



FIRST RECORD OF THE GENUS *PSEUDOCHELES* CHACE & BROWN, 1978 (DECAPODA, CARIDEA, PSEUDOCHELIDAE) FROM THE EASTERN ATLANTIC WITH AN ANALYSIS OF THE PHYLOGENETIC POSITION OF THE PSEUDOCHELIDAE

BY

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ABSTRACT

Four specimens belonging to the shrimp genus *Pseudocheles* Chace & Brown, 1978 were collected during fieldwork on São Tomé from cracks in rocks in an underwater tunnel through Santana Islet. The specimens are here described, figured and compared with the two known Atlantic species, *P. chacei* Kensley, 1983 from Florida and Belize, and *P. falsapinca* Anker, 2012 from Espírito Santo, Brazil. It is most likely that the present specimens are conspecific with *P. falsapinca*. The phylogenetic position of the family Pseudochelidae is reconstructed on the basis of 16S and 18S gene sequences. The family is most closely related to the Disciadiidae.

Key words. — Decapoda, Caridea, Pseudochelidae, shrimp, São Tomé, East Atlantic, phylogeny

ZUSAMMENFASSUNG

Vier Exemplare der Garnelengattung *Pseudocheles* Chace & Brown, 1978 wurden aus Spalten im Fels in einem Tunnel durch das Inselchen Santana bei der Insel São Tomé gefangen. Sie werden hier beschrieben, abgebildet und mit den beiden bekannten atlantischen Arten verglichen, mit *P. chacei* Kensley, 1983 von Florida und Belize und mit *P. falsapinca* Anker, 2012 von Espírito Santo, Brasilien. Wahrscheinlich sind die Exemplare von São Tomé artgleich mit *P. falsapinca*. Die phylogenetische Stellung der Familie Pseudochelidae wird anhand der 16S- und 18S-Gensequenzen rekonstruiert. Die Familie ist am nächsten mit den Disciadiidae verwandt.

Schlüsselwörter. — Decapoda, Caridea, Pseudochelidae, Garnele, São Tomé, Ostatlantik, Phylogenie

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## INTRODUCTION

The shrimp genus *Pseudocheles* Chace & Brown, 1978 is the only genus in the family Pseudochelidae De Grave & Moosa, 2004 and known from only few specimens of the four species recognized: *P. enigma* Chace & Brown, 1978 (Australia); *P. chacei* Kensley, 1983 (Florida and Belize); *P. neutra* De Grave & Moosa, 2004 (Indonesia); and *P. falsapinca* Anker, 2012 (Brazil) (Chace & Brown, 1978; Kensley, 1983; De Grave & Moosa, 2004; De Grave & Fransen, 2011; Anker, 2012; Poore & Ah Yong, 2023).

Members of this genus can be easily recognized by the pseudochelate third, fourth and fifth pereopods, ending in a pectinate dactylus and several adjacent spiniform setae, including a particularly long and stout one that resembles an immovable finger.

The systematic position of the Pseudochelidae within the superfamily Bresilioidea Calman, 1896 was discussed by De Grave & Moosa (2009) based on morphological characters. They placed *Pseudocheles* in its own family, removing it from the Disciadidae Rathbun, 1902 sensu Christoffersen (1986) and Vereshchaka (1997) and restricting the Disciadidae to the genera *Discias* Rathbun, 1902, *Tridiscias* Kensley, 1983, and *Lucaya* Chace, 1939. The familial placement of the genera *Kirnasia* Burukovsky, 1988 and *Encantada* Wicksten, 1989 remained problematic at that time. The Bresilioidea presently comprise the families Agostocarididae Hart & Manning, 1986, Alvinocarididae Christoffersen, 1986, Anchialocarididae Mejía-Ortíz, Yañez & López-Mejía, 2017, Bresiliidae, Disciadidae and Pseudochelidae. Recent molecular analyses of caridean families showed the Bresilioidea to be polyphyletic with several separate clades within the Caridea (Bracken et al., 2009; Aznar-Cormano et al., 2014; De Grave et al., 2015). In these analyses only the Agostocarididae, Alvinocarididae, Bresiliidae and Disciadidae were represented. The systematic position of the Pseudochelidae thus remains unclear.

During fieldwork by the second author on São Tomé, four specimens of *Pseudocheles* were collected from cracks in rocks in an underwater tunnel through Santana Islet. These specimens are similar to the two West Atlantic species: *P. falsapinca* which is only known from the holotype and a paratype ovigerous female collected off Espírito Santo, Brazil (Anker, 2012); and to *P. chacei*, known from 15 specimens collected at Looe Key, Florida and Carrie Bow Cay, Belize (Kensley, 1983). The four specimens from São Tomé are described, illustrated and compared with the two Atlantic species of *Pseudocheles*.

We obtained sequences of the mitochondrial marker 16S, as well as of the nuclear markers 18S of the *Pseudocheles* specimens from São Tomé and several related species. From GenBank we obtained sequences of species representing caridean superfamilies, families and outgroups (table I) to analyse the phylogenetic position of the Pseudochelidae within the Caridea.

TABLE I

Selected species representing caridean superfamilies, families and outgroups (DecaNet, 2025) with newly obtained sequences (in italics) and sequences obtained from GenBank used in phylogenetic analyses

Superfamily	Family	Species	Voucher	Reference	GenBank accession Nos		
					16S	18S	
Alpheoidea	Alpheidae	<i>Alpheus gracilipes</i> Stimpson, 1860	not indicated	Mitsuhashi et al. (2007)	DQ642885	DQ642859	
	Barbouriidae	<i>Parhippolyte antiquensis</i> (Chace, 1972)	OUMH.ZC.2004-15-002	Li et al. (2011)	NA	JF346262	
	Hippolytidae	<i>Hippolyte varians</i> Leach, 1814	OUMH.ZC.2004-15-002 ULLZ 6970	De Grave et al. (2014) Bracken et al. (2009)	KF023112 EU868662	NA EU868753	
	Lysmatidae	<i>Lysmata debelius</i> Bruce, 1983	MLP121	Porter et al. (2005)	DQ079718	DQ079752	
	Ogyrididae	<i>Ogyrides</i> sp.1	ULLZ 7755	Bracken et al. (2009)	EU868679	EU868772	
	Thoridae	<i>Eualus cranchii</i> (Leach, 1817)	ULLZ 6969	Bracken et al. (2009)	EU868667	EU868758	
		<i>Lebbeus jiaolongi</i> (Xu, Liu, Ding & Wang, 2016)	not indicated	Sun et al. (2021)	MH398078	MH398107	
	Atoidea	Atyidae	<i>Atyopsis moluccensis</i> (De Haan, 1849)	not indicated	Page et al. (2007)	DQ681281	NA
			<i>Caridina serratirostris</i> De Man, 1892	NTOU:M00728 MNHN-IU-2013-11821	Li et al. (2011) Aznar-Cormano et al. (2015)	NA KP725509	JF346252 KP725708

TABLE I  
(Continued)

Superfamily	Family	Species	Voucher	Reference	GenBank accession Nos	
					16S	18S
Bresilioidea	Agostocarididae	<i>Agostocaris</i> sp.	USNM 1014071	Bracken et al. (2009)	EU868626	EU868716
	Alvinocarididae	<i>Alvinocaris lusca</i> Williams & Chace, 1982	MNHN (no voucher)	Aznar-Cormano et al. (2015)	KP215284	KP215299
Bresiliidae		<i>Bresilia antipodarum</i> Bruce, 1990	MNHN-IU-2011-5978	Aznar-Cormano et al. (2015)	NA	KP725705
		<i>Bresilia saldanhai</i> Calado, Chevaldonné & dos Santos, 2004	MNHN-IU-2013-15658	Aznar-Cormano et al. (2015)	KP725505	KP725706
Disciadiidae		<i>Discias atlanticus</i> Gurney, 1939	ULLZ 8953	Bracken et al. (2009)	EU868652	EU868743
		<i>Discias</i> sp. AT-2008	RMNH.CRUS.D.59489	This study	PV918503	PV918499
		<i>Discias</i> sp. AL-2010	KC3108	Toon et al. (2009)	EU920921	EU920941
		<i>Discias verbergi</i> Booth & Heard, 1987	not indicated	Chan et al. (2010)	GQ131913	GQ131937
		<i>Lucaya bigelowi</i> Chace, 1939	RMNH.CRUS.D.57264	This study	PV918502	PV918498
			HBG5216	Varela & Bracken-Grisson (2021)	MF197214	NA
Pseudocheilidae			HBG4627	Varela & Bracken-Grisson (2021)	MF197213	NA
		<i>Pseudocheles</i> <i>falsapinca</i> Anker, 2012	RMNH.CRUS.D.59487	This study	PV918504	PV918500
			RMNH.CRUS.D.59488	This study	PV918505	PV918501

TABLE I  
(Continued)

Superfamily	Family	Species	Voucher	Reference	GenBank accession Nos	
					16S	18S
Campylonotoidea	Campylonotidae	<i>Campylonotus capensis</i> Spence Bate, 1888	MNHN-IU-2008-16733	Aznar-Cormano et al. (2015)	KP725506	KP725707
		<i>Bathypalaemonella serratipalma</i> Pequegnat, 1970	MNHN-IU-2008-16757	Aznar-Cormano et al. (2015)	KP725503	KP725701
Crangonoidea	Crangonidae	<i>Crangon crangon</i> (Linnaeus, 1758)	ULLZ 6967	Bracken et al. (2009)	EU868649	EU868740
		<i>Pontophilus norvegicus</i> (M. Sars, 1861)	KC3053	Bracken et al. (2010)	GQ487496	GQ487504
Nematocarinoidea	Glyphocrangonidae	<i>Glyphocrangon armata</i> Komai, 2004	MNHN-IU-2008-14552	Boisselier-Dubayle et al. (2010)	HQ241513	HQ241525
		<i>Eugonatonotus chacei</i> Chan & Yu, 1991	MNHN-IU-2011-3650	Aznar-Cormano et al. (2015)	KP725518	KP725717
	Nematocarcinidae	<i>Nematocarcinus africanus</i> Crosnier & Forest, 1973	MNHN-IU-2008-17048	Aznar-Cormano et al. (2015)	KP725566	KP725769
Oplophoroidea	Rhynchocinetidae	<i>Cinetorhynchus erythrosicticus</i> Okuno, 1997	MNHN-IU-2010-4994	Aznar-Cormano et al. (2015)	KP725512	KP725712
	Acanthephyridae	<i>Acanthephyra smithi</i> Kemp, 1939	not indicated	Sun et al. (2021)	MH398079	MH398108
	Oplophoridae	<i>Oplophorus typus</i> H. Milne Edwards, 1837	not indicated	Sun et al. (2021)	MH398081	MH398110

TABLE I  
(Continued)

Superfamily	Family	Species	Voucher	Reference	GenBank accession Nos	
					16S	18S
Palaemonoidea	Palaemonidae	<i>Macrobrachium aemulum</i> (Nobili, 1906)	MNHN (no voucher)	Aznar-Cormano et al. (2015)	KP215286	KP215301
Pandalioidea	Pandalidae	<i>Palaemon elegans</i> Rathke, 1836	ULLZ 6968	Bracken et al. (2009)	EU868696	EU868790
		<i>Bitias brevis</i> (Rathbun, 1906)	not indicated	Sun et al. (2021)	MH398080	MH398109
Pasiphaeoidea	Pasiphaeidae	<i>Pandalus montagui</i> Leach, 1814	KC3144	Bracken et al. (2010)	GQ487498	GQ487506
		<i>Pasiphaea sivado</i> (Risso, 1816)	MNHN-IU-2008-16750	Aznar-Cormano et al. (2015)	KP725630	KP725825
Processoidea	Processidae	<i>Processa guyanae</i> Holthuis, 1959	ULLZ 7150	Bracken et al. (2009)	EU868708	EU868803
Procarioidea	Procaridae	<i>Procaris mexicana</i> von Sternberg & Schotte, 2004	ULLZ 9224	Bracken et al. (2009)	EU868715	EU868811
Psalidopodoidea	Psalidopidae	<i>Procaris ascensionis</i> Chace & Manning, 1972	KC4273	Bracken et al. (2010)	GQ487494	GQ487502
		<i>Psalidopus huaxleyi</i> Wood-Mason in Wood-Mason & Alcock, 1892	MNHN-IU-2011-2655	Aznar-Cormano et al. (2015)	KP725641	KP725842

TABLE I  
(Continued)

Superfamily	Family	Species	Voucher	Reference	GenBank accession Nos	
					16S	18S
Styloactyloidea	Styloactylidae	<i>Neostyloactylus amarynthii</i> (De Man, 1902)	MNHN-IU-2008-10355	Aznar-Cormano et al. (2015)	KP725601	KP725804
		<i>Styloactylus multidentatus</i> Kubo, 1942	ULLZ 8881	Bracken et al. (2009)	EU868711	EU868806
Outgroup						
Stenopodidea	Stenopodidae	<i>Stenopus hispidus</i> (Olivier, 1811)	not indicated	Ahyong & O'Meally (2004)	AY583884	AY743957
Dendrobranchiata	Penaeidae	<i>Penaeus semisulcatus</i> De Haan, 1844	KC1269	Porter et al. (2005)	DQ079731	DQ079766

HBG, specimens in the Florida International University Crustacean Collection (FICC), Miami, FL, U.S.A.; KC and MLP, Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT, U.S.A.; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NTOU, National Taiwan Ocean University, Keelung, Taiwan; OUMH, Oxford University Museum of Natural History, Oxford, U.K.; ULLZ, University of Louisiana at Lafayette Zoological Collection, Lafayette, LA, U.S.A.; USNM, Smithsonian United States National Museum, Washington, DC, U.S.A.

## MATERIAL AND METHODS

## Taxon sampling

The São Tomé specimens were collected in 11-13 m depth by spraying clove oil (diluted with ethanol) into cracks in the rock in a completely dark side-branch near the western end of the channel through Santana Islet, São Tomé. Newly obtained sequences as well as sequences obtained from GenBank (table I) representing selected caridean families were used for phylogenetic analyses.

## Morphological analysis

Specimens were studied using a dissecting stereomicroscope (Zeiss Discovery.V8) and a compound microscope (Olympus BX53), both provided with a drawing tube. Drawings were scanned (Canon Canoscan 9000F) with a resolution of 600 dpi and subsequently mounted into plates using Adobe Photoshop software (Adobe Systems). Post-orbital carapace length (pocl.) was measured from the posterior margin of the orbit to the posterior margin of the carapace in dorsal midline; rostral characters (R) are formulated as  $R = \text{number of dorsal teeth}/\text{number of ventral teeth}$ . Specimens were deposited in the Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie, RMNH), Leiden, The Netherlands.

## DNA analyses

Total genomic DNA was extracted from the abdominal muscle tissues, pleopods or eggs using the DNeasy Blood and Tissue Kit or Qiamp DNA Micro Kit (Qiagen) following the manufacturer's protocols.

For resolving phylogenetic relationships, partial mitochondrial 16S ribosomal RNA (16S; 500-520 bp), and nuclear 18S ribosomal RNA (18S; approx. 653 bp) were sequenced. Target gene regions were amplified by polymerase chain reaction (PCR) using primer pairs: 16Sar/16Sbr (Palumbi et al., 1991) for 16S rRNA and 18S-2.0/18S-9R (Whiting, 2002) for 18S rRNA.

Polymerase chain reactions of newly sequenced samples followed the protocols used by Brinkmann & Fransen (2016). PCR products were submitted to Macro-gen (Amsterdam, The Netherlands) for sequencing using the Sanger sequencing reaction with an ABI3730XL DNA Sequencer.

Aligning was carried out using the software MUSCLE (Edgar, 2004), with default setting, as implemented in MEGA-X (Kumar et al., 2018). Highly variable and divergent positions as well as poorly aligned ones were detected and eliminated from the alignment using Gblocks v0.91b (Castresana, 2000) with default parameters except for allowing gap positions. This resulted in 1282 nucleotides

determined to be suitable for phylogenetic analysis in the 18S marker and 453 in the 16S marker.

The best-fit model for the nucleotide substitution (i.e., GTR + G + I for both markers) was selected based on AICc (Akaike Information Criterion, corrected) implemented in MEGA-X (Kumar et al., 2018). The 18S and 16S were combined in a concatenated alignment. Maximum Likelihood (ML) analysis was conducted with the web server W-IQ-TREE (see <http://iqtree.cibiv.univie.ac.at/>; Trifinopoulos et al., 2016) using the best-fit substitution model automatically selected by the software according Akaike information criterion (AIC) and ultrafast bootstrap (UFB) (Minh et al., 2013) with 10 000 replicates to assess branch support. Bayesian Inference (BI) was conducted in MrBayes 3.2.1 (Ronquist et al., 2012). The Markov chain Monte Carlo (MCMC) algorithm was run for 5 million generations and sampled trees every 1000 generations; the burn-in was set to 25%.

The final tree was displayed using FigTree v1.4.4 software (Rambaut, 2018).

## RESULTS

### Taxonomy

Family PSEUDOCHELIDAE De Grave & Moosa, 2004

Genus *Pseudocheles* Chace & Brown, 1978

***Pseudocheles falsapinca* Anker, 2012**

(figs. 1-10)

Material examined.— São Tomé, Santana Islet. One male, pochl. 2.1 mm, R = 6/1 (RMNH.CRUS.D.59486), from cracks in the rock, dark side-branch of tunnel through Santana Islet, 0°14'28"N 6°45'33"E, 18.xi.2023, depth 13 m, scuba diving, collected by Peter Wirtz. One male, pochl. 1.9 mm, R = 6/1, and one ovigerous female, pochl. 2.9 mm, R = 6/1 (RMNH.CRUS.D.59487), dark side-branch of tunnel through Santana Islet, 0°14'28"N 6°45'33"E, 26.xi.2023, depth 11 m, scuba diving, collected by Peter Wirtz. One ovigerous female, pochl. 2.6 mm, R = 6/1 (RMNH.CRUS.D.59488), dark side-branch of tunnel through Santana Islet, 0°14'28"N 6°45'33"E, 27.xi.2023, depth 11 m, scuba diving, collected by Peter Wirtz.

Material of *Pseudocheles chacei* for comparison.— Paratypes: one male, pochl. 2.0 mm, R = 6/1, and one juvenile, pochl. 1.3 mm, R = 6/1 (RMNH.CRUS.D.36167), Looe Key, Florida, 27.i.1983, depth 6 m, coll. B. Kensley and M. Schotte.

Material of *Discias verbergi* Boothe & Heard, 1987 for comparison.— 1 ovigerous female (pochl. 5.1 mm), 7 females (pochl. 2.2 to 3.6 mm), 8 males (pochl. 1.8 to 3.5 mm) (RMNH.CRUS.D.57264), Netherlands Antilles, Bonaire, 12°04'47"N, 068°17'37"W, depth 246 m, 31.v.2013, dive with Curasub submersible BON4/BDR050, in sponge, collected by L. E. Becking and H. W. G. Meesters.

Material of *Discias atlanticus* Gurney, 1939 for comparison.— 2 non-ovigerous females, pochl. 2.7 and 3.0 mm (RMNH.CRUS.D.59489) Cape Verde Islands, Santiago Island, Tarrafal, close to diving base, 5.v.2024, depth 15-20 m, below stones, scuba diving, collected by P. Wirtz.

Description and comparison of newly collected specimens.— Like in the types of *P. falsapinca* and *P. chacei*, the rostrum of the present specimens is moderately

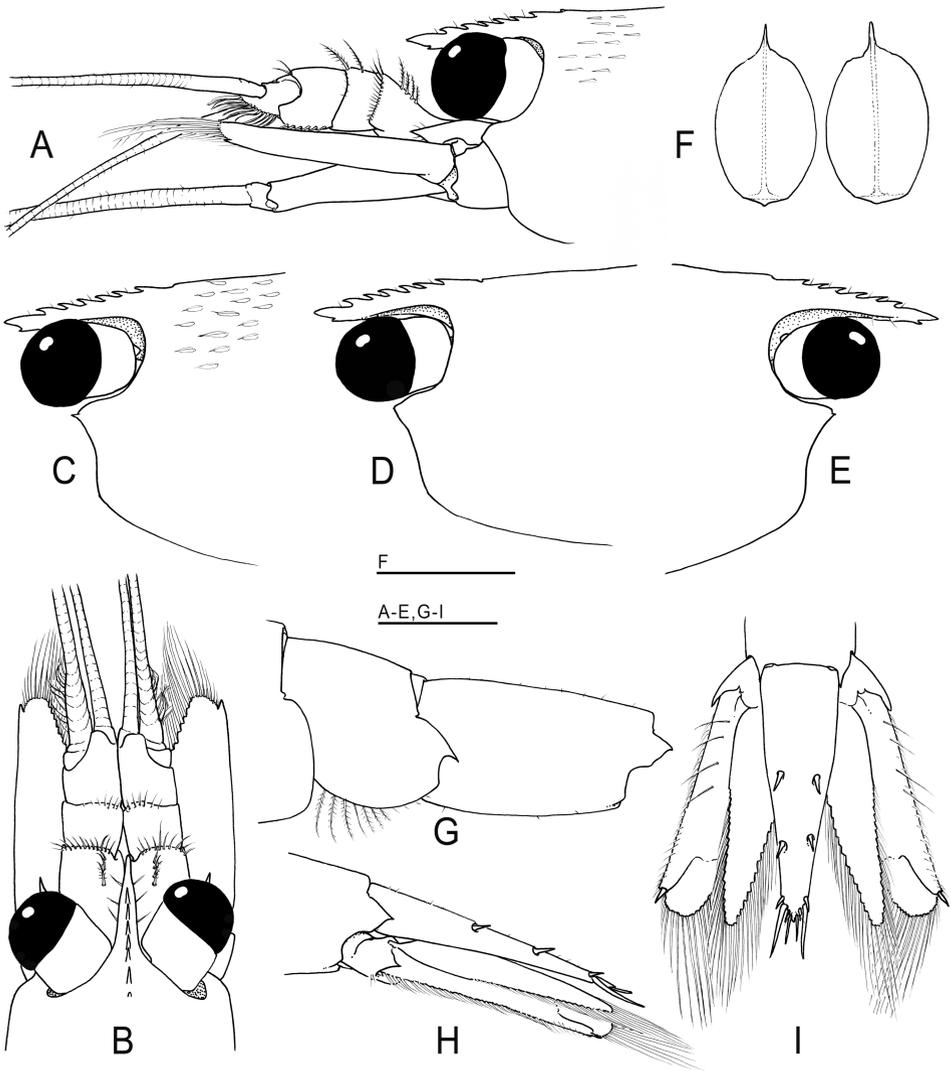


Fig. 1. *Pseudocheles falsapinca* Anker, 2012. A, B, F-I, male, pochl. 1.9 mm (RMNH.CRUS.D.59487); C, ovigerous female, pochl. 2.9 mm (RMNH.CRUS.D.59487); D, male, pochl. 2.1 mm (RMNH.CRUS.D.59486); E, ovigerous female, pochl. 2.6 mm (RMNH.CRUS.D.59488). A, Anterior appendages and anterior part carapace, lateral view; B, idem, dorsal view (tegumental scales omitted); C-E, anterior part carapace, lateral view (tegumental scales omitted in D and E); F, tegumental scales from dorsal surface of carapace, dorsal view; G, fifth and sixth abdominal somites, lateral view (tegumental scales omitted); H, caudal fan, lateral view (tegumental scales omitted); I, idem, dorsal view. Scale bars: A-E, G-I = 1 mm; F = 0.125 mm.

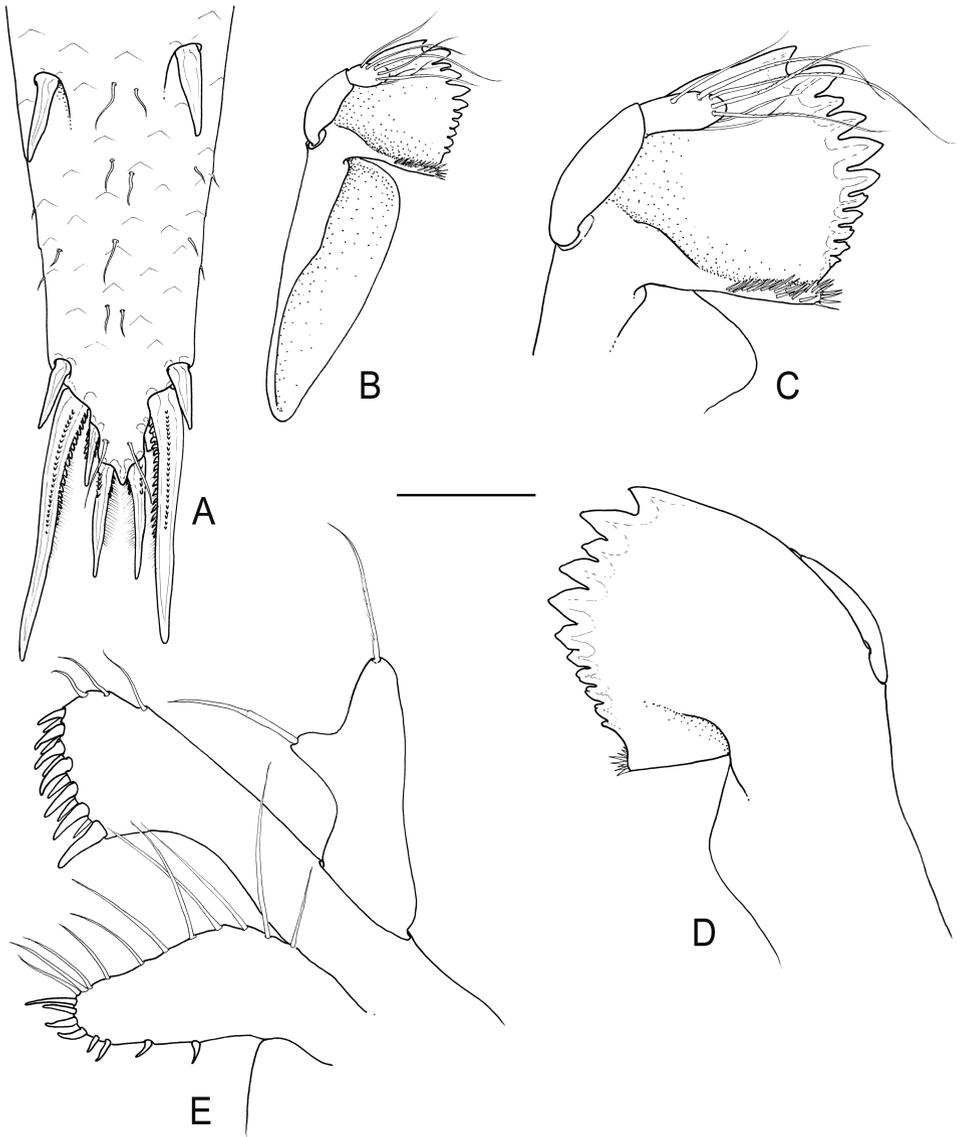


Fig. 2. *Pseudosquilla falsapinca* Anker, 2012, male, pochl. 1.9 mm (RMNH.CRUS.D.59487). A, Telson, tip, dorsal view; B, C, left mandible, dorsal view; D, idem, ventral view; E, left maxillula, ventral view. Scale bars: A, C-E = 0.25 mm; B = 0.5 mm.

slender, barely reaching the distal margin of the first article of the antennular peduncle (figs. 1A-E, 8). In all four specimens at hand, the rostrum bears six anteriorly directed dorsal teeth of about equal size and at equal distances. The types of *P. falsapinca* have five dorsal rostral teeth (see Anker, 2012, fig. 1a-c, m). The 15 type specimens of *P. chacei* have 5-8 (usually 6) dorsal rostral

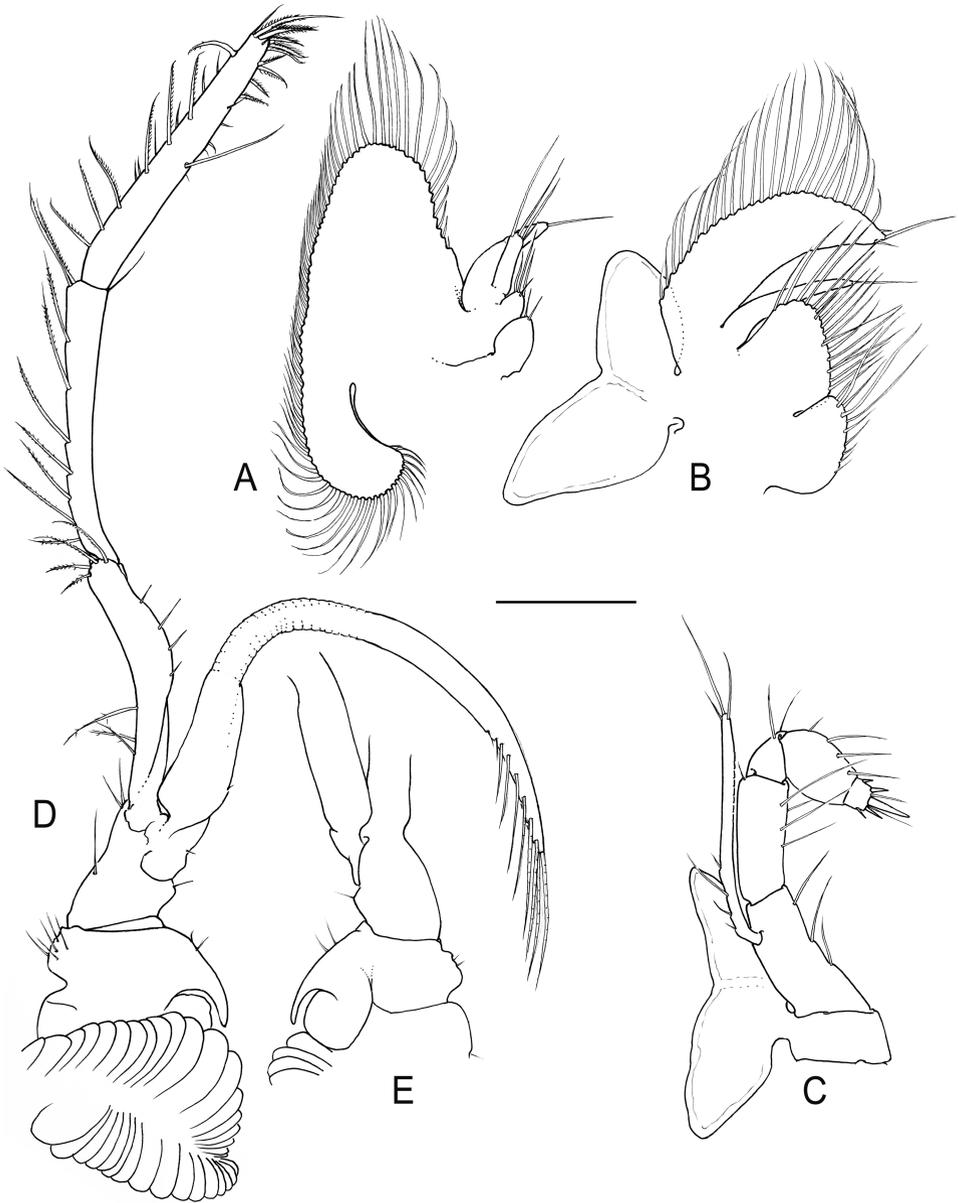


Fig. 3. *Pseudocheles falsapinca* Anker, 2012, male, pocl. 1.9 mm (RMNH.CRUS.D.59487). A, Right maxilla, ventral view; B, right first maxilliped, posterior view; C, right second maxilliped, posterior view; D, right third maxilliped, lateral view; E, idem, mesial view proximal part. Scale bar = 0.5 mm.

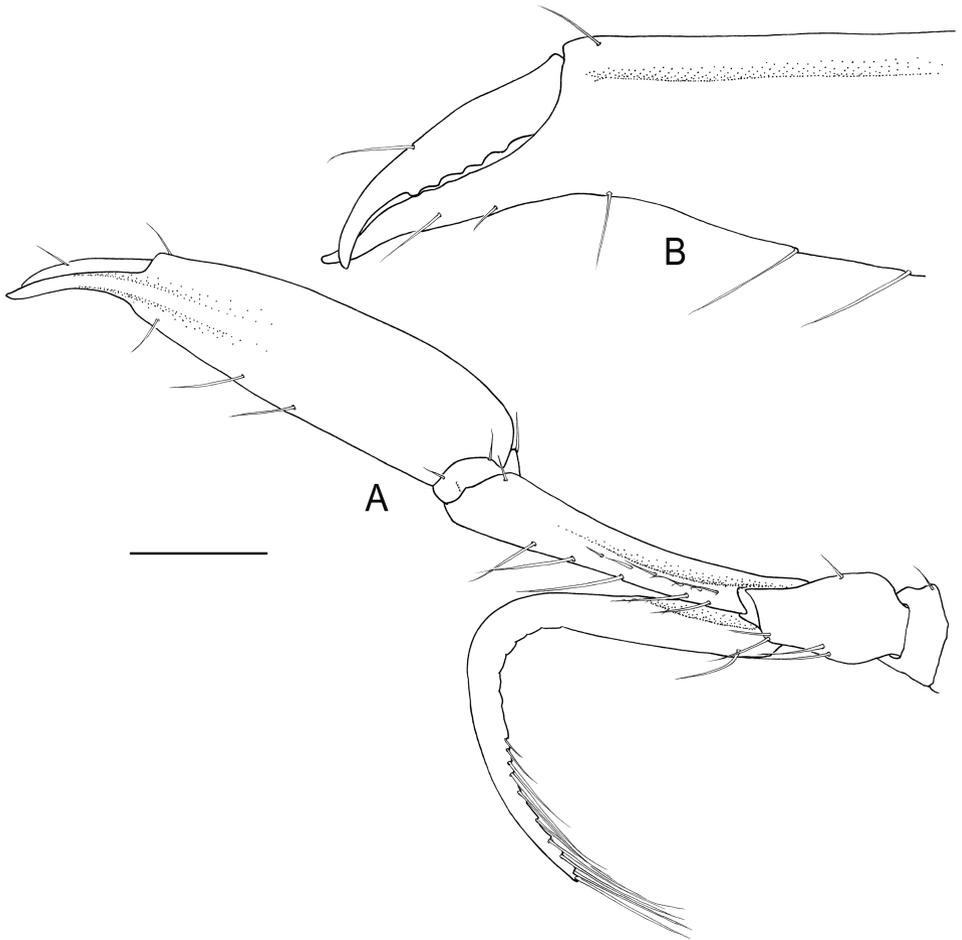


Fig. 4. *Pseudocheles falsapinca* Anker, 2012, male, pochl. 1.9 mm (RMNH.CRUS.D.59487). A, Right first pereiopod, lateral view; B, idem, chela, mesial view. Scale bars: A = 0.5 mm; B = 0.25 mm.

teeth. In the middle of each tooth there is a single dorsal simple seta present except for the posteriormost tooth; this feature is also present in the paratypes (RMNH.CRUS.D.36167) of *P. chacei* and the types of *P. falsapinca* (see Anker, 2012, fig. 2c). Just behind the six dorsal rostral teeth, a small anterior tubercle or notch, is present at a slightly larger distance from the posteriormost tooth than the distance between the anterior six teeth. This tubercle or notch was also noted in the types of *P. falsapinca* (Anker, 2012, fig1a-c, m) but not observed in the paratypes (RMNH.CRUS.D.36167) of *P. chacei*. The low middorsal tubercle in the posterior seventh of the carapace as described for *P. chacei* was not observed in the present material nor noted for *P. falsapinca*. The ventral margin of the rostrum is straight and bears one small subdistal tooth as in *P. chacei* (see Kensley, 1983,

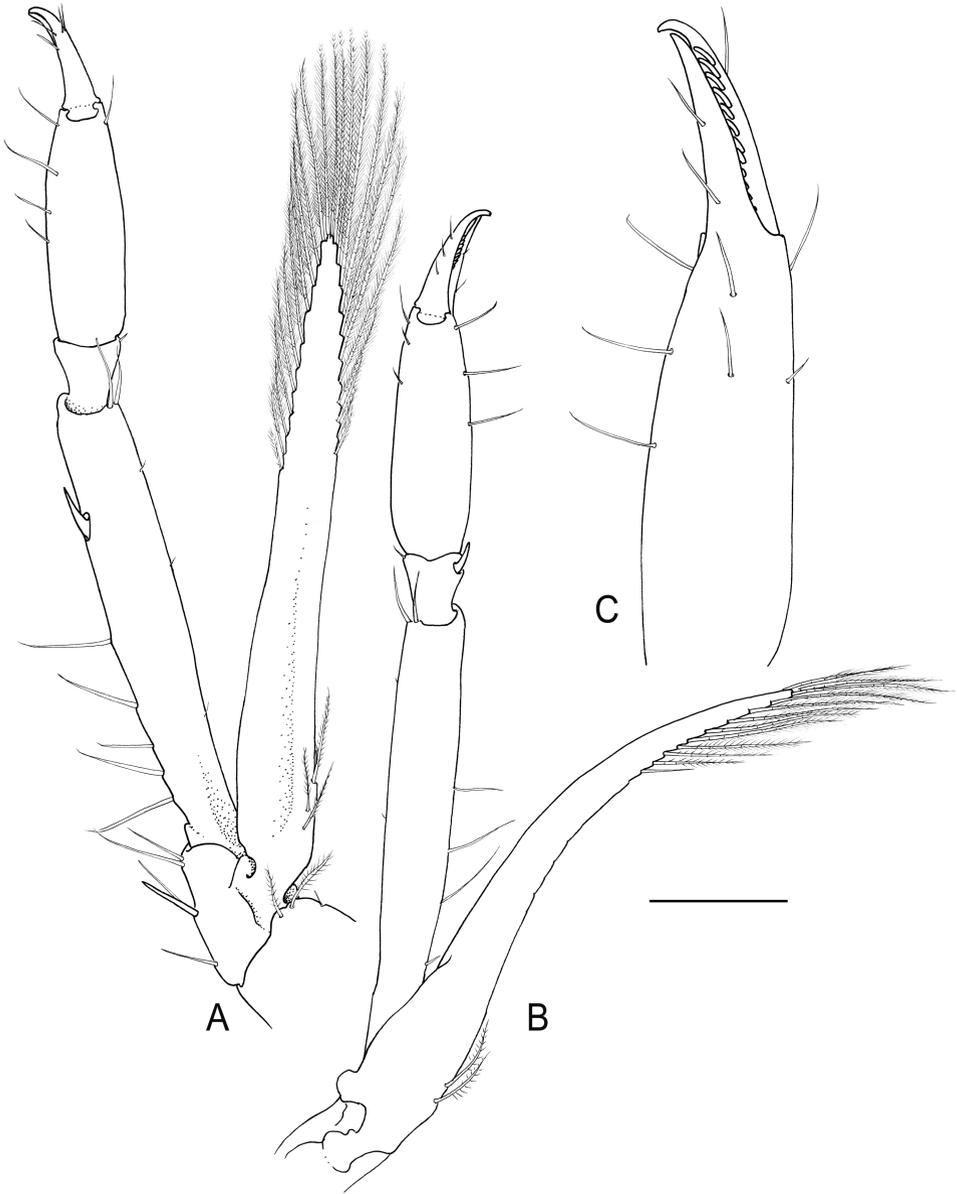


Fig. 5. *Pseudocheles falsapinca* Anker, 2012, male, pochl. 1.9 mm (RMNH.CRUS.D.59487). A, Left second pereiopod, lateral view; B, right second pereiopod, lateral view; C, idem, chela. Scale bars: A, B = 0.5 mm; C = 0.25 mm.

fig. 18) and the types of *P. falsapinca* (see Anker, 2012, fig. 1b, c, m). A lateral carina is present in the lower part of the rostrum forming a narrow supraorbital eave widening posteriorly. On the lower margin of this carina few simple setae are

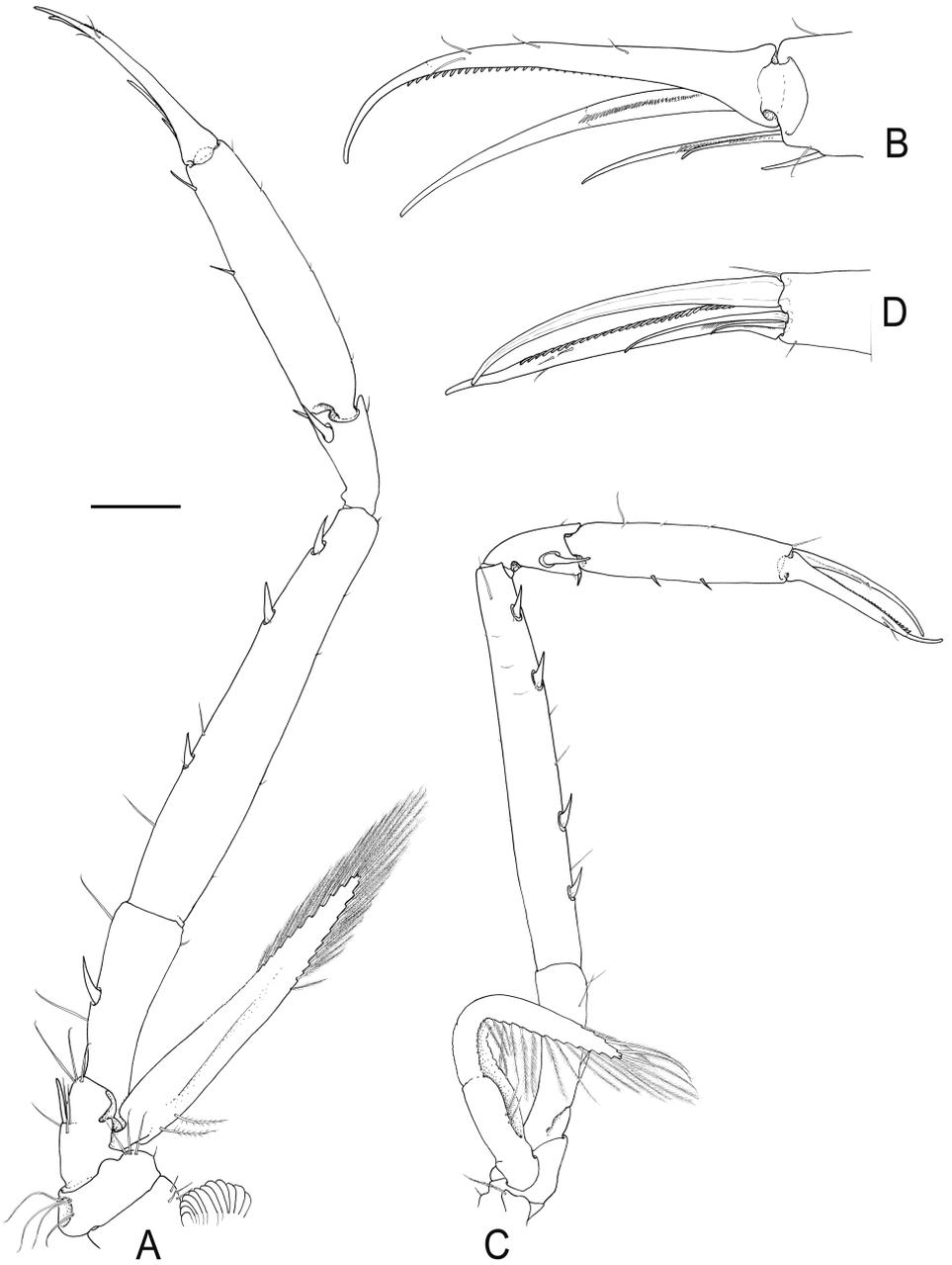


Fig. 6. *Pseudocheles falsapinca* Anker, 2012. A, ovigerous female, pochl. 2.9 mm (RMNH.CRUS.D.59487), left third pereiopod, lateral view; B, idem, chela; C, male, pochl. 1.9 mm (RMNH.CRUS.D.59487), right fourth pereiopod, lateral view; D, idem, chela, mesial view. Scale bars: A, C = 0.5 mm; B, D = 0.25 mm.

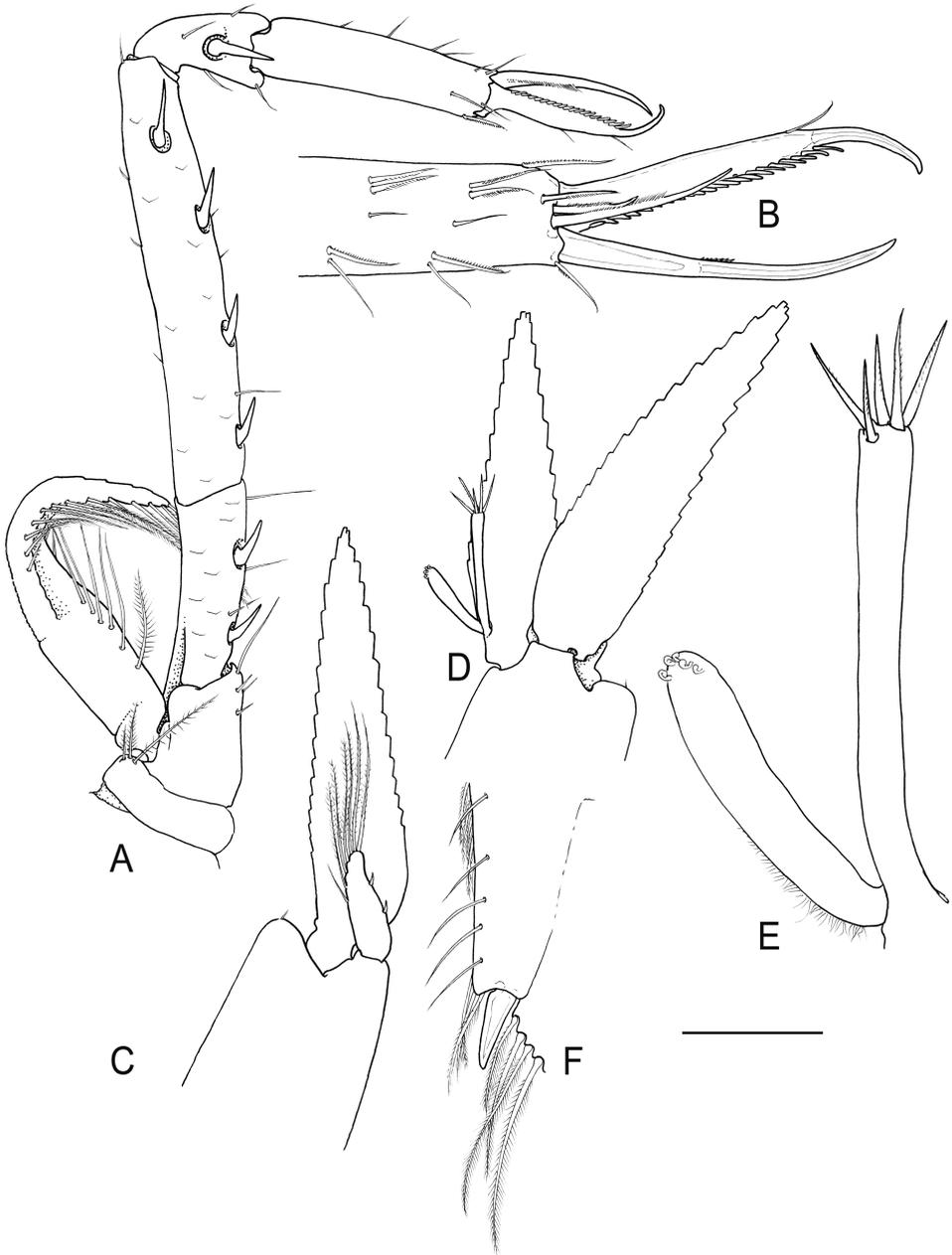


Fig. 7. *Pseudocheles falsapinca* Anker, 2012. A, Male, pochl. 1.9 mm (RMNH.CRUS.D.59487), right fifth pereiopod, lateral view; B, idem, chela, mesial view; C, left first pleopod, posterior view; D, left second pleopod, posterior view; E, idem, appendix interna and appendix masculina; F, left uropodal exopod, distolateral part, dorsal view. Scale bars: A, C, D = 0.5 mm; B, F = 0.25 mm; E = 0.125 mm.

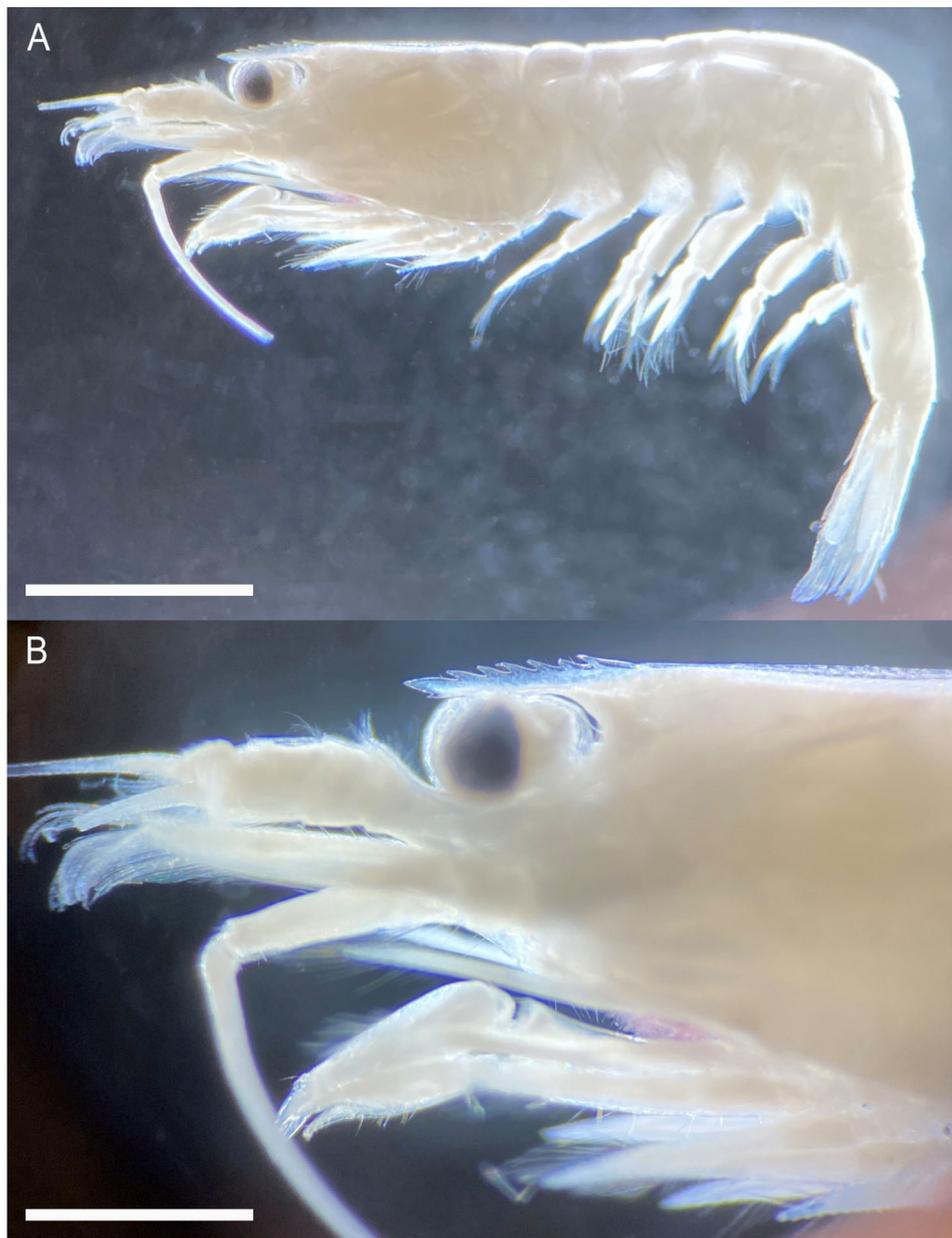


Fig. 8. *Pseudocheles falsapinca* Anker, 2012. A, male, pochl. 1.9 mm (RMNH.CRUS.D.59487). A, Habitus, lateral view; B, anterior part carapace and anterior appendages, lateral view. Scale bars: A = 2 mm; B = 1 mm.

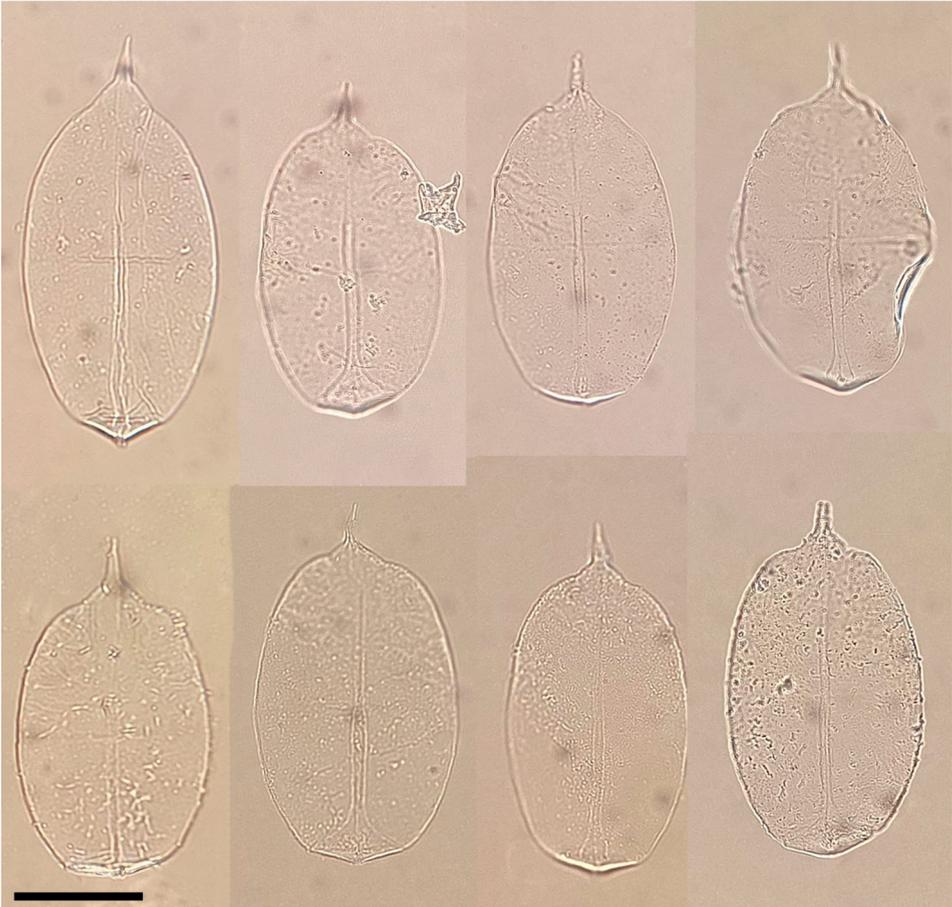


Fig. 9. *Pseudocheiles falsapinca* Anker, 2012, male, pochl. 1.9 mm (RMNH.CRUS.D.59487), tegumental scales from dorsal surface of carapace, dorsal view. Scale bar = 0.05 mm.

present. The carapace is slightly compressed laterally, covered with tegumental scales (figs. 1A, C, F, 9). When tegumental scales have abraded, they leave a scar, giving the carapace a finely pitted surface as described by Anker (2012, fig. 1c, m) for *P. falsapinca*. In the paratypes (RMNH.CRUS.D.36167) of *P. chacei*, tegumental scales are also present on the carapace. The infra-orbital lobe has a very small to obsolete antennal tooth (fig. 1A, C-E). The pterygostomial angle is rounded (fig. 1A, C-E). The thoracic sternites are very narrow, all unarmed.

The pleon of both males and females is covered with tegumental scales. Tegumental scales are directed forward on the anterior three somites. Tegumental scales on the anterior dorsal margins of the anterior three somites are slightly longer than those on the somites proper. Tegumental scales on the posterior three somites are directed backwards. Tegumental scales on the posterior dorsal margins

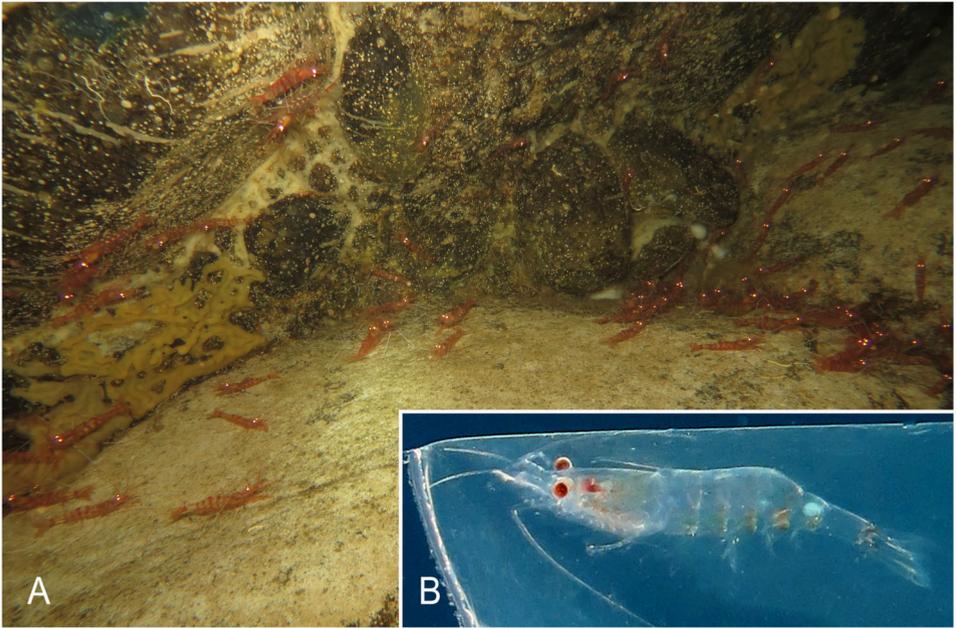


Fig. 10. A, Habitat inside Santana tunnel with *Parhippolyte antiguensis* (Chace, 1972) shrimps; B, *Pseudosquilla falsapinca* Anker, 2012, photographed through a plastic bag just after collecting. Photo credits: Peter Wirtz.

are slightly longer than on the somites proper. The first and second pleura are broadened ventrally and have a row of setae along their dorsal anterior margins. The third somite is narrower ventrally, the posterior dorsal margin is projecting and distinctly overhanging part of the fourth somite, forming a short hump. The fifth pleuron has a sharp, posteroventrally curved tooth on its posterior margin. The sixth somite is elongate, almost twice as long as high, and has a sharply projecting tooth near the base of the telson (fig. 1G).

The telson (fig. 1H, I) is slender, almost four times as long as wide proximally, tapering posteriorly. The dorsal surface has two pairs of spiniform setae inserted slightly posterior to about 0.4 and at 0.7 of the telson length, at some distance from the lateral margin. Tegumental scales are present (fig. 2A, scars of the tegumental scales indicated). The posterior margin (fig. 2A) ends in a sharp triangular point, with four pairs of spiniform setae as described for *P. falsapinca* (Anker, 2012, fig. 1d, f, g) and *P. chacei*. The anteriormost pair of spiniform setae is short, about as long as the dorsal pairs of spiniform setae, laterally located and without special features. The sublateral pair of spiniform setae, inserted slightly more posteriorly is much longer than the lateral pair and have dorsal and mesial rows of denticles in their proximal half as well as fine setae mesially. A pair of short, distinctly more posterior submedian spiniform setae have few rows of denticles proximally.

A pair of long median spiniform setae, shorter and more slender than the sublateral spiniform setae, are flanking the median point of the posterior margin, with rows of denticles in their proximal part and fine setae mesially. The features of the four pairs of terminal spines described here for the São Tomé specimens were also observed in the paratype male (RMNH.CRUS.D.36167) of *P. chacei*.

The eyestalks are divergent, with large, globular eyes. The corneas are well pigmented, occupying most of the eyestalk's terminal portion (fig. 1A-E).

The antennular peduncle (fig. 1A, B) does not reach the distal margin of the scaphocerite. The basal article has a small stylocerite ending in an acute point, not reaching the distal margin of basal article, and a ventromesial triangular rounded tooth at mid-length. The ultimate article is slightly longer than the penultimate article. The lateral flagellum is without distinct accessory ramus, with tufts of long aesthetascs in its proximal part, starting from its first article. The mesial flagellum is shorter than the lateral flagellum as in *P. chacei* (Kensley, 1983, fig. 18) and *P. falsapinca* (Anker, 2012, fig. 1).

The antenna is similar to that of *P. chacei* and *P. falsapinca*. It has a relatively small basicerite with its ventrolateral margin ending in a blunt tooth. The scaphocerite is elongate, with a slightly convex lateral margin and a broadly convex mesial margin. The distolateral tooth is small, not reaching beyond the anterior margin of the blade. The carpopocerite reaches to about the end of the antennular peduncle, not to the end of the scaphocerite. The flagellum is longer than the antennular flagella, more than five times as long as the poel.

The mandible (fig. 2B-D) has the molar and incisor processes partly fused. The molar process is very small, with short setae along its mesioventral margin. The incisor process of the dissected mandible has 11 triangular, distally sharp teeth of varying size identical to adult specimens of *P. chacei* (Kensley, 1983, fig. 19a); these teeth are smaller and lower in number in juveniles (Kensley, 1983, fig. 21a). The incisor process of the mandible of *P. falsapinca* (Anker, 2012, fig. 3a, b) is similar to that of the present material with 10 teeth. The palp has two articles (fig. 2C, C) as in the two other Atlantic species, with the ultimate segment bearing several long serrulate setae and being slightly shorter than the oblong basal segment.

The maxillula (fig. 2E) is identical with that of *P. chacei* (Kensley, 1983, fig. 19b) and *P. falsapinca* (Anker, 2012, fig. 3c). It has a bilobed endopod, each lobe has one slender seta. The dorsal endite has two rows of stout spiniform setae on its distal margin. The ventral endite is oblong with slender long setae dorsally, and stouter, shorter setae ventrally.

The maxilla (fig. 3A) has the scaphognathite much broader dorsally than ventrally. The endopod has two articles, although the subdivision is very subtle, like described for *P. falsapinca* (Anker, 2012, fig. 3d). This subdivision is not

mentioned in the description of *P. chacei* (Kensley, 1983, fig. 19c). The terminal segment of the palp bears one long simple seta. The dorsal endite is elongate, narrow, furnished with long setae distally. The ventral endite is short, also with few long simple setae.

The first maxilliped (fig. 3B) is identical with that of the *P. chacei* (Kensley, 1983, fig. 19d) and *P. falsapinca* (Anker, 2023, fig. 3e). It has a large, broadly subtriangular bilobed epipod. The exopod has a large caridean lobe, is distally truncate, without lash. The endopod is simple, falling short of the exopod, with one long distal simple seta. The dorsal and ventral endites have rows of long setae on their mesial surface.

The second maxilliped (fig. 3C) is similar to that of *P. chacei* (Kensley, 1983, fig. 20a) and *P. falsapinca* (Anker, 2023, fig. 3f). It has a narrow, ear-shaped, bilobed epipod. The exopod is narrow, just overreaching the third (carpal) article of the endopod, with few setae proximolaterally and few setae distally. The endopod has five articles. The first two are subequal in length. The carpal article is distinctly shorter than second and triangular in shape. The propodal article is broader and slightly longer than the carpal article. The dactylar article is short, armed with 4 very stout spiniform setae distally.

The third maxilliped (fig. 3D, E) is similar to those described for *P. chacei* (Kensley, 1983, fig. 20b) and *P. falsapinca* (Anker, 2023, fig. 3g-i). It is slender, pediform. The coxa has an acutely produced lateral plate and a rounded epipod. The exopod is well developed, reaching the distal margin of the penultimate article. The antepenultimate article is slightly twisted, about as long as the penultimate article. Both articles have long, stiff, curving setae on their dorsal margins and numerous more straight setae on their ventral margins. The ultimate article is slightly longer than the penultimate article, with 7-9 transverse rows of serrulate setae. The tip is rod-shaped, with several long, stout setae.

The first pereopod (= first cheliped) (fig. 4) are as described for *P. chacei* (Kensley, 1983, figs. 20c, 22b) and *P. falsapinca* (Anker, 1983, fig. 4a-c). It has the coxa robust. The basis has several groups of long, stiff setae. The exopod is well developed, reaching far beyond the carpus, with plumose setae along one-third of its distal margin. The ischiomerus is somewhat angular in cross-section, elongate, distally widening, scarcely setose. The carpus is very short, plate-shaped, much wider than long. The chela is moderately swollen, has its palm smooth, subcylindrical, more or less rounded in cross-section. The ventrolateral surface bears a few stiff setae. The fingers are about 0.4 times as long as the palm, slightly gaping, with smoothly curving, crossing tips. The cutting edge of the dactylus has small, rounded teeth. The cutting edge of the pollex has shallow, irregularly shaped teeth.

The second pereopods (= second chelipeds) (fig. 5) are similar to those of *P. chacei* (Kensley, 1983, fig. 20d, e) and *P. falsapinca* (Anker, 2012, fig. 4d, e). They have almost the same length as the first pereopod, but are more slender. The coxa is not projecting ventrally. The basis has one slender spiniform seta on its ventral surface. The exopod is well developed, reaching to the distal margin of the carpus. The ischiomerus is slender, elongate, not widening distally, with few long setae along its ventrolateral margin and with a stout spiniform seta in its distal part as described for *P. chacei* (Kensley, 1983, fig. 20d) and *P. falsapinca* (Anker, 2012, fig. 4d), except for the right second pereopod of a male (fig. 5B) which lacks this spiniform seta. The carpus is short, cup-shaped without spiniform setae except for the right second pereopod of this male which has a stout spiniform seta on the ventrolateral side in its distal part (fig. 5B). The chela is feebly swollen, with the palm smooth, subcylindrical, rounded in cross-section. The ventrolateral surface has three or four long, stiff setae. The fingers are half as long as the palm, slightly gaping, with curving, crossing tips. The cutting edges of both dactylus and pollex are pectinate from about 0.2 to 0.9 of the cutting edge length, with the size of the teeth gradually increasing distally.

The third pereopod (fig. 6A, B) is the longest of all pereopods, reaching far beyond the antennular peduncle and scaphocerite when fully extended. The coxa is slightly projecting ventrally. It does not possess the elongate spine described for *P. chacei* (Kensley, 1983, fig. 20f). The basis is short, with a slender spiniform seta and several stiff setae ventrally. A spinose process as described for *P. chacei* (Kensley, 1983, fig. 20f) was not observed. In the male paratype (RMNH.CRUS.D.36167) of *P. chacei*, the elongate spine on the coxa nor the spinose process on the basis were observed. The exopod is reaching to about 0.3 of the merus length, it has one mesial slender spiniform setae and several stiff setae. The ischium has one stout spiniform seta on its ventrolateral surface. The merus is long, about seven times as long as its greatest width. Its ventrolateral surface has three stout spiniform setae, like in the description of *P. chacei* (Kensley, 1983, fig. 20f), whereas Anker (2012, fig. 5a) noted four stout spiniform setae ventrolaterally in *P. falsapinca*. The carpus is short, vase-shaped, distally widening, with a stout spiniform seta on its ventrolateral surface, and a small spiniform seta on its distomesial margin. The chela is slender, with the palm smooth, cylindrical, rounded in cross-section. Its ventrolateral surface has two spiniform setae, the first at about mid-length of the palm, the second subdistally. The distoventral margin of the palm has three spiniform setae of different length and thickness. The ventral spiniform seta is elongate, reaching to and crossing with the dactylus tip, thick, with a row of denticles along its mesial margin, the row of denticles stops at about half-length of the seta. The first ventrolateral spiniform seta is distinctly more slender and shorter than the ventral spiniform seta, reaching to about mid-length of

the dactylus, also with a row of minute denticles in its proximal half. The second ventrolateral spiniform seta is about half as long as the first ventrolateral spiniform seta, again with a row of minute denticles in its proximal half. The dactylus is elongate, almost as long as the palm, slender, curving towards the tip, with its cutting edge pectinate from the dactylar base to about 0.9 of the dactylar length.

The fourth pereopod (fig. 6C, D) is generally similar to the third pereopod, although somewhat shorter and more slender; also similar to the fourth pereopods of *P. chacei* (Kensley, 1983, fig. 20g) and *P. falsapinca* (Anker, 2012, fig. 5f, g). The basis lacks the slender spiniform setae. The ischium has one or two stout spiniform setae ventrally. The merus is about 7.5 times as long as its greatest width and bears four stout spiniform setae ventrolaterally. Both ischium and merus show few transverse striae with pits, probably of abraded tegumental scales. The carpus is vase-shaped, with one stout spiniform seta on its ventrolateral surface and a more slender short spiniform seta distoventrally. The chela has the palm and fingers shorter than in the third pereopod, but is otherwise similar.

The fifth pereopod (fig. 7A, B) is shorter than the third and fourth pereopods. It is similar to that of *P. chacei* (Kensley, 1983, fig. 20h) and *P. falsapinca* (Anker, 2012, fig. 5h, i). The exopod is reaching half-length of the merus. The armature of basis, merus and carpus is similar to that of the fourth pereopod. The ischium has two stout spiniform setae in all specimens. Both ischium and merus show few transverse striae with pits, probably of abraded tegumental scales. The chela is generally similar to that of the fourth pereopod, with a slightly more slender palm with more serrulate setae than in pereopod three and four.

The pleopods of females are without specific features. The second to fifth pleopods have a short appendix interna near the base of the endopod. The first pleopod in males (fig. 7C) has a short endopod, about one-fourth of the exopod length, distally narrowed, with a row of long plumose setae laterodistally and two short simple setae on its mesial margin. The second pleopod in males (fig. 7D, E) has the endopod slightly shorter than the exopod, with the appendix interna about two-thirds of the length of the appendix masculina, with several distal coupling hooks and a row of short slender setae posteromesially. The appendix masculina has five stiff, serrulate setae of various lengths distally. The male first and second pleopods are similar to those of *P. chacei* (Kensley, 1983, figs. 19h, i, and 21d, e), those of *P. falsapinca* are not known.

The uropod (figs. 1H, I, 7F) has a stout protopod, its distolateral lobe ending in a sharp tooth; the endopod is slender, tapering distally; the exopod is also slender, not tapering; the distolateral area has a small tooth and adjacent, stout spiniform seta; the diaeresis is irregularly curved, as illustrated (fig. 1I). Both endopod and exopod with tegumental scales. The uropods are similar to those of *P. chacei* (Kensley, 1983, fig. 19e), and *P. falsapinca* (Anker, 2012, fig. 2d, i).

The gill-exopod formula is as described for *P. falsapinca*: five pleurobranchs (P1-5), no arthrobranch, no podobranch, three epipods (Mxp1-3), and eight exopods (Mxp1-3, P1-5).

Size.— The present male specimens have a pochl. of 1.9 and 2.1 mm. The ovigerous female specimens are somewhat larger in size with a pochl. of 2.6 and 2.9 mm. The holotype female of *P. falsapinca* from Brazil has a pochl. of 2.60 mm, the paratype ovigerous female 2.73 mm. The males of *P. chacei* have a pochl. between 1.6 and 2.8 mm, the females between 1.3 and 2.2 mm.

Colour in life (fig. 10B).— Only few rather vague photographs have been taken of the specimens. They appear largely translucent with a slight yellowish tinge on carapace and abdomen. The colouration of *P. falsapinca* is not known. That of *P. chacei* was noted by Kensley (1983) as: 'Animal almost completely transparent, except for gut, when alive. Single red chromatophores present at following positions: on ventral eyestalk; dorsum of proventriculus, on propodus, carpus, and ischiomerus of pereopod I; on carpus and ischiomerus of pereopod 2; on coxae of pereopods 1-5; on outer base of pleopods 1-5; on sternum of abdominal segments 1-5'.

Habitat.— The present specimens were collected at 11 and 13 m depth, from cracks in the rock of the completely dark side-branch near the semi-dark western end of the underwater tunnel through Santana Islet. Several individuals of the shrimp *Parhippolyte antiguensis* (Chace, 1972) were observed in the same side-branch (fig. 10A). The specimens of *P. falsapinca* from Brazil were dredged on a marl-type bottom, consisting of fragments and nodules of calcareous algae, at a depth range of 68-71 m. The microhabitat of the specimens of *P. chacei* is not known. They were collected at depths between 6 and 28 m.

Remarks.— Integumental scales have hitherto been observed in eight caridean shrimp families: Acanthephyridae, Bresiliidae, Calliasmatidae, Crangonidae, Lysmatidae, Oplophoridae, Pandalidae, and Rhynchocinetidae (Holthuis, 1973; De Grave & Wood, 2011). These scales are here recorded for the first time for the family Pseudochelidae. As was noted before for Lysmatidae and Rhynchocinetidae (see De Grave & Wood, 2011), tegumental scales are facing anteriorly on the carapace and first three abdominal pleonites, whereas they are facing posteriorly on the last three abdominal pleonites, telson and uropods. The tegumental scales (figs. 1F, 9) have a rather broad basal part which is falling in a broadly V-shaped pit in the surface of the carapace or abdomen, followed by an oval part with entire margins, distally ending in a short, slender, acute tip; a longitudinal midrib is present. When the tegumental scales are abraded away, they leave a V-shaped scar on the surface.

It is interesting to note that the spiniform setae of the pseudochelae as well as the terminal three pair of the telson show the same configuration of serrations and microsetules.

DNA analyses

New sequences of two genes (18S, 16S) were obtained (table I).

Molecular phylogenetic analyses based on the concatenated alignment of the two markers of selected species representing most of the caridean families indicate with high branch support that the Pseudochelelidae are most closely related to the Disciadiidae (fig. 11). In the present analyses, the Pseudochelelidae are located within the Disciadiidae, though with low support. The clade with both Pseudochelelidae and

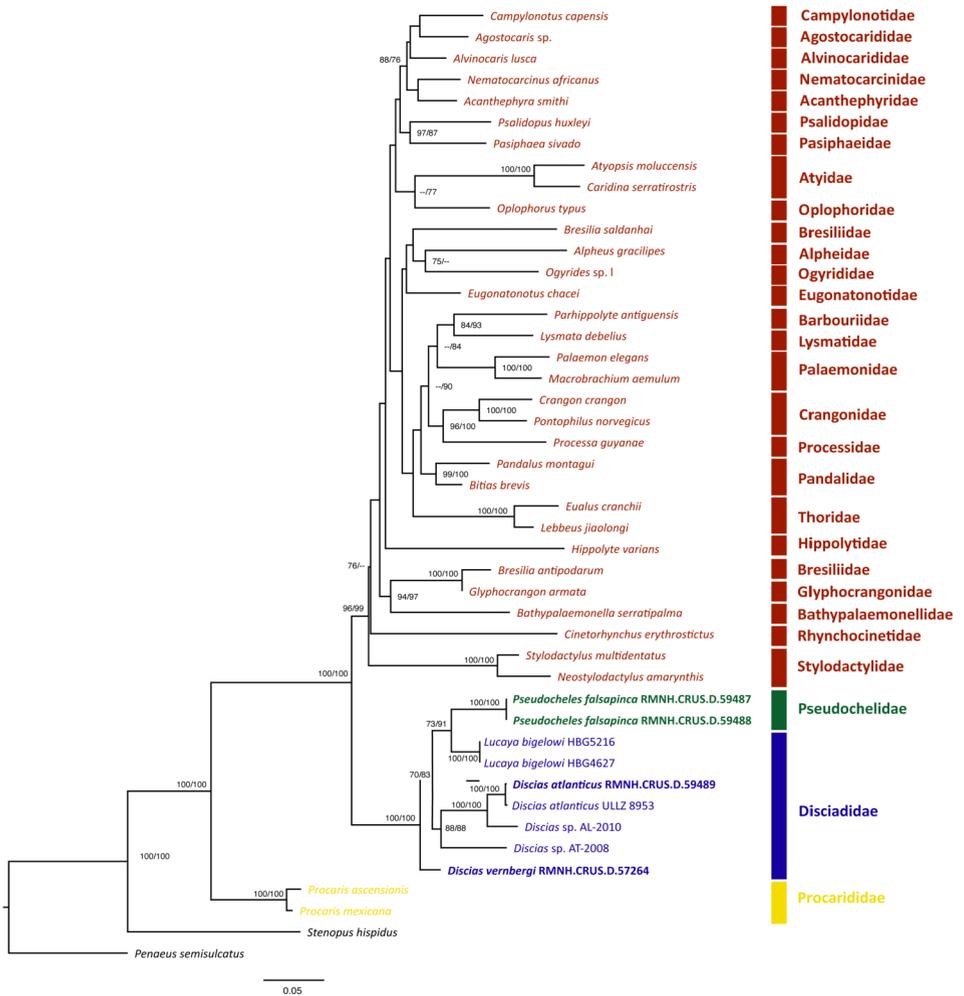


Fig. 11. Phylogenetic tree of selected species carideans resolved by Maximum Likelihood (ML) based on the combined dataset of the 18S (nDNA) and 16S (mtDNA) genes. ML bootstrap support and Bayesian Inference (BI) posterior probabilities are expressed as percentages noted near the nodes (ML/BI). Support values <75% are not shown. New sequences are indicated in boldface.

Disciadidae is located basally in the caridean tree, between the basal Procarididae and all other families. Both ML and BI analyses resulted in highly similar phylogenies. Branch support values within families was high; branch support values among families was generally low. The ML topology was selected as the basis for discussion with bootstrap values and posterior probabilities (BI) included.

## DISCUSSION

### Morphology

The four specimens from São Tomé are very similar to both *P. chacei* and *P. falsapinca*. As only few specimens of these species are hitherto known, it is difficult to estimate the infraspecific variation. Anker (2012) distinguished *P. falsapinca* from *P. chacei* based on: (1) the absence of spine-like mesial projections on the coxae of the third and fourth pereopod, which also holds for the present material from São Tomé; (2) the absence of an acute mesial projection on the basis of the third pereopod, which is also absent in the present material São Tomé; (3) a rostrum with fewer dorsal teeth (5 vs. 6-8 in *P. chacei*), all of which are anterior to post-orbital margin (vs. 1 or 2 most-posterior teeth posterior to post-orbital margin in *P. chacei*). With regard to this character the present material from São Tomé falls within the rostral variation noted for *P. chacei*. However, as only few specimens of Atlantic *Pseudocheles* species are known, the variation in the rostral dentition cannot be established properly. The presence of mesial spine-like projections on the coxae of third and fourth pereopods and the mesial projection on the basis of the third pereopod in *P. chacei* seems a solid character although these were not observed in the small paratype of the species examined (RMNH.CRUS.D.36167). Just behind the posteriormost dorsal rostral tooth, a small anterior tubercle or notch is present. This tubercle or notch was also noted in the types of *P. falsapinca* (Anker, 2012, fig1a-c, m) but not described for *P. chacei*, nor observed in the paratypes (RMNH.CRUS.D.36167) of *P. chacei*. The low middorsal tubercle in the posterior seventh of the carapace as described for *P. chacei* was not observed in the present material nor noted for *P. falsapinca*. Therefore, the present material from São Tomé is for the time being identified as *P. falsapinca*. More material of *Pseudocheles* from the Caribbean, Brazil, and the East Atlantic is needed, preferably accompanied with good colour photographs and DNA sequences, to clarify the taxonomic status of these Atlantic *Pseudocheles* populations.

### DNA analyses

The basal position of the Disciadidae in the caridean tree, between the Procarididae and all other families as previously established (Bracken et al., 2009, 2010;

Aznar-Cormano et al., 2014; De Grave et al., 2015; Davis et al., 2018), is confirmed. The present phylogenetic analyses indicate a close phylogenetic relationship between the Pseudochelidae and Disciadidae. Whether the Pseudochelidae fall within the Disciadidae or are a separate clade outside the Disciadidae remains doubtful as in the present analyses based on two genes, the branch support values concerned are low. More genes and a larger set of taxa within these families are needed to get a better picture of the phylogenetic relationship between the two families.

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