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Three new species of acanthocephalans (Palaeacanthocephala) from marine fishes collected off the East Coast of South Africa

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Abstract: Three new species of acanthocephalans are described from marine fishes collected in Sodwana Bay, South Africa: *Rhadinorhynchus gerberi* n. sp. from *Trachinotus botla* (Shaw), *Pararhadinorhynchus sodwanensis* n. sp. from *Pomadasys furcatus* (Bloch et Schneider) and *Transvena pichelinae* n. sp. from *Thalassoma purpureum* (Forsskål). *Transvena pichelinae* n. sp. differs from the single existing species of the genus *Transvena annulospinosa* Pichelin et Cribb, 2001, by the lower number of longitudinal rows of hooks (10–12 *vs* 12–14, respectively) and fewer hooks in a row (5 *vs* 6–8), shorter blades of anterior hooks (55–63 *vs* 98), more posterior location of the ganglion (close to the posterior margin of the proboscis receptacle *vs* mid-level of the proboscis receptacle) and smaller eggs (50–58 × 13 µm *vs* 62–66 × 13–19 µm). *Pararhadinorhynchus sodwanensis* n. sp. differs from all known species of the genus by a combination of characters. It closely resembles unidentified species *Pararhadinorhynchus* sp. *sensu* Weaver and Smales (2014) in the presence of a similar number of longitudinal rows of hooks on the proboscis (16–18 *vs* 18) and hooks in a row (11–13 *vs* 13–14), but differs in the position of the lemnisci (extend to the level of the posterior end of the proboscis receptacle or slightly posterior *vs* extend to the mid-level of the receptacle), length of the proboscis receptacle (910–1180 µm *vs* 1,460 µm) and cement glands (870–880 µm *vs* 335–350 µm). *Rhadinorhynchus gerberi* n. sp. is distinguishable from all its congeners by a single field of 19–26 irregular circular rows of the tegumental spines on the anterior part of the trunk, 10 longitudinal rows of hooks on the proboscis with 29–32 hooks in each row, subterminal genital pore in both sexes, and distinct separation of the opening of the genital pore from the posterior edge of the trunk (240–480 µm) in females. Sequences for the 18S rDNA, 28S rDNA and *cox*1 genes were generated to molecularly characterise the species and assess their phylogenetic position. This study provides the first report based on molecular evidence for the presence of species of *Transvena* Pichelin et Cribb, 2001 and *Pararhadinorhynchus* Johnston et Edmonds, 1947 in African coastal fishes.

Key words: Echinornhynchida, *Transvena*, *Pararhadinorhynchus*, *Rhadinorhynchus*, morphology, Sodwana Bay, DNA

The parasite diversity of South African marine fishes has rarely been studied and the discoveries of new species from numerous groups of parasites including acanthocephalans are highly expected (Smit and Hadfield 2015). Our knowledge of the acanthocephalan fauna of marine fishes from the waters around South Africa is restricted to two articles published by Dollfus and Golvan (1963) and Bray (1974). To date, only a single species of *Rhadinorhynchus* Lühe, 1911, *Rhadinorhynchus capensis* Bray, 1974, and another of *Longicollum* Yamaguti, 1935, *Longicollum chabanaudi* Dollfus et Golvan, 1963, are known.

During a parasitological survey of the marine fishes in Sodwana Bay, KwaZulu-Natal Province, South Africa in 2016 and 2017, specimens of acanthocephalans were found in the evileye blaasop *Amblyrhynchotes honckenii* (Bloch) (Tetraodontiformes: Tetraodontidae), white seabream *Diplodus sargus* (Linnaeus) (Perciformes: Sparidae), *Plectorhinchus* sp. (Perciformes: Haemulidae), banded grunter *Pomadasys furcatus* (Bloch et Schneider) (Perciformes: Haemulidae), Jarbua terapon *Terapon jarbua* (Forsskål) (Perciformes: Terapontidae), surge wrasse *Thalassoma purpureum* (Forsskål) (Perciformes: Labridae) and largespotted dart *Trachinotus botla* (Shaw) (Perciformes: Carangidae). Detailed morphological examination and molecular analyses based on the 18S and 28S rRNA and mitochondrial cytochrome *c* oxidase 1 (*cox*1) genes of our material revealed the presence of three undescribed species, belonging to the genera *Transvena* Pichelin et Cribb, 2001 and *Pararhadinorhynchus* Johnston et Edmonds, 1947 within the Transvenidae (Echinorhynchida) and *Rhadinorhynchus* within the Rhadinorhynchidae (Echinorhynchida).

The Transvenidae is a small family of acanthocephalans presently including only four genera and nine species. The

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family was established to accommodate the genera *Trajectura* Pichelin et Cribb, 2001, *Transvena* and *Pararhadinorhynchus* based on the presence of only two cement glands (Pichelin and Cribb 2001). Recently, the fourth genus of the family, *Paratrajectura* Amin, Heckmann et Ali, 2018, was described (Amin et al. 2018).

The genus *Pararhadinorhynchus* was described within the family Rhadinorhynchidae (see Johnston and Edmonds 1947) and later transferred into the Transvenidae on the basis of the lack of trunk spines and the presence of two cement glands (Pichelin and Cribb 2001). This was supported by Weaver and Smales (2014) and Smales (2015), but rejected by Amin (2013), Amin et al. (2018), Ha et al. (2018) and Smales et al. (2018). Ha et al. (2018) consider this genus as a member of the family Diplosentidae Meyer, 1932 (Echinorhynchida). The genus *Pararhadinorhynchus* consists of four species: *P. coorongensis* Edmonds, 1973, *P. mugilis* Johnston et Edmonds, 1947, *P. upenei* Wang, Wang et Wu, 1993 and *P. magnus* Ha, Amin, Ngo et Heckmann, 2018 that parasitise a wide variety of marine fishes in Indo-Pacific. *Transvena* is a monotypic genus with its single species, *T. annulospinosa* Pichelin et Cribb, 2001, described from the wrasse *Anampses neoguinaicus* Bleeker and six other species of Labridae from Heron Island, Great Barrier Reef, Australia (Pichelin and Cribb 2001).

The members of the Rhadinorhynchidae parasitise both freshwater and marine fishes. The systematics of this family has long been controversial and is presently unsatisfactory due to the significant morphological differences between genera and species included in the family. In particular, the family includes taxa with different numbers of cement glands and with or without spines on the trunk (Pichelin and Cribb 2001). According to the most recent morphology-based classification system of the Acanthocephala by Amin (2013), the Rhadinorhynchidae is represented by 24 genera in five subfamilies: Golvanacanthinae (monotypic), Gorgorhynchinae (12 genera), Rhadinorhynchinae (9 genera), Serrasentinae (monotypic) and Serrasentoidinae (monotypic). Phylogenetic studies, however, have shown the remote positions of the Serrasentinae and three genera of the Gorgorhynchinae, *Gorgorhynchoides* Cable et Linderoth, 1963, *Leptorhynchoides* Kostylew, 1924 and *Pseudoleptorhynchoides* Salgado-Maldonado, 1976 from other Rhadinorhynchidae (García-Varela and Nadler 2005, 2006, Verweyen et al. 2011). Some of the results of the phylogenetic studies were accepted in the classification of the Acanthocephala by Smales (2015). For example, the genera *Leptorhynchoides* and *Pseudoleptorhynchoides* were excluded from the Rhadinorhynchidae and transferred to the Illiosentidae (Echinorhynchida). However, the morphology-based systematic concept of the family requires further molecular phylogenetic studies to clarify the relationships at the suprageneric level.

Rhadinorhynchus is the type genus of the Rhadinorhynchidae. It currently comprises 42 valid species with 26 of those described from Indo-West Pacific (Amin et al. 2011, Amin 2013, Smales 2014, Pichelin et al. 2016, Amin and Heckmann 2017). In Africa, seven species of *Rhadinorhynchus* have been reported from various marine teleosts: *R. africanus* (Golvan, Houin et Deltour, 1963), *R. atheri* (Farooqi, 1981), *R. cadenati* (Golvan et Houin, 1964), *R. camerounensis* Golvan, 1969, *R. saltatrix* Troncy et Vassiliadès, 1973, *R. capensis*, and *R. lintoni* Cable et Linderoth, 1963 (Cable and Linderoth 1963, Golvan 1969, Troncy and Vassiliadès 1973, Bray 1974, Farooqi 1981).

The present paper contributes to our knowledge of the acanthocephalans in marine fishes in South Africa by providing the first molecular data accompanied with morphological descriptions of three new species, *Pararhadinorhynchus sodwanensis* n. sp., *Rhadinorhynchus gerberi* n. sp. and *Transvena pichelinae* n. sp.

MATERIALS AND METHODS

Specimen collection and morphological examination

Eight *Amblyrhynchotes honckenii* (total length 10.2–13.2 cm), 13 *Diplodus sargus* (total length 14–23.7 cm), one Plectorhinchus sp. (total length 28 cm), five *Pomadasys furcatus* (total length 20.5–28 cm), three *Terapon jarbua* (total length 11.8–12 cm), three *Thalassoma purpureum* (total length 18–21.8 cm) and seven *Trachinotus botla* (total length 18.5–29.5 cm) were collected in Sodwana Bay, KwaZulu-Natal Province, South Africa (32°40'46"E; 27°32'24"S) during July 2016 and October 2017. Fishes were dissected fresh and examined for the presence of parasites. When found, the acanthocephalans were washed with saline and fixed in 80% ethanol for morphological and molecular analyses. Morphology of the acanthocephalans was studied on temporary total mounts cleared in Berlese's medium using a compound Zeiss Axio Imager M1 microscope equipped with DIC optics. Drawings were made with the aid of a drawing tube. All measurements in the text and tables are in micrometres unless otherwise stated. Trunk length does not include proboscis, neck and evaginated bursa.

Specimens selected for scanning electron microscopy (SEM) were dehydrated through an ethanol series and critical point dried using liquid carbon dioxide (Bio-Rad, Bio-Rad Microscience Division, London, United Kingdom). They were then mounted onto 12 mm aluminium stubs with double-sided carbon tape and sputter-coated for 2 min with a gold palladium alloy, in argon gas at a pressure of 2 atm (SPI-ModuleTM Sputter Coater, SPI Supplies, West Chester, PA, USA) and examined with a Phenom PRO Desktop SEM (Phenom PRO Desktop SEM, Phenom-World B., Eindhoven, Netherlands) at an accelerated voltage of 10 kV.

The type material was deposited in the Parasite Collection of the National Museum (NMB), Bloemfontein, South Africa and in the Helminthological Collection of the Institute of Parasitology (IPCAS), Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic. The hologenophores (anterior part of the worms not used for molecular analysis) were deposited in the IPCAS.

Sequence generation

Genomic DNA was isolated from the posterior part of specimens representing each species using the standard protocol for the Kapa Express Extract kit (Kapa Biosystems, Cape Town, South Africa). Partial fragments of the 18S rRNA gene was amplified using the forward primer (5'-AGA TTA AGC CAT GCA TGC GTA AG-3') and the reverse primer (5'-TGA TCC TTC

Table 1. Sequence data for the Echinorhynchida taxa included in the phylogenetic analyses

Species	Host	GenBank No.		Reference
		18S	*cox*1	
Arhythmacanthidae				
Acanthocephaloides propinquus (Dujardin, 1845)	*Gobius bucchichii* Steindachner	AY830149	DQ089713	García-Varela and Nadler (2005, 2006)
Cavisomidae				
Filisoma bucerium Van Cleave, 1940	*Kyphosus elegans* (Peters)	AF064814	DQ089722	García-Varela et al. (2000), García-Varela and Nadler (2006)
F. rizalinum Tubangui et Masilungan, 1946	*Scatophagus argus* (Linnaeus)	JX014229	–	Verweyen et al. (2011)
Neorhadinorhynchus nudus (Harada, 1938)	*Auxis thazard* (Lacepede)	–	MG757444	Li et al. (2018)
Echinorhynchidae				
Acanthocephalus anguillae (Müller, 1780)	*Perca fluviatilis* Linnaeus	–	AM039865	Benesh et al. (2006)
A. clavula (Dujardin, 1845)	*P. fluviatilis*	–	AM039866	Benesh et al. (2006)
A. dirus (Van Cleave, 1931)	*Asellus aquaticus* (Linnaeus)	AY830151	DQ089718	García-Varela and Nadler (2005, 2006)
A. lucii (Müller, 1776)	*Perca fluviatilis* Linnaeus	AY830152	AM039837	García-Varela and Nadler (2005), Benesh et al. (2006)
A. nanus Van Cleave, 1925	*Cynops pyrrhogaster* (Boie)	LC129889	–	Nakao (2016)
Echinorhynchus bothniensis Zdzitowiecki et Valtonen, 1987	*Osmerus eperlanus* (Linnaeus)	–	KP261018	Wayland et al. (2015)
E. brayi Wayland, Sommerville et Gibson, 1999	*Pachycara crassiceps* (Roule)	–	KP261015	Wayland et al. (2015)
E. cinctulus Porta, 1905	*Lota lota* (Linnaeus)	–	KP261014	Wayland et al. (2015)
E. gadi Müller, 1776	not determined	AY218123	AY218095	Giribet et al. (2004)
E. salmonis Müller, 1784	*Coregonus lavaretus* (Linnaeus)	–	KP261017	Wayland et al. (2015)
E. truttae Schrank, 1788	*Thymallus thymallus* (Linnaeus)	AY830156	DQ089710	García-Varela and Nadler (2005, 2006)
Pseudoacanthocephalus lucidus Van Cleave, 1925	*Rana ornativentris* Werner	LC129279	LC100057	Nakao (2016)
P. toshimai Nakao, 2016	*Rana pirica* Matsui	LC129278	LC100044	Nakao (2016)
Illiosentidae				
Dentitruncus truttae Sinzar, 1955	*Salmo trutta* Linnaeus	JX460865	JX460877	Vardić Smrzlić et al. (2013)
Dollfusentis chandleri Golvan, 1969	–	–	DQ320484	Baker and Sotka (unpublished data)
Illiosentis sp.	not determined	AY830158	DQ089705	García-Varela and Nadler (2005, 2006)
Koronacantha mexicana Monks et Pérez-Ponce de León, 1996	*Haemulopsis leuciscus* (Günther)	AY830157	DQ089708	García-Varela and Nadler (2005, 2006)
K. pectinaria (Van Cleave, 1940)	*Microlepidotus brevipinnis* (Steindachner)	AF092433	DQ089707	García-Varela and Nadler (2005, 2006)
Leptorhynchoides thecatus (Linton, 1891)	*Lepomis cyanellus* Rafinesque	AF001840	DQ089706	Near et al. (1998), García-Varela and Nadler (2006)
Pseudoleptorhynchoides lamothei Salgado-Maldonado, 1976	*Ariopsis guatemalensis* (Günter)	EU090950	EU090949	García-Varela and Gonzalez-Oliver (2008)
Pomphorhynchidae				
Longicollum pagrosomi Yamaguti, 1935	*Pagrus major* (Temmink et Schlegel)	LC195887	–	Mekata et al. (unpublished data)
L. pagrosomi	*Oplegnathus fasciatus* (Temminck et Schlegel)	–	KY490048	Li et al. (2017)
Pomphorhynchus bulbocolli Linkins, 1919	*Oncorhynchus mykiss* (Walbaum)	AF001841	–	Near et al. (1998)
P. bulbocolli	*Lepomis macrochirus* Rafinesque	–	DQ089709	García-Varela and Nadler (2006)
P. laevis (Zoega in Müller, 1776)	*Gammarus pulex* (Linnaeus)	AY423346	AY423348	Perrot-Minnot (2004)
P. purhepechus García-Varela, Mendoza-Garfias, Choudhury et Pérez-Ponce de León, 2017	*Moxostoma austrinum* Bean	–	KY911281	García-Varela et al. (2017)
P. tereticollis (Rudolphi, 1809)	*G. pulex*	AY423347	AY423351	Perrot-Minnot (2004)
P. zhoushanensis Li, Chen, Amin et Yang, 2017	*O. fasciatus*	–	KY490045	Li et al. (2017)
Tenuiproboscis sp.	*Epinephelus malabaricus* (Bloch et Schneider)	–	JF694273	Vijayan et al. (unpublished)
Rhadinorhynchidae				
Gorgorhynchoides bullocki Cable et Mafarachisi, 1970	*Eugerres plumieri* (Cuvier)	AY830154	DQ089715	García-Varela and Nadler (2005, 2006)
Gymnorhadinorhynchus decapteri Braicovich, Lanfranchi, Farber, Marvaldi, Luque et Timi, 2014	*Decapterus punctatus* (Cuvier)	KJ590123	KJ590125	Braicovich et al. (2014)
Gymnorhadinorhynchus mariserpentis Steinauer, Garcia-Vedrenne, Weinstein et Kuris, 2019	*Regalecus russelii* (Cuvier)	MK014866	MK012665	Steinauer et al. (2019)
Rhadinorhynchus laterospinosus Amin, Heckmann et Van Ha, 2011	*Auxis rochei* (Risso)	MK457183	MK572744	Amin et al. (2019)
Rhadinorhynchus lintoni Cable et Linderoth, 1963	*Selar crumenophthalmus* (Bloch)	JX014224	–	Verweyen et al. (2011)
***R. gerberi* n. sp.**	*Trachinotus botla* (Shaw)	MN105739	MN104897	Present study
***R. gerberi* n. sp.**	*Amblyrhynchotes honckenii* (Bloch)	MN105740	MN104898	Present study
***R. gerberi* n. sp.**	*Terapon jarbua* (Forsskål)	MN105741	–	Present study
R. pristis (Rudolphi, 1802)	*Gempylus serpens* Cuvier	JX014226	–	Verweyen et al. (2011)
R. pristis	*Alosa alosa* (Linnaeus)	KR349116	–	Bao et al. (2015)
Rhadinorhynchus sp.	*Nyctiphanes couchii* (Bell)	JQ061133	–	Gregori et al. (2013)
Rhadinorhynchus sp.	Sciaenidae	AY062433	DQ089712	García-Varela et al. (2002), García-Varela and Nadler (2006)
Serrasentis sagittifer (Linton, 1889)	*Johnius coitor* (Hamilton)	JX014227	–	Verweyen et al. (2011)
S. sagittifer	*Lutjanus sebae* (Cuvier)	–	MF134296	Barton et al. (2018)
S. nadakali George et Nadakal, 1978	not determined	KC291715	KC291713	Paul et al. (unpublished)
Transvenidae				
Transvena annulospinosa Pichelin et Cribb, 2001	*Anampses neoguinaicus* Bleeker	AY830153	DQ089711	García-Varela and Nadler (2005, 2006)
***T. pichelinae* sp. n.**	*Thalassoma purpureum* (Forsskål)	MN105736, MN105737	MN104895, MN104896	Present study
***P. sodwanensis* sp. n.**	*Pomadasys furcatus* (Bloch et Schneider)	MN105738	–	Present study
Pararhadinorhynchus sp.	*Siganus fuscescens* (Houttuyn)	HM545903	–	Wang et al. (unpublished data)
Diplosentidae				
Sharpilosentis peruviensis Lisitsyna, Scholz et Kuchta, 2015	*Duopalatinus* cf. *peruanus*	–	KP967562	Lisitsyna et al. (2015)
Outgroup				
Andracantha gravida (Alegret, 1941)	*Phalacrocorax auritus* (Lesson)	EU267802	–	García-Varela et al. (2009)
Andracantha phalacrocoracis (Yamaguti, 1939)	*Zalophus californianus* (Lesson)	–	MK119254	Lisitsyna et al. (2019)
Ibirhynchus dimorpha (Schmidt, 1973)	*Eudocimus albus* (Linnaeus)	GQ981436	GQ981438	García-Varela et al. (2011)
Southwellina hispida (Van Cleave, 1925)	not determined	EU267809	EF467866	García-Varela et al. (2009)

TGC AGG TTC ACC TAC-3') (Garey et al. 1996) or the forward primer 18SU467F (5'-ATC CAA GGA AGG CAG CAG GC-3') and the reverse primer 18SL1310R (5'-CTC CAC CAA CTA AGA ACG GC-3') (Suzuki et al. 2006). The PCR thermocycling profile comprised initial denaturation at 94 °C for 4 min, followed by 30 cycles (30 s denaturation at 94 °C, 30 s primer annealing at 60 °C or 55 °C and 90 s at 72 °C for primer extension), with a final extension step of 5 min at 72 °C. Partial fragments of the mitochondrial cytochrome *c* oxidase 1 (*cox*1) gene was amplified using the forward primer #507 (5'-AGT TCT AAT CAT AAR GAT ATY GG-3') (Nadler et al. 2006) and the reverse primer HC02198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al. 1994) under the following thermocycling conditions: initial denaturation at 94 °C for 5 min, followed by 35 cycles (60 s denaturation at 94 °C, 60 s primer annealing at 40 °C, and 60 s at 72 °C for primer extension), with a final extension step of 5 min at 72 °C. Partial fragments of the 28S rRNA gene was amplified using the forward primer LSU5 (5'-TAG GTC GAC CCG CTG AAY TTA AGC A-3') (Littlewood 1994) and the reverse primer 1200R (5'-GCA TAG TTC ACC ATC TTT CGG G-3') (Lockyer et al. 2003) under the following thermocycling conditions: initial denaturation at 94 °C for 5 min, followed by 35 cycles (30 s denaturation at 94 °C, 30 s primer annealing at 55 °C, and 90 s at 72 °C for primer extension), with a final extension step of 5 min at 72 °C.

PCR amplicons were visualised on 1% agarose gel and then sent to a sequencing company (Inqaba Biotechnical Industries (Pty) Ltd. Pretoria, South Africa) for purification and sequencing. Sequencing was performed using the PCR primers. Contiguous sequences were assembled and edited using Geneious ver. 9.1 (Biomatters, Auckland, New Zealand) and submitted to GenBank.

Molecular phylogenetic analysis

To complete morphological description of the new species with molecular data, we sequenced PRC amplicons for the 18S rRNA (850 nt and 1,570 nt), 28S rRNA (882 nt) and *cox*1 (670 nt) genes. The newly-generated sequences for 18S rRNA and *cox*1 together with sequences representing eight families of Echinorhynchida retrieved from GenBank were used for the phylogenetic analyses (Table 1). Sequences for *Andracantha* spp. (Polymorphida: Polymorphidae), *Ibirhynchus dimorpha* (Schmidt, 1973) (Polymorphida: Polymorphidae) and *Southwellina hispida* (Van Cleave, 1925) (Polymorphida: Polymorphidae) were used as the outgroup for both, 18S and *cox*1 analyses (Table 1).

Two alignment were constructed using MUSCLE v3.7 implemented in Geneious ver. 9.1. The *cox*1 sequences were aligned with reference to the amino acid translation using the invertebrate mitochondrial code (transl_table = 5) (Telford et al. 2000). The final alignment for 18S rDNA resulted in a total of 800 characters and for *cox*1 in a total of 489 characters available for analyses. Phylogenetic trees were constructed through Bayesian inference (BI) and maximum likelihood (ML) analyses. The best-fitting model was estimated prior to analyses using jModelTest 2.1.2 (Guindon and Gascuel 2003, Darriba et al. 2012). This was the general time-reversible model incorporating invariant sites and gamma distributed among-site rate variations (GTR + I + G) for both alignments.

BI analysis was performed using MrBayes software (ver. 3.2.3) (Ronquist et al. 2012). Markov Chain Monte Carlo (MCMC) searches were performed on two simultaneous runs for 10,000,000 generations of four chains and sampled every 1,000th generation. The 'burn-in' was set for the first 2,500 sampled trees which were discarded prior to analyses. Consensus topology and nodal support estimated as posterior probability values (Huelsenbeck et al. 2001) were calculated from the remaining trees. ML analysis was performed using PhyML version 3.0 (Guindon et al. 2010) run on the ATGC bioinformatics platform (http://www.atgc-montpellier.fr/ngs). Nodal support in the ML analyses was estimated from 100 bootstrap pseudoreplicates. Trees were visualised using the FigTree ver. 1.4 software (Rambaut 2012).

The newly-generated sequences of the partial 28S rDNA were not consistent with the 28S rDNA sequences for most acanthocephlans currently available in GenBank and were not included in the phylogenetic analyses. These sequences were submitted to GenBank for future studies.

RESULTS

Family Transvenidae

Genus *Transvena* Pichelin et Cribb, 2001

***Transvena pichelinae* n. sp.** Figs. 1, 2

ZooBank number for species: urn:lsid:zoobank.org:act:74BA03EE-BFE9-4D4C-823F-4242A351CDEC

General (based on five specimens: three males and two females; one female without proboscis).

With characters of the genus *Transvena*. Body small. Size of males and females commensurable. Trunk spindle-shaped, with one ring of tiny spines at or near junction of neck and trunk (Fig. 1A, D). Prominent paired protrusions at posteroventral end of trunk (Fig. 2A, B) in both sexes, 390–558 × 110–140 (width of base). Trunk spines obtuse, short, 5–8 long, approximately 50–64 spines on ring, closely adjacent to each other. Each spine embedded in trunk wall. Proboscis claviform with 10–12 longitudinal rows of hooks; each row with 5 hooks (Figs. 1F, 2C). Hooks in apical and subapical rows differ in size: 3 large hooks with simple roots and 2 small hooks with short root processes in apical row; 2 and 3 in subapical row, respectively (Fig. 1B,C). Blades of third hook in each apical row S-shaped (Fig. 1C). Neck short. Proboscis receptacle double-walled with ganglion towards posterior end of proboscis receptacle (Figs. 1A,D, 2C). Ganglion 92–112 × 50–55. Lemnisci equal in length, 360–500 × 80–170, extend beyond proboscis receptacle. Genital pore subterminal in both sexes.

Males (metrical data for holotype given in parentheses; size of proboscis hooks with same number in apical and subapical rows differ substantially and are separated with "/"). Trunk 1,800–2,600 × 550–670 (1,800 × 550). Trunk spines obtuse, short, 5–6 long, approximately 50–54 spines on ring, closely adjacent to each other. Proboscis 150–160 × 130–140 (160 × 140). Proboscis with 11–12 longitudinal rows of hooks; each row with 5 hooks. Hook blades length: 1, 28–30/43–45 (28/45); 2, 55–58/58 (58/58); 3, 40–45/20–22 (43/22); 4, 17–20/17 (20/17); 5, 15/15 (15/15). Hook roots length: 1, 17–22/ 28–33 (22/30); 2, 33–43/38 (33/38); 3, 28–30/17 (30/17); 4, 17/17 (17/17); 5, 15/15 (15/15). Proboscis receptacle 360–410 × 130 (360 × 130). Lemnisci 420–580 (580) long, extend to level of testes. Testes two, oval, dorsal slightly more anterior than ventral. Anterior testis 300–420 ×

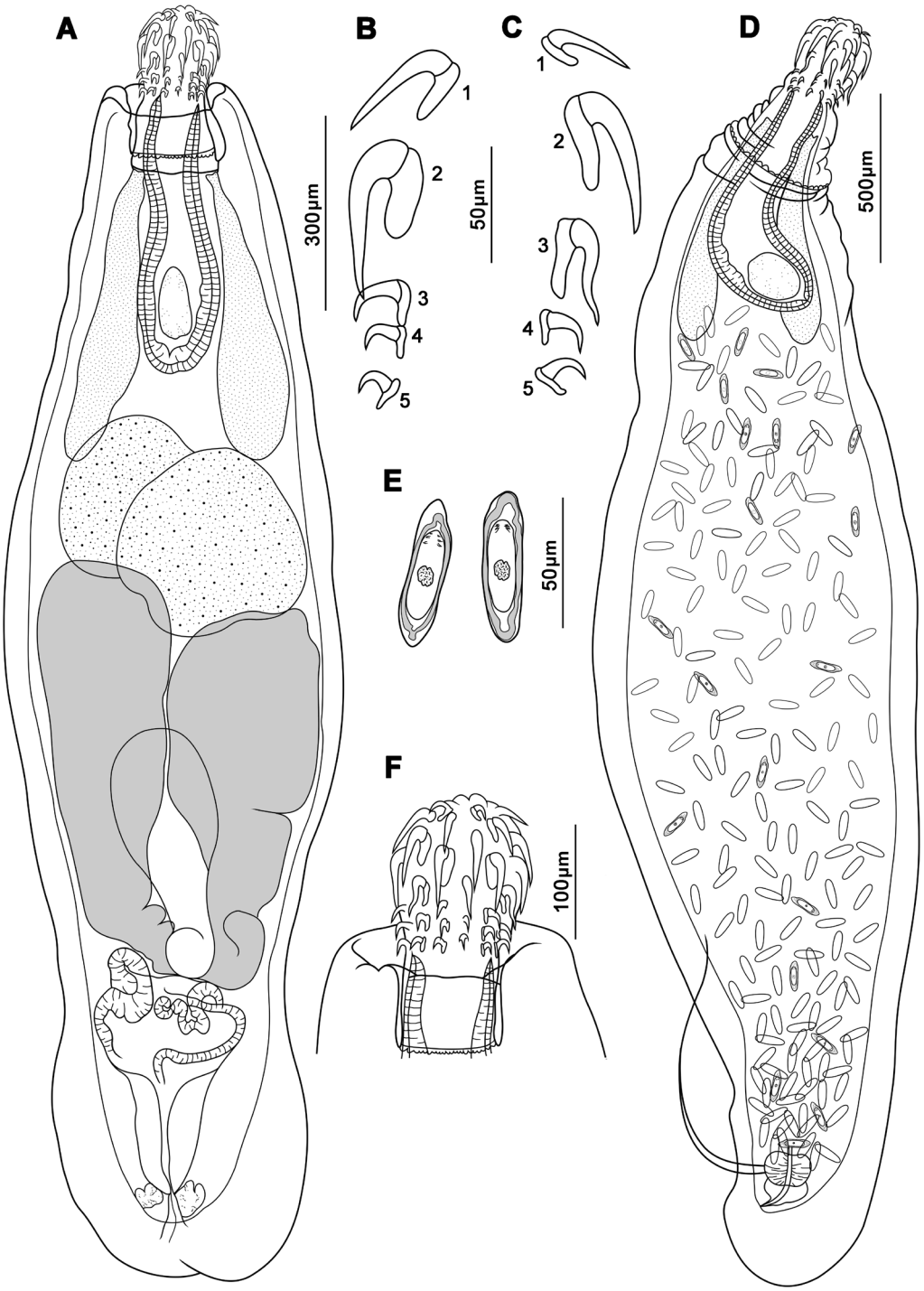

Fig. 1. *Transvena pichelinae* sp. n. from *Thalassoma purpureum* (Forsskål). **A** – total view of male, holotype; **B** – hooks of subapical row; **C** – hooks of apical row; **D** – total view of female; **E** – eggs; **F** – proboscis of male, holotype.

270–290 (360 × 290). Posterior testis 300–450 × 180–270 (300 × 270). Cement glands 2, tubular to pyriform, 580–780 × 220–360 (780 × 320). Säfftigen's pouch pyriform, between cement glands, 360–430 × 170–260 (420 × 200). Small genital ganglion present, at level of genital pore.

Females (metrical data for allotype is given in parentheses. Measurements of hooks, proboscis and proboscis receptacle were taken only from allotype; size of proboscis hooks with same number in apical and subapical rows differ substantially and are separated with "/"). Trunk 2,040–2,280 × 560–760 (2,040 × 560). Trunk spines obtuse, short, 5–8 long, approximately 60–64 (64) spines on ring, closely adjacent to each other. Proboscis 160 × 130. Proboscis with 10 longitudinal rows of hooks; each row with 5 hooks. Hook blade length: 1, 20–28/43–45; 2, 55–58/60–63; 3, 48–50/20–25; 4, 17–20/17; 5, 17/17. Hook roots length: 1, 15–20/ 30–33; 2, 30–33/38–45; 3, 30–33/17; 4, 15–17/15–17; 5, 15–17/15–17. Proboscis receptacle 410–420 × 130–140. Reproductive system obscured by fusiform eggs. Vagina with one muscle sphincter. Eggs fusiform with polar prolon-

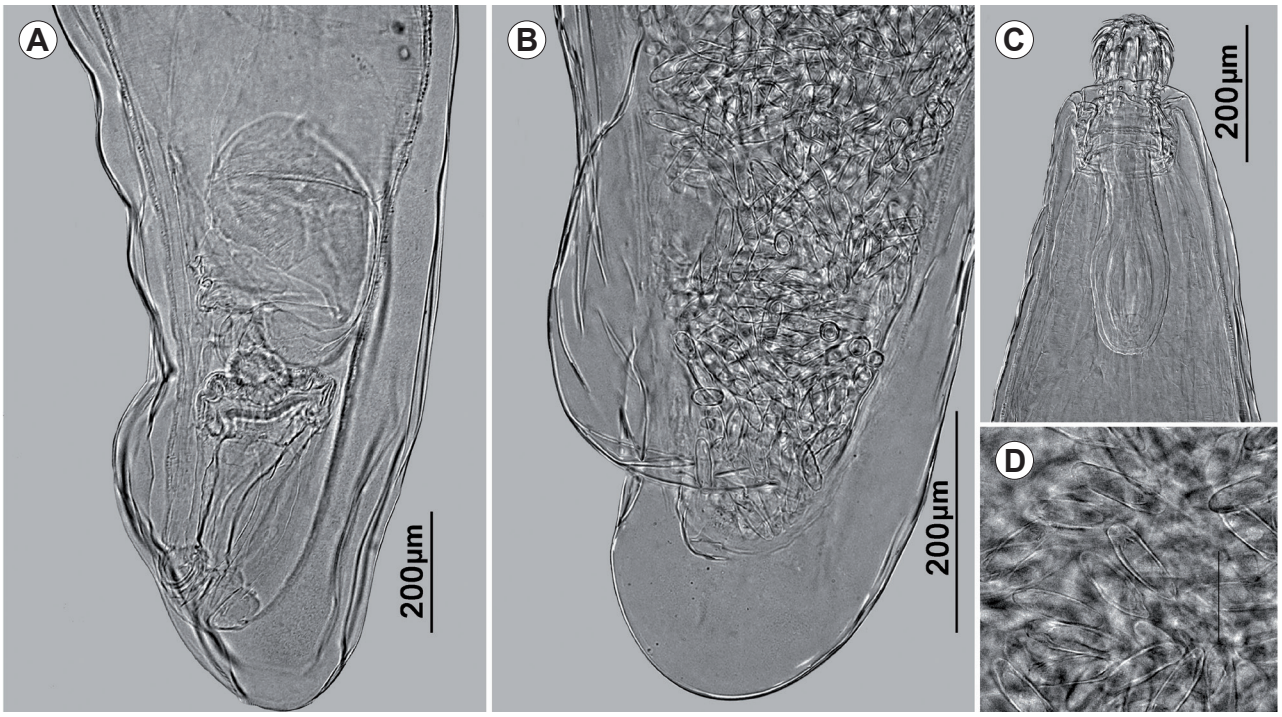

Fig. 2. Light microscopy photomicrographs of *Transvena pichelinae* sp. n. from *Thalassoma purpureum* (Forsskål). **A** – lateral view of posterior end of male; **B** – lateral view of posterior end of female; **C** – anterior end of male; **D** – eggs.

gation of E2 membrane, 55–58 × 15–17 (55–58 × 17) (Figs. 1E, 2D). Acanthor oval, 37–38 × 13 (37–38 × 13).

Type host: Surge wrasse *Thalassoma purpureum* (Forsskål) (Perciformes: Labridae).

Type locality: Sodwana Bay, South Africa (32°40'46"E; 27°32'24"S).

Site of infection: Intestine.

Infection rates: Prevalence, 2 of 3, intensity, 2–3 worms per host.

Type-material: Holotype and allotype (NMB P 499-500), and one paratype (NMB P 501); one paratype and two hologenophores (IPCAS A-121).

Molecular data: The fragments of 850 nucleotides (nt) of the 18S rDNA, 887 nt of the 28S rDNA and 670 nt of the cox1 genes of two specimens of *T. pichelinae* n. sp. from two individuals of *T. purpureum* were amplified. The nucleotide sequences are available in the GenBank database (Accession No. MN105736–MN105737 (18S), MN105742–MN105743 (28S), MN104895–MN104896 (cox1)).

Etymology: The species in named for Sylvie Pichelin (The University of Queensland, Brisbane, Australia) in recognition of her important contribution to the knowledge of acanthocephalans from marine fishes.

Remarks. Specimens of *T. pichelinae* n. sp. possess features that are fully consistent with the generic diagnosis for *Transvena* (see Pichelin and Cribb 2001). The new species differs from *T. annulospinosa*, the only other species, by having fewer longitudinal rows of hooks on the proboscis (10–12 *vs* 12–14, respectively), fewer hooks in each row (5 *vs* 6–8), shorter blades of anterior hooks (55–63 µm *vs* 98 µm), more posterior location of the ganglion (close to posterior margin of the proboscis receptacle *vs* the mid-level of the proboscis receptacle) and smaller eggs (50–58 × 13 µm *vs* 62–66 × 13–19 µm). Males and females of *T. pichelinae* n. sp. both possess prominent paired protrusions present at posteroventral end of the trunk, whereas only males of *T. annulospinosa* possess this structure.

Transvena annulospinosa, the type-species, has been reported from seven fish species of the family Labridae in Australia (Pichelin and Cribb 2001). *Transvena pichelinae* n. sp. was found in fish from the same family. This may indicate the high level of specificity of *Transvena* spp. to the fishes from the family Labridae.

Genus *Pararhadinorhynchus* Johnston et Edmonds, 1947

Pararhadinorhynchus sodwanensis n. sp. Figs. 3, 4

ZooBank number for species: urn:lsid:zoobank.org:act:C4061ED3-BC8E-43D7-A1CB-50313CF0A688

General (based on four specimens: two males and two females). With characters of the genus *Pararhadinorhynchus*. Trunk elongate, almost cylindrical, smooth, without spines. Females larger than males. Proboscis cylindrical, with 16–18 longitudinal rows of 11–13 hooks each. Hooks of similar shape without dorsoventral differentiation in size. All hooks with simple roots. Neck short. Lemnisci elongate, with maximum width in posterior part, extend beyond to proboscis receptacle. Proboscis receptacle cylindrical, double-walled with cerebral ganglion towards posterior end of proboscis receptacle. Testes oval, tandem. Cement glands 2, tubular, similar in length. Vagina with single muscular sphincter.

Males (metrical data for holotype given in parentheses). Trunk cylindrical, 4,850–5,600 × 530–670 (5,600 × 670). Proboscis 670–680 × 200–250 (680 × 250), armed with 16 (16) longitudinal rows of 11–12 hooks in a row. Anterior hooks slightly inverted in both specimens. Blades of middle hooks 50–53 long, blades

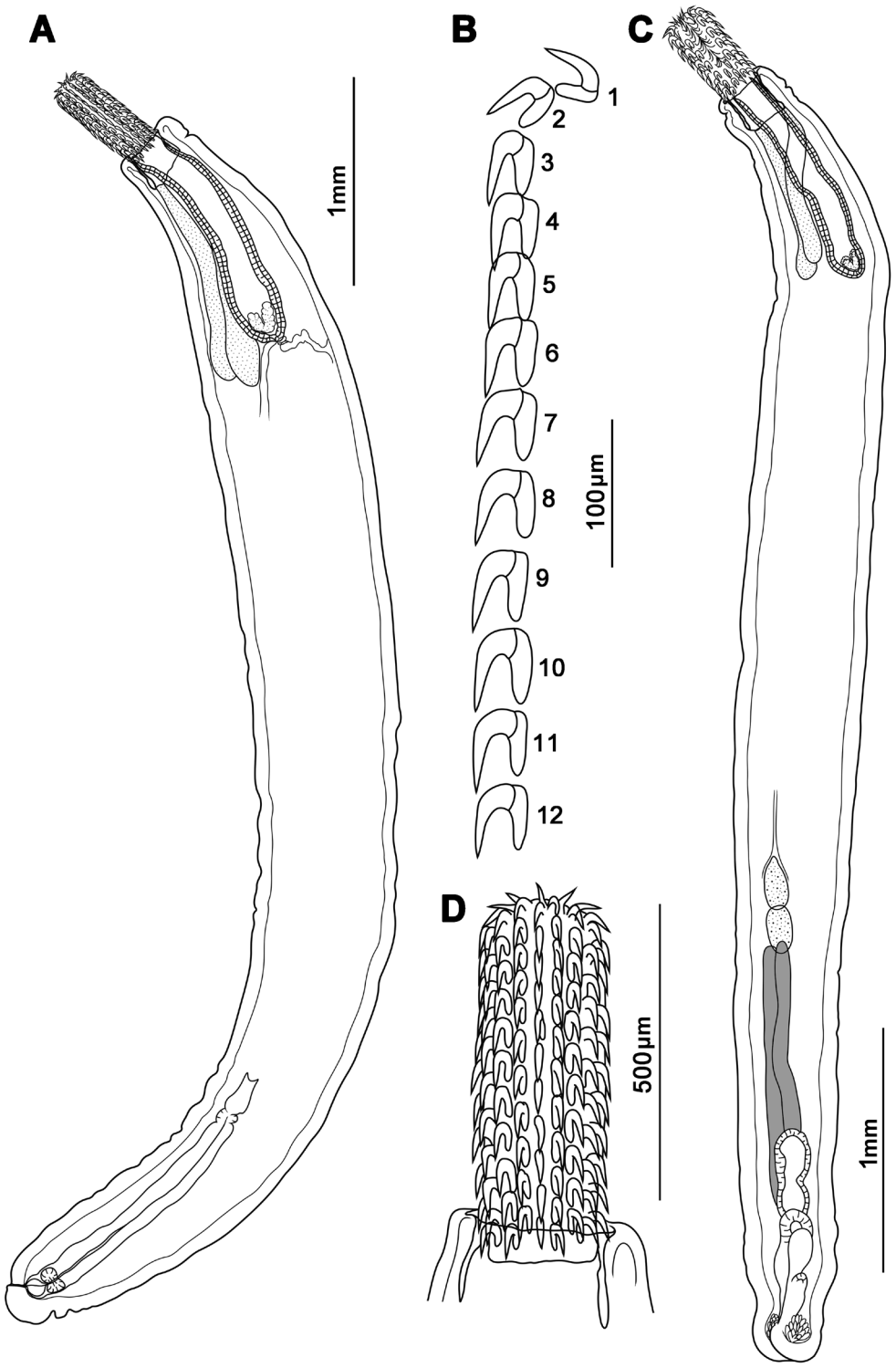

Fig. 3. *Pararhadinorhynchus sodwanensis* sp. n. from *Plectorhinchus schotaf* (Forsskål) (A, B, D) and from *Pomadasys furcatus* (Bloch et Schneider) (type host, C). **A** – total view of female; **B** – hooks of a longitudinal row of female; **C** – total view of holotype; **D** – proboscis of female.

of basal hooks 50 long. Roots of middle hooks 50 long, roots of basal hooks 38 long. Proboscis receptacle 910–1,110 × 160–220 (1,110 × 220). Neck 160–180 (160) long. Lemnisci 780–1,000 (1,000) long. Reproductive system occupies 40% of trunk posteriorly. Distance between posterior margin of proboscis receptacle and anterior margin of anterior testis 1,420–1,800. Testes two, elongate-oval, tandem. Anterior testis 210–290 × 90–180 (290 × 180), posterior testis 200–250 × 100–160 (250 × 160). Cement glands 870–880 (880) long, extend to posterior testis. Genital ganglion prominent. Genital pore terminal.

Female. Trunk cylindrical, falcate curved, 7,140 × 760. Proboscis 620 × 220, armed with 18 longitudinal rows of 12–13 hooks in a row. Anterior hook blades 50–53 long, middle hooks blades 58–60 long, basal hooks blades 53–58 long. Anterior hook

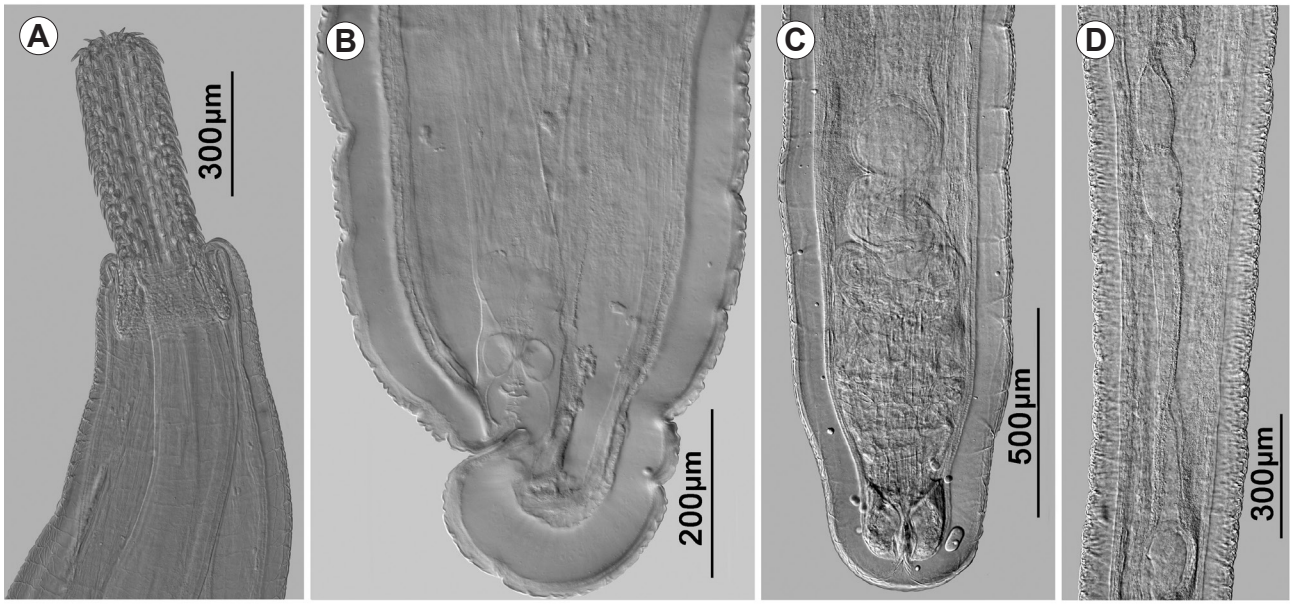

Fig. 4. Light microscopy photomicrographs of *Pararhadinorhynchus sodwanensis* sp. n. from *Pomadasys furcatus* (Bloch et Schneider). **A** – anterior part of female; **B** – posterior part of female; **C** – posterior part of male; **D** – middle part of holotype.

roots of 35 long, 2–7 hooks 38–43 long, 8–11 hooks 48–50 long, 12–13 hooks 33–40 long. Proboscis receptacle 1,180 × 260. Neck 170 long. Lemnisci 900–950 × 90–95. Reproductive system 1,100 long. Vagina with single muscular sphincter. Genital pore subterminal (Fig. 3A). Eggs unknown.

Type host: Banded grunter *Pomadasys furcatus* (Bloch et Schneider) (Perciformes: Haemulidae).

Other hosts: *Plectorhinchus* sp. (Perciformes: Haemulidae).

Type locality: Sodwana Bay, South Africa (32°40'46"E; 27°32'24"S).

Site of infection: Intestine.

Infection rates: Prevalence, 1 of 5; intensity, 3 in *P. furcatus*; 1 of 1 in *Plectorhinchus* sp.

Type material: Holotype (NMB P 502) and one paratype (NMB P 503); one paratype and one hologenophore (IPCAS A-120).

Molecular data: A fragment of 1,570 nt of the 18S rDNA and of 884 nt of 28S rDNA genes of one specimen of *P. sodwanensis* n. sp. ex *P. furcatus* was amplified. The nucleotide sequence is available in the GenBank database (Accession No. MN105738 (18S), MN105744 (28S)).

Etymology: The specific name is derived from the type locality, Sodwana.

Remarks. *Pararhadinorhynchus sodwanensis* n. sp. belongs to the family Transvenidae based on the presence of two cement glands and absence of the trunk spines. It exhibits features consistent with the genus *Pararhadinorhynchus*: it has a cylindrical trunk, cylindrical proboscis with an armature of longitudinal rows of hooks decreasing in length from the apex to the base of the proboscis, double-walled proboscis receptacle; and lemnisci not extending as far as the anterior testis (Pichelin and Cribb 2001, Weaver and Smales 2014).

The new species differs from *Pararhadinorhynchus mugilis* Johnston and Edmonds (1947) in having a smaller number of hooks per row (11–13 *vs* 16–17), a shorter proboscis (620–680 µm *vs* 889–940 µm), in shape of posterior hooks (with roots *vs* without roots) and in the position of the genital pore in females (subterminal *vs* terminal). It differs from *Pararhadinorhynchus coorongensis* Edmonds (1973) in the number of hooks in a row (11–13 *vs* 8–10), shorter lemnisci (almost the same length as the proboscis receptacle *vs* twice as long as the proboscis receptacle) and position of the genital pore in females (subterminal *vs* terminal).

Pararhadinorhynchus sodwanensis n. sp. differs from *Pararhadinorhynchus upenei* Wang et al. (1993) only in the number of hooks in a row (11–13 vs 26–28). *Pararhadinorhynchus sodwanensis* n. sp. differs from *P. magnus* Ha et al. (2018) in the length of blades of hooks (50–60 *vs* 22–35), length of root of hooks (35–50 *vs* 22–35), and the number of hooks in longitudinal rows (11–13 *vs* 23–27).

The new species closely resembles an unidentified species of *Pararhadinorhynchus, Pararhadinorhynchus* sp. *sensu* Weaver et Smales (2014) collected from *Urogymnus granulatus* (Macleay) from Lizard Island, Australia (Weaver and Smales 2014). Both species possess a similar number of longitudinal rows of hooks on the proboscis (16–18 *vs* 18) and hooks in a row (11–13 *vs* 13–14). However, the present specimens differ from *Pararhadinorhynchus* sp. by the position of lemnisci (extend to the level of posterior end of the proboscis receptacle or slightly posterior *vs* extend to the mid-level of the proboscis receptacle), length of proboscis receptacle (910–1180 µm *vs* 1460 µm) and cement glands (870–880 µm *vs* 335–350 µm).

Acanthocephalans of the genus *Pararhadinorhynchus* have been reported from marine fishes of the families Mugilidae, Mullidae and Scatophagidae and freshwater fishes of the family Gobiidae (Smales et al. 2018). The new species, *P. sodwanen-*

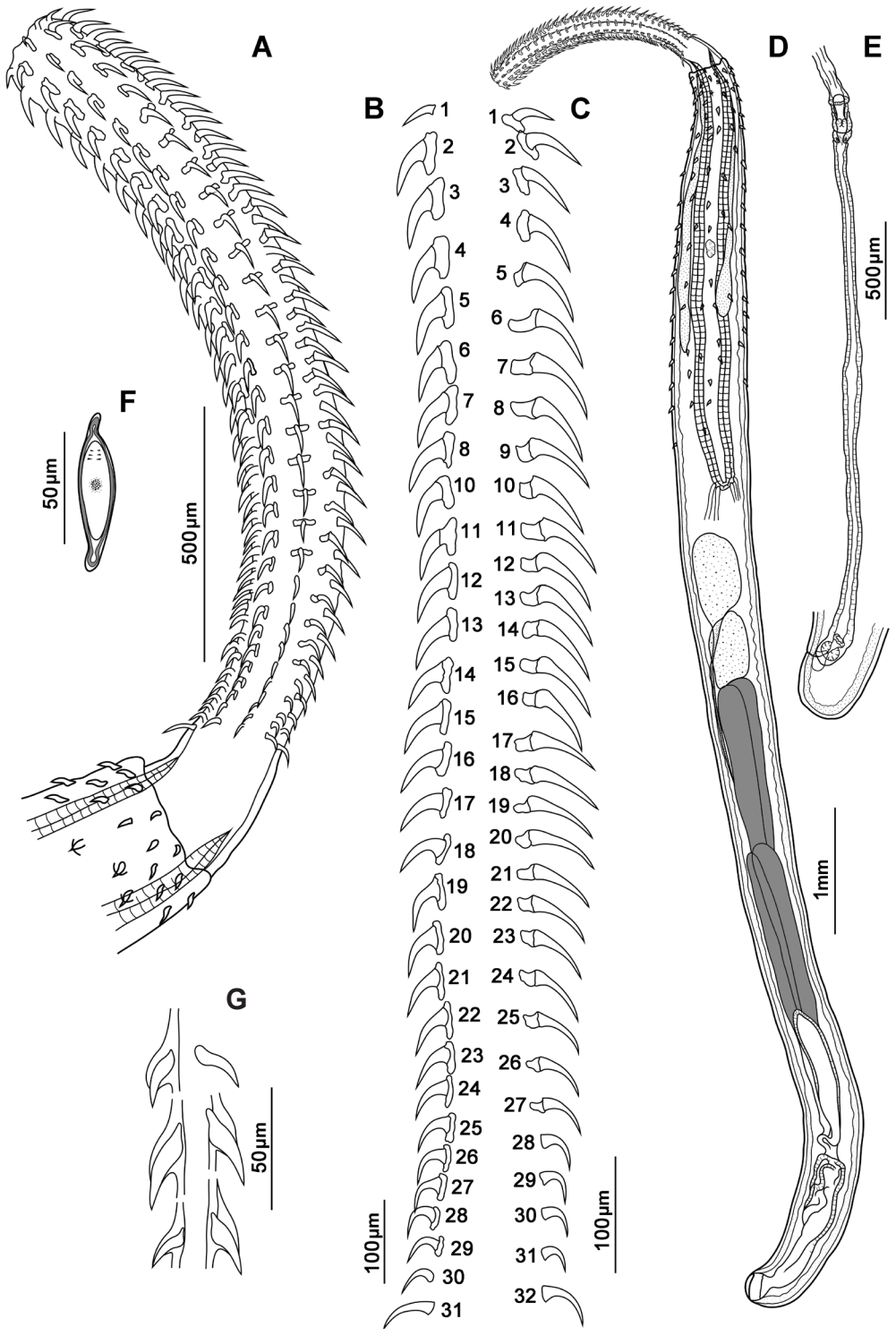

Fig. 5. *Rhadinorhynchus gerberi* sp. n. from *Trachinotus botla* (Shaw). **A** – proboscis of holotype; **B** – hooks of ventral longitudinal row, holotype; **C** – hooks of dorsal longitudinal row, holotype; **D** – total view of holotype; **E** – female reproductive tract; **F** – egg, allotype; **G** – ventral and dorsal tegumental spines, holotype.

sis n. sp., was found in two species of the Haemulidae. Thus, acanthocephalans from this genus demonstrate low host specificity, even up to family level of the definitive hosts.

Family Rhadinorhynchidae

Genus Rhadinorhynchus Lühe, 1911

Rhadinorhynchus gerberi n. sp. Figs. 5–8

ZooBank number for species: urn:lsid:zoobank.org:act:C221B6A3-4F90-4381-987E-1F0F4ACA4628

General (based on 19 specimens. Metrical data for the holotype and allotype are given in the description; ranges and means for the type-series are provided in Table 2. Metric data for proboscis hooks are provided in Table 3). With characters of the ge-

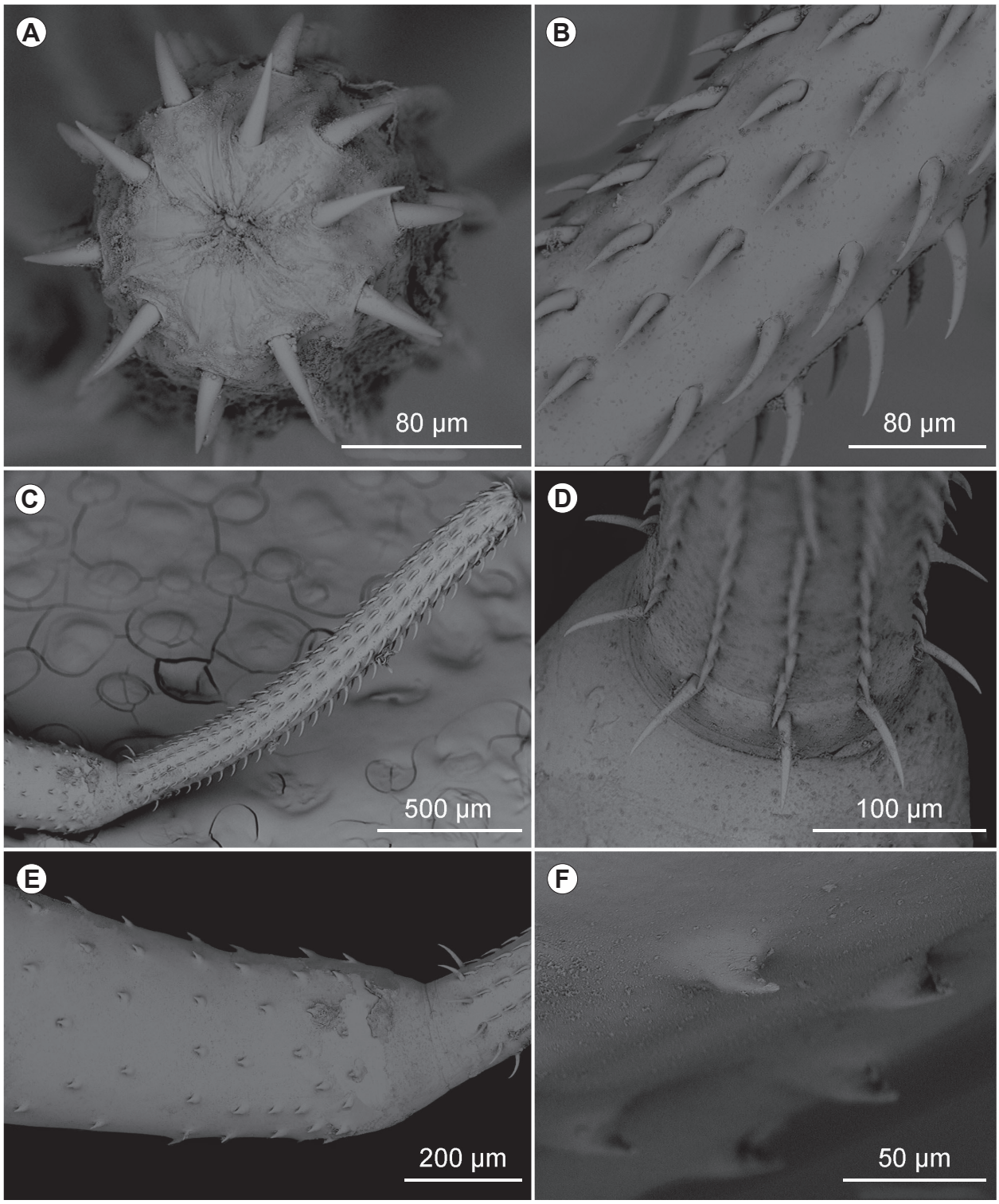

Fig. 6. Scanning electron photomicrographs of *Rhadinorhynchus gerberi* sp. n. from *Trachinotus botla* (Shaw). **A** – apical view of proboscis, male; **B** – hooks in the midsection of proboscis, male; **C** – proboscis, male; **D** – basal hooks of proboscis, male; **E** – anterior part of trunk with tegumental spines as single field, male; **F** – middle tegumental spines, male.

nus *Rhadinorhynchus*. Shared structures larger in females than in males. Trunk long with a single field of 19–26 irregular circular rows of the tegumental spines on anterior part (Figs. 5D, 6E, 7E). Posterior circles incomplete dorsally. Length of spines similar in males and females, increases from anterior, dorsal 20–30 and ventral 23–35, to median, dorsal 25–38 and ventral 25–40, and decreases to posterior, dorsal 25–35, ventral 18–35. Proboscis long, cylindrical, curved to ventral, widely anterior than posterior (Figs. 5A, 6C). Proboscis with 9 (in one male) or 10 (in six males and ten females) longitudinal rows of 28–32 hooks each. Ventral hooks thicker than dorsal (Fig. 5B,C). First anterior ventral hook without root. Next 25–29 ventral hooks with simple roots 25–43 long, directed posteriorly. Posterior 2–3 hooks, without roots (Fig. 5B). Anterior 4–5 dorsal hooks, with simple roots

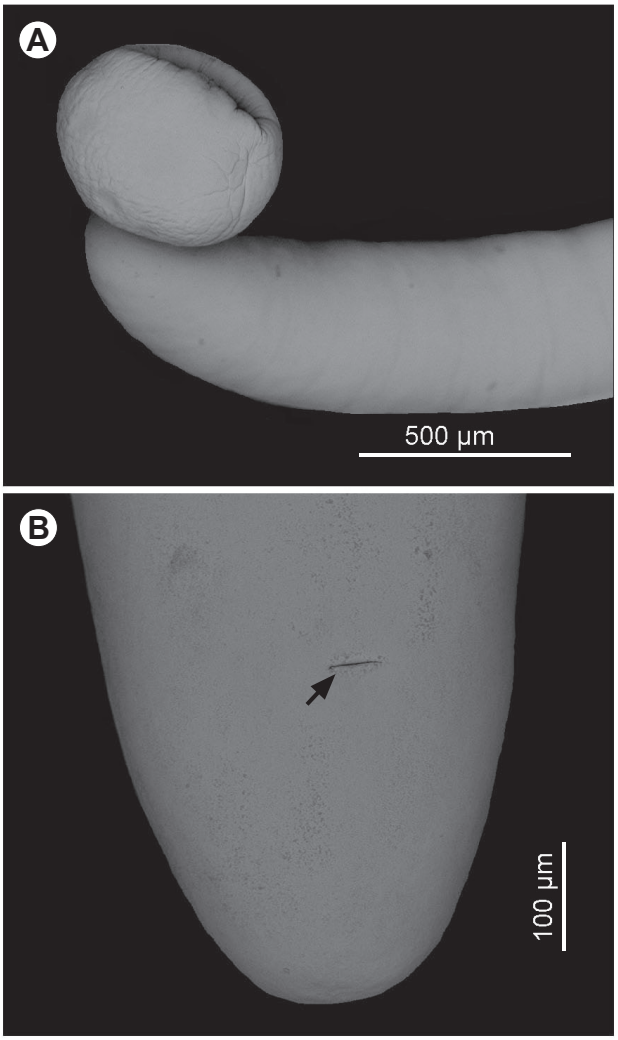

Fig. 7. Scanning electron photomicrographs of *Rhadinorhynchus gerberi* sp. n. from *Trachinotus botla* (Shaw). **A** – bursa of male showing the subventral position of the gonopore; **B** – posterior end of female showing horizontal slit-like subterminal genital pore (arrow).

25–35 long, directed posteriorly. Next 18–20 dorsal hook roots with two manubrium directed horizontally. Posterior 2–5 dorsal hooks without roots (Figs. 3C, 6F). Hooks of basal circle longer than hooks of penultimate circle (Figs. 5B,C, 6D, 8D). Neck prominent, conical, longer dorsal than ventral. Proboscis receptacle elongate, cylindrical, with cephalic ganglion near its middle. Lemnisci elongate, about twice as short as proboscis receptacle, with maximal width in posterior part. Distance between bottom of proboscis receptacle and anterior edge of anterior testis, 300–1,940 (904). Testes oblong, contiguous. Cement glands 4, in two pairs of different length. Copulatory bursa hemispherical (Fig. 7A). Female reproductive tract long, 1,675–2,145 (1,953). Uterine bell cup-shaped, with lateral pockets (Fig. 8C). Vagina with single muscular sphincter. Genital pore subterminal in both sexes (Figs. 5D,E, 7A,B).

Holotype. Trunk 10.40 mm long, 620 width at level of middle part of proboscis receptacle. Trunk spines in 19 irregular circles, extend to 2,850 ventrally and 2,200 dorsally. Length of dorsal spines: anterior 28, middle 35–40, posterior 35. Length of ventral spines: anterior 35, middle 38–43, posterior 25. Proboscis 1,600 long, 250 wide anteriorly, 200 wide posteriorly. Proboscis with 10 longitudinal rows of 31–32 hooks each. Proboscis receptacle 3,580 × 300. Neck 220 long dorsally, 120 long ventrally. Lemnisci 2,250 × 100 and 2,330 × 100. Distance between anterior edge of anterior testis and bottom of proboscis receptacle, 440. Testes two, elongate-oval, tandem. Anterior testis 760 × 350 longer than posterior testis. Posterior testis 650 × 300. Longer pair of cement glands 2,950 long, extends to posterior edge of posterior testis; shorter pair 1,550 long. Säeftigen's pouch clavate, 1,150 × 180. Genital pore transverse slit-like, median, opens on ventral side.

Allotype. Trunk 16.2 mm long, 830 width at level of middle part of proboscis receptacle. Trunk spines in 26 irregular circles, extend to 3,490 ventrally and to 2,370 dorsal. Length of dorsal spines: anterior 23, middle 30, posterior 28. Length of ventral spines: anterior 25, middle 33, posterior 38. Proboscis 1,520 long, 250 wide anteriorly, 200 wide posteriorly. Proboscis with 10 longitudinal rows of 30–31 hooks each. Proboscis receptacle 3,950 × 300. Neck 250 long dorsally, 170 long ventrally. Lemnisci 2,700 × 150 and 1,870 × 110. Reproductive system obscured by fusiform eggs. Eggs 65–68 × 15 with polar prolongations of middle membranes (Figs. 5F, 8G). Acanthor 48 × 13. Genital pore subterminal, at 460 from posterior edge of trunk.

Type host: Largespotted dart *Trachinotus botla* (Perciformes: Carangidae).

Other hosts: White seabream *Diplodus sargus* Linnaeus (Perciformes: Sparidae); evileye blaasop *Amblyrhynchotes honckenii* Bloch (Tetraodontiformes: Tetraodontidae); Jarbua terapon *Terapon jarbua* (Forsskål) (Perciformes: Terapontidae).

Type locality: Sodwana Bay, South Africa (32°40'46"E; 27°32'24"S).

Site of infection: Intestine.

Infection rates: Prevalence, 6 of 7, intensity, 12–116 in *T. botla*; 1 of 13; 1 in *D. sargus*; 3 of 8; 1–9 *A. honckenii*. 2 of 3; 1–4 *T. jarbua*.

Type material: Holotype and allotype (NMB P 504) and 13 paratypes (NMB P 505); five paratypes and three hologenophores (IPCAS A-108).

Molecular data: The fragments of 1,570 and 850 nucleotides (nt) of the 18S rDNA, 882 nt of 28S rDNA and 670 nt of the cox1 genes of *R. gerberi* n. sp. from *A. honckenii*, *T. jarbua* (no cox1 sequence), *T. botla* were amplified. The nucleotide sequences are available in the GenBank database (Accession No. MN105739–MN105741 (18S), MN105745–MN105747 (28S), MN104897–MN104898 (cox1)).

Etymology: The species in named for Ruan Gerber (North-West University, Potchefstroom, South Africa) in recognition of his continued assistance with fish collection.

Remarks. *Rhadinorhynchus gerberi* n. sp. is characterised by an elongate cylindrical trunk covered with tegumental spines anteriorly, elongate cylindrical proboscis with longitudinal rows of hooks that differ in shape and size dorsally and ventrally, position of cephalic ganglion in the middle of proboscis receptacle, and presence of four cement glands. This combination of morphological characters clearly allocates this species into the genus *Rhadinorhynchus* (see Golvan 1969, Amin et al. 2011, Smales 2014). The new species possesses a single uninterrupted field of tegumental spines covering the anterior part of the body and shares this feature with 15 species of *Rhadinorhynchus* (see Amin et al.

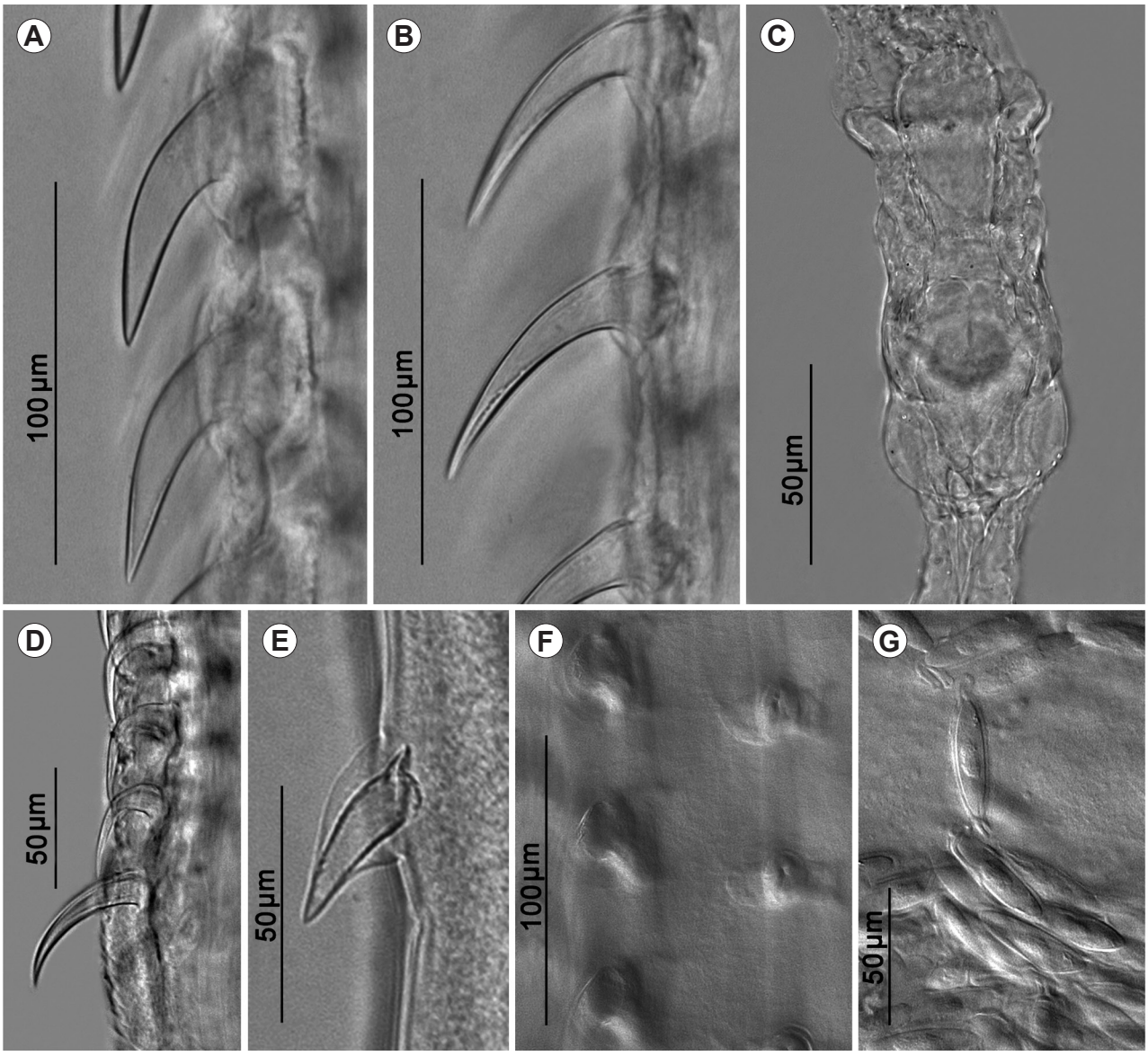

Fig. 8. Light microscopy photomicrographs of *Rhadinorhynchus gerberi* sp. n. from *Trachinotus botla* (Shaw). **A** – proboscis hooks of ventral longitudinal row, holotype; **B** – proboscis hooks of dorsal longitudinal row, holotype; **C** – uterine bell of female; **D** – ventral prebasal and basal proboscis hooks, holotype; **E** – one tegumental spine, holotype; **F** – hook roots of midsection of proboscis, holotype; **G** – eggs, allotype.

2011, Smales 2014). Of these, only six species possess proboscis armature similar to that of *R. gerberi* n. sp., namely *R. carangis* Yamaguti, 1939, *R. plotosi* Parukhin, 1985, *R. decapteri* Parukhin et Kovalenko, 1976, *R. pichelinae* Smales, 2014, *R. polydactyli* Smales, 2014 and *R. polynemi* Gupta et Lata, 1967.

Rhadinorhynchus gerberi n. sp. differs from *R. carangis* as described by Yamaguti (1939) in the smaller number of the hooks in longitudinal row (28–32 *vs* 34–38), location of the genital pore (subterminal in both sexes *vs* terminal in males) and position of the testes in males [300–1,940 (904) from the posterior margin of proboscis receptacle *vs* testes overlap proboscis receptacle posteriorly]. The new species differs from the single male of *R. plotosi* described by Parukhin (1985) in possessing a smaller number of the hooks in longitudinal rows on the proboscis (10 *vs* 12), longer trunk (8.40–15.11 mm *vs* 4.43 mm) and shorter lemnisci (extend to the middle of the proboscis receptacle *vs* extend to the posterior margin of proboscis receptacle). The males of *R. gerberi* n. sp. differ from those of *R. decapteri* described by Parukhin and Kovalenko (1976) in the smaller number of the hooks in longitudinal rows on the proboscis (10 *vs* 12), much shorter length of the trunk (8.40–15.11 *vs* 18.57–22.10 mm) and location of the genital pore (subterminal *vs* terminal). The new species differs from *R. polydactyli* described by Smales (2014) in the smaller number of hooks in longitudinal rows on the proboscis (28–32 *vs* 34) and shorter neck length in females (100–280 µm *vs* 1,300 µm).

The South African species closely resembles *R. polynemi* and *R. pichelinae* in having 10 longitudinal row of hooks on the proboscis, numbers of circular rows of the tegumental spines, and in similar dimensions for a number of structures (Table 2). *Rhadinorhynchus polynemi* was described from the Javanese threadfin *Filimanus heptadactylus* (Cuvier) (syn. *Polynemus heptadactylus*) (Perciformes: Polynemidae) in India (Gupta and Lata 1967) and later reported from the same host from Moreton Bay, Australia (Smales 2014). *Rhadinorhynchus pichelinae* was described

Table 2. Comparative metrical data (in µm) for *Rhadinorhynchus* spp.

Species	*Rhadinorhynchus pichelinae* Smales, 2014				*Rhadinorhynchus polynemi* Smales, 2014				*Rhadinorhynchus gerberi* sp. n.			
Host	*Upeneichthys vlamingi*				*Filimanus heptadactylus*				*Trachinotus botla*			
Locality	Australia				Australia				South Africa			
Source	Smales (2014)				Smales (2014)				Present study			
Sex, n	♂ (n = 10)		♀ (n = 10)		♂ (n = 7)		♀ (n = 10)		♂ (n = 7)		♀ (n = 10)	
	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean
TL*	9–12	9.7	11–18	12.9	4.5–9.0	6.5	15–17	15.7	8.40–15.11	10.61	11.95–18.12	14.88
TW	510–815	577	560–935	742	290–630	384	255–510	408	490–780	612.86	600–900	740
SFDL*	–	–	–	–	–	–	–	–	1.62–2.20	2.05	2.37–3.32	1.62
SFVL*	–	–	–	–	–	–	–	–	2.20–3.00	2.57	2.73–3.53	3.23
NRS	21–24	21–24	19–25	28–37	21–24	21–24	19–25	28–37	19–21	19.57	19–26	23.10
PL	1,020–1,360	1,113	1,360–1,530	1,458	1,055–1,305	1,185	1200–1530	1448	1,520–1,880	1,631.43	1,500–1,950	1,679
PWmax	175–230	205	204–290	253	105–155	127	153–155	153.5	210–260	234.29	230–270	248
PWmin	–	–	–	–	–	–	–	–	120–200	171.43	190–220	201
HR	10	–	10	–	10	–	10	–	9–10	–	10	–
HPR	24–28	–	24–28	–	30–34	–	30–34	–	30–32	–	28–32	–
LHD	85.8–89.1	–	85.8–89.1	–	62.9	–	59.5	–	63–80	71.50	70–83	77.75
LHV	75.9–82.5	–	75.9–82.5	–	47.6	–	46	–	65–73	67	63–75	68.63
PRL*	2.78–4.34	3.28	3.06–4.53	3.,57	1.78–3.32	1.97	3.06–3.40	3.20	3.24–3.90	3.61	3.45–4.35	3.88
PRW	270–510	312	280–375	324	155–255	197	255–340	298	200–320	262.86	200–320	283
NDL	100–201	127	168–200	171	80–135	102	99–101	100	180–200	222.86	190–280	232
NVL	–	–	–	–	–	–	–	–	100–150	120	100–150	122
LL	1,280–2,010	1,737	1,410–2,380	1671	1,105–2,210	1,752	–	–	1,480–2,460	1,170	2,210–3,780	2,550
LW	–	–	–	–	–	–	–	–	100–160	121.43	100–190	130
TAL	603–1020	775	–	–	300–680	501	–	–	720–2,000	1,204.29	–	–
TAW	255–425	316	–	–	140–460	242	–	–	210–500	325.71	–	–
TPL	590–1020	788	–	–	302–850	514	–	–	702–1,000	678.86	–	–
TPW	221–357	239	–	–	135–390	220	–	–	200–350	238.57	–	–
CGL	804–1,820	1,300	–	–	335–720	561	–	–	2,300–5,970	3,260	–	–
RTL	–	–	1,675–2,145	1,953	–	–	3,265–3,655	3,514	–	–	3,000–6,700	4,320
AL	–	–	–	–	–	–	–	–	–	–	43–50	45.8
AW	–	–	–	–	–	–	–	–	–	–	13–15	14.2
EL	–	–	59.5–66	59.5	–	–	42.5–56.1	50.6	–	–	65–73	68.5
EW	–	–	11.2–13.6	12.6	–	–	11.9–13.6	12.6	–	–	15–18	16.8
GPE	–	–	–	–	–	–	–	–	–	–	240–480	341

*Measurements age given in mm. *Abbreviations:* TL, trunk length; TW, trunk width; SFDL, length of spine field dorsal; SFVL, length of spines field ventral; NRS, number of spine rows; PL, proboscis length; PWmax, proboscis maximum width; PWmin, proboscis minimum width; HR, number of hook rows; HPR, number of hooks per row; LHD, dorsal largest hooks length, LHV, ventral largest hooks length; PRL, proboscis receptacle length; PRW, proboscis receptacle width; NDL, neck length dorsally; NVL, neck length ventrally; LL, lemnisci length; LW, lemnisci width; TAL, anterior testis length; TAW, anterior testis width; TPL, posterior testis length; TPW, posterior testis width; CGL, cement glands complex length; RTL, reproductive tract length; AL, acanthor length; AW, acanthor width; EL, eggs length; EW, eggs width; GPE, distance from gonophore to posterior edge.

from the southern goat fish, *Upenechthys olamingi* Cuvier (Perciformes: Mullidae), from Point Peron, Western Australia and Kangaroo Island, South Australia (Smales 2014).

However, the present specimens differ from *R. polynemi* and *R. pichelinae* in possessing much larger hooks in males (longest hook blade length: dorsal 63–80 µm and ventral 65–73 µm *vs* dorsal 63 µm and ventral 48 µm *vs* dorsal 89 µm and ventral 83 µm, respectively) and larger eggs (65–73 µm *vs* 42.5–56 µm *vs* 60–66 µm, respectively). In addition, the new species differs from *R. polynemi* in possession of larger number of hooks in longitudinal rows on the proboscis (28–32 *vs* 24–28) and from *R. pichelinae* in the location of the genital pore of females (far from the posterior edge of the trunk *vs* close to posterior edge of the trunk).

Rhadinorhynchus gerberi n. sp. was found in four species of three families marine fishes the Carangidae, Sparidae and Tetraodontidae. Thus, the host specificity of this species to family of the definitive hosts is rather low.

Molecular analysis

A total of 16 sequences were generated during this study: *R. gerberi* n. sp. ex *T. botla* (18S, 28S and *cox*1), ex *A. honckenii* (18S, 28S and *cox*1) and ex *T. jarbua* (18S and 28S); *T. pichelinae* n. sp. ex *T. purpureum* (18S, 28S and *cox*1); and *P. sodwanensis* n. sp. ex *P. furcatus* (18S and 28S) (Table 1).

The 18S rDNA dataset (800 nt) included 36 sequences for species of eight families within the Echinorhynchida and novel sequences for the new species, *R. gerberi* n. sp., *T. pichelinae* n. sp. and *P. sodwanensis* n. sp. The *cox*1 dataset (489 nt) included 39 sequences for species of eight families of Echinorhynchida and four novel sequences: two of *R. gerberi* n. sp. and two of *T. pichelinae* n. sp. BI and ML phylogenetic analyses using both 18S rDNA and *cox*1 datasets produced a tree topology (Fig. 9) consistent with those of previous studies (i.e. Gregory et al. 2013, Braicovich et al. 2014, Bao et al. 2015). Sequences for *R. gerberi* n. sp., *T. pichelinae* n. sp. and *P. sodwanensis* n. sp. in both 18S rDNA and *cox*1 analyses fell into a strongly-supported clade represented by species belonging to the three families Gymnorhadinorhynchidae, Rhadinorhynchidae and Transvenidae.

Table 3. Comparative metrical data (in μm) for dorsal and ventral proboscis hooks of males and females of *Rhadinorhynchus gerberi* n. sp.

No	Length of hooks blades, ♂ (7 sp.)						Length of hooks blades, ♀ (10 sp.)					
	dorsal			ventral			dorsal			ventral		
	holotype	range	mean	holotype	range	mean	allotype	range	mean	allotype	range	mean
1	45	38–58	47	45	35–53	47	45	50–65	56	43	43–65	51
2	68	55–68	61	75	53–75	62	55	55–70	67	65	63–70	66
3	70	58–70	63	75	60–75	65	58	58–73	68	65	63–70	66
4	70	58–70	64	75	63–75	67	68	65–73	70	65	63–75	69
5	75	63–75	67	75	63–75	67	68	65–73	71	65	63–75	68
6	75	63–75	70	73	63–73	69	73	68–78	74	68	63–75	69
7	78	63–75	70	73	65–73	68	73	70–78	75	65	60–73	68
8	78	63–80	72	73	63–73	67	75	68–80	76	65	63–75	69
9	78	63–78	71	70	63–70	67	75	70–80	76	65	63–70	68
10	75	63–78	71	68	63–70	66	80	70–80	77	63	63–70	67
11	75	63–78	71	70	65–70	67	78	70–80	76	65	63–70	68
12	75	63–78	72	65	63–68	65	78	73–80	77	65	63–70	68
13	75	63–75	70	65	63–68	65	78	70–83	77	65	63–70	67
14	75	58–75	69	65	63–70	63	78	70–83	78	65	63–70	67
15	78	58–78	70	65	60–70	64	80	68–83	77	63	60–73	66
16	73	53–73	68	65	58–70	64	80	68–80	76	63	60–70	66
17	75	48–75	67	63	58–68	63	80	65–80	76	60	60–70	66
18	75	45–75	66	63	55–65	61	75	65–80	75	60	60–73	67
19	75	45–75	66	60	55–65	60	73	65–80	75	65	63–70	67
20	75	45–75	64	60	53–65	59	73	65–80	74	65	60–73	66
21	73	45–73	62	60	53–63	59	68	60–80	72	63	60–70	65
22	70	45–73	62	60	45–60	56	65	55–80	70	63	58–68	63
23	68	38–68	58	58	38–60	54	63	53–80	66	60	55–65	62
24	65	30–65	52	53	33–58	52	55	48–73	62	55	50–63	59
25	65	25–65	50	55	30–55	48	48	43–70	54	50	50–60	55
26	53	25–53	44	50	38–63	48	45	38–65	49	50	50–60	53
27	50	30–50	41	48	38–53	46	38	35–60	44	45	45–55	50
28	50	28–50	37	45	38–48	42	35	35–50	41	38	38–50	46
29	43	25–43	34	43	38–48	41	35	35–50	39	35	35–53	46
30	38	30–45	36	40	33–45	39	35	35–45	38	35	35–48	43
Basal	60	43–60	51	63	50–68	63	48	48–75	61	63	63–78	72

Based on the results of the 18S rDNA analyses (Fig. 9), *T. pichelinae* n. sp. clustered with *T. annulospinosa* and *P. sodwanensis* n. sp. clustered with unidentified species of *Pararhadinorhynchus* (GenBank accession number HM545903) with strong support. The sequence of *R. gerberi* n. sp. branched apart from the members of the Transvenidae, *Rhadinorhynchus* spp. and *Gymnorhadinorhynchus mariserpentis* Steinauer, Garcia-Vedrenne, Weinstein et Kuris, 2019. The sequence of *Gymnorhadinorhynchus decapteri* Braicovich, Lanfranchi, Farber, Marvaldi, Luque et Timi, 2014 appeared at the basal position to the members of the clade. Within the 800 nt long alignment, the interspecific divergence between species of *Transvena* was 0.7% (5 nt) and between species of *Pararhadinorhynchus* was 0.3% (2 nt). Sequences of *G. mariserpentis*, *Rhadinorhynchus laterospinosus* Amin, Heckmann et Nguyen Van Ha, 2011 and *Rhadinorhynchus pristis* (Rudolphi, 1802) appeared to be identical. The interspecific divergence between *R. gerberi* n. sp. and *Rhadinorhynchus* spp. was 1.1% (8 nt). The sequence divergence between *R. gerberi* n. sp. and *G. decapteri* was 3.8% (27 nt) and between *G. decapteri* and *G. mariserpentis* was 3.9% (28 nt).

Within the *cox*1 dataset analyses, two identical sequences for *T. pichelinae* n. sp. clustered with that of *T. annulospinosa* in a strongly supported clade (Fig. 10). The interspecific divergence between the two species was 25.3% (123 nt). The clade comprising the sequences of two isolates of *R. gerberi* n. sp., two sequences of *Gymnorhadinorhynchus* spp., two sequences of *Rhadinorhynchus* spp. and the sequence of *Neorhadinorhynchus nudus* (Harada, 1938), received a negligible support. The intraspecific divergence between two isolates for *R. gerberi* n. sp. was 0.4% (2 nt). The genetic divergence within this clade ranged between 2.3–26.5% (11–129 nt) with *N. nudus* and *G. mariserpentis* exhibiting the lowest percentage of sequence divergence and *R. laterospinosus* and *G. decapteri* exhibiting the highest percentage of sequence divergence. The sequence difference between *G. mariserpentis* and *G. decapteri* was 26.1 % (127 nt).

DISCUSSION

Despite the increasing number of molecular studies on acanthocephalans (García-Varela et al. 2002, García-Varela and Nadler 2005, 2006, Verweyen et al. 2011), very little molecular phylogenetic work has been done on the Rhadinorhynchidae and Transvenidae. The first study of the relationship of the Rhadinorhynchidae within Acanthocephala based on the 18S rRNA gene including sequences for a *Rhadinorhynchus* sp. was by García-Varela et al. (2002). Subsequent phylogenetic studies (García-Varela and Nadler 2005, 2006, García-Varela and González-Oliver 2008) including sequences for additional rhadinorhynchid taxa, revealed that the genus *Gorgorhynchoides* clustered apart from *Rhadinorhynchus* sp. Two rhadinorhynchid genera *Leptorhynchoides* and *Pseudoleptorhynchoides* clustered within the family Illiosentidae, which is consistent with their morphological similarities (the absence of spines on the trunk and presence of 8 cement glands) and is accepted

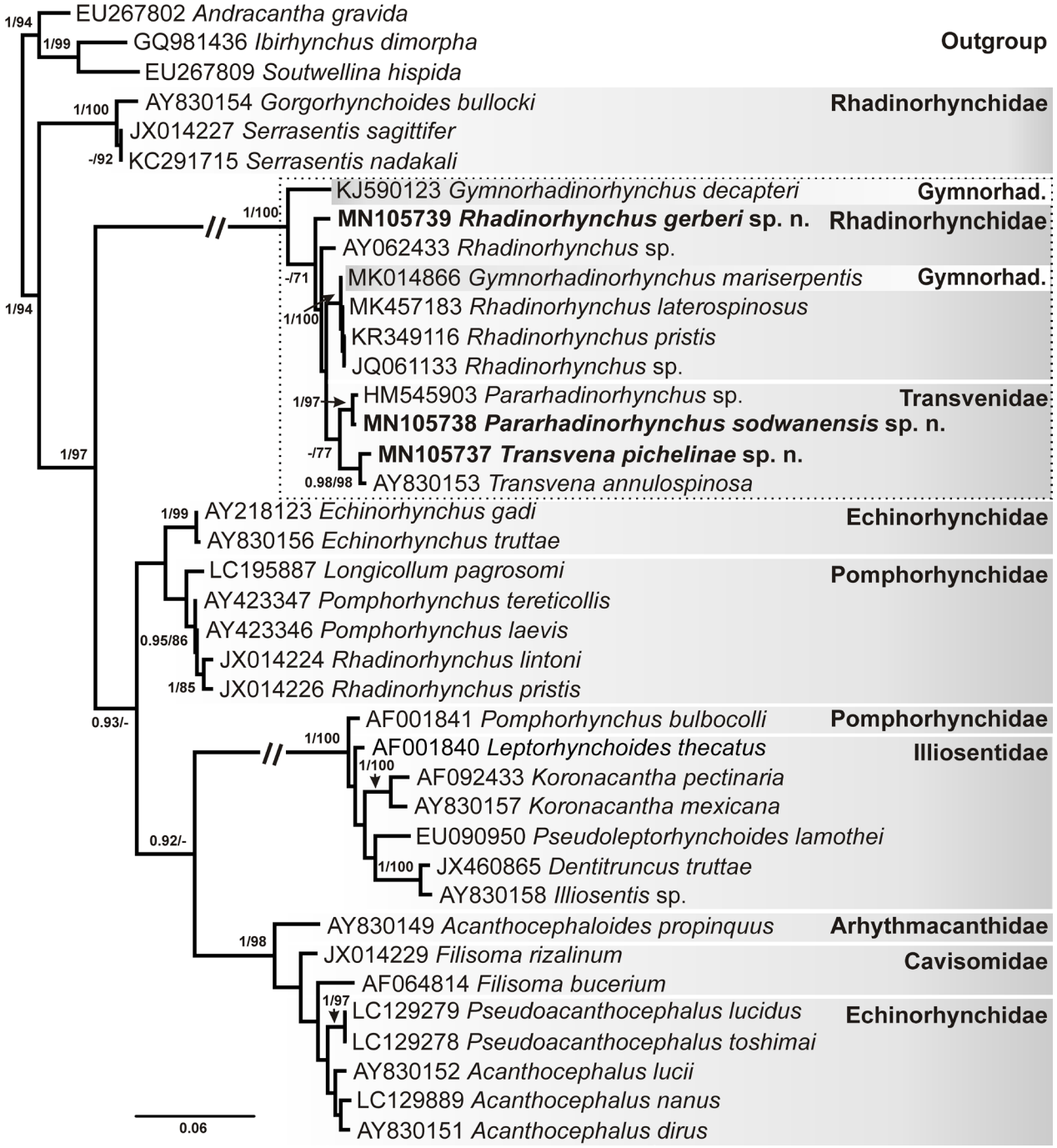

Fig. 9. Bayesian inference (BI) tree for the order Echinorhynchida based on partial 18S rDNA sequences. Numbers above branches indicate nodal support as posterior probabilities from BI followed by bootstrap values from maximum likelihood (ML) analysis. Support values lower than 0.90 (BI) and 70 (ML) are not shown. The scale-bar indicates the expected number of substitutions per site. Newly generated sequences are highlighted in bold. Abbreviation: Gymnorhad., Gymnorhadinorhynchidae.

in the recent classification of the Acanthocephala (Smales, 2015).

Verweyen et al. (2011) provided an updated analysis of the Acanthocephala incorporating the new sequence data for several taxa from the Palaeacanthocephala, including sequences for species from *Rhadinorhynchus* and *Serrasentis* Van Cleave, 1923. Their analysis demonstrated the position of the genus *Serrasentis* in the same clade as *Gorgorhynchoides*. Surprisingly, in contrast to the results of García-Varela and Nadler (2005, 2006), sequences generated for *Rhadinorhynchus* spp. by Verweyen et al. (2011) clustered together with *Pomphorhynchus* spp. (family Pomphorhynchidae). It should be noted that the sequence for *Rhadinorhynchus* sp. published by García-Varela et al. (2002) was not included in the analysis of Verweyen et al. (2011).

Later, Gregory et al. (2013) reported a cystacanth of *Rhadinorhynchus* sp. from bucchich's goby *Nyctiphanes couchii* (Bell) in the Mediterranean. Their phylogenetic analysis included all available sequences for rhadinorhy-

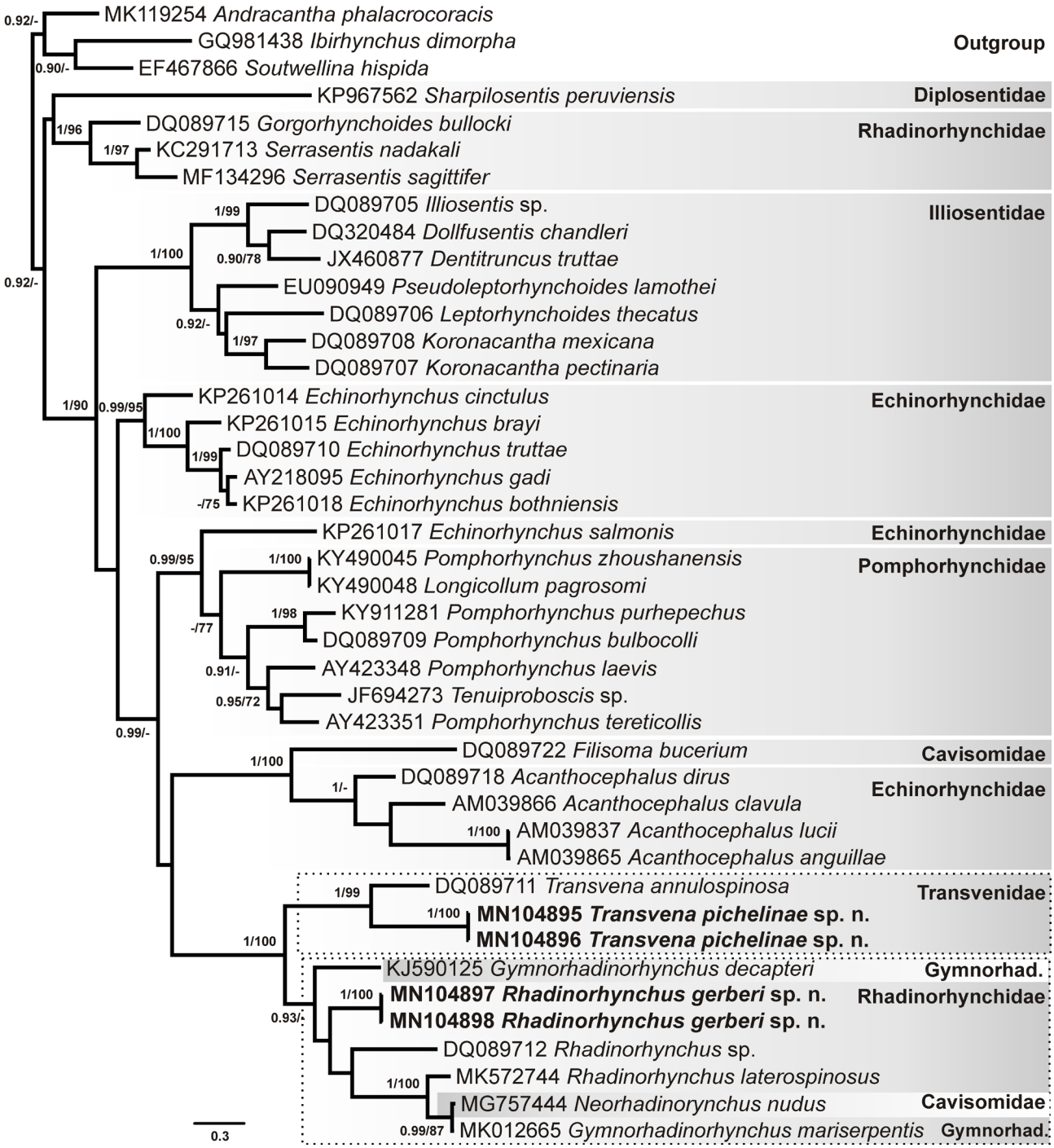

Fig. 10. Bayesian inference (BI) tree for the order Echinorhynchida based on *cox*1 sequences. Numbers above branches indicate nodal support as posterior probabilities from BI followed by bootstrap values from maximum likelihood (ML) analysis. Support values lower than 0.90 (BI) and 70 (ML) are not shown. The scale-bar indicates the expected number of substitutions per site. Newly generated sequences are highlighted in bold. Abbreviation: Gymnorhad., Gymnorhadinorhynchidae.

nchids in GenBank and raised a question as to the identification of *Rhadinorhynchus* spp. by Verweyen et al. (2011). The sequence for *Rhadinorhynchus* sp. of Gregory et al. (2013) clustered in a highly supported clade with *Rhadinorhynchus* sp. of García-Varela et al. (2002), *Pararhadinorhynchus* sp. and *Transvena annulospinosa*, whereas sequences for *Rhadinorhynchus pristis* and *R. lintoni* of Verweyen et al. (2011) clustered within the family Pomphorhynchidae. It should be mentioned that the sequences of an unidentified species *Rhadinorhynchus* by Gregory et al. (2013) is listed as *R. pristis* in GenBank (GenBank accession numbers JQ061133−JQ061135).

Bao et al. (2015) found specimens of *Rhadinorhynchus* in the allis shad *Alosa alosa* (Linnaeus) in rivers of the Western Iberian Peninsula. Their material was sequenced and identified using BLAST searches of the GenBank database as *R. pristis* by a 100% match with sequences of

Gregory et al. (2013) and in fact represents *Rhadinorhynchus* sp.

Amin et al. (2019) updated the description of *Rhadinorhynchus laterospinosus* based on novel material collected from *Auxis rochei* (Risso) and *Auxis thazard* (Lacépède) off the Pacific coast of Vietnam and provided the 18S rDNA and *cox*1 sequences for this species.

Recently, Braicovich et al. (2014) erected the family Gymnorhadinorhynchidae to accommodate the new genus and species *Gymnorhadinorhynchus decapteri* which possesses a combination of morphological features consistent with the Rhadinorhynchidae (dorsoventral asymmetry of the proboscis hooks, greatly enlarged hooks forming a ring at the base of the proboscis, four tubular cement glands) and Cavisomidae (unarmed trunk). Molecular phylogenetic analysis placed *G. decapteri* within a clade comprising *Rhadinorhynchus* sp. of García-Varela et al. (2002) and two species that belong to the Transvenidae.

According to Braicovich et al. (2014), the sequence for a new taxon clustered apart from members of the Rhadinorhynchidae (*Rhadinorhynchus* spp. of Verweyen et al. (2011) and Cavisomidae (*Filisoma bucerium* Van Cleave, 1940 and *Filisoma rizalinum* Tubangui et Masiluñgan, 1946). Therefore, the authors assumed that the unidentified sequence of García-Varela et al. (2002) may represent a member of a new family. However, sequences for *Rhadinorhynchus* sp. of Gregory et al. (2013) were not included in the analyses of Braicovich et al. (2014).

In the latest classification of the Acanthocephala by Smales (2015), the genus *Gymnorhadinorhynchus* Braicovich, Lanfranchi, Farber, Marvaldi, Luque et Timi, 2014 was considered as a member of the Rhadinorhynchidae. This was not considered by Steinauer et al. (2019) since the authors described the second species of the genus *Gymnorhadinorhynchus* within the Gymnorhadinorhynchidae, *Gymnorhadinorhynchus mariserpentis* recorded in the intestine of the oarfish *Regalecus russelii* (Cuvier) collected in Hibiki-nada Sea, Japan. Our phylogenetic analyses revealed an association between *G. decapteri*, *G. mariserpentis* and *Rhadinorhynchus* spp. and we thus suggest that the erection of the family Gymnorhadinorhynchidae was rather premature.

The results of *cox* 1 analyses raise a question regarding the taxonomic identity of *Neorhadinorhynchus nudus,* which is presently recognised as a member of the Cavisomidae. The sequence of *N. nudus* falls within the clade of Rhadinorhynchidae and is distant to another member of the Cavisomidae, *F. bucerium*. The genus *Neorhadinorhynchus* Yamaguti, 1939 was initially described within the family Rhadinorhynchidae as a subgenus of *Rhadinorhynchus* (see Yamaguti 1939). It was later elevated to full genus status (Yamaguti 1963) and transferred to the Cavisomidae, presumably on the basis of the presence of four cement glands and the lack of trunk spines (see Pichelin and Cribb 2001, Amin 2013, Smales 2015).

Based on the results of our molecular analyses, although without strong support, the acanthocephalans with four cement glands and lacking trunk spines (*N. nudus*, *G. decapteri* and *G. mariserpentis*) clustered together with the species that bear four cement glands and trunk spines (*Rhadinorhynchus* spp. and *R. gerberi* n. sp.), i.e. with the members of the Rhadinorhynchidae, and distant to another member of the Cavisomidae (*F. bucerium*). However, as previously stated by Pichelin and Cribb (2001), the presence or lack of trunk spines is a valuable taxonomic character but can cause considerable difficulties when wrongly interpreted (spines may be easily lost or overlooked). Thus, this feature cannot be considered as significant at the family level and, thus, the transfer of *N. nudus* into the Cavisomidae as well as the erection of the Gymnorhadinorhynchidae is questionable.

The phylogenetic analysis based on the *cox*1 dataset demonstrated the close relationships between *G. mariserpentis* and *N. nudus*. The sequence divergence between these species was rather low (2.3%, 11 nt), especially when compared with interspecific difference of *G. mariserpentis* and *G. decapteri* (26.1%, 127 nt). This suggest that such low sequence divergence between the isolates of *G. mariserpentis* and *N. nudus* may be intraspecific. Morphologically, *G. mariserpentis* differs from *N. nudus* by only one major characteristic. The basal proboscis hooks of *G. mariserpentis* are larger than prebasal, whereas the basal hooks in *N. nudus* are of the same size as prebasal (Li et al. 2018, Steinauer et al. 2019). Thus, both molecular and morphological results suggest that *G. mariserpentis* was erroneously assigened into the genus *Gymnorhadinorhynchus* and should be considered as a member of *Neorhadinorhynchus*.

The present genus-level structure within the Rhadinorychidae remains controversial. Much wider sampling and sufficient molecular data are required in order to satisfactorily resolve the problems of its composition. Out of 23 genera currently recognised within the family (Smales 2015), species of only four genera (*Gorgorhynchoides*, *Gymnorhadinorhynchus*, *Rhadinorhynchus* and *Serrasentis*) were molecularly characterised with *Gorgorhynchoides* and *Serrasentis* being phylogenetically distant from other rhardinorhynchids in a number of molecular studies (García-Varela and Nadler 2005, 2006, García-Varela and González-Oliver 2008, Verweyen et al. 2011, present study).

The systematic position of the genus *Pararhadinorhynchus* has also been controversial and opinions of authors on its systematic position and content are contradictory (Johnston and Edmonds 1947, Golvan 1969, Pichelin and Cribb 2001, Amin 2013, Amin et al. 2018, Ha et al. 2018, Smales et al. 2018). This genus was initially described by Johnston and Edmonds (1947) within the family Rhadinorhynchidae and later transferred in the Diplosentidae by Golvan (1969). This was corrected by Pichelin and Cribb (2001) based on the re-examination of the type material. The genus was transferred into the family Transvenidae.

However, Amin (2013), Amin et al. (2018), Ha et al. (2018) and Smales et al. (2018), without providing any clear reasons, consider *Pararhadinorhynchus* to have affinities with the family Diplosentidae. The 18S rDNA analyses in the present study strengthens the close relationship of *Pararhadinorhynchus* and *Transvena*, albeit without

high support. Moreover, the sequence of only a single representative of the Diplosentidae, *Sharpilosentis peruviensis* Lisitsyna, Scholz et Kuchta, 2015 currently available in GenBank (Lisitsyna et al. 2015), formed a branch distant from the clade with the Transvenidae (Fig. 10). This provides additional support for considering *Pararhadinorhynchus* as a member of the Transvenidae.

The discussion above once again demonstrates the importance of considering morphological and molecular approaches in the study of the acanthocephalans and necessity for morphological evidence (described and deposited in the museum collection specimens) for molecular data.

The present study improves our knowledge of the diversity of acanthocephalans from marine fishes in South Africa. Both, *Transvena* and *Pararhadinorhynchus* are reported for the first time from the waters around the African continent. *Rhadinorhynchus gerberi* n. sp. is the eighth species of this genus collected from fishes in Africa and the 43nd species within the genus. The observation of three distinct species of acanthocephalans belonging to the three genera collected from a relatively few fishes in one locality at Sodwana Bay, highlights the necessity for dedicated studies on this group of parasites in marine fishes in South Africa.

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