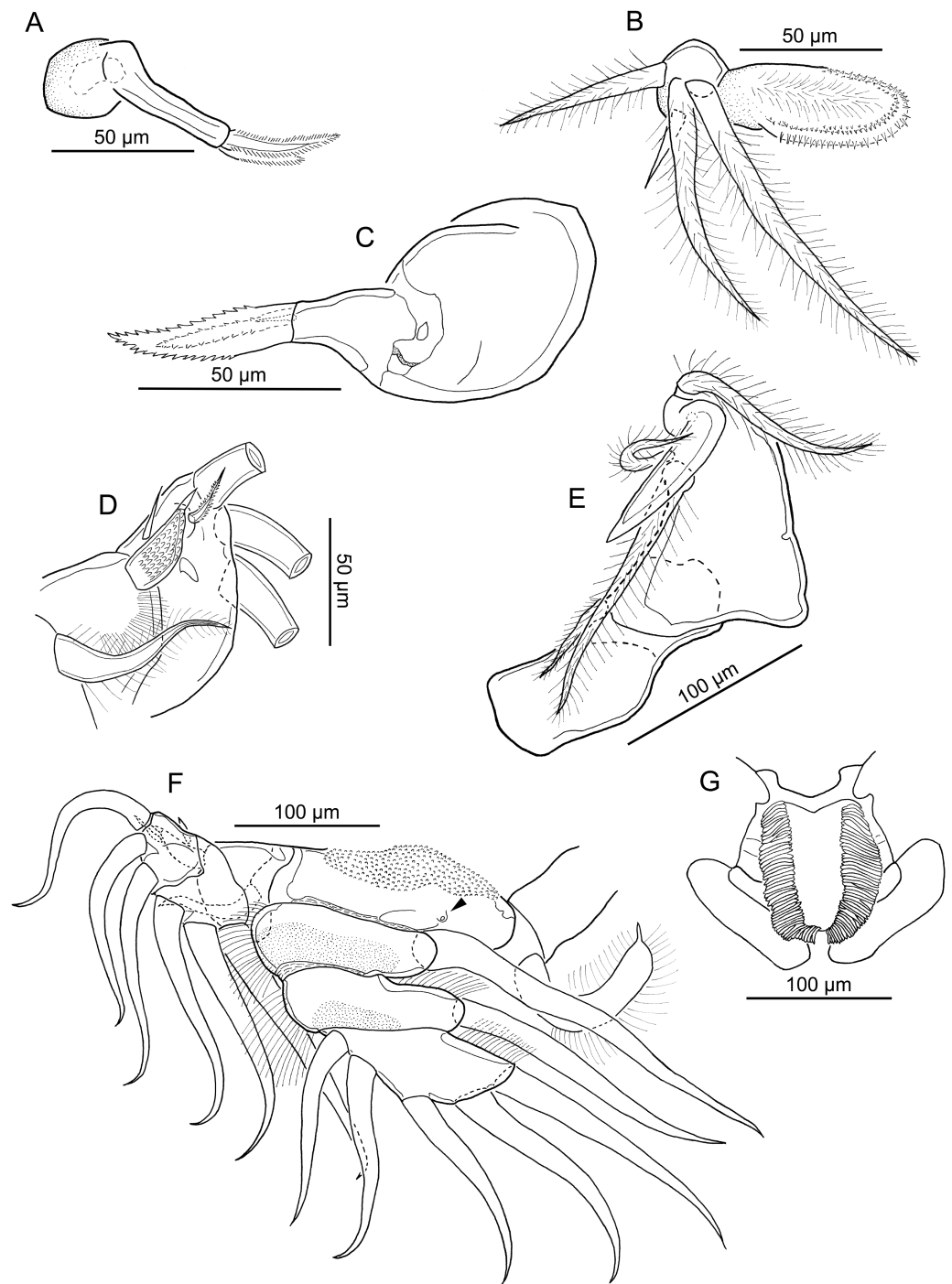
Figure 2 **Line drawings of *Nothobomolochus johndaveorum* n. sp.** (A) Mandible, ventral view (dissected paratype). (B) Maxillule and paragnath, ventral view (dissected paratype). (C) Maxilla, ventral view (dissected paratype). (D) Outer spines on leg 1 exopod, dorsal view (dissected paratype). (E) Maxilliped, ventral view (dissected paratype). (F) Leg 1, ventral view (dissected paratype), plumosity on setae not illustrated; arrowhead indicating inner seta represented by small rounded tubercle. (G) Intercoxal sclerite of leg 1, ventral view (holotype QM W29438). Drawing credit: James P. Bernot.
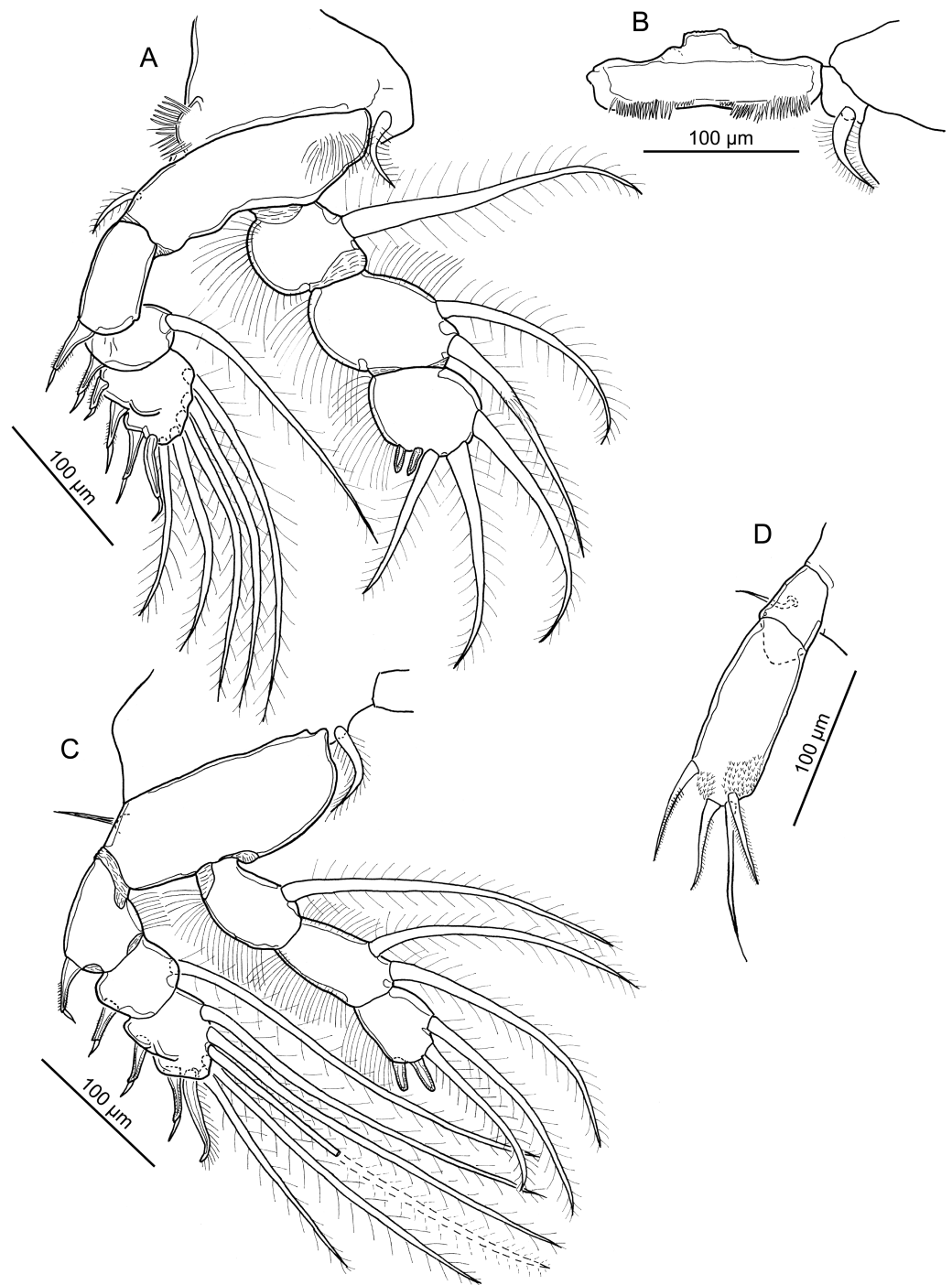
Figure 3 **Line drawings of *Nothobomolochus johndaveorum* n. sp.** (A) Leg 2, ventral view (dissected paratype). (B) Intercoxal sclerite of leg 2, ventral view (dissected paratype). (C) Leg 3, ventral view (dissected paratype). (D) Leg 5, ventral view (dissected paratype). Drawing credit: James P. Bernot.
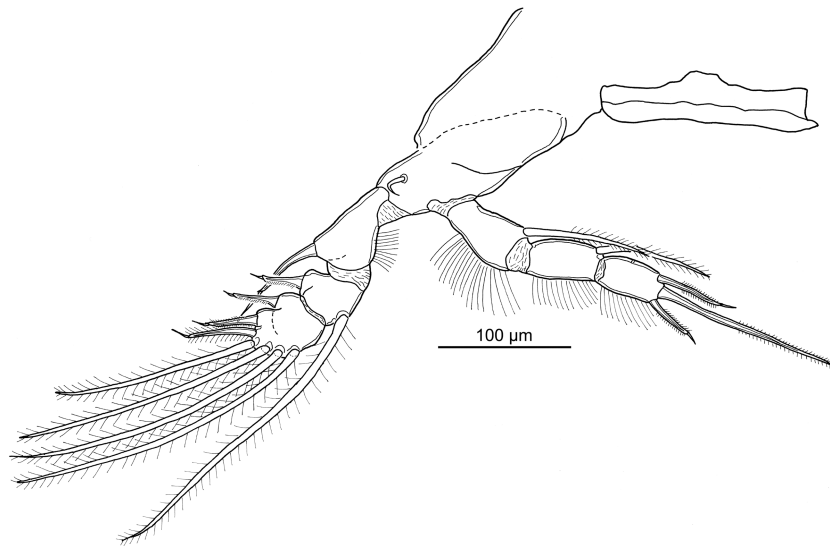
Figure 4 **Line drawing of *Nothobomolochus johndaveorum* n. sp.** Leg 4 and intercoxal sclerite, dorsal view (dissected paratype). Drawing credit: James P. Bernot.

Table 1 *Nothobomolochus johndaveorum* n. sp. swimming leg armature.

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-0; II, 6	0-1; 0-1; 5
Leg 2	0-1	1-0	I-0; I-1; IV, 5	0-1; 0-2; II, 3
Leg 3	0-1	1-0	I-0; I-1; II, I, 5	0-1; 0-2; II, 2
Leg 4	0-0	1-0	I-0; I-1; III, 4	0-1; 0-1; III

extending distally and one medial, fan-like pectinate process; distal armature comprising 4 claw-like setae and 4 naked setae of unequal lengths.

Mandible (Fig. 2A) bearing two spinulate blades; ventral blade slightly longer than dorsal. Paragnath (Fig. 2B) ovoid, ornamented with multiple rows of small tooth-like spinules on margin and hairs along midline. Maxillule (Fig. 2B) consisting of rounded lobe with 3 hirsute setae and 1 small naked seta. Maxilla (Fig. 2C) indistinctly 2-segmented; proximal segment unarmed; distal segment with 2 unequal spinulate processes and 1 dorsal, small naked seta. Maxilliped (Fig. 2E) 3-segmented, comprising long syncoxa armed with one hirsute seta; middle segment tapering distally, armed with 2 unequal hirsute setae on medial margin; distal segment incorporated into claw and bearing hirsute seta; claw simple, lacking accessory process.

Leg 1 (Fig. 2F) biramous, with flattened lamellate rami; members of leg pair joined by intercoxal sclerite (Fig. 2G) bearing lingulate process ornamented with elongate spinules on lateral margins. Coxa with inflated plumose seta, with blunt-apex drawn out into elongate tip. Basis ornamented with patch of rounded spinules proximally, outer plumose seta (Figs. 2D and 2F), and inner seta reduced to small rounded tubercle (arrowhead in Fig. 2F). Exopod (Figs. 2D and 2F) 2-segmented; proximal segment armed with large spine

on dorsal surface ornamented with lingulate spinules and narrow tip; compound distal segment formed by fusion of segments 2 and 3, bearing 6 plumose setae (only 3 shown in Fig. 2D; plumosity not figured in Figs. 2D and 2F), 1 naked spine and 1 serrated spine on dorsal surface (Fig. 2D). Secondary cuticular thickenings present on ventral surface of compound distal segment, not indicative of original segmental articulations. Endopod 3-segmented; all segments flattened and expanded transversely; first and second segments each with inner plumose seta and ornamented with patch of small spinules on ventral surface and hair-like setules on outer margin; second segment with additional hair-like setules along inner margin; third segment armed with 5 plumose setae and with hair-like setules along inner margin.

Leg 2 (Fig. 3A) biramous; intercoxal sclerite (Fig. 3B) ornamented with 2 lateral fields of spinules. Coxa with inner plumose seta and outer swelling ornamented with elongate, blunt-tipped spinules. Basis with outer plumose seta and inner patch of hair-like setules proximally. Exopod 3-segmented, with setal formula: I-0; I-1; IV, 5. All spines bearing subterminal flagellum, and all but terminal 2 spines with bilateral spinulation. Endopod 3-segmented; first segment with plumose inner seta and hair-like setules on outer margin; second segment with 2 plumose inner setae and hair-like setules on inner and outer margins; third segment with 2 short, bilaterally spinulate spines and 3 plumose setae, and ornamented with hair-like setules on outer margin.

Leg 3 (Fig. 3C) biramous, with unornamented intercoxal sclerite. Coxa with inner plumose seta. Basis with outer naked seta on raised base. Exopod 3-segmented; first segment with outer spine and hair-like setules on inner margin; second segment with outer spine and inner seta; third segment with formula: II, I, 5. All outer spines with bilateral spinulation and subterminal flagellum. Terminal spine with spinulation on inner margin only and lacking flagellum. Endopod 3-segmented; first segment with plumose inner seta and hair-like setules along outer margin; second segment with 2 plumose setae and setules along inner and outer margins; third segment with 2 inner setae plus 2 spines bearing fine spinulation bilaterally, and ornamented with hair-like setules along outer margin.

Leg 4 (Fig. 4) biramous, with broad unornamented intercoxal sclerite. Coxa lacking inner seta. Basis with naked outer seta on slightly raised base. Exopod 3-segmented; first segment with long outer spine bearing elongate subterminal flagellum and ornamented with hair-like setules along inner margin of segment; second segment bearing plumose seta and outer spine ornamented with flagellum and unilateral spinulation; third segment with setal formula: III, 4; all spines with flagellum; proximal spine with unilateral spinulation; distal 2 spines with bilateral spinulation. Endopod 3-segmented; all segments ornamented with row of long hair-like setules along outer margin: first segment bearing plumose seta extending just beyond middle of third segment; second segment with inner plumose seta extending beyond tip of ramus, about to middle of outer distal spine; third segment with 3 bilaterally-spinulate spines distally; inner and outer distal spines each with flagellate tip; inner distal spine 30% longer than outer but only 40% as long as apical spine.

Leg 5 (Fig. 3D) 2-segmented: protopodal segment with naked outer seta; exopodal segment with 4 setae; outer 2 setae each with unilateral spinulation; terminal seta naked, inner seta with bilateral spinulation; terminal seta markedly longer than other elements

but just shorter than segment. Leg 6 (Fig. 1E) represented by 3 setae on raised base near oviduct opening.

Remarks

The genus *Nothobomolochus* currently comprises 39 valid species (*Walter & Boxshall, 2019*), and the most recent key to species was provided by *El-Rashidy & Boxshall (2014)*, although this does not include *N. ilhoikimi Venmathi Maran et al., 2014*. *Nothobomolochus johndaveorum* n. sp. can be readily distinguished from *N. fradei Marques, 1965*, *N. ilhoikimi*, *N. lateolabracis* (*Yamaguti & Yamasu, 1959*) *Vervoort, 1962*, *N. lizae* Ho and Lin, 2005, and *N. sagaxi Avdeev, 1986* in its possession of 3, rather than 2, apical elements on the distal endopodal segment of leg 4. The new species differs from *N. cornutus* (*Claus, 1864*) *Vervoort, 1962*, *N. cresseyi Timi & Sardella, 1997*, *N. cypseluri* (*Yamaguti, 1953*) *Vervoort, 1962*, *N. exocoeti Avdeev, 1978*, *N. gibber* (*Shiino, 1957*) *Vervoort, 1962*, *N. monodi El-Rashidy & Boxshall, 2014*, *N. oxyporhamphi Avdeev, 1977*, *N. paruchini Avdeev, 1978*, *N. scomberesocis* (*Krøyer, 1863*) *Vervoort, 1962*, *N. teres* (*Wilson, 1911*) *Pillai, 1967*, and *N. trichiuri Pillai & Natarajan, 1977* in possessing 3 modified setae on the pedestal on the first antennulary segment that are of approximately the same length, rather than possessing a proximal element at least 20–60% shorter than the 2 more distal processes. The new species can be differentiated from *N. epulus Vervoort, 1962*, *N. gazzae* (*Shen, 1957*) *Vervoort, 1969*, *N. kanagurta* (*Pillai, 1965*) *Cressey & Cressey, 1980*, *N. longisaccus* Ho and Lin, 2005, *N. neomediterraneus* El-Rashidy and Boxshall, 2001, *N. ovalis Avdeev, 1977*, and *N. sigani Hameed & Kumar, 1988* in its lack of an accessory process on the female maxilliped claw.

The new species differs from *N. multispinosus* (*Gnanamuthu, 1949*) *Vervoort, 1962*, *N. triceros* (*Bassett-Smith, 1898*) *Vervoort, 1962*, and *N. vervoorti Avdeev, 1986* in its possession of modified setae on the antennulary pedestal that are less than 1/3 the length of the cephalothorax, rather than greater than 1/3 the length. *Nothobomolochus johndaveorum* n. sp. further differs from the former two species in its possession of caudal rami that are shorter than the anal somite. The new species is readily distinguished from *N. atlanticus Avdeev, 1978*, *N. chilensis Avdeev, 1974*, *N. elegans Avdeev, 1977*, *N. marginatus Avdeev, 1986*, and *N. pulicatensis Kaliyamurthy, 1990* in having a leg 4 distal exopod formula of II, I, 4 rather than II, I, 5.

Nothobomolochus johndaveorum n. sp. differs from *N. saetiger* (*Wilson, 1911*) *Vervoort, 1962* in its possession of caudal rami that are longer than wide. It can be differentiated from *N. denticulatus* (*Bassett-Smith, 1898*) *Vervoort, 1962*, *N. digitatus* Cressey, 1970, *N. gerresi Pillai, 1973*, and *N. thambus Ho, Do & Kasahara, 1983* in its possession of a robust, modified seta on the second antennulary segment adjacent to the 3 modified setae on the pedestal of the first segment, that gives the appearance of a fourth modified process, rather than a typical unmodified seta. The new species further differs from these 4 species in possessing a much shorter third pedigerous somite rather than a swollen third pedigerous somite that completely, or nearly completely, overlaps the fourth pedigerous somite, concealing it in dorsal view.

The new species closely resembles *N. leiognathicola El-Rashidy & Boxshall, 2014* and *N. quadriceros Pillai, 1973* in that all species possess a robust, modified seta on the

second antennulary segment adjacent to the 3 modified setae on the first segment so that, superficially, they appear to have 4 modified setae on the antennule. It can be differentiated from *N. leiognathicola* in its possession of an outer element on the distal endopodal segment of leg 4 that is 3/4 the length of the inner element, rather than $\frac{1}{2}$ the length as in *N. leiognathicola*. The new species also possesses mandibular blades that are less asymmetrical: the shorter blade is 3/4 the length of the longer blade vs less than $\frac{1}{2}$ the length in *N. leiognathicola*. In addition, the inner setae on the first 2 endopodal segments of leg 4 are much longer in the new species: the seta on endopodal segment 1 extends past the midline of the distal segment in the new species vs just past the margin of segment 2 in *N. leiognathicola*, and the seta on segment 2 extends well beyond the distal margin of the endopod in the new species vs just to the margin in *N. leiognathicola*. *Nothobomolochus johndaveorum* n. sp. is most similar to *N. quadriceros* but differs in the number of rows of spinules along the distal segment of the antenna. Whereas the new species possesses 4 rows of spinules, *N. quadriceros* as figured by *Pillai (1973)* possesses 9 rows of spinules. The new species can also be distinguished from *N. quadriceros* as figured by *Pillai (1973)* in the lengths of setal elements on leg 4: the outer spine on segment 2 of the exopod is relatively longer in the new species, extending past the midpoint of the third exopodal segment rather than just past the distal margin of the second exopodal segment; likewise the seta of endopodal segment 1 is relatively longer in the new species, extending past the midpoint of the third endopodal segment rather than to the distal margin of the second segment; and the distal endopodal segment of the new species bears an inner setal element that is 30% longer than the outer setal element, rather than approximately the same length.

One other species of *Nothobomolochus* has been reported parasitizing a species of *Gerres*. *Nothobomolochus gerresi* was described from *Gerres filamentosus* Cuvier by *Pillai (1973)* from Trivandrum (now Thiruvananthapuram), India. In addition to the characters noted above, the new species can be further distinguished from *N. gerresi* in its possession of a longer outer spine on the first exopodal segment of leg 4, which extends past the midpoint of the third endopodal segment rather than to the distal margin of the second segment, and its possession of 4, rather than 10, rows of spinules along the distal segment of the antenna.

Nothobomolochus host associations and biogeography

The hosts and localities of all known species of *Nothobomolochus* are summarized in Table 2. The 39 species of *Nothobomolochus* have collectively been reported 112 times, excluding the suspect host reports identified by *El-Rashidy & Boxshall (2014)*. Following the revised classification of bony fishes by *Betancur et al. (2017)*, the genus *Nothobomolochus* parasitizes at least 11 orders of fish (Acanthuriformes, Atheriniformes, Beloniformes, Carangiformes, Chaetodontiformes, Clupeiformes, Gerreiformes, Lobotiformes, Lutjaniformes, Mugiliformes, and Scombriformes) and 22 different families, with some host orders currently *incertae sedis* in the Eupercaria and Carangaria series. The vast majority of host reports come from the orders Beloniformes ($n = 56$; 50%), Scombriformes ($n = 17$; 15%), and Clupeiformes ($n = 14$; 13%), with 6 or fewer reports (<5%) from the other 8 host orders. Most reports are from the families Belonidae ($n = 41$; 37%), followed by

Table 2 *Nothobomolochus* **species hosts and localities.** Records in bold indicate type hosts and localities.

Species	Host	Host family	Host order	Locality	Marine Ecoregion	Source
N. atlanticus *Avdeev, 1978*	***Exocoetus volitans***	Exocoetidae	Beloniformes	**Tropical Atlantic**	Tropical Atlantic	*Avdeev (1978)*
N. chilensis Avdeev, 1974	***Scomberesox saurus***	Belonidae	Beloniformes	**SE Pacific Ocean**	Eastern Indo Pacific	*Avdeev (1974)*
	Cheilopogon furcatus	Exocoetidae	Beloniformes	Tropical Atlantic	Tropical Atlantic	*Avdeev (1978)*
	Exocoetidae	Exocoetidae	Beloniformes	Gulf of Carpentaria, Australia	Central Indo Pacific	*Avdeev (1977)*
	Exocoetidae	Exocoetidae	Beloniformes	Japan	Temperate Northern Pacific	*Avdeev (1977)*
N. cornutus (Claus, 1864) Vervoort, 1962	***Luvarus imperialis***	Luvaridae	Acanthuriformes	**Messina Straits, Italy**	Temperate Northern Atlantic	*Claus (1864)*
N. cresseyi Timi & Sardella, 1997	***Engraulis anchoita***	Engraulidae	Clupeiformes	**Argentina**	Temperate South American	*Timi & Sardella (1997)*
N. cypseluri (Yamaguti, 1953) Vervoort, 1962	***Cheilopogon agoo***	Exocoetidae	Beloniformes	**Mie Prefecture, Japan**	Temperate Northern Pacific	*Yamaguti (1953)*
	Cheilopogon cyanopterus	Exocoetidae	Beloniformes	Northern Indian Ocean	Western Indo Pacific	*Avdeev (1977)*
	Cypselurus oligolepis	Exocoetidae	Beloniformes	Taiwan	Central Indo Pacific	*Ho & Lin (2005)*
	Cypselurus sp.	Exocoetidae	Beloniformes	Japan	Temperate Northern Pacific	*Avdeev (1977)*
N. denticulatus (Bassett-Smith, 1898) Vervoort, 1962	***Sphyraena jello***	Sphyraenidae	Order *incertae sedis* in Carangaria	**Trincomalee, Sri Lanka**	Western Indo Pacific	*Bassett-Smith (1898)*
	Selar crumenophthalmus	Carangidae	Carangiformes	Coral Sea; Port Moresby	Central Indo Pacific	*Avdeev (1986)*
	Sphyraena chrysotaenia	Sphyraenidae	Order *incertae sedis* in Carangaria	Mediterranean Sea, off Egypt	Temperate Northern Atlantic	*El-Rashidy & Boxshall (2014)*
	Sphyraena jello	Sphyraenidae	Order *incertae sedis* in Carangaria	Trivandrum, India	Western Indo Pacific	*Pillai (1965)*
	Sphyraena jello	Sphyraenidae	Order *incertae sedis* in Carangaria	Vietnam	Central Indo Pacific	*Avdeev (1986)*
N. digitatus Cressey & Collette, 1970	***Strongylura strongylura***	Belonidae	Beloniformes	**Penang, Malaysia**	Central Indo Pacific	*Cressey & Collette (1970)*
	Strongylura leiura	Belonidae	Beloniformes	Island of Java	Central Indo Pacific	*Cressey & Collette (1970)*
	Strongylura leiura	Belonidae	Beloniformes	Philippines	Central Indo Pacific	*Cressey & Collette (1970)*

Table 2 (*continued*)

Species	Host	Host family	Host order	Locality	Marine Ecoregion	Source
	Strongylura leiura	Belonidae	Beloniformes	Gulf of Thailand	Central Indo Pacific	*Cressey & Collette (1970)*
	Strongylura strongylura	Belonidae	Beloniformes	Australia	Central Indo Pacific	*Cressey & Collette (1970)*
	Strongylura strongylura	Belonidae	Beloniformes	Calicut, Bombay	Western Indo Pacific	*Cressey & Collette (1970)*
	Strongylura strongylura	Belonidae	Beloniformes	Hong Kong	Central Indo Pacific	*Cressey & Collette (1970)*
	Strongylura strongylura	Belonidae	Beloniformes	India	Western Indo Pacific	*Cressey & Collette (1970)*
	Tylosurus crocodilus	Belonidae	Beloniformes	Northern Borneo	Central Indo Pacific	*Cressey & Collette (1970)*
	Tylosurus punctulatus	Belonidae	Beloniformes	New Guinea	Central Indo Pacific	*Cressey & Collette (1970)*
N. elegans Avdeev, 1977	**Scomberesox saurus**	Belonidae	Beloniformes	**Southeastern Pacific Ocean**	Eastern Indo Pacific	*Avdeev (1977)*
N. epulus Vervoort, 1962	**Plectorhinchus macrolepis**	Haemulidae	Lutjaniformes	**Niger Delta, Nigeria**	Tropical Atlantic	*Vervoort (1962)*
N. exocoeti Avdeev, 1978	**Exocoetus volitans**	Exocoetidae	Beloniformes	**Tropical Atlantic**	Tropical Atlantic	*Avdeev (1978)*
N. fradei Marques, 1965	**Sardinella maderensis**	Clupeidae	Clupeiformes	**Sao Tome, Gulf of Guinea**	Tropical Atlantic	*Marques (1965)*
	Atherinomorus lacunosus [as *Allanetta forskali*]	Atherinidae	Atheriniformes	Arabian Gulf	Western Indo Pacific	*Ho & Sey (1996)*
	Herklotsichthys punctatus	Clupeidae	Clupeiformes	Mediterranean Sea, off Egypt	Temperate Northern Atlantic	*El-Rashidy & Boxshall (2009)*
	Sardina pilchardus	Clupeidae	Clupeiformes	Mediterranean Sea, off Egypt	Temperate Northern Atlantic	*El-Rashidy & Boxshall (2009)*
N. gazzae (Shen, 1957) Vervoort, 1969	**Gazza minuta**	Leiognathidae	Chaetodontiformes	**Hainan Island, China**	Central Indo Pacific	*Shen (1957)*
	Siganus fuscescens	Siganidae	Order *incertae sedis* in Eupercaria	Chiayi County, Taiwan	Central Indo Pacific	*Lin & Ho (2008)*
N. gerresi Pillai, 1973	**Gerres filamentosus**	Gerreidae	Gerreiformes	**Trivandrum, India**	Western Indo Pacific	*Pillai (1973)*
N. gibber (Shiino, 1957) Vervoort, 1962	**Tylosurus crocodilus** [as **Tylosus** [sic] **giganteus**]	Belonidae	Beloniformes	**Owase, Mie, Japan**	Temperate Northern Pacific	*Shiino (1957)*
	Ablennes hians	Belonidae	Beloniformes	Andaman Island	Western Indo Pacific	*Cressey & Collette (1970)*
	Ablennes hians	Belonidae	Beloniformes	Bay of Bengal	Western Indo Pacific	*Cressey & Collette (1970)*
	Ablennes hians	Belonidae	Beloniformes	Borneo	Central Indo Pacific	*Cressey & Collette (1970)*

Table 2 (*continued*)

Species	Host	Host family	Host order	Locality	Marine Ecoregion	Source
	Ablennes hians	Belonidae	Beloniformes	Japan	Temperate Northern Pacific	*Cressey & Collette (1970)*
	Ablennes hians	Belonidae	Beloniformes	Philippines	Central Indo Pacific	*Cressey & Collette (1970)*
	Ablennes hians	Belonidae	Beloniformes	Torres Straits	Central Indo Pacific	*Cressey & Collette (1970)*
	Belone belone	Belonidae	Beloniformes	Funchal, Madeira	Temperate Northern Atlantic	*Cressey & Collette (1970)*
	Belone svetovidovi	Belonidae	Beloniformes	Genoa, Italy	Temperate Northern Atlantic	*Cressey & Collette (1970)*
	Belone svetovidovi	Belonidae	Beloniformes	Tunisia	Temperate Northern Atlantic	*Cressey & Collette (1970)*
	Belones platyura	Belonidae	Beloniformes	Eniwetok Atoll	Eastern Indo Pacific	*Lewis (1968)*
	Euleptorhamphus viridis	Hemiramphidae	Beloniformes	Timor Sea	Central Indo Pacific	*Avdeev (1977)*
	Platybelone argalus	Belonidae	Beloniformes	Aldabra	Western Indo Pacific	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Ascension Island	Tropical Atlantic	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Fakaofo Atoll	Eastern Indo Pacific	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Fanning Island	Eastern Indo Pacific	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Gulf of Guinea	Tropical Atlantic	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Line Islands	Eastern Indo Pacific	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Marshall Island	Eastern Indo Pacific	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Somoa	Eastern Indo Pacific	*Cressey & Collette (1970)*
	Platybelone argalus	Belonidae	Beloniformes	Tokelau Island	Eastern Indo Pacific	*Cressey & Collette (1970)*
	Strongylura leiura	Belonidae	Beloniformes	Taiwan	Central Indo Pacific	*Ho & Lin (2005)*
	Tylosurus acus	Belonidae	Beloniformes	Taiwan	Central Indo Pacific	*Cressey & Collette (1970)*
	Tylosurus crocodilus	Belonidae	Beloniformes	Kerala, India	Central Indo Pacific	*Cressey & Collette (1970)*
	Tylosurus crocodilus	Belonidae	Beloniformes	Madagascar	Western Indo Pacific	*Cressey & Collette (1970)*
	Tylosurus crocodilus	Belonidae	Beloniformes	Red Sea	Western Indo Pacific	*Cressey & Collette (1970)*
	Tylosurus crocodilus	Belonidae	Beloniformes	Seychelles	Western Indo Pacific	*Cressey & Collette (1970)*

Species	Host	Host family	Host order	Locality	Marine Ecoregion	Source
	Tylosurus crocodilus	Belonidae	Beloniformes	Zanzibar	Western Indo Pacific	*Cressey & Collette (1970)*
N. ilhoikimi Venmathi Maran et al., 2014	**Tenualosa ilisha**	Clupeidae	Clupeiformes	**Al-Faw City, Iraq**	Western Indo Pacific	*Venmathi Maran et al. (2014)*
N. johndaveorum n. sp.	**Gerres subfasciatus**	Gerreidae	Gerreiformes	**Moreton Bay, Queensland, Australia** 27°22′**S**, 153°13′**E**	Central Indo Pacific	Present study
	Gerres oyena	Gerreidae	Gerreiformes	Moreton Bay, Queensland, Australia 27°26′S, 153°24′E	Central Indo Pacific	Present study
N. kanagurta (Pillai, 1965) Cressey & Cressey, 1980	**Rastrelliger kanagurta**	Scombridae	Scombriformes	**Kerala, India**	Central Indo Pacific	*Pillai (1965)*
	Rastrelliger faughni	Scombridae	Scombriformes	Philippines	Central Indo Pacific	*Cressey & Cressey (1980)*
	Rastrelliger kanagurta	Scombridae	Scombriformes	China	Central Indo Pacific	*Cressey & Cressey (1980)*
	Rastrelliger kanagurta	Scombridae	Scombriformes	Madras, India	Western Indo Pacific	*Cressey & Cressey (1980)*
	Rastrelliger kanagurta	Scombridae	Scombriformes	Red Sea	Western Indo Pacific	*Cressey & Cressey (1980)*
	Rastrelliger kanagurta	Scombridae	Scombriformes	Taiwan	Central Indo Pacific	*Ho & Lin (2005)*
	Scomber japonicus	Scombridae	Scombriformes	Gulf of Mannar, India	Western Indo Pacific	*Avdeev (1978)*
N. lateolabracis (Yamaguti & Yamasu, 1959) Vervoort, 1962	**Lateolabrax japonicus**	Sillaginidae	Order *incertae sedis* in Eupercaria	**Inland Sea, Japan**	Temperate Northern Pacific	*Yamaguti & Yamasu (1959)*
	Lateolabrax japonicus	Sillaginidae	Order *incertae sedis* in Eupercaria	Ashai River, Japan	Temperate Northern Pacific	*Ho, Do & Kasahara (1983)*
	Sillago sihama	Sillaginidae	Order *incertae sedis* in Eupercaria	Taiwan	Central Indo Pacific	*Ho & Lin (2005)*
N. leiognathicola El-Rashidy & Boxshall, 2014	**Leiognathus klunzingeri**	Leiognathidae	Chaetodontiformes	**Mediterranean Sea, off Egypt**	Temperate Northern Atlantic	*El-Rashidy & Boxshall (2014)*
N. lizae Ho & Lin, 2005	**Liza macrolepis**	Mugilidae	Mugiliformes	**Taiwan**	Central Indo Pacific	*Ho & Lin (2005)*
N. longisaccus Ho & Lin, 2005	**Thryssa hamiltonii**	Engraulidae	Clupeiformes	**Taiwan**	Central Indo Pacific	*Ho & Lin (2005)*
N. marginatus Avdeev, 1986	unknown	NA	NA	10°07′S 145°57′E	Central Indo Pacific	*Avdeev (1986)*

Table 2 (*continued*)

Species	Host	Host family	Host order	Locality	Marine Ecoregion	Source
N. monodi El-Rashidy & Boxshall, 2014	**Hemiramphus far**	Hemiramphidae	Beloniformes	**Madagascar**	Western Indo Pacific	*Monod (1970)*
N. multispinosus (*Gnanamuthu, 1949*) *Vervoort, 1962*	**Dussumiera acuta**	Dussumieridae	Clupeiformes	**Madras, India**	Western Indo Pacific	*Gnanamuthu (1949)*
	Dussumiera elopsoides	Dussumieridae	Clupeiformes	Kerala, India	Western Indo Pacific	*Pillai (1985)*
N. neomediterraneus El-Rashidy & Boxshall, 2011	**Siganus rivulatus**	Siganidae	Order *incertae sedis* in Eupercaria	**Mediterranean Sea, off Egypt**	Temperate Northern Atlantic	*El-Rashidy & Boxshall (2011)*
N. ovalis Avdeev, 1977	**Siganus stellatus**	Siganidae	Order *incertae sedis* in Eupercaria	**Mannar Straits, Indian Ocean**	Western Indo Pacific	*Avdeev (1977)*
N. oxyporhamphi Avdeev, 1977	**Oxyporhamphus micropterus**	Hemiramphidae	Beloniformes	**Galapagos Islands**	Tropical Eastern Pacific	*Avdeev (1977)*
N. paruchini Avdeev, 1978	**Exocoetus volitans**	Exocoetidae	Beloniformes	**Tropical Atlantic**	Tropical Atlantic	*Avdeev (1978)*
N. pulicatensis Kaliyamurthy, 1990	**Hyporhamphus quoyi**	Hemiramphidae	Beloniformes	**Pulicat Lake, India**	Western Indo Pacific	*Kaliyamurthy (1990)*
N. quadriceros Pillai, 1973	**Gazza minuta**	Leiognathidae	Chaetodontiformes	**Trivandrum, India**	Western Indo Pacific	*Pillai (1973)*
N. saetiger (*Wilson, 1911*) *Vervoort, 1962*	**Exocoetus volitans**	Exocoetidae	Beloniformes	**Massachusetts, USA**	Temperate Northern Atlantic	*Wilson (1911)*
	Menidia menidia	Atherinopsidae	Atheriniformes	North Carolina, USA	Temperate Northern Atlantic	*Pearse (1947)*
N. sagaxi Avdeev, 1986	**Sardinops sagax**	Clupeidae	Clupeiformes	**South Kuril Island** 43°42′N 148°30′E	Temperate Northern Pacific	*Avdeev (1986)*
N. scomberesocis (*Krøyer, 1863*) *Vervoort, 1962*	**Scomberesox sp.**	Belonidae	Beloniformes	**Atlantic Ocean**	NA	*Krøyer (1863)*
	Scomberesox saurus [as S. rondeletii]	Belonidae	Beloniformes	Cabo Creus, Spain	Temperate Northern Atlantic	*Deboutteville & Nunes-Ruivo (1958)*
N. sigani Hameed & Kumar, 1988	**Siganus canaliculatus [as Siganus oramin]**	Siganidae	Order *incertae sedis* in Eupercaria	**Trivandrum, India**	Western Indo Pacific	*Hameed & Kumar (1988)*
N. teres (*Wilson, 1911*) *Pillai, 1967*	**Brevoortia tyrannus**	Clupeidae	Clupeiformes	**Massachusetts, USA**	Temperate Northern Atlantic	*Wilson (1911)*
	Brevoortia smithi	Clupeidae	Clupeiformes	Charlotte Harbor, Florida, USA	Tropical Atlantic	*Cressey (1983)*
	Brevoortia tyrannus	Clupeidae	Clupeiformes	Charlotte Harbor, Florida, USA	Tropical Atlantic	*Cressey (1983)*

Table 2 (*continued*)

Species	Host	Host family	Host order	Locality	Marine Ecoregion	Source
N. thambus Ho, Do & Kasahara, 1983	***Konosirus punctatus***	Clupeidae	Clupeiformes	**Ashai River, Japan**	Temperate Northern Pacific	*Ho, Do & Kasahara (1983)*
N. triceros (Bassett-Smith, 1898) Vervoort, 1962	***Pampus argenteus [as Stromateus cinereus]***	Stromateidae	Scombriformes	**Arabian Sea**	Western Indo Pacific	*Bassett-Smith (1898)*
	Lobotes surinamensis	Lobotidae	Lobotiformes	Taiwan	Central Indo Pacific	*Ho & Lin (2005)*
	Pampus argenteus	Stromateidae	Scombriformes	Ashai River, Japan	Temperate Northern Pacific	*Ho, Do & Kasahara (1983)*
	Pampus argenteus	Stromateidae	Scombriformes	Kuwait Bay	Western Indo Pacific	*Ho, Kim & Sey (2000)*
	Pampus argenteus	Stromateidae	Scombriformes	Pacific Ocean	NA	*Yamaguti (1939)*
	Pampus argenteus	Stromateidae	Scombriformes	Persian Gulf, Iran	Western Indo Pacific	*Khosheghbal & Pazooki (2015)*
	Pampus argenteus	Stromateidae	Scombriformes	Taiwan	Central Indo Pacific	*Ho & Lin (2005)*
	Pampus argenteus [as Stromateoides argentus]	Stromateidae	Scombriformes	Kwangtung, China	Central Indo Pacific	*Shen (1957)*
N. trichiuri Pillai & Natarajan, 1977	***Lepturacanthus savala [as Trichiurus savala]***	Trichiuridae	Scombriformes	**Trivandrum, India**	Western Indo Pacific	*Pillai & Natarajan (1977)*
	Lepturacanthus savala [as Trichiurus savala]	Trichiuridae	Scombriformes	Trivandrum, India	Western Indo Pacific	*Hameed & Kumar (1988)*
	Trichiurus lepturus	Trichiuridae	Scombriformes	Taiwan	Central Indo Pacific	*Ho & Lin (2005)*
N. vervoorti Avdeev, 1986	***Ilisha elongata***	Pristigasteridae	Clupeiformes	**Vietnam**	Central Indo Pacific	*Avdeev (1986)*

the Exocoetidae ($n = 11$; 10%), Clupeidae ($n = 9$; 8%), and Scombridae and Stromateidae ($n = 7$ each; 6%) with 4 or fewer reports (<4%) from the 17 other host families.

Following the marine realms established by *Spalding et al. (2007)*, we observe the following distribution for the genus *Nothobomolochus* as currently understood. Of the 112 reports of species of *Nothobomolochus,* 36 (33%) come from the Central Indo-Pacific realm, followed by 30 (27%) from the Western Indo-Pacific, 13 (12%) in the Temperate Northern Atlantic, and 10 or fewer (<9% each) in the following 5 realms: Temperate Northern Pacific (10), Tropical Atlantic (10), Eastern Indo-Pacific (9), Temperate South American (1), and Tropical Eastern Pacific (1). The report of *N. scomberesocis* from the Atlantic Ocean by *Krøyer (1863)* and *N. triceros* from the Pacific Ocean by *Yamaguti (1939)* could not be unambiguously assigned to a realm because the reports lack precise locality information. There are currently no reports of *Nothobomolochus* from the Temperate Australasia, Temperate Southern Africa, Arctic, or Southern Ocean realms.

Genus *Unicolax* Cressey & Cressey, 1980
Unicolax longicrus n. sp.
(Figs. 5–9).

LSID: urn:lsid:zoobank.org:act:0E24C5F0-29C1-49C9-830D-7124D27D3FAE
Type-host: *Sillago maculata* Quoy & Gaimard, 1824 (Order-level *incertae sedis* in Eupercaria: Sillaginidae).
Other host: Sillago ciliata Cuvier, 1829 (Order-level *incertae sedis* in Eupercaria: Sillaginidae).
Type-locality: Moreton Bay, Queensland, Australia (27°26′S, 153°24′E).
Site: Nasal cavity.
Type-material: Holotype female (QM W29434) and 5 female paratypes (1 paratype QM W29435; 2 paratypes NHMUK 2018.198–2018.199; 2 paratypes USNM 1532294–1532295). Allotype male (QM W29436) and 4 male paratypes (2 paratypes NHMUK 2018.200–2018.201; 2 paratypes USNM 1532296–1532297).
Etymology: The name of this species is derived from the Latin *longus* (long) and *crus* (leg), in reference to the elongate endopodal segments of leg 4.

Adult female.
Body (Fig. 5A) 980–1430 (1171 ± 183; $n = 6$) long, measured along midline from frontal margin of rostrum to posterior margin of caudal rami excluding caudal setae; greatest width 432–600 (501 ± 64; 6) at posterior of dorsal cephalothoracic shield. Prosome 490–770 (641 ± 115; 6) long by 432–600 (501 ± 64; 6) wide, comprising broad cephalothorax and 3 free pedigerous somites. Urosome 450–650 (553 ± 85; 6) long by 162–210 (192 ± 19; 6) wide, comprising 5th pedigerous somite, genital double-somite, and 3 free abdominal somites. Genital double-somite (Fig. 5A) bearing paired genital apertures dorso-laterally. Anal somite (Fig. 5E) bearing paired caudal rami; ornamented with 2 patches of spinules, anal slit deeply incised. Caudal rami (Fig. 5E) longer than wide, bearing principal seta and 5 smaller setae, ornamented with patch of spinules. Egg sacs elongate, multiseriate. Swimming leg armature summarized in Table 3.

Antennule (Fig. 5B) 7-segmented; first segment heavily sclerotized at base; second to fourth segments partially fused, 3 distal segments cylindrical. First segment bearing single broad, spine-like fourth seta plus 4 hirsute setae. Second segment bearing 5 hirsute setae and 5 naked setae along anterior margin, and 5 hirsute setae arrayed across ventral surface extending posteriorly. Third segment bearing 3 hirsute and 2 naked setae. Fourth segment bearing 2 hirsute plus 1 naked seta. Distal 3 segments with setal formula: 4; 2 + 1 ae; 7 + 1 ae.

Antenna (Fig. 5C) uniramous, 3-segmented, comprising elongate coxobasis bearing hirsute seta, short first endopodal segment bearing naked seta, and heavily armed compound distal segment. Distal segment ornamented with 3 irregular rows of spinules, 2 rows of spinules extending onto elongate distal process, bearing one pectinate process
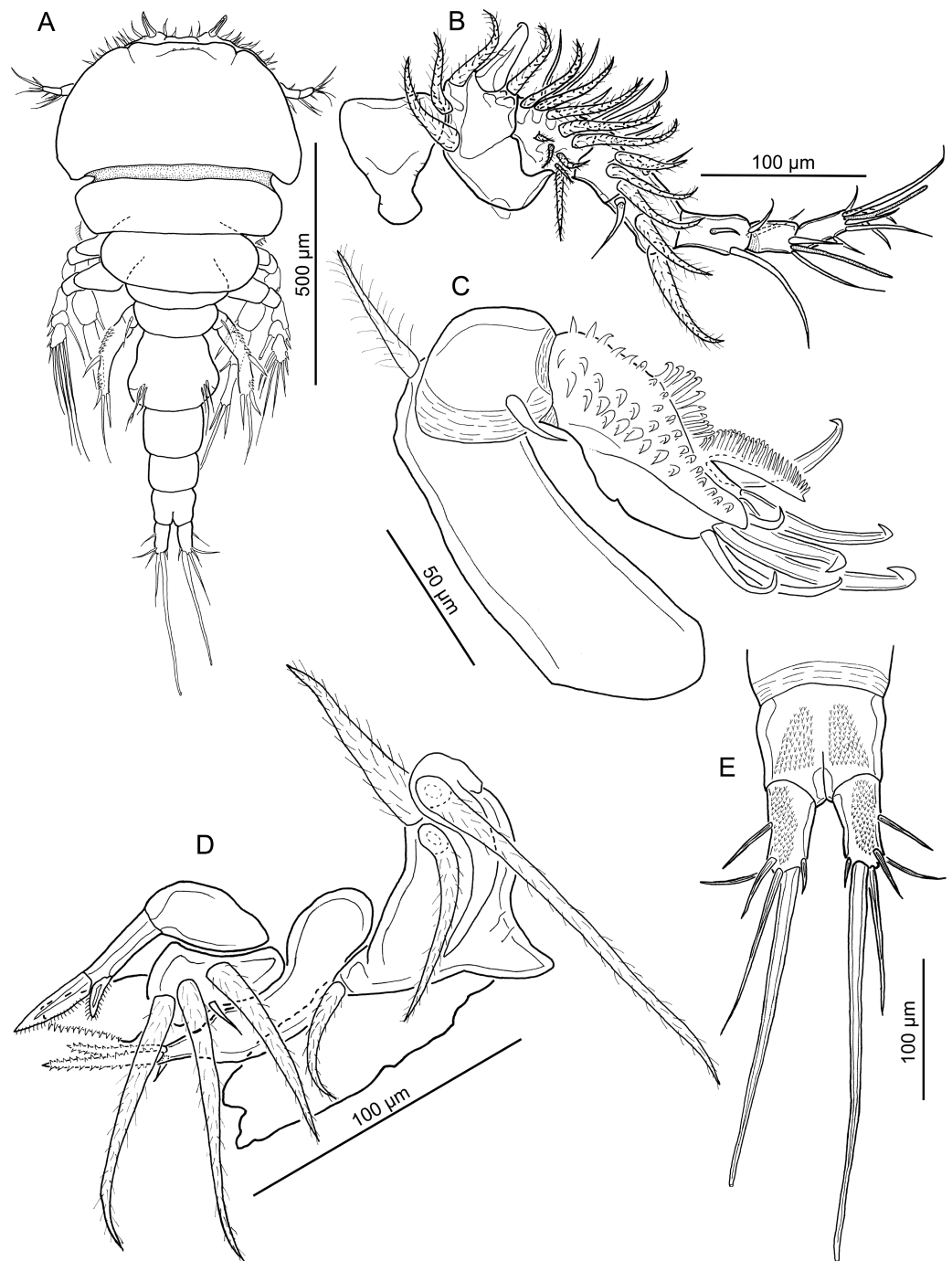
Figure 5   Line drawings of *Unicolax longicrus* n. sp. female. (A) Habitus, dorsal view (holotype QM W29434). (B) Antennule, ventral view (holotype QM W29434). (C) Antenna, ventral view (paratype NHMUK 2018.198). (D) Oral area showing mandible, maxillule, paragnath, maxilla, and maxilliped, *in situ* (holotype QM W29434). (E) Caudal rami and anal somite, ventral view (holotype QM W29434). Drawing credit: James P. Bernot.
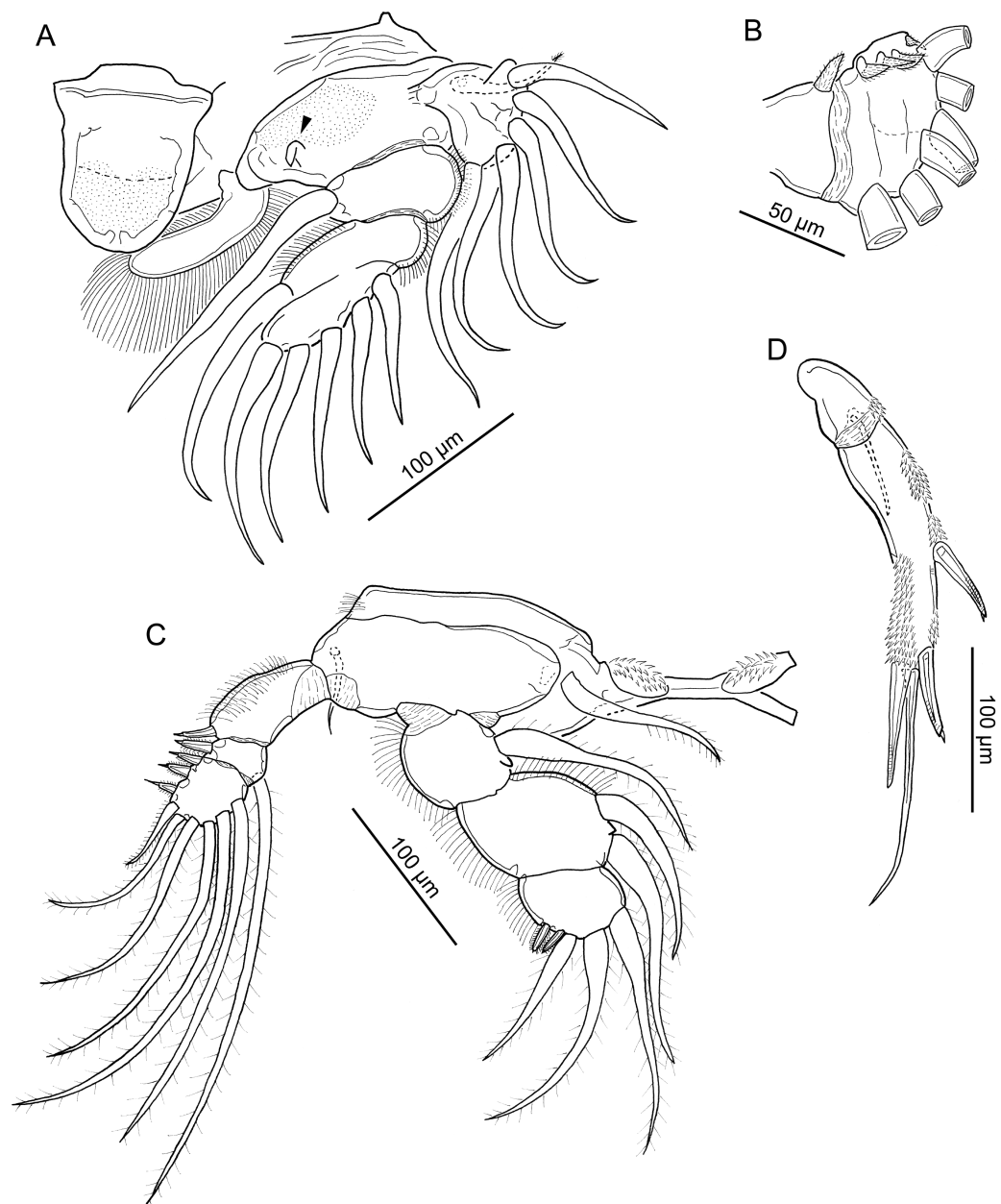
Figure 6 **Line drawings of *Unicolax longicrus* n. sp. female.** (A) Leg 1 and intercoxal sclerite, ventral view (holotype QM W29434); plumosity on setae not illustrated; arrowhead indicating inner seta represented by hooked tubercle. (B) Outer spines on Leg 1 exopod, dorsal view (paratype NHMUK 2018.198). (C) Leg 2 and intercoxal sclerite, ventral view (paratype NHMUK 2018.198). (D) Leg 5, ventral view (holotype QM W29434). Drawing credit: James P. Bernot.

extending distally and enlarged teeth medially; distal armature comprising 4 claw-like setae, 2 elongate naked setae, and 1 short naked seta.

Mandible (Fig. 5D) bearing two spinulate blades of unequal length. Paragnath (Fig. 5D) tapering distally, with tooth-like spinules on posterior margin. Maxillule (Fig. 5D)
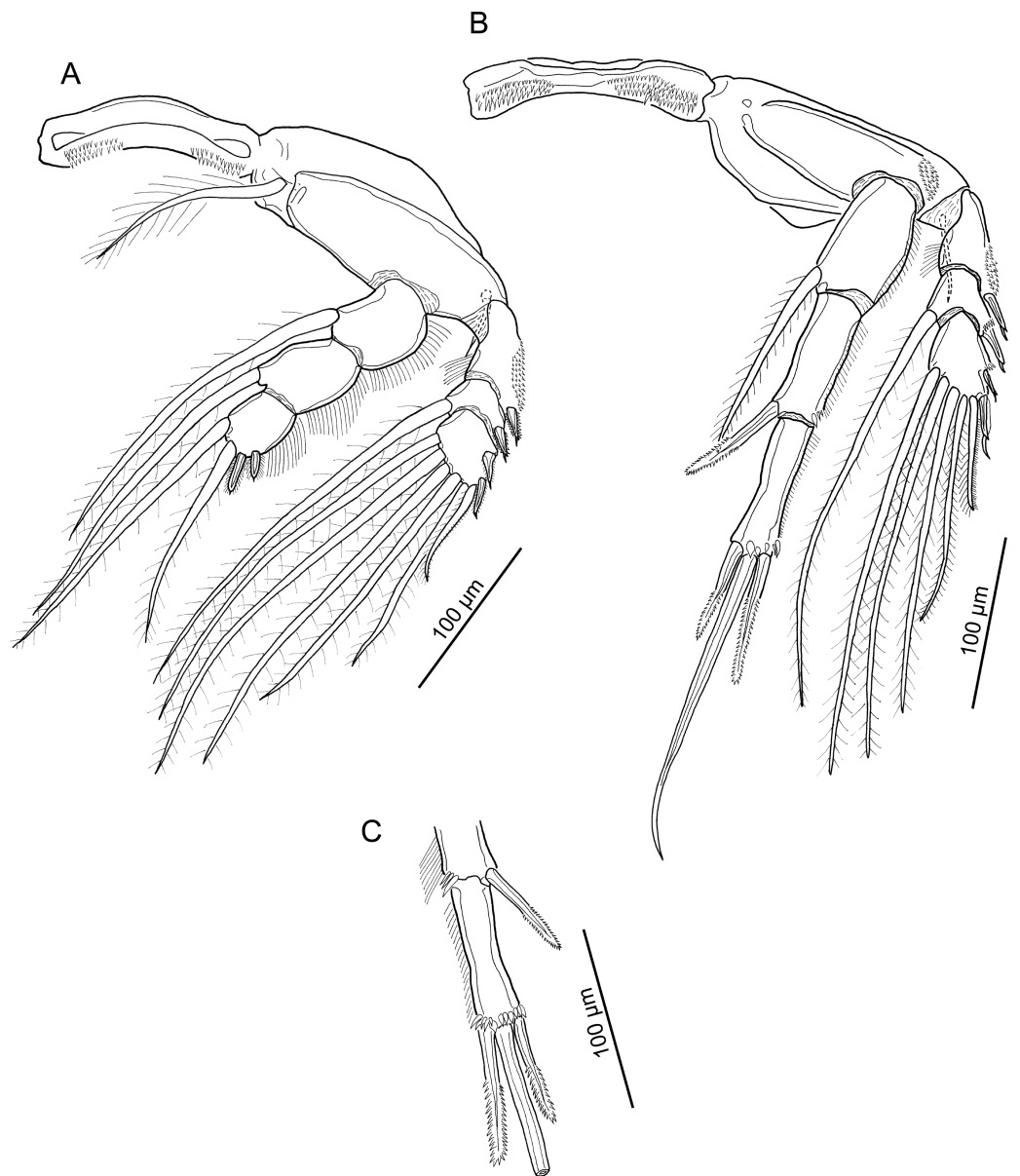
Figure 7 **Line drawings of *Unicolax longicrus* n. sp. female.** (A) Leg 3 and intercoxal sclerite, ventral view (holotype QM W29434). (B) Leg 4 and intercoxal sclerite, ventral view (holotype QM W29434). (C) Detail of leg 4 endopod distal armature, same specimen as 7B, opposite leg (holotype QM W29434).

consisting of irregular lobe with 3 large hirsute setae and 1 small naked seta. Maxilla (Fig. 5D) indistinctly 2-segmented; proximal segment unarmed; distal segment with 2 unequal spinulate apical processes and 1 small naked seta dorsally. Maxilliped (Fig. 5D) 3-segmented, comprising long syncoxa armed with hirsute seta; middle segment tapering distally, armed with 2 large hirsute setae on medial margin; distal segment incorporated into claw and bearing long hirsute seta; claw simple, lacking accessory process.
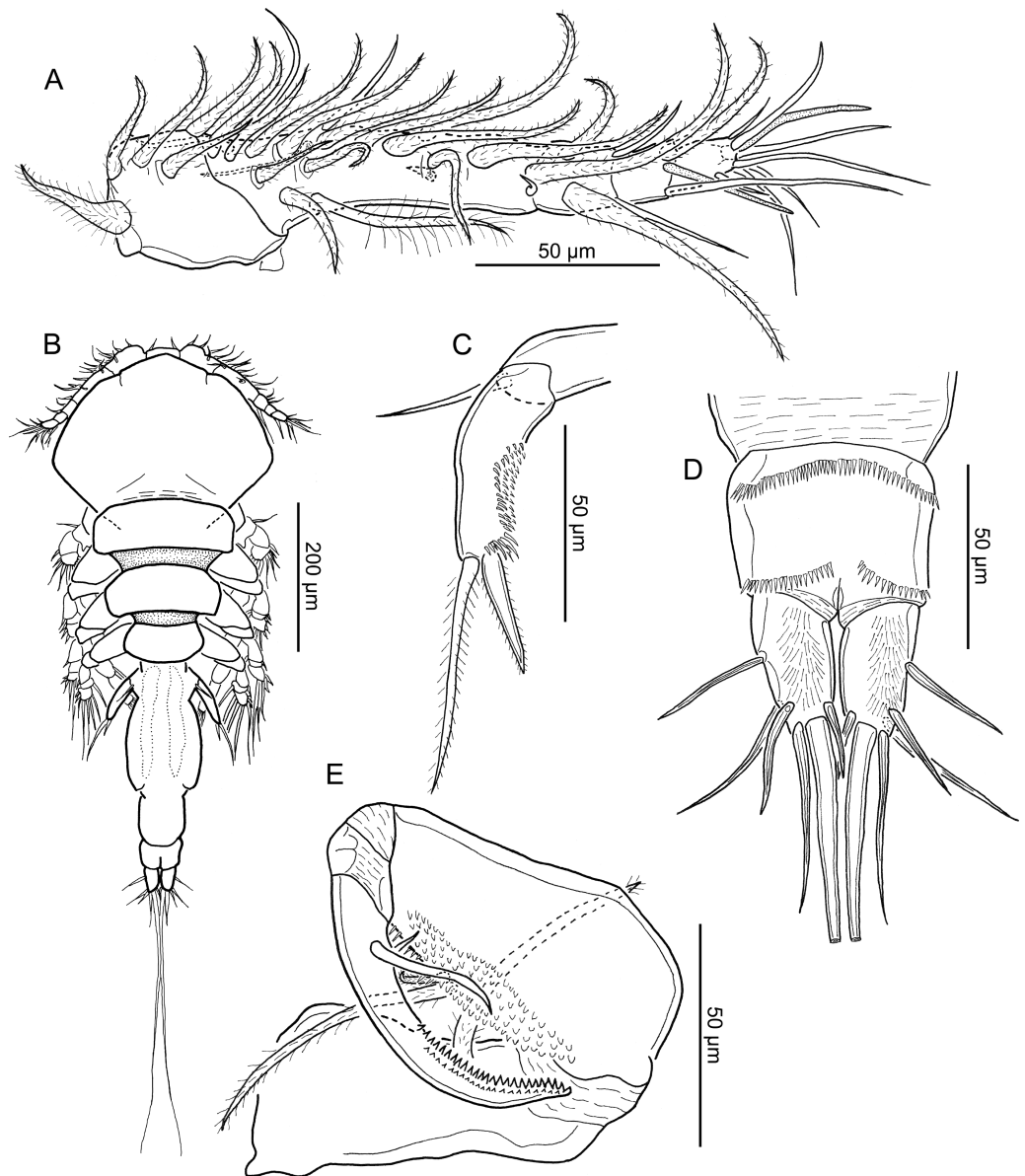
Figure 8 Line drawings of *Unicolax longicrus* n. sp. male. (A) Antennule, ventral view (allotype QM W29436). (B) Habitus, dorsal view (allotype QM W29436). (C) Leg 5, ventral view (allotype QM W29436). (D) Caudal rami and anal somite, ventral view (allotype QM W29436). (E) Maxilliped, ventral view (allotype QM W29436). Drawing credit: James P. Bernot.

Leg 1 (Fig. 6A) biramous, with flattened lamellate rami; members of leg pair joined by intercoxal sclerite bearing lingulate process ornamented with patch of small spinules distally. Coxa with numerous ridge-like cuticular thickenings and inflated inner plumose seta. Basis ornamented with patch of small spinules proximally, outer plumose seta, and inner seta reduced to hooked tubercle (arrowhead in Fig. 6A). Exopod (Figs. 6A and 6B) indistinctly 2-segmented; proximal segment armed with short hirsute spine on dorsal
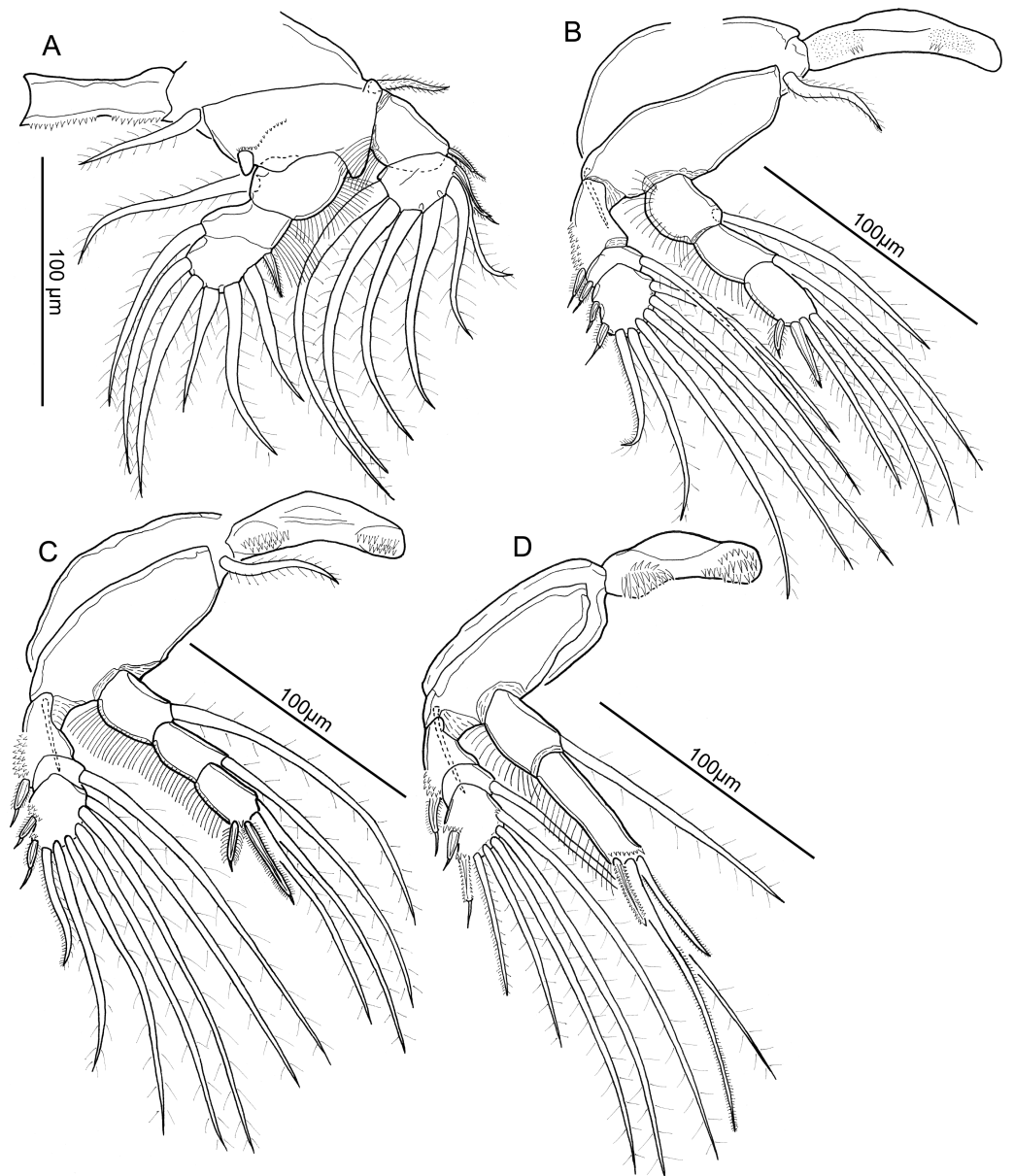
Figure 9 Line drawings of *Unicolax longicrus* n. sp. male. (A) Leg 1 and intercoxal sclerite, ventral view (allotype QM W29436). (B) Leg 2 and intercoxal sclerite, ventral view (allotype QM W29436). (C) Leg 3 and intercoxal sclerite, ventral view (allotype QM W29436). (D) Leg 4 and intercoxal sclerite, ventral view (allotype QM W29436). Drawing credit: James P. Bernot.

surface; compound distal segment formed by fusion of segments 2 and 3, bearing 6 plumose setae (plumosity not figured in Figs. 6A and 6B), and 4 short hirsute spines on dorsal surface (Fig. 6B). Endopod 3-segmented; all segments flattened and expanded transversely; first segment with inner plumose seta and hair-like setules on outer margin; second segment partially fused to third, with inner plumose seta and hair-like setules on inner and outer margins; third segment armed with 5 plumose setae.

Table 3 *Unicolax longicrus* n. sp. swimming leg armature.

	Coxa	Basis	Exopod	Endopod
Female				
Leg 1	0-1	1-I	I-0; IV, 6	0-1; 0-1; 5
Leg 2	0-1	1-0	I-0; I-1; III, 1, 5	0-1; 0-2; II, 3
Leg 3	0-1	1-0	I-0; I-1; II, 1, 5	0-1; 0-1; II, 2
Leg 4	0-0	1-0	I-0; I-1; II, 1, 4	0-1; 0-I; III
Male				
Leg 1	0-1	1-I	I-0; I, 1, 5	0-1; 0-1; I, 5
Leg 2	0-1	1-0	I-0; I-1; II, 1, 5	0-1; 0-1; II, 3
Leg 3	0-1	1-0	I-0; 0-1; II, 1, 5	0-1; 0-1; II, 2
Leg 4	0-0	1-0	I-0; 0-1; II, 1, 4	0-1; III

Leg 2 (Fig. 6C) biramous; intercoxal sclerite ornamented with paired lateral fields of spinules on raised expansions. Coxa with inner plumose seta and patch of hair-like setules on outer margin. Basis with outer naked seta. Exopod 3-segmented; first segment bearing outer spine and ornamented with hair-like setules in patch on outer surface; distal segments with setal formula I-1; III, 1, 5. All spines bearing subterminal flagellum, and all but segment 1 spine with bilateral spinulation. Endopod 3-segmented; first segment with plumose inner seta and hair-like setules on outer margin; second segment with 2 plumose inner setae and hair-like setules on inner and outer margins; third segment with hair-like setules on outer margin, 3 plumose setae, and 2 spines with very fine spinulation on margins.

Leg 3 (Fig. 7A) biramous; intercoxal sclerite with rows of spinules in paired lateral fields and cuticular folds. Coxa with inner plumose seta. Basis with outer naked seta. Exopod 3-segmented; first segment with outer spine, segment ornamented with patch of spinules on outer margin and hair-like setules on inner margin; second segment with outer spine and inner seta; third segment with formula: II, 1, 5. All outer spines with bilateral spinulation and subterminal flagellum; proximal 2 spines with more robust bilateral serrations. Endopod 3-segmented; first and second segments each with plumose inner seta and hair-like setules along outer margin; third segment with 2 inner setae plus 2 spines bearing fine spinulation bilaterally, and ornamented with hair-like setules along outer margin.

Leg 4 (Fig. 7B) biramous, with intercoxal sclerite ornamented with spinules in paired lateral fields. Coxa lacking inner seta. Basis with naked outer seta and ornamented with patch of spinules near base of exopod. Exopod 3-segmented; first segment with outer spine bearing subterminal flagellum, segment ornamented with patch of spinules on outer margin and hair-like setules along inner margin; second segment bearing plumose seta, outer spine with flagellum, and spinules at base of spine; third segment with setal formula: II, 1, 4; all spines with flagellum; spinules present at base of proximal spine; distal spine bearing flange on outer margin. Endopod 3-segmented; all segments ornamented with row of short hair-like setules along outer margin; first segment bearing plumose seta extending to 30% of length of third segment; second segment (Figs. 7B and 7C) elongate, length:width ratio 2.5, bearing large spinules in cluster on outer distal margin and spine-like seta extending

just beyond midline of distal segment; seta with marginal serrations on distal half; third segment (Figs. 7B and 7C) highly elongate, length:width ratio 3.8, bearing 3 spines along distal margin with large spinules at bases of spines; inner and outer distal spines of unequal length, outer spine as long as segment and 20% longer than inner; both ornamented with lateral serrations distally; middle spine naked, more than 2x longer than outer distal spine.

Leg 5 (Fig. 6D) 2-segmented: protopodal segment with naked outer seta and small patch of spinules on outer distal margin; exopodal segment with 4 patches of spinules and 4 setal elements; outer 2 spines each with subterminal flagellum; terminal seta and inner spine naked; inner spine approximately 30% longer than outer; terminal seta markedly longer than other elements, just longer than segment, nearly twice as long as inner spine and 2.5x longer than outer spine. Leg 6 (Fig. 5A) represented by 3 setae near oviduct opening.

Adult male.

Body (Fig. 8B) 650–770 (715 ± 46; $n = 5$) long, measured along midline from frontal margin of rostrum to posterior margin of caudal rami excluding caudal setae; greatest width 270–320 (291 ± 22; 5) at posterior of dorsal cephalothoracic shield. Prosome 370–460 (410 ± 34; 5) long by 270–320 (291 ± 22; 5) wide, comprising broad cephalothorax and 3 free pedigerous somites. Urosome 270–344 (306 ± 30; 5) long by 80–130 (108 ± 22; 5) wide, comprising fused fifth pedigerous somite, genital somite, and 2 abdominal somites, plus 1 free abdominal (anal) somite. Anal somite (Fig. 8D) bearing paired caudal rami; ornamented with anterior row of spinules plus 2 lateral rows of spinules posteriorly. Caudal rami longer than wide, bearing principal seta and 5 smaller setae, ventral surface ornamented with extensive patch of hair-like setules. Swimming leg armature summarized in Table 3.

Most appendages sexually dimorphic, except antenna, mandible, paragnath, maxillule, and maxilla as in female. Antennule (Fig. 8A) 5-segmented; first segment heavily sclerotized at base; second to fourth segments partially fused, 3 distal segments cylindrical. First segment bearing 5 hirsute setae. Second segment bearing 13 hirsute setae and 2 naked setae along anterior margin, and 2 hirsute setae and 1 naked seta on posterior ventral surface; 2 long and 1 short seta present on dorsal surface. Third segment with 2 hirsute and 2 naked setae. Fourth segment bearing 1 hirsute seta, 1 naked seta, and 1 aesthetasc. Distal segment with setal formula: 7 + 1 ae; setae naked.

Maxilliped (Fig. 8E) 3-segmented, comprising long syncoxa bearing hirsute seta; middle segment tapering distally, with 1 long and 1 short hirsute setae on medial margin, ornamented with patch of blunt spinules along inner surface and row of elongate spinules along inner margin distally; distal segment incorporated into claw and bearing 1 long and 1 short naked setae; claw with 2 rows of teeth in distal half of concave margin.

Leg 1 (Fig. 9A) biramous, with flattened lamellate rami; intercoxal sclerite flattened, ornamented with row of spinules along free posterior margin. Coxa with inner plumose seta. Basis ornamented with row of spinules proximally, outer hirsute seta, and short inner seta reduced to rounded tubercle. Exopod 2-segmented; proximal segment with outer spine and hair-like setules along inner margin; spine armed with subterminal flagellum and bilateral spinulation; distal segment bearing 6 plumose setae and 1 spine with subterminal

flagellum and bilateral spinulation. Endopod indistinctly 3-segmented; first segment with inner plumose seta and hair-like setules on outer margin; second segment partially fused to third, with inner plumose seta and hair-like setules on outer margins; third segment armed with 5 plumose setae and 1 spine with bilateral spinulation; terminal seta shorter than adjacent 4 setae.

Leg 2 (Fig. 9B) biramous; intercoxal sclerite ornamented with paired lateral fields of small spinules with three larger spinules on inner margin of each field. Coxa with inner plumose seta. Basis with outer seta. Exopod 3-segmented; first segment bearing outer spine and spinules in patch on outer margin; distal segments with setal formula I-1; II, 1, 5; all outer spines bearing subterminal flagellum and bilateral spinulation. Endopod 3-segmented; first and second segments each with plumose inner seta and hair-like setules on outer margin; third segment with hair-like setules on outer margin and setal formula II, 3; spines with subterminal flagellum and bilateral spinulation; terminal spine twice as long as proximal, with spinulation only on distal 25%.

Leg 3 (Fig. 9C) biramous; intercoxal sclerite ornamented with cuticular folds and paired lateral fields of spinules on raised expansions. Coxa with plumose inner seta. Basis with outer seta. Exopod 3-segmented; first segment with outer spine and patch of spinules on outer margin; second segment lacking outer spine, armed with inner seta; third segment with formula: II, 1, 5, ornamented with small patches of spinules at base of spines; all spines with bilateral spinulation and subterminal flagellum. Endopod 3-segmented; first and second segments each with plumose inner seta and hair-like setules along outer margin; third segment ornamented with hair-like setules along outer margin and 2 inner setae plus 2 spines bearing subterminal flagella and bilateral spinulation; terminal spine twice as long as proximal spine.

Leg 4 (Fig. 9D) biramous, with intercoxal sclerite ornamented with spinules in paired lateral fields on raised bases. Coxa lacking inner seta. Basis with outer seta. Exopod 3-segmented; first segment with outer spine bearing subterminal flagellum and bilateral spinulation, segment ornamented with patch of spinules on outer margin; second segment lacking outer spine but bearing plumose seta; third segment with setal formula: II, 1, 4; small patches of spinules present at bases of spines and innermost seta; all spines with subterminal flagella; first spine otherwise unornamented; terminal spine with serrated margins; terminal setal element with asymmetrical spinulation on inner and outer margins. Endopod 2-segmented; both segments ornamented with row of long hair-like setules along outer margin; first segment bearing plumose seta; second segment elongate, bearing row of spinules on posterior margin and 3 terminal elements; medial element longest; inner and medial element with bilateral spinulation; outer element shortest, with serrated margins.

Leg 5 (Fig. 8C) 2-segmented; protopodal segment with naked outer seta; exopodal segment bearing 2 terminal setal elements and patch of spinules; spinules becoming more elongate towards outer posterior margin; both setal elements with bilateral spinulation; outer element twice as long as inner. Leg 6 not seen.

Remarks

There are 8 nominal species of *Unicolax*: *U. anonymous* (*Vervoort, 1965*) *Cressey & Cressey, 1980*; *U. ciliatus Cressey & Cressey, 1980*; *U. collateralis Cressey & Cressey, 1980*; *U. longispinus Lin & Ho, 2006*; *U. mycterobius* (*Vervoort, 1965*) *Cressey & Cressey, 1980*; *U. quadrispinulus Lin & Ho, 2006*; *U. reductus Cressey & Cressey, 1980*, and *U. longicrus* n. sp. The most recent key to *Unicolax* is by *Lin & Ho (2006)* and includes all species but *U. longicrus* n. sp.

The new species is distinguished from *U. reductus* in its lack of conspicuous dorsolateral aliform expansions of the second pedigerous somite. It further differs in having a leg 4 exopod formula of II, I, 4 rather than II, I, 3. The new species can be differentiated from *U. ciliatus*, *U. collateralis*, *U. mycterobius*, *U. longispinus,* and *U. quadrispinulus* by its possession of a leg 4 exopod with the setal formula II, I, 4 rather than II, I, 5. The new species resembles *U. anonymous* in this feature, but differs in its possession of a leg 5 that is relatively longer and less wide. The setation of the fifth leg also differs, whereas *U. anonymous* possesses inner and outer distal spines on leg 5 that are approximately the same length, those of the new species are relatively longer and asymmetrical (outer spine approximately 40% the length of terminal seta, inner spine approximately 50% the length of terminal seta). *Unicolax longicrus* n. sp. can also be differentiated from *U. anonymous* in its possession of a leg 4 with much more elongate endopodal segments 2 and 3. The new species further differs from *U. anonymous*, *U. collateralis*, *U. reductus,* and, to a lesser degree, *U. ciliatus*, in its possession of outer spines on the exopodal segments, particularly of legs 3 and 4, with smaller, less robust serrations on their margins.

The new species is most similar to *U. quadrispinulus*, the only other species of *Unicolax* known to parasitize a host species of the genus *Sillago*. Both species possess four spines on the distal exopodal segment of leg 1. The new species differs from *U. quadrispinulus* in a number of features. There are numerous differences in leg 4 between the new species and *U. quadrispinulus*: the distal exopodal segment is II, I, 4 in the new species and II, I, 5 in *U. quadrispinulus*; the setal element on the second endopodal segment is much shorter and more spine-like in the new species, extending only to the midline of the distal endopodal segment, while in *U. quadrispinulus* this element is a plumose seta that extends well beyond the end of the ramus and is more than $1.5\times$ the length of distal segment. The new species is unusual among species of *Unicolax* in possessing elongate endopodal segments in leg 4: in the new species the second endopodal segment of leg 4 has a length:width ratio of 2.5 vs. 1.6 in *U. quadrispinulus* and the distal segment has a length:width ratio of 3.8 vs. 2.4 in *U. quadrispinulus*. In addition to the differences in leg 4, the lateral terminal spines of leg 5 in *U. quadrispinulus* are the same length, whereas in the new species the inner distal spine is 30% longer than the outer distal spine. The spinules on the antenna of the new species are also larger and less densely arrayed relative to those on *U. quadrispinulus* (see *Lin & Ho, 2006*: fig. 13B). Furthermore, the terminal spine of the distal endopodal segment of leg 3 is longer than the segment itself in *U. quadrispinulus* while the terminal spine of the new species is shorter than the segment and more blunt.

Unicolax host associations and biogeography

The hosts and localities of all known species of *Unicolax* are summarized in Table 4. The 8 species of *Unicolax* have collectively been reported 83 times. The genus parasitizes the nasal cavity of at least 2 orders of fish. Six of 8 known species of *Unicolax* parasitize fish of the order Scombriformes. *Unicolax quadrispinulus* and *U. longricrus* parasitize species of *Sillago* (family Sillaginidae, Order *incertae sedis* in Eupercaria). Three fish families are known to host *Unicolax*. Five species of *Unicolax* are known to parasitize the Scombridae, 2 the Sillaginidae, and *U. longispinus* the Centrolophidae.

Species of *Unicolax* are known from 9 of the 12 marine realms established by *Spalding et al. (2007)*. Of the 83 reports of *Unicolax* reviewed, 26 (31%) come from the Central Indo-Pacific realm, followed by 15 (18%) from the Western Indo-Pacific, 10 each (12%) in the Temperate Northern Pacific and Tropical Atlantic, and 9 or fewer in the following 5 realms: Temperate Northern Atlantic ($n = 9$; 11%), Tropical Eastern Pacific ($n = 4$; 5%), Eastern Indo-Pacific ($n = 3$; 4%), Temperate Australasia ($n = 3$; 4%), and Temperate Southern Africa ($n = 1$; 1%) . There are currently no reports of *Unicolax* from the Arctic, Temperate South America, or Southern Ocean realms. Two reports of *U. ciliatus* by *Cressey & Cressey (1980)* could not be assigned to a realm. The locality was given only as ''China'' (*Cressey & Cressey, 1980* pg. 15), and given that the coast of China spans the Central Indo-Pacific and Temperate Northern Pacific realms, a biogeographic realm could not be unambiguously assigned to these records.

DISCUSSION

Current reports suggest *Nothobomolochus* has a predominately tropical distribution, with 86 reports from tropical ecoregions and 24 reports from temperate regions. The west coast of North America and the east and west coasts of South America remain largely unexplored for species of *Nothobomolochus*. Given the diversity of potential hosts there, we suspect many new species remain to be described from beloniform, scombriform, and clupeiform fishes in these waters.

Of the 39 species of *Nothobomolochus*, 25 have been reported a single time, only from the host from which they were described. By far the most widely reported species of *Nothobomolochus* is *N. gibber*, which has been reported 28 times from beloniform fish of the families Belonidae and Hemiramphidae. The global distribution of this species, ranging from the Mediterranean Sea to Ascension Island in the Atlantic and a variety of localities spanning the Indian and Pacific Oceans calls into question whether these specimens are, in fact, conspecific. Because of the limited nature of host reports for species of *Nothobomolochus*, few negative host data available, and questionable conspecificity of specimens reported from a variety of hosts and geographic regions, a precise measure of the host specificity of the genus remains elusive.

Most reports of *Unicolax* come from host species of the family Scombridae. The report of *U. longispinus* from *Psenopsis anomala* (Temminck & Schlegel, 1844) (Centrolophidae), the first species reported from a non-scombrid host, is not particularly surprising given that the Centrolophidae are closely related to the Scombridae, an affinity supported by

Table 4 *Unicolax* species hosts and localities. Records in bold indicate type hosts and localities.

Species	Host	Host family	Host order	Locality	Marine ecoregion	Source
U. anonymus (*Vervoort, 1965*) *Cressey & Cressey, 1980*	**Euthynnus alletteratus**	Scombridae	Scombriformes	**Abidjan, Côte dTvoire, Gulf of Guinea**	Tropical Atlantic	*Vervoort (1965)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Ghana	Tropical Atlantic	*Cressey & Cressey (1980)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Gulf of Mexico	Tropical Atlantic	*Cressey & Cressey (1980)*
U. ciliatus *Cressey & Cressey, 1980*	**Scomberomorus plurilineatus**	Scombridae	Scombriformes	**Zanzibar Channel**	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus commerson	Scombridae	Scombriformes	Batavia, Java	Central Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus commerson	Scombridae	Scombriformes	Hong Kong	Central Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus commerson	Scombridae	Scombriformes	Mi-Tuo fishing port, Taiwan	Central Indo Pacific	*Lin & Ho (2006)*
	Scomberomorus commerson	Scombridae	Scombriformes	Philippines	Central Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus commerson	Scombridae	Scombriformes	Cochin, India	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus commerson	Scombridae	Scombriformes	Madagascar	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus commerson	Scombridae	Scombriformes	Phuket, Thailand	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus commerson	Scombridae	Scombriformes	Travancore, India	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus guttatus	Scombridae	Scombriformes	Batavia, Java	Central Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus guttatus	Scombridae	Scombriformes	Hong Kong	Central Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus guttatus	Scombridae	Scombriformes	Singapore	Central Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus guttatus	Scombridae	Scombriformes	Calicut, India	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus guttatus	Scombridae	Scombriformes	Padang, Sumatra	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus guttatus	Scombridae	Scombriformes	Phuket, Thailand	Western Indo Pacific	*Cressey & Cressey (1980)*
	Scomberomorus guttatus	Scombridae	Scombriformes	China	NA	*Cressey & Cressey (1980)*
	Scomberomorus niphonius	Scombridae	Scombriformes	Korea	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Scomberomorus niphonius	Scombridae	Scombriformes	China	NA	*Cressey & Cressey (1980)*
	Scomberomorus semifasciatus	Scombridae	Scombriformes	New Guinea	Central Indo Pacific	*Cressey & Cressey (1980)*

Species	Host	Host family	Host order	Locality	Marine ecoregion	Source
	Scomberomorus tritor	Scombridae	Scombriformes	Ghana	Tropical Atlantic	*Cressey & Cressey (1980)*
	Scomberomorus tritor	Scombridae	Scombriformes	Lagos, Nigeria	Tropical Atlantic	*Cressey & Cressey (1980)*
	Scomberomorus tritor	Scombridae	Scombriformes	Liberia	Tropical Atlantic	*Cressey & Cressey (1980)*
U. collateralis Cressey & Cressey, 1980	**Euthynnus alletteratus**	Scombridae	Scombriformes	**Saint George Bay, Lebanon**	Temperate Northern Atlantic	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Hong Kong	Central Indo Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Philippines	Central Indo Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Hawaii	Eastern Indo Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Saint George Bay, Lebanon	Temperate Northern Atlantic	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Woods Hole, Massachusetts	Temperate Northern Atlantic	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Chusan, China	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Japan	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Ghardaqa, Egypt	Western Indo Pacific	*Cressey & Cressey (1980)*
	Cybiosarda elegans	Scombridae	Scombriformes	Brisbane, Australia	Central Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Caribbean 9°11′N, 77°50′W	Tropical Atlantic	*Cressey & Cressey (1980)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Brazil	Tropical Atlantic	*Cressey & Cressey (1980)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Southeastern Iberia	Temperate Northern Atlantic	*Mele et al. (2016)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Saint George Bay, Lebanon	Temperate Northern Atlantic	*Cressey & Cressey (1980)*
	Euthynnus lineatus	Scombridae	Scombriformes	Galapagos	Tropical Eastern Pacific	*Cressey & Cressey (1980)*
	Euthynnus lineatus	Scombridae	Scombriformes	Lower California	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Euthynnus lineatus	Scombridae	Scombriformes	Mexico (Pacific)	Tropical Eastern Pacific	*Cressey & Cressey (1980)*
	Euthynnus lineatus	Scombridae	Scombriformes	Costa Rica (Pacific)	Tropical Eastern Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Brisbane, Australia	Central Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Formosa	Central Indo Pacific	*Cressey & Cressey (1980)*

Table 4 (*continued*)

Species	Host	Host family	Host order	Locality	Marine ecoregion	Source
	Euthynnus affinis	Scombridae	Scombriformes	Gulf of Thailand	Central Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Hong Kong	Central Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Java	Central Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Palau	Central Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Phillipines	Central Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Okinawa	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Tokyo	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Arabian Sea	Western Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Madagascar	Western Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Mozambique	Western Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Seychelles	Western Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Elat, Israel	Western Indo Pacific	*Cressey & Cressey (1980)*
	Orcynopsis unicolor	Scombridae	Scombriformes	Saint George Bay, Lebanon	Temperate Northern Atlantic	*Cressey & Cressey (1980)*
	Sarda australis	Scombridae	Scombriformes	New South Wales, Australia	Temperate Australasia	*Cressey & Cressey (1980)*
	Sarda orientalis	Scombridae	Scombriformes	Durban, South Africa	Temperate Southern Africa	*Cressey & Cressey (1980)*
	Sarda orientalis	Scombridae	Scombriformes	Pearl Island, Panama	Tropical Eastern Pacific	*Cressey & Cressey (1980)*
U. longicrus n. sp.	**Sillgao maculata**	Sillaginidae	Order *incertae sedis* in Eupercaria	**Moreton Bay, Queensland, Australia** 27°26′**S**, 153°24′**E**	Central Indo Pacific	Present study
	Sillago ciliata	Sillaginidae	Order *incertae sedis* in Eupercaria	Moreton Bay, Queensland, Australia 27°22′S, 153°13′E	Central Indo Pacific	Present study
U. longispinus Lin & Ho, 2006	**Psenopsis anomala**	Centrolophidae	Scombriformes	**Hsing-Dah fishing port, Taiwan (Kaohsiung County)**	Central Indo Pacific	*Lin & Ho (2006)*
	Psenopsis anomala	Centrolophidae	Scombriformes	Dong-Shih fishing port, Taiwan	Central Indo Pacific	*Lin & Ho (2006)*

Species	Host	Host family	Host order	Locality	Marine ecoregion	Source
U. mycterobius (*Vervoort, 1965*) *Cressey & Cressey, 1980*	**Auxis thazard**	Scombridae	Scombriformes	**Gulf of Guinea, off Abidjan, Côte dTvoire**	Tropical Atlantic	*Vervoort (1965)*
	Auxis rochei	Scombridae	Scombriformes	Strait of Gibraltar	Temperate Northern Atlantic	*Mele et al. (2015)*
	Auxis sp.	Scombridae	Scombriformes	Formosa	Central Indo Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Luzon, Phillipines	Central Indo Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Hawaii	Eastern Indo Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	New South Wales, Australia	Temperate Australasia	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Massachusetts	Temperate Northern Atlantic	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Tokyo	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Auxis sp.	Scombridae	Scombriformes	Ghardaqa, Egypt	Western Indo Pacific	*Cressey & Cressey (1980)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Saint George Bay, Lebanon	Temperate Northern Atlantic	*Cressey & Cressey (1980)*
	Euthynnus alletteratus	Scombridae	Scombriformes	Pensacola, Florida	Tropical Atlantic	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Kagoshima, Japan	Temperate Northern Pacific	*Cressey & Cressey (1980)*
	Euthynnus affinis	Scombridae	Scombriformes	Tokyo	Temperate Northern Pacific	*Cressey & Cressey (1980)*
U. quadrispinulus *Lin & Ho, 2006*	**Sillago sihama**	Sillaginidae	Order *incertae sedis* in Eupercaria	**Hsing-Dah fishing port, Taiwan (Kaohsiung County)**	Central Indo Pacific	*Lin & Ho (2006)*
	Sillago sihama	Sillaginidae	Order *incertae sedis* in Eupercaria	Dong-Shih fishing port, Taiwan	Central Indo Pacific	*Lin & Ho (2006)*
U. reductus *Cressey & Cressey, 1980*	**Katsuwonus pelamis**	Scombridae	Scombriformes	**New South Wales**	Temperate Australasia	*Cressey & Cressey (1980)*
	Katsuwonus pelamis	Scombridae	Scombriformes	Tahiti	Eastern Indo Pacific	*Cressey & Cressey (1980)*
	Katsuwonus pelamis	Scombridae	Scombriformes	Japan	Temperate Northern Pacific	*Cressey & Cressey (1980)*

mulitlocus phylogenetic analyses (*Betancur et al., 2017*). Both families, in fact, are now recognized as members of the order Scombriformes (*Betancur et al., 2017*). However, the discovery of *U. quadrispinulus* and *U. longicrus* parasitizing species of *Sillago* is unexpected given the distant phylogenetic relationship of these hosts with the Scombridae (see *Betancur et al., 2017* fig. 2). This suggests that, not only are other scombrids and related families (i.e., Amarsipidae, Ariommatidae, Arripidae, Bramidae, Caristiidae, Chiasmodontidae, Gempylidae, Icosteidae, Nomeidae, Pomatomidae, Scombropidae, Scombrolabracidae, Stromateidae, Tetragonuridae, and Trichiuridae) candidate hosts of *Unicolax*, but also that much of the Eupercaria, the largest series of fishes, containing over 6,000 species in 161 families and at least 17 orders, are potential hosts.

The fact that most known hosts of *Unicolax* are widely harvested, economically important fish species is likely a reflection of sampling bias rather than true host distribution. Both the inaccessible microhabitat (i.e., the nasal sinuses) parasitized by these copepods and their small size (0.6–3 mm) has contributed to the slow discovery of species of *Unicolax*. Given the phylogenetic diversity of fish species hosting members of *Unicolax*, we predict that careful observation of the nasal sinuses of marine fish will reveal numerous additional scombriform and eupercarian fish host species of *Unicolax*, many of which are likely new to science. It is likely that diversity of this genus is substantially higher than current records suggest, and this also likely applies to other copepod genera that predominately inhabit fish nostrils.

Five genera of bomolochids are known to live almost exclusively in the nostrils of teleosts: *Acanthocolax Vervoort, 1969*, *Ceratocolax Vervoort, 1965*, *Naricolax Ho, Do & Kasahara, 1983*, *Tegobomolochus* Izawa, 1976, and *Unicolax*. These genera share a number of morphological similarities and are thought to be closely related (*Huys et al., 2012*). It is interesting to consider the potential functional significance of shared morphological features in this group. For instance, the second leg of *Ceratocolax, Naricolax, Unicolax*, and *Tegobomolochus* have flattened endopods, and *Huys et al. (2012)* proposed this modification may help seal the suction cup formed by the ventral cephalothorax, a process documented in other parasitic copepods (e.g., leg 3 of Caligidae by *Kabata & Hewitt (1971)*). Similarly, males of *Naricolax, Unicolax,* and *Tegobomolochus* possess a flattened leg 1, which may assist in sealing the cephalothoracic suction cup.

Other structures have arisen in a number of nostril inhabiting copepods. A pincer-like structure arising from projections of anterior cephalothorax and dorsal projections of the antennae is present in *Acanthocolax, Ceratocolax*, and *Tegobomolochus* (*Huys et al., 2012*). There may be some evidence of this, albeit to a lesser degree, in species of *Unicolax*. *Vervoort (1965)* shows *U. anonymous* to have a protrusion at the anterior margin of the cephalothorax (fig. 1) and *Cressey & Cressey (1980)* illustrated a similar protrusion in *U. collateralis* (see fig. 9A). Perhaps a pincer-like structure is formed between this anterior protrusion of the cephalothorax and the modified spine-like seta of the antennule of these species, which may provide a functional explanation for the heavily sclerotized fourth seta of the antennule in *Unicolax*. It would be interesting to explore if these pincer-like structures are used for attachment in the nostril, perhaps to the lamellae of the olfactory rosette. A number of nostril inhabiting copepods have also developed dorsal extensions on

their body somites (e.g., *Ceratocolax, Tegobomolochus, U. anonymous* [see *Vervoort, 1965* fig. 1], and *U. reductus* [*Cressey & Cressey, 1980* fig. 23a]). Given that dorsal extensions appear to have arisen multiple times in nostril-inhabiting copepods, it is possible that they have functional significance; for instance, they may reduce shearing forces on the copepods or enable them to wedge themselves in small cavities of the nasal passage.

There is considerable variation in the ornamentation on *Unicolax* appendages. In particular, ornamentation on the margins of spines on legs 2–4 varies from relatively few, robust serrations in *U. anonymous, U. collateralis*, and *U. reductus*, to numerous fine serrations along the margins of the spines in *U. ciliatus, U. longicrus, U. longispinus, U. mycterobius,* and *U. quadrispinulus*. The inner seta on leg 4 also varies from a typical plumose seta, as seen in *U. quadrispinulus*, to a more spine-like element in most other species of *Unicolax*; this element is highly reduced to a short spine-like element in *U. reductus*. We recommend researchers pay careful attention to the ornamentation of setal elements in species of *Unicolax*, as these are likely to be useful taxonomic characters.

ACKNOWLEDGEMENTS

We are grateful to Dr. Tom Cribb, Dr. Scott Cutmore, and all members of the Cribb Lab for their vision and effort on the collecting expedition. We thank all members of the Moreton Bay parasite survey team for collecting hosts and parasites. We also thank Pavel Avdeyev for translating Russian locality information from *Avdeev (1977)* and *Avdeev (1978)*.

Funding

This study was funded by an Australian Biological Resources Study (ABRS) National Taxonomy Research Grant RF215-40 to Thomas Cribb and Scott Cutmore (University of Queensland). This work was supported in part by funding from the Society of Systematic Biologists mini ARTS award to James P. Bernot, the GWU Knowledge in Action Career Internship Fund to James P. Bernot, the Smithsonian NMNH Reed Fellowship for Copepod Research to James P. Bernot, and the AMNH Lerner-Gray Fund for Marine Research to James P. Bernot. There was no additional external funding received for this study. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
Australian Biological Resources Study (ABRS) National Taxonomy Research: RF215-40.
University of Queensland.
Society of Systematic Biologists mini ARTS.
GWU Knowledge in Action Career Internship Fund.
Smithsonian NMNH Reed Fellowship for Copepod Research.
AMNH Lerner-Gray Fund for Marine Research.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- James P. Bernot conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Geoffrey A. Boxshall conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

The Animal Welfare Unit at the University of Queensland provided approval for the ethical use of animals for this research (SBS/248/15/ABRS/ARC).

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

Australian Department of Agriculture, Fisheries, and Forestry provided permit number 187264.

Data Availability

The raw data used in the beogeography and host association summaries are available in Tables S1 and S2.

Museum accession numbers are:

Nothobomolochus johndaveorum n. sp.

Holotype female (QM W29438) and 10 female paratypes (2 paratypes QM W29439; 4 paratypes NHMUK 2018.194–2018.197; 4 paratypes USNM 1532298–1532300).

Unicolax longicrus n. sp.

Holotype female (QM W29434) and 5 female paratypes (1 paratype QM W29435; 2 paratypes NHMUK 2018.198–2018.199; 2 paratypes USNM 1532294–1532295). Allotype male (QM W29436) and 4 male paratypes (2 paratypes NHMUK 2018.200–2018.201; 2 paratypes USNM 1532296–1532297).

New Species Registration

The following information was supplied regarding the registration of a newly described species:

Publication LSID:

urn:lsid:zoobank.org:pub:E8663AB9-EF47-4382-8096-C45B10A879A7.

Nothobomolochus johndaveorum LSID: urn:lsid:zoobank.org:act:D5F768DE-686A-4B00-B241-8BBA061BF4A9.

Unicolax longicrus LSID: urn:lsid:zoobank.org:act:0E24C5F0-29C1-49C9-830D-7124D27D3FAE.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.6858#supplemental-information.

REFERENCES

Avdeev GV. 1974. New species of crustacean, *Nothobomolochus chilensis* sp. n. (Copepoda, Cyclopoida), parasitic on *Scomberesox saurus* (Wahlbaum). *Parazitologiia* **8**:39–44.

Avdeev GV. 1977. New and some known species of copepods of the genus *Nothobomolochus* Vervoort (Cyclopoida, Bomolochidae) parasitizing on marine fishes from the Pacific and Indian Oceans. *Biologiya Morya* **6**:12–30.

Avdeev GV. 1978. Copepods of the genus *Nothobomolochus* Vervoort (Cyclopoida. Bomolochidae) parasitizing on marine fishes. II; Three new and one known species from tropical waters of the Atlantic Ocean. *Biologiya Morya* **1**:24–35.

Avdeev GV. 1986. Three new and one well-known species of parasitic copepods in the genus *Nothobomolochus* (Bomolochidae, Poecilostomatoida) from the Pacific Ocean fishes. *Zoologicheskii Zhurnal* **65**:55–65.

Bassett-Smith PW. 1898. Some new or rare parasitic copepods found on fish in the Indo-Tropic Region. *Annals and Magazine of Natural History* **2**:357–372 DOI 10.1080/00222939808678056.

Betancur R, Wiley EO, Arratia G, Acero A, Bailly N, Miya M, Lecointre C, Orti G. 2017. Phylogenetic classification of bony fishes. *BMC Evolutionary Biology* **17**:162 DOI 10.1186/s12862-017-0958-3.

Claus C. 1864. Beiträge Zur Kenntnis Der Schmarotzerkrebse. The genus *Bomolochus* and its relatives. *Zeitschrift Für Wissenschaftliche Zoologie* **14**:365–383.

Cressey R. 1983. Parasitic copepods from the Gulf of Mexico and Caribbean Sea, II: Bomolochidae. *Smithsonian Contributions to Zoology* **389**:1–35.

Cressey R, Collette B. 1970. Copepods and needlefishes: a study in host-parasite relationships. *Fishery Bulletin, United States National Marine Fisheries Service* **63**:347–432.

Cressey R, Cressey HB. 1980. Parasitic copepods of mackerel- and tuna-like fishes (Scombridae) of the world. *Smithsonian Contributions to Zoology* **311**:1–186.

Deboutteville CD, Nunes-Ruivo LP. 1958. Copépodes parasites des Poissons méditerranéens. *Vie et Milieu* **9**:215–235.

El-Rashidy H, Boxshall GA. 2009. Parasites gained: alien parasites switching to native hosts. *Journal of Parasitology* **95**:1326–1329 DOI 10.1645/GE-2190.1.

El-Rashidy H, Boxshall GA. 2011. Two new species of parasitic copepods (Crustacea) on two immigrant rabbitfishes (family Siganidae) from the Red Sea. *Systematic Parasitology* **79**:175–193 DOI 10.1007/s11230-011-9298-7.

El-Rashidy H, Boxshall GA. 2014. A new parasitic copepod (Cyclopoida: Bomolochidae) from a ponyfish (Leiognathidae) caught in Egyptian Mediterranean waters, with a review of hosts and key to species of *Nothobomolochus*. *Systematic Parasitology* **87**:111–126 DOI 10.1007/s11230-013-9462-3.

Froese R, Pauly D. 2018. FishBase. *Available at http://www.fishbase.org* (accessed on 25 December 2018).

Gnanamuthu CP. 1949. *Bomolochus multispinosa*, sp. nov.: an ergasilid copepod observed in copulation. *Records of the Indian Museum, Calcutta* **45**:309–319.

Hameed MS, Kumar KA. 1988. Two new species of *Nothobomolochus* (Copepoda: Bomolochidae) from Kerala. *Journal of the Marine Biological Association of India* **28**:257–273.

Ho J-S, Do TT, Kasahara S. 1983. Copepods of the family Bomolochidae parasitic on fishes of Kojima Bay, Okayama Prefecture. *Journal of the Faculty of Applied Fisheries* **22**:1–41.

Ho J-S, Kim I-H, Sey O. 2000. Two species of bomolochid copepods (Crustacea) parasitic on marine fishes of Kuwait. *Proceedings of the Biological Society of Washington* **113**:670–680.

Ho J-S, Lin C-L. 2005. Two new species of *Nothobomolochus Vervoort, 1962* (Copepoda, Bomolochidae) parasitic on marine fishes of Taiwan. *Crustaceana* **77**:1389–1402 DOI 10.1163/1568540043165994.

Ho J-S, Sey O. 1996. Parasitic Copepoda of marine fishes from Kuwait: a preliminary report. *Kuwait Journal of Science & Engineering* **23**:61–69.

Huys R, Boxshall G. 1991. *Copepod evolution.* London: The Ray Society.

Huys R, Fatih F, Ohtsuka S, Llewellyn-Hughes J. 2012. Evolution of the bomolochiform superfamily complex (Copepoda: Cyclopoida): new insights from ssrdna and morphology, and origin of umazuracolids from polychaete-infesting ancestors rejected. *International Journal for Parasitology* **42**:71–92 DOI 10.1016/j.ijpara.2011.10.009.

International Commission on Zoological Nomenclature. 2012. Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Zootaxa* **3450**:1–7.

Kabata Z, Hewitt GC. 1971. Locomotory mechanisms in Caligidae (Crustacea: Copepoda). *Journal of the Fisheries Board of Canada* **28**:1143–1151 DOI 10.1139/f71-169.

Kaliyamurthy M. 1990. On a new species of copepod, *Nothobomolochus pulicatensis* sp. nov., parasitic on *Hemirhamphus gaimardi* Valenciennes from the Pulicat Lake, east coast of India. *Records of the Zoological Survey of India* **86**:515–518.

Khosheghbal M, Pazooki J. 2015. First report of two parasitic copepods of Pampus argenteus (Stromateidae) in west of Persian Gulf, Iran. *Iranian Journal of Animal Biosystematics* **11**:1–6.

Krøyer H. 1863. Bidrag til kundskab om snyltekrebsene. *Naturhistorisk Tidsskrift* **3**:75–426.

Lewis A. 1968. Copepod crustaceans parasitic on fishes of Eniwetok Atoll. *Proceedings of the United States National Museum* **125**:1–78.

Lin C-L, Ho J-S. 2006. Four species of *Unicolax* Cressey & Cressey, 1980 (Copepoda: Bomolochidae) parasitic on marine fishes of Taiwan. *Zoological Studies* **45**:339–356.

Lin CL, Ho JS. 2008. *Nothobomolochus gazzae* (Shen, 1957), a rare parasitic copepod found on marine fish of Taiwan. *Journal of the Fisheries Society of Taiwan* **35(2)**:167–174.

Marques E. 1965. Copépodes parasitas de peixes marinhos de S. Tomé. *Garcia de Orta, Lisbon* **13(2)**:185–192.

Mele S, Pennino MG, Piras MC, Macias D, Gómez-Vives MJ, Alemany F, Montero FE, Garippa G, Merella P. 2016. Ecology of the Atlantic black skipjack Euthynnus alletteratus (Osteichthyes: Scombridae) in the western Mediterranean Sea inferred by parasitological analysis. *Parasitology* **143**:1330–1339 DOI 10.1017/s0031182016000792.

Mele S, Saber S, Gómez-Vives MJ, Garippa G, Alemany F, Macías D, Merella P. 2015. Metazoan parasites in the head region of the bullet tuna Auxis rochei (Osteichthyes: Scombridae) from the western Mediterranean Sea. *Journal of Helminthology* **89**:734–739 DOI 10.1017/s0022149x14000662.

Monod T. 1970. Sur un *Nothobomolochus* (Crust., Copepodes) parasite d'un hemiramphe he Madagascar. *Bulletin du Museum National d'Histoire Naturelle, Paris, Section A Zoologie. Biologie et Écologie Animales* **42**:401–409.

Pearse AS. 1947. Parasitic copepods from Beaufort, North Carolina. *Journal of the Elisha Mitchell Scientific Society* **63**:1–16.

Pillai NK. 1965. Copepods parasitic on South Indian fishes: family Bomolochidae—3. *Journal of the Bombay Natural History Society* **62**:38–55.

Pillai NK. 1967. Redescription of seven species of bomolochids from the collections of the United States National Museum. *Journal of the Marine Biological Association of India* **7(2)**:243–276.

Pillai NK. 1973. Three new bomolochids parasitic on fishes of the Kerala coast. *Indian Journal of Fisheries* **20**:487–496.

Pillai NK. 1985. Copepod parasites of marine fishes. In: *The Fauna of India.* Calcutta: Zoological Society of India.

Pillai NK, Natarajan P. 1977. Copepods parasitic on fishes of the Kerala Coast. *Aquatic Biology* **2**:19–43.

Shen CJ. 1957. Parasitic copepods from fishes of China, Part I. Cyclopoida (1). *Acta Zoologica Sinica* **9**:297–327.

Shiino SM. 1957. Copepods parasitic on Japanese fishes, 16. Bomolochidae and Taeniacanthidae. *Reports of the Faculty of Fisheries, Prefectural University of Mie* **2**:411–428.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana AL, Lourie SA. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *AIBS Bulletin* **57**:573–583 DOI 10.1641/b570707.

Timi JT, Sardella NH. 1997. A new species of *Nothobomolochus* (Copepoda: Bomolochidae) parasitic on Engraulis anchoita (Pisces: Engraulidae) from Argentina. *Folia Parasitologica, Ceske Budejovice* **44**:305–308.

Venmathi Maran BA, Moon SY, Adday TK, Khamees NR, Myoung JG. 2014. A new species of parasitic copepod *Nothobomolochus* and redescription of Orbitacolax hapalogenyos (Yamaguti and Yamasu, 1959) (Cyclopoida: Bomolochidae) off Iraq. *Acta Parasitologica* **59**:675–685 DOI 10.2478/s11686-014-0300-9.

Vervoort W. 1962. A review of the genera and species of the Bomolochidae (Crustacea, Copepoda), including the description of some old and new species. *Zoologische Verhandelingen* **56**:1–111.

Vervoort W. 1965. Three new species of Bomolochidae (Copepoda, Cyclopoida) from tropical Atlantic tunnies. *Zoologische Verhandelingen* **76**:1–40.

Vervoort W. 1969. Caribbean Bomolochidae (Copepoda: Cyclopoida). *Studies on the Fauna of Curaçao and Other Caribbean Islands* **28(105)**:1–125.

Walter TC, Boxshall G. 2019. World of Copepods database. Nothobomolochus Vervoort, 1962. Accessed through: World Register of Marine Species. *Available at http://www.marinespecies.org/aphia.php?p=taxdetails&id=128611* (accessed on 11 April 2019).

Wilson CB. 1911. North American parasitic copepods belonging to the family Ergasilidae. *Proceedings of the US National Museum* **39**:263–400 DOI 10.5479/si.00963801.39-1788.263.

Yamaguti S. 1939. Parasitic copepods from fishes of Japan. Part 4. Cyclopoida, II. *Volume Jubilare Pro Prof. Sadao Yoshida* **2**:391–415.

Yamaguti S. 1953. Parasitic copepods from fishes of Japan. Part 7. Cyclopoida, III and Caligoida, IV. *Publications of the Seto Marine Biological Laboratory* **3**:221–231 DOI 10.5134/174466.

Yamaguti S, Yamasu T. 1959. Parasitic copepods from fishes of Japan with descriptions of 26 new species and remarks on two known species. *Biological Journal of Okayama University* **5(3–4)**:89–165.