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A review of *Palaemonella* (Decapoda: Caridea: Palaemonidae), with clarification of the taxonomic status of *Cuapetes americanus*, *Eupontonia* and *Vir*

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ABSTRACT

The pantropical genus *Palaemonella* Dana, 1852 (Caridea: Palaemonidae) currently includes 27 species of free-living and symbiotic marine shrimps. The monophyly of *Palaemonella* with respect to several closely related genera, however, has been questioned by recent analyses. We tested the monophyly of *Palaemonella* based on multigene phylogenetic analysis and the genus was revealed to be a paraphyletic assemblage by inclusion of species of the genera *Eupontonia* Bruce, 1971 and *Vir* Holthuis, 1952, and two genetic lineages of the western Atlantic *Cuapetes americanus* (Kingsley, 1878). We recognise one of the latter lineages as the previously described *Periclimenes rhizophorae* Lebour, 1949. *Eupontonia* and *Vir* are synonymised with *Palaemonella*. We also transfer *Cuapetes americanus* and *Periclimenes rhizophorae* to *Palaemonella*. Species previously assigned to *Vir* were revised; *V. colemani* Bruce, 2003, *V. orientalis* (Dana, 1852), *V. philippinensis* Bruce & Svoboda, 1984 and *V. smiti* Fransen & Holthuis, 2007 are regarded as valid species of *Palaemonella*; *Vir longidactylus* Marin, 2008 is synonymised with *P. smiti*; and the status of *V. euphyllius* Marin & Anker, 2005 remains unresolved. *Palaemonella* is currently regarded as a taxon with variable states of two main diagnostic characters, i.e. the plesiomorphic mandibular palp (fully reduced in *P. americana*) and the hepatic tooth (fully reduced in former species of *Vir* and *Eupontonia* – evidently due to symbiotic modes of life).

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Keywords: Caridea, Crustacea, Decapoda, *Eupontonia*, molecular phylogeny, *Palaemonella*, Palaemonidae, revision, *Vir*.

Introduction

Palaemonidae is the most speciose family of caridean shrimps. The family has a remarkably high composition of freshwater and marine, predominantly symbiotic species, while non-symbiotic marine representatives of the family are less frequent. The symbiotic forms were previously included in subfamily Pontoniinae (currently an unaccepted taxon; see De Grave *et al.* 2015) that is currently represented by two sister genetic assemblages within the family in recent phylogenetic studies (e.g. Horká *et al.* 2016; Chow *et al.* 2020, 2021). These include the major clade consisting almost exclusively of symbionts of hosts of different marine invertebrate phyla, and a smaller clade with only 11 genera of predominantly free-living species and a limited number of ectosymbiotic species or species-poor genera. The latter assemblage was provisionally named the ‘Pon-I group’ by Chow *et al.* (2020, 2021) or the ‘*Palaemonella*–*Cuapetes* group’ of genera by Frolová *et al.* (2022) to highlight the most speciose genera of the assemblage.

Dana (1852) established the genus *Palaemonella* for the species *P. tenuipes* Dana, 1852. Currently, 27 valid species of *Palaemonella* with marine pantropic-temperate distributions are known (De Grave and Fransen 2011; Komai and Yamada 2015; Okuno 2017; Fransen *et al.* 2022a; Anker and Assayie 2023; Anker and Benzoni 2023). *P. atlantica* Holthuis, 1951 occurs in the eastern Atlantic (Holthuis 1951a), whereas *P. asymmetrica* Holthuis, 1951 and *P. holmesi* (Nobili, 1907) occur in the eastern Pacific

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(Nobili 1907; Holthuis 1951b; Fransen 1987). The remaining 24 species are distributed in the Indo-West Pacific (IWP) biogeographic area (Bruce 1970, 1975, 1978, 1991, 2002a, 2002b, 2005, 2008, 2010a; Okuno 1999, 2017; Li and Bruce 2006; Marin 2008; Hayashi 2009; Komai and Yamada 2015).

Most species of *Palaemonella* are free-living (Hayashi 2001; Bruce 2002a, 2002b; Frolová et al. 2022), however several individual species are symbiotic, e.g. *P. pottsii* (Borradaile, 1915) associated with crinoids (Bruce 1970; Minemizu 2000, 2013; Kato and Okuno 2001; Kawamoto and Okuno 2003), *P. aliska* Marin, 2008, *P. jamila* Anker & Benzoni, 2023 and *P. shirakawai* Okuno, 2017, suggested to be inquilinists in burrows of alpheid shrimp or opisthognathid fish (Marin 2008; Okuno 2017; Anker and De Grave 2019; Anker and Benzoni 2023; present report) and *P. rubrolineata* Fransen, van der Veer and Frolová, 2022 with *P. sandyi* Fransen, van der Veer & Ďuriš, 2023 living on scleractinian corals (Fransen et al. 2022a, 2023). Nevertheless, these taxa do not display remarkable characters adaptive to the symbiotic lifestyle. The general morphology of *Palaemonella* is relatively ordinary and ‘*Palaemon*-like’, with the cylindrical body, carapace with a toothed rostrum and usual set of the main carapacial teeth (epigastric, antennal, hepatic, often also supraorbital), the fourth thoracic sternite with a finger-like median process and simple, not specialised, ambulatory dactyli (Bruce 2002a; Komai and Yamada 2015). The bathymetric range of *Palaemonella* is wide, ranging from the intertidal zone down to 519 m (Hayashi 2001; Bruce 2002a, 2008; Li and Bruce 2006).

The present multigene molecular revision of the genus *Palaemonella* covers most of the diversity of the currently valid taxa, with 19 analysed from 27 currently known species from all main tropical marine geographic regions. Representatives of other genera, showing a close relationship with *Palaemonella* (see Frolová et al. 2022) are also included to highlight their evolutionary and taxonomic position in relation to the target genus.

The aim of our study is therefore to reveal the infrageneric structure of *Palaemonella*, and examine the relationships of the related IWP genera *Eupontonia* Bruce, 1971, *Vir* Holthuis, 1952 and the western Atlantic species *Cuapetes americanus* (Kingsley, 1878) to the former genus. We hypothesise that *Palaemonella* is an aphyletic taxon (as evident from the study by Frolová et al. 2022) and needs a deeper taxonomic revision based on multigene molecular analyses as is presented below.

Materials and methods

Sampling

A total of 130 specimens of *Palaemonella*, *Vir*, *Eupontonia* and related genera included in this study were collected by

the authors during biodiversity expeditions organised by the National Museum of Natural History, Paris (MNHN) and the Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden (RMNH), and during field trips of the authors organised by the National Taiwan Ocean University, Keelung (NTOU) and National Museum of Marine Biology and Aquarium, Kenting, Taiwan (NMMBA). Some specimens were obtained on loans from the latter institutions or other international museums (e.g. NTM, Darwin – *V. colemani*; OUMNH, Oxford – *P. atlantica*; WAM, Perth – *P. foresti*), or as tissues for DNA provided directly by researchers (A. Anker – *P. aliska*, *P. holmesi*, *E. nudirostris*), along with permissions to use these in molecular analyses. Specimens were collected by standard sampling methods using hand nets in tidal pools, hand picking while scuba diving or bulk methods (suction pump, rock brushing) or from a boat (dredging) and preserved in 80% ethanol. Species identifications were made by means of stereomicroscopic examinations; selected specimens were photographed alive and preserved in 80% ethanol; and pieces of tissue were held in 96–99% ethanol for subsequent molecular analyses.

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, Inc.) following the manufacturer’s protocols. For resolving phylogenetic relationships, partial mitochondrial 16S ribosomal RNA (16S; ~454 bp), the cytochrome c oxidase subunit mitochondrial DNA (*COI*; ~596 bp), nuclear 18S ribosomal RNA (18S; ~653 bp) and nuclear histone 3 (*H3*; ~269 bp) were sequenced. Target gene regions were amplified by polymerase chain reaction (PCR) using primer pairs: 16S-ar (5′-CGCCTGTTTATCAAAAACAT-3′) and 1472 (5′-AGATAGAAACCAACCTGG-3′) (Palumbi et al. 1991; Crandall and Fitzpatrick 1996) for 16S rRNA; Crust-F1/LCO1490 (5′-TTT TCTACAAATCATAAAGACATTGG-3′/5′-GGTCAACAAATCA TAAAGATATTGG-3′) and HCO2198 (5′-TAACTTCAGGGTG ACCAAAAAATCA-3′) (Folmer et al. 1994; Costa et al. 2007) for *COI*; H3af (5′-ATGGCTCGTACCAAGCAGACVGC-3′) and H3ar (5′-ATATCCTTRGGCATRATRGTGAC-3′) (Colgan et al. 2008) for histone *H3*; and 2.0 (5′-ATGGTTGCAAAGCTGA AAC-3′) and 9R (5′-GATCCTTCCGCAGGTTACCTAC-3′) (Whiting 2002) for 18S rRNA. Polymerase chain reactions of newly sequenced samples were performed in a 20-μL volume containing DNA template, 10 μM of each primer, MyTaq Red DNA polymerase, 1 U of MyTaq Red Polymerase buffer and 20 mg mL⁻¹ of bovine serum albumin. Thermal cycling profiles followed those of Frolová et al. (2022). The amplified DNA was purified with a Gel/PCR DNA Fragments Extraction Kit (GENAID, Taiwan) and submitted to Macrogen, Inc. (Amsterdam, Netherlands) for sequencing using the Sanger sequencing reaction with an ABI3730XL DNA Sequencer. Resulting sequences were

submitted to GenBank (Supplementary Tables S1 and S2). Remaining sequences, including outgroup sequences, were obtained from previous studies of the current authors (Horká *et al.* 2016, 2018; Fransen *et al.* 2022a, 2023; Frolová *et al.* 2022) or from GenBank (Supplementary Tables S1, S2; Porter *et al.* 2005).

Phylogenetic analyses

Sequences were aligned using the MUSCLE (ver. 5, see <http://www.drive5.com/muscle>; Edgar 2004) algorithm and protein coding genes (*H3* and *COI*) were translated to amino acids to control frameshift mutation and stop codons in MEGA X software (ver. 11.0.11, see <http://www.mega-software.net>; Kumar *et al.* 2018). Substitution saturation of all genes was tested in Dambe (ver. 6.4, <http://dambe.bio.uottawa.ca>; Xia 2017) according to an index by Xia *et al.* (2003). At the 3rd codon position of the *COI*, saturation was detected and therefore excluded from further analyses. GBLOCKS (ver. 0.91b; Talavera and Castresana 2007; http://phylogeny.lirmm.fr/phylo.cgi/one_task.cgi?task_type=gblocks) was used to omit highly divergent and poorly aligned regions on the individual datasets of ribosomal genes *16S* and *18S*. A multigene dataset was concatenated using SequenceMatrix software (ver. 1.8, see <http://code.google.com/p/sequence-matrix/>; Vaidya *et al.* 2011) consisting of 1759 characters. Sequences were aligned with the MUSCLE algorithm (Edgar 2004) using the web server NGPhylogeny.fr (see <https://ngphylogeny.fr>; Lemoine *et al.* 2019) for the phylogeny of representatives of the genus *Vir* based on the *16S* gene. Highly divergent and poorly aligned regions were excluded from the analysis using GBLOCKS (ver. 0.91b) through the web server Phylogeny.fr (see <http://www.phylogeny.fr/>; Dereeper *et al.* 2008) with a less stringent selection approach.

Phylogenies were inferred using both Maximum Likelihood (ML) and Bayesian inference (BI). ML analyses were 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). An ultrafast bootstrap (UFB) (Minh *et al.* 2013) with 10,000 replicates was used in the analyses to assess branch support. BI analyses were conducted in MrBayes on XSEDE (ver. 3.2.7a, see <https://github.com/NBISweden/MrBayes/>; Ronquist *et al.* 2012) with the online CIPRES Science Gateway (ver. 3.3, see <https://www.phylo.org/>; Miller *et al.* 2010) using substitution models selected by Partition Finder (ver. 2.1.1, see <https://www.robertlanfear.com/partitionfinder/>; Lanfear *et al.* 2017) (Supplementary Table S3). The Markov chain Monte Carlo (MCMC) algorithm was run for 5 million and 10 million generations (for concatenated and single gene data sets respectively) and sampled trees every 500 generations. The convergence of the BI was checked in Tracer (ver. 1.7 see <http://tree.bio.ed.ac.uk/software/tracer/>; Rambaut *et al.* 2018). All

resulting phylogenetic trees were displayed in the online application ITOL (Interactive Tree of Life, ver. 6.6, see <https://itol.embl.de/>; Letunic and Bork 2021).

Abbreviations

EA, eastern Atlantic; EP, eastern Pacific; IWP, Indo-West Pacific biogeographic area; pocl, post-orbital carapace length (measured on the dorsal midline from the level of the posterior orbital margin to the posterior margin of the carapace); fcn, the unique field collection number and photographic voucher; PI, principal investigator; RF, rostral formula ($RF = x + y \div z$), i.e. teeth number = postrostral (x) + rostral dorsal (y) \div ventral (z); PNG, Papua New Guinea; stn, station; *v.* (*versus*), in comparison with; WA, western Atlantic. Institutions: AIMS, Australian Institute of Marine Science, Cairns, Australia; CBM-ZC, Natural History Museum and Institute (Zoology, Crustacea), Chiba, Japan; FMNH, Florida Museum of Natural History, Gainesville, USA; IO VAST, Institute of Oceanology, Vietnam Academy of Science and Technology, Nha Trang, Vietnam; MNHN, Muséum national d'Histoire naturelle, Paris, France; MTQ, Museum of Tropical Queensland, Townsville, Australia; NBC/RMNH, Naturalis Biodiversity Center, Leiden, Netherlands; NMMBA/NMMBCD, National Museum of Marine Biology and Aquarium (CD – Crustacea Decapoda collection), Pingtung, Taiwan; NTM, Museum and Art Gallery of the Northern Territory, Darwin, Australia; NTOU, National Taiwan Ocean University, Keelung, Taiwan; UO, University of Ostrava, Czechia; USP, University of São Paulo, Brazil (MZUSP – museum collections); WAM, Western Australian Museum, Perth, Australia; ZMMSU, Zoological Museum of Moscow State University, Moscow, Russian Federation.

Results

Molecular analysis

Molecular phylogenetic analyses based on the concatenated alignment of four gene markers (*COI*, *16S*, *H3* and *18S*) supported the hypothesis of the paraphyly of *Palaemonella*. We obtained identical results using BI and ML analyses; BI topology was selected as the basis for discussion with posterior probabilities and including bootstrap values for ML analyses (Fig. 1). The analysed dataset of specimens contained 70% of the described species of *Palaemonella* (19/27), 50% of the described *Eupontonia* species (2/4) and covered all currently described species of *Vir* (6).

The most basally positioned clade is composed of specimens of the eastern Pacific species *P. asymmetrica*. The further supported clade contains a lineage of another eastern Pacific species, *P. holmesi*, with the supported assemblage of the Atlantic species, *Cuapetes americanus* and

P. atlantica. *Cuapetes americanus* is split into two genetically separated branches with the mutual genetic distances 16.8–18% in *COI* and 12.5–13.4% in *16S*.

The last marginally supported clade is composed of the IWP representatives of the genera *Palaemonella*, *Eupontonia* and *Vir*, and can be divided into five major supported

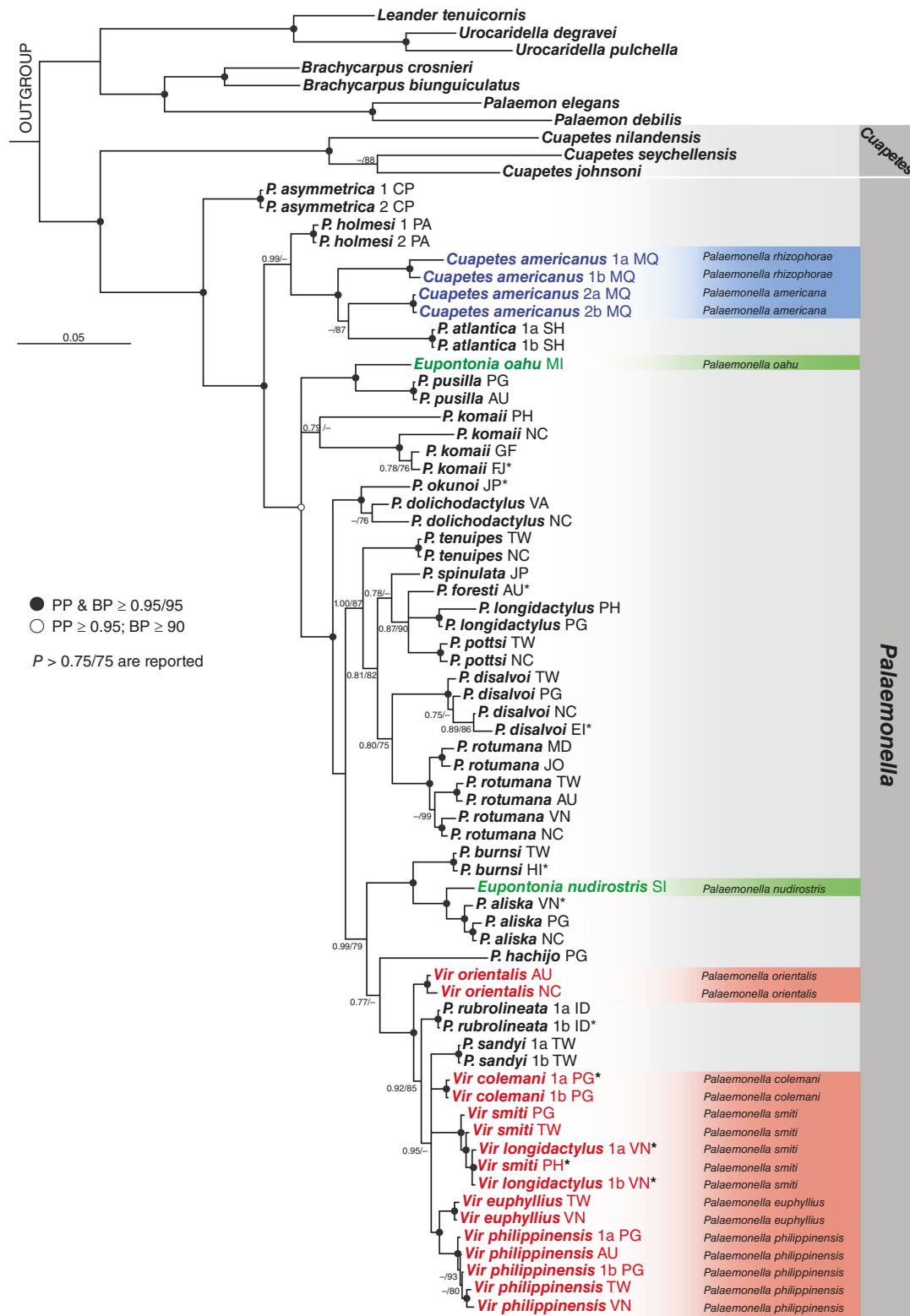


Fig. 1. (Caption on next page)

Fig. 1. Phylogenetic tree of *Palaemonella* species resolved by BI based on the combined dataset for four genes (*COI*, *16S*, *H3* and *18S*). UFB support is expressed as a percentage. Dash (–) indicates PP/BP values <75/0.75. Current generic names shown on the tree, corrected names in right column. Asterisk (*) indicates type specimens, the latter shown under original names. Abbreviations: AU, Australia; CP, Clipperton Island; EI, Easter Island; FJ, Fiji; GF, French Guiana; HI, Hawaii; ID, Indonesia; JO, Jordan; JP, Japan; MD, Madagascar; MI, Marquesas Islands; MQ, Martinique; NC, New Caledonia; PA, Panama; PG, Papua New Guinea; PH, Philippines; SH, Saint Helena; SI, Solomon Islands; TW, Taiwan; VA, Vanuatu; VN, Vietnam. For other data see Supplementary Table S1.

subclades. The first subclade is formed by a sister-positioned species, scleractinian coral-associated *Eupontonia oahu* and non-associated *P. pusilla*. The second subclade includes *P. okunoi* and representatives of *P. dolichodactylus*. The third basally supported (by BI) subclade contains an assemblage of *P. tenuipes*, *P. spinulata*, *P. foresti*, *P. longidactylus*, *P. disalvoi* and *P. rotumana*, and the crinoid-associated *P. pottsii*. The fourth subclade contains specimens of tidal pools inhabiting *P. burnsi* and a pair of sister-positioned *P. aliska* and *E. nudirostris* (both suggested to live with burrowing animals). The remaining subclade is composed of scleractinian coral-associated representatives of *Vir* and *Palaemonella*, namely *V. orientalis*, *V. colemani*, *V. longidactylus*, *V. smiti*, *V. euphyllius*, *V. philippinensis*, *P. sandyi* and *P. rubrolineata*. The latter species is positioned between the most basally separated *V. orientalis* and remaining congeners of *Vir*. Internal relationships between those species are not entirely clear, however, analysed specimens of *V. smiti* and *V. longidactylus* form a common clade, with very low genetic divergences varying from 0–1.1% in *16S*. *Palaemonella sandyi* is most closely related to *V. colemani* and *V. euphyllius*, with the genetic divergences reaching 3.8–4.1% on the *16S* gene marker.

The remaining species, *P. komaii* and *P. hachijo*, are nested separately in the main clade with other congeners. The distinct phylogenetic relationships to other species remain unresolved because of unsupported phylogenetic positions. Some genetic structuring can be observed within the clade of *P. komaii* specimens. This may be an indication that this concerns a complex of cryptic species.

The molecular analysis based on the single gene marker, *16S* rRNA, of a wider set of 75 specimens of the previous *Vir* species (Fig. 2), currently a species complex within *Palaemonella*, revealed seven to eight subclades respective to separate species (Fig. 2). A new species, recently described as *Palaemonella sandyi* by Fransen *et al.* (2023), was separated basally; morphologically the species shows an affiliation to the previous *Vir* (owing to the lack of the hepatic tooth and symbiosis with euphylliid corals); and the direct affiliation to *Palaemonella* was based on our phylogenetic results revealing all *Vir* species to be members of *Palaemonella*. The second subdivision separates *Vir smiti* (also containing the holotype and the holotype of *V. longidactylus*), and the third subdivision two subclades respective to *Vir orientalis* and another new species, sharing the hepatic tooth with *Palaemonella* (in the previous concept);

the latter species has recently been described as *P. rubrolineata* by Fransen *et al.* (2022a). The remaining part of the evolutionary tree contains two basally supported clades respective to the species *V. philippinensis* (also containing specimens with the colouration traditionally affiliated with *V. colemani*) and the clade composed of specimens identifiable as *V. euphyllius*, subdivided in two or three subclades. One of the latter subclades also contains the holotype of *V. colemani*, therefore corresponding with that species; the second one can either be *V. euphyllius* or form a common assemblage with the previous clade, therefore being conspecific with *V. colemani* (see '*P. colemani-euphyllius*' in Fransen *et al.* 2023). A paratype of *V. philippinensis* is nested within the current '*V. euphyllius*' clade and the affiliation is discussed under Remarks for *P. colemani* and *P. euphyllius*. The persisting lack of DNA sequences of *V. euphyllius* types (currently not reachable from ZMMSU) does not permit us to closely ascertain the phylogenetic position of the latter two subclades, or resolve the taxonomic status of *V. euphyllius* as the valid name or as a synonym of *V. colemani*.

Results of the molecular analysis therefore reveal five or six current species respective to the previous *Vir*, including one new species described recently (Fransen *et al.* 2023) and another new species of *Palaemonella* (see Fransen *et al.* 2022) clustered among the *Vir* species. *Vir longidactylus* is a junior synonym of *V. smiti* and the status of *V. euphyllius* remains unresolved.

Systematics

Family PALAEMONIDAE Rafinesque, 1815

Genus *Palaemonella* Dana, 1852

Palaemonella Dana, 1852 (*type species: Palaemonella tenuipes* Dana, 1852, designated by Kingsley (1880), gender feminine; name placed on the Official List of Generic Names in Zoology in Opinion 470; Hemming 1957). = *Vir* Holthuis, 1952 (*type species: Palaemonella orientalis* Dana, 1852, by original designation and monotypy, gender masculine). = *Eupontonia* Bruce, 1971 (*type species: Eupontonia noctalbata* Bruce, 1971, by original designation and monotypy, gender feminine).

Type species: Palaemonella tenuipes Dana, 1852.

Included species

Thirty-eight: *Palaemonella aliska* Marin, 2008, *P. americana* (Kingsley, 1878) **comb. nov.**, *P. asymmetrica* Holthuis,

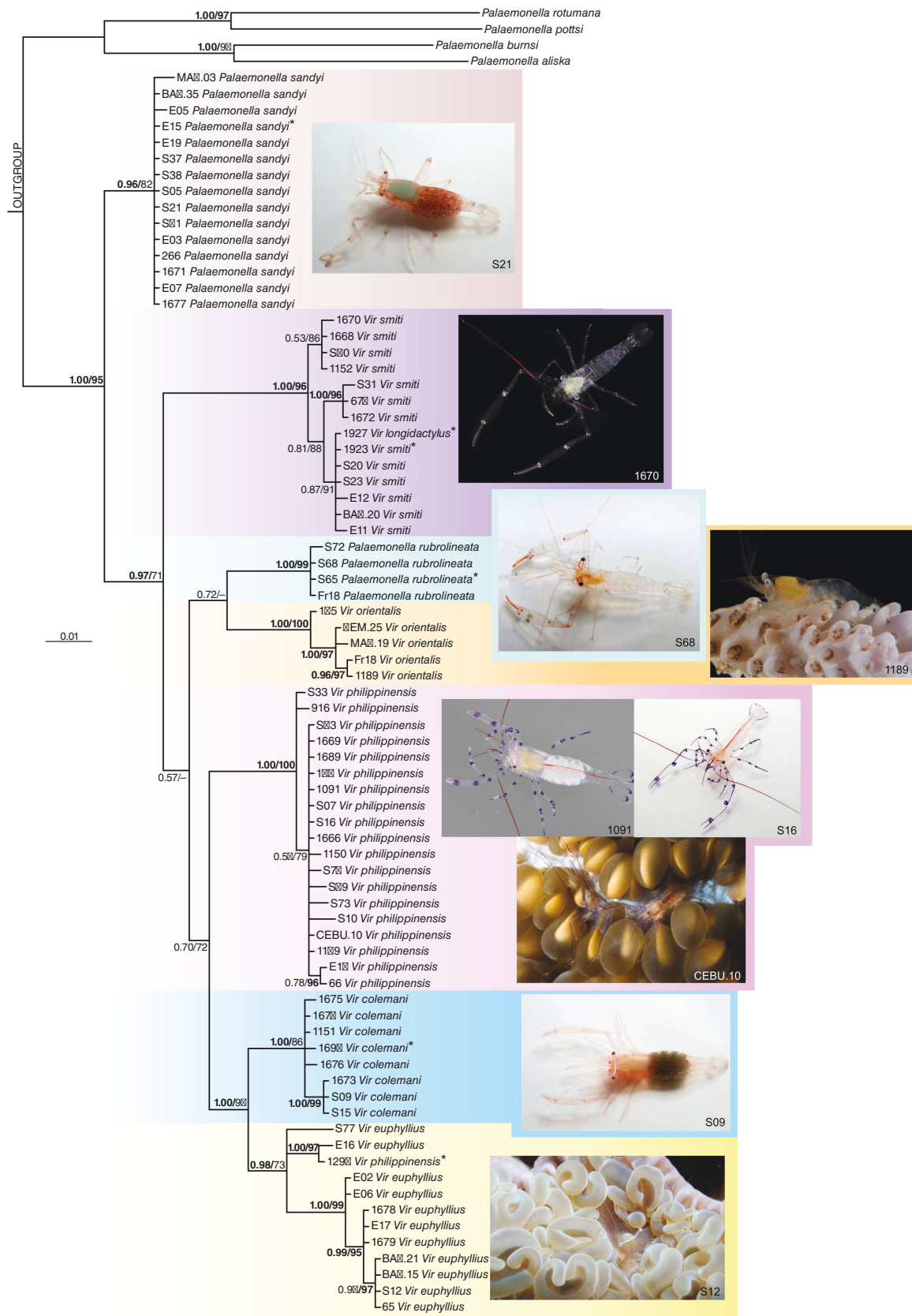


Fig. 2. (Caption on next page)

Fig. 2. Phylogenetic tree of *Vir* species resolved by BI based on 16S gene. UFB support is expressed as a percentage. Dash (–) indicates BP values <50. Highlighted PP/BP values indicate values >0.95/95. Current generic names shown on the tree. Asterisk (*) indicates type specimens shown under original names. Photographs of selected specimens from the main clades: (S21) *P. sandyi* RMNH.CRUS.D.53060; (1670) *V. smiti* MNHN-IU-2013-10769; (S68) *P. rubrolineata* RMNH.CRUS.D.53067; (1189) *V. orientalis* MNHN-IU-2018-844; (1091) *V. philippinensis* MNHN-IU-2013-10955; (S16) *V. philippinensis* RMNH.CRUS.D.53086; (CEBU.10) *V. philippinensis* RMNH.CRUS.D.48528; (S09) *V. colemani* RMNH.CRUS.D.53094; (S12) *V. euphyllius* RMNH.CRUS.D.53095. For other data see Supplementary Tables S1, S2. (Photographs: 1670, 1189, 1091, Z. Đuriš; S21, S68, S16, CEBU.10, S09, S12, C. H. J. M. Fransen).

1951, *P. atlantica* Holthuis, 1951, *P. burnsi* Holthuis, 1973, *P. colemani* (Bruce, 2003) **comb. nov.**, *P. crosnieri* Bruce, 1978, *P. dijonesae* Bruce, 2010, *P. disalvoi* Fransen, 1987, *P. dolichodactylus* Bruce, 1991, *P. euphyllius* (Marin & Anker, 2005) **comb. nov.**, *P. foresti* Bruce, 2002, *P. gracilipes* (Komai & Minemizu, 2014) **comb. nov.**, *P. hachijo* Okuno, 1999, *P. holmesi* (Nobili, 1907), *P. jamila* Anker & Benzoni, 2023, *P. komaii* Li & Bruce, 2006, *P. lata* Kemp, 1922, *P. longidactylus* Hayashi, 2009, *P. maziwi* Bruce, 2002, *P. meteorae* Bruce, 2008, *P. noctalbata* (Bruce, 1971) **comb. nov.**, *P. nudirostris* (Marin, 2014) **comb. nov.**, *P. oahu* (Bruce, 2010) **comb. nov.**, *P. okunoi* Komai & Yamada, 2015, *P. orientalis* Dana, 1852, *P. philippinensis* (Bruce & Svoboda, 1984) **comb. nov.**, *P. pottsi* (Borradaile, 1915), *P. pusilla* Bruce, 1975, *P. rhizophorae* (Lebour, 1949), **comb. nov.**, *P. rotumana* (Borradaile, 1898), *P. rubrolineata* Fransen, van der Veer & Frolová, 2022, *P. shirakawai* Okuno, 2017, *P. sandyi* Fransen, van der Veer & Đuriš, 2023, *P. smiti* (Fransen & Holthuis, 2007) **comb. nov.**, *P. spinulata* Yokoya, 1936, *P. tenuipes* Dana, 1852 and *P. yalla* Anker & Assayie, 2023.

Diagnosis (modified from Bruce 1995)

Small shrimps of slender subcylindrical body form. Rostrum well developed, slender, dorsal and ventral carinae generally dentate (rarely ventral or both entire), lateral carinae feeble. Carapace glabrous, smooth, supraorbital, epigastric and hepatic teeth present or absent, antennal tooth present, inferior orbital angle distinct, orbit feebly developed; anterolateral angle of branchiostegite bluntly angular. Antennule slender, flagella well developed, upper flagellum biramous. Antenna with basicerite laterally dentate, scaphocerite well developed. Eye with large globular cornea. Epistome unarmed. Mandible with small 1 or 2-segmented palp (palp absent in *P. americana*), molar process strongly dentate, incisor process normal, maxillula with bilobed palp, laciniae slender; maxilla with slender palp, basal endite bilobed, coxal endite obsolete, scaphognathite broad, anterior lobe narrow; first maxilliped with simple palp, basal endite broad, coxal endite distinct, exopod with small caridean lobe, flagellum with plumose setae distally, epipod triangular; second maxilliped with normal endopod, dactylar segment small, exopod with plumose setae distally, epipod simple, with or without rudimentary podobranch;

third maxilliped with long slender endopod, ischiomerus and basis distinct, exopod with plumose setae distally, coxa with large oval lateral plate, with or without small arthrobranch. Fourth thoracic sternite with long slender median process. First pereopods slender, chela with fingers slender, simple. Second pereopods well developed, usually overreaching rostrum by chela and carpus, subequal, similar or dissimilar, carpus usually constricted subdistally and markedly expanded distally, simple or with 1–2 acute or obtuse marginal teeth, chela with compressed dentate fingers shorter than or subequal to slightly swollen palm. Ambulatory pereopods slender, dactyli simple. Pleon smooth, glabrous; third pleonal segment not produced posterodorsally, pleura of first segments broadly rounded, fourth rounded or angular, fifth rounded, angular or pointed. Telson with two pairs of dorsal spines, three pairs of posterior spines. Uropod with protopodite posterolaterally acute, exopod with posterolateral tooth with mobile spine medially.

Remarks

The genus *Palaemonella* currently includes all species of the previous *Vir* Holthuis, 1952 and *Eupontonia* Bruce, 1971, and also two western Atlantic species, *Cuapetes americanus* (Kingsley, 1878) and *Palaemonella rhizophorae* (Lebour, 1949) – see Remarks to respective species and Discussion. The generic diagnosis (above) is therefore modified to incorporate the variable state of some important diagnostic characters, i.e. the presence or absence of the hepatic and antennal tooth on the carapace. The absence of the mandibular palp in *C. americanus* (= *Palaemonella americana*), unique in the whole present assemblage of *Palaemonella*, is well illustrative as an example of the evolutionary loss of an otherwise important generic character.

Within the complex of the palaemonid genera related to *Palaemonella* (all with the symplesiomorphic thoracic sternal spine) examined by Frolová *et al.* (2022), from the remaining eight genera (i.e. *Anapontonia* Bruce, 1966, *Cuapetes* Clark, 1919, *Exoclimenella* Bruce, 1995, *Harpilius* Dana, 1852, *Ischnopontonia* Bruce, 1966, *Madangella* Frolová & Đuriš, 2018, *Periclimenella* Bruce, 1995 and *Philarius* Holthuis, 1952), only *Exoclimenella* possesses the plesiomorphic mandibular palp. The latter generally differs from *Palaemonella* (in the current extent) in the presence of the strongly dissimilar second pereopods with a massive

dactylus of the major chela bearing one or few subrectangular cutting teeth (however, a similar feature may also be present in *P. atlantica*) and with subspatulate chelae of the first pereopods with denticulate cutting edges (Đuriš and Bruce 1995). Among these genera, *Cuapetes* is the most similar to *Palaemonella*, both in very conservative body and leg shape. The lack of the mandibular palp was suggested to be the only remarkable character distinguishing these genera. Nevertheless, this may also be variable. Although the mandibular palp is 2-segmented in most IWP species (Bruce 1995), the palp is small and single-segmented in the eastern Pacific and Atlantic species (Holthuis 1951a, 1951b, 1952), extremely minute in *P. rhizophorae* and fully lacking in *P. americana* (present report). The latter species was therefore long affiliated to *Periclimenes* or *Cuapetes*.

Key to species of *Palaemonella*

(modified mainly after Komai and Minemizu 2014, Komai and Yamada 2015, and Fransen and Holthuis 2007; EA, eastern Atlantic; Ind.O, Indian Ocean; EP, eastern Pacific; IWP, Indo-West Pacific; Pac., Pacific Ocean; WA, western Atlantic)

1. Mandibular palp absent.....*P. americana* (Holthuis, 1951) [WA]
Mandibular palp present.....2
2. Hepatic tooth absent.....3
Hepatic tooth present.....4
3. Postorbital ridge on carapace absent; cornea well developed, eyestalk not wider than cornea; propodi of third and fourth pereopods smooth posteriorly (minute distal spines may be present); symbiotic with scleractinian corals.....32
Postorbital ridge on carapace present; cornea reduced, eyestalk wider than cornea; propodi of third and fourth pereopods spinulose; possibly symbiotic with burrowing animals or gorgonarians.....37
4. Ambulatory propodi with numerous setae distally.....
.....*P. rubrolineata* Fransen, van der Veer & Frolová, 2022 [IWP: Pac.]
Ambulatory propodi with sparse setae distally.....5
5. Supraorbital tooth present.....6
Supraorbital tooth absent.....14
6. Ischium of second pereopod with distoventral tooth.....7
Ischium of second pereopod without distoventral tooth.....8
7. Rostral formula $RF = 8 \div 3$
.....*P. crosnieri* Bruce, 1978 [IWP: Ind.O]
 $RF = 6-7 \div 2$*P. disalvoi* Fransen, 1987 [IWP: Pac.]
8. Postorbital ridge on carapace distinct.....9
Postorbital ridge on carapace obscure or absent.....13
9. Fingers of second pereopod subequal to half length of palm or shorter [EP, EA].....10
Fingers of second pereopod distinctly longer than half length of palm [IWP].....12
10. Second pereopods subequal, similar in shape, major distinctly stronger; rostrum moderately deep, with 3 ventral teeth.....
.....*P. holmesi* Nobili, 1907 [EP]
Second pereopods distinctly unequal.....11
11. Rostrum slender, with 2 ventral teeth; second pereopods slender.....*P. asymmetrica* Holthuis, 1951 [EP]
Rostrum moderately deep, with 3 ventral teeth; second pereopods stout.....*P. atlantica* Holthuis 1951 [EA]
12. Ambulatory dactyli long, slender, ~9–11× as long as basal width.....*P. longidactylus* Hayashi, 2009 [IWP]
Ambulatory dactyli relatively short and moderately slender, 4.6–6.0× as long as basal width.....
.....*P. spinulata* Yokoya, 1936 [IWP]
13. Rostrum as long as or longer than carapace.....
.....*P. dijonesae* Bruce, 2010 [IWP: Ind.O]
Rostrum shorter than carapace.....
.....*P. maziwi* Bruce, 2002 [IWP: Ind.O]
14. Ambulatory dactyli slender, more than 8.0× longer than basal width.....15
Ambulatory dactyli moderately slender, less than 8.0× longer than basal width.....22
15. Hepatic tooth in branchiostegal position.....16
Hepatic tooth not in branchiostegal position.....18
16. Carapace without postorbital ridge; posteriormost tooth of dorsal rostral series located at 0.25 of carapace length.....
.....*P. meteorae* Bruce, 2008 [IWP: Ind.O]
Carapace with distinct postorbital ridge; posteriormost tooth of dorsal rostral series located at ~0.3 of carapace length.....17
17. Carapace with large antennal tooth.....
.....*P. komaii* Li & Bruce, 2006 [IWP: Pac.]
Carapace with small antennal tooth.....
.....*Palaemonella* sp. (sensu Li, Mitsuhashi & Chan 2008) [IWP: Pac.]
18. Rostrum longer than poel.....*P. rhizophorae* (Lebour, 1949) [WA]
Rostrum subequal to or shorter than poel.....19
19. Ambulatory propodi subdivided.....
.....*P. dolichodactylus* Bruce, 1991 [IWP: Pac.]
Ambulatory propodi not subdivided.....20
20. Chela of second pereopod with fingers longer than palm; dactylus of third pereopod 0.2× as long as propodus length.....
.....*P. hachijo* Okuno, 1999 [IWP: Pac.]
Chela of second pereopod with fingers subequal to or slightly shorter than palm; dactylus of third pereopod 0.3–0.4× as long as propodus length.....21
21. Rostrum with single ventral tooth; dactylus of third pereopod 0.4× as long as propodus length, propodus with single distoventral spine only, otherwise unarmed ventrally: third maxilliped with 4 spinules on antepenultimate segment.....
.....*Palaemonella* sp. (sensu Bruce 2003) [IWP]
Rostrum with 3 ventral teeth; dactylus of third pereopod 0.3× as long as propodus length, propodus with pair of distoventral spines and 4 smaller spines along ventral margin: third maxilliped with 7 spinules on antepenultimate segment.....
.....*P. yalla* Anker & Assayie, 2023 [IWP: Ind.O.]
22. Merus of second pereopod without conspicuous tooth at distoventral angle.....23
Merus of second pereopod with conspicuous tooth at distoventral angle.....29
23. Carapace with 3 postrostral teeth, of which 2–3 located posterior to level of hepatic tooth, posteriormost one located at dorsal midlength of carapace.....24
Carapace with 1 or 2 postrostral teeth, of which only 1 or none located posterior to level of hepatic tooth, posteriormost tooth located anterior to dorsal midlength of carapace.....26
24. Second pereopods stout, carpus subequal to palm length; symbiotic with burrowing *Alpheus* aff. *bellulus*; $RF = 3 + (5-6) \div (2-3)$
.....*P. aliska* Marin, 2008 [IWP: Pac.]
Second pereopods slender, carpus 1.5–2.0× longer than palm length.....25

25. Scaphocerite elongated, 5× longer than broad, lateral margin distinctly concave; ventral rostral tooth subterminal; second pereopod carpus distinctly longer than 1.5× pocl; RF = 3 + 3 ÷ 1; symbiotic with burrowing opistognathid fish.....*P. shirakawai* Okuno, 2017 [IWP: Pac.]
Scaphocerite 3× longer than broad, lateral margin almost straight; ventral rostral tooth near midlength of rostrum; second pereopod carpus distinctly shorter than 1.5 pocl; RF = 3 + 6 ÷ 1; symbiotic with burrowing *Alpheus* spp.....*P. jamila* Anker & Benzoni, 2023 [IWP: Ind.O.]
26. Rostrum slightly descending; carapace with distinct postorbital ridge; second pereopod carpus 1.2× longer than palm length.....*P. okunoi* Komai & Yamada, 2015 [IWP: Pac.]
Rostrum horizontal; carapace without distinct postorbital ridge; second pereopod carpus shorter than or subequal to palm.....27
27. Carpus of second pereopod with 2 conspicuous distomedial teeth.....*P. lata* Kemp, 1922 [IWP]
Carpus of second pereopod unarmed on distomedial margin.....28
28. Rostrum not reaching distal end of antennular peduncle, RF = 1 + 5 ÷ 2; eye with cornea not wider than eyestalk, eyestalk not narrowing proximally.....*P. pusilla* Bruce, 1975 [IWP]
Rostrum overreaching distal end of antennular peduncle, RF = 2 + 6 ÷ 2; eye with cornea wider than eyestalk, eyestalk narrowing proximally.....*P. burnsi* Holthuis, 1973 [IWP: Pac.]
29. Distoventral tooth on carpus of second pereopod distinctly subterminal.....*P. tenuipes* Dana, 1852 [IWP]
Distoventral tooth on carpus of second pereopod terminal.....30
30. Postorbital ridge on carapace absent; dorsal rostral teeth slender, curved.....*P. foresti* Bruce, 2002 [IWP: Ind.O.]
Postorbital ridge on carapace distinct; dorsal rostral teeth moderately not markedly stout.....31
31. Ambulatory dactyli with flexor margin ventrally concave, flexor distal spines on propodi long, ~0.5 of dactylus length; free-living.....*P. rotumana* (Borradaile, 1898) [IWP; EA]
Ambulatory dactyli with flexor margin sinuous or biconcave, flexor distal spines on propodi short, ~0.25 of dactylus length; symbiotic with crinoids.....*P. pottsi* (Borradaile, 1915) [IWP]
32. Third pereopod propodus with brush of setae distally, dactylus short and curved; RF = 7 ÷ 1; associated with *Acropora* and *Pocillopora*.....*P. orientalis* Dana, 1852 [IWP]
Third pereopod propodus sparsely setose distally, dactylus more elongated, weakly curved.....33
33. Third ambulatory propodus with pair of distinct distoventral propodal spinules.....34
Third ambulatory propodus distoventral spinules minute or lacking.....35
34. Rostrum reaching end of antennular peduncle, subequal to 0.5 of pocl; associated with *Fimbriaphyllia*.....*P. colemani* Bruce, 2003 [IWP: Pac.]
Rostrum exceeds antennular peduncle, distinctly longer than 0.5 of pocl; associated with *Plerogyra* and *Physogyra*.....36
35. Rostrum dentition RF = 1 + (7–8) ÷ (1–2); mandibular palp short, simple; associated with *Plerogyra* and *Physogyra*.....*P. philippinensis* (Bruce & Svoboda, 1984) [IWP]
Rostrum dentition RF = 1 + (3–4) ÷ 1; mandibular palp elongated, 2-segmented; associated with *Euphyllia* and *Fimbriaphyllia*.....*P. euphyllius* Marin & Anker, 2005 [IWP: Pac.]
36. Rostrum distinctly longer than 0.5 of pocl, RF = (1–2) + (6–8) ÷ (1–2); associated with *Physogyra*.....*P. smiti* (Fransen & Holthuis, 2007) [IWP: Pac.]
Rostrum subequal to 0.5 of pocl, RF = (1–2) + (3–6) ÷ (0–1); associated with *Euphyllia*.....*P. sandyi* Fransen, van der Veer & Đuriš, 2023 [IWP: Pac.]
37. Dorsal and ventral margin of rostrum armed with well-developed teeth.....38
Rostrum unarmed, with apex rounded; associated with burrow of echinurid worm.....*P. nudirostris* (Marin, 2014) [IWP: Pac.]
38. Carapace with supraorbital tooth; (association unknown).....*P. noctalbata* (Bruce, 1971) [IWP: Pac.]
Carapace without supraorbital tooth.....39
39. Posteriormost tooth of dorsal rostral series distinctly postrostral; second pereopod with carpus distinctly longer than palm, unarmed; (association unknown).....*P. gracilipes* (Komai & Minemizu, 2014) [IWP: Pac.]
Posteriormost tooth of dorsal rostral series not postrostral; second pereopod with carpus distinctly shorter than palm, armed with small distomesial tooth; associated with *Pocillopora*.....*P. oahu* (Bruce, 2010) [IWP: Pac.]

List of species

Palaemonella aliska Marin, 2008

(Fig. 3a.)

Palaemonella aliska Marin, 2008, p. 376, fig. 1–5, 9a. [South China Sea, Vietnam, Nha Trang Bay, Tré Island, Tré Bay].

Material examined

Vietnam: Allotype male, pocl. 4.2 mm, RMNH.CRUS.D.51910, South China Sea, Nha Trang Bay, Tre Island, Tre Bay, mangrove littoral, yabby-pump, inside the holes occupied by *Alpheus* cf. *bellulus* and unidentified gobiid fish, 12.vii.2006, leg. I.N. Marin. **Papua New Guinea:** 1 spm, MNHN-IU-2013-11044, PAPUA NIUGINI Expedition, PS46, N Riwo mangrove and seagrass, 05°08.7'S, 45°48.2'E, depth 2 m, 10 Dec. 2012, leg. A. Anker, Z. Đuriš (fcn UO.628H-Png12). **Solomon Islands:** 1 spm, OUMNH, SOL 212, Sep. 2016, leg. A. Anker. **New Caledonia:** 1 ovig. female, MNHN-IU-2019-3493, KOUMAC 2.3, KR910, New Caledonia: back barrier reef, 20°38.4'S, 164°11'E, sandy bottom with dead coral boulders; under boulder together with *Alpheus* aff. *bellulus*, depth 3 m, 11 Nov. 2019, leg. Z. Đuriš, A. Šobáňová.

Remarks

For *P. aliska*, the symbiotic association is known – suggested inquilinism in burrows of alpheid shrimp *Alpheus* aff. *bellulus* Miya & Miyake, 1967 (Marin 2008; Anker and De Grave 2019; present report). An undescribed species assigned to *P.* aff. *aliska*, associated with opistognathid jaw fish, was recorded from Japan; based on published photographs (Minemizu 2013, p. 42), the latter species is remarkable by the long, slender second pereopods with the carpus distinctly longer than the chela and dense red colouration of the appendages.

Palaemonella aliska shows a closer phylogenetic relationship to *P. nudirostris* (both suggested inquilinistic forms; see above) and *P. burnsi* (tidal or landlocked saltwater pools; Holthuis 1973). The both inquilinistic forms are remarkable because of a partial reduction of the eye, with the cornea distinctly smaller in diameter than the swollen eyestalk. Such corneal reduction is also observed in other species living with burrowing animals, e.g. *P. jamila* or in remaining

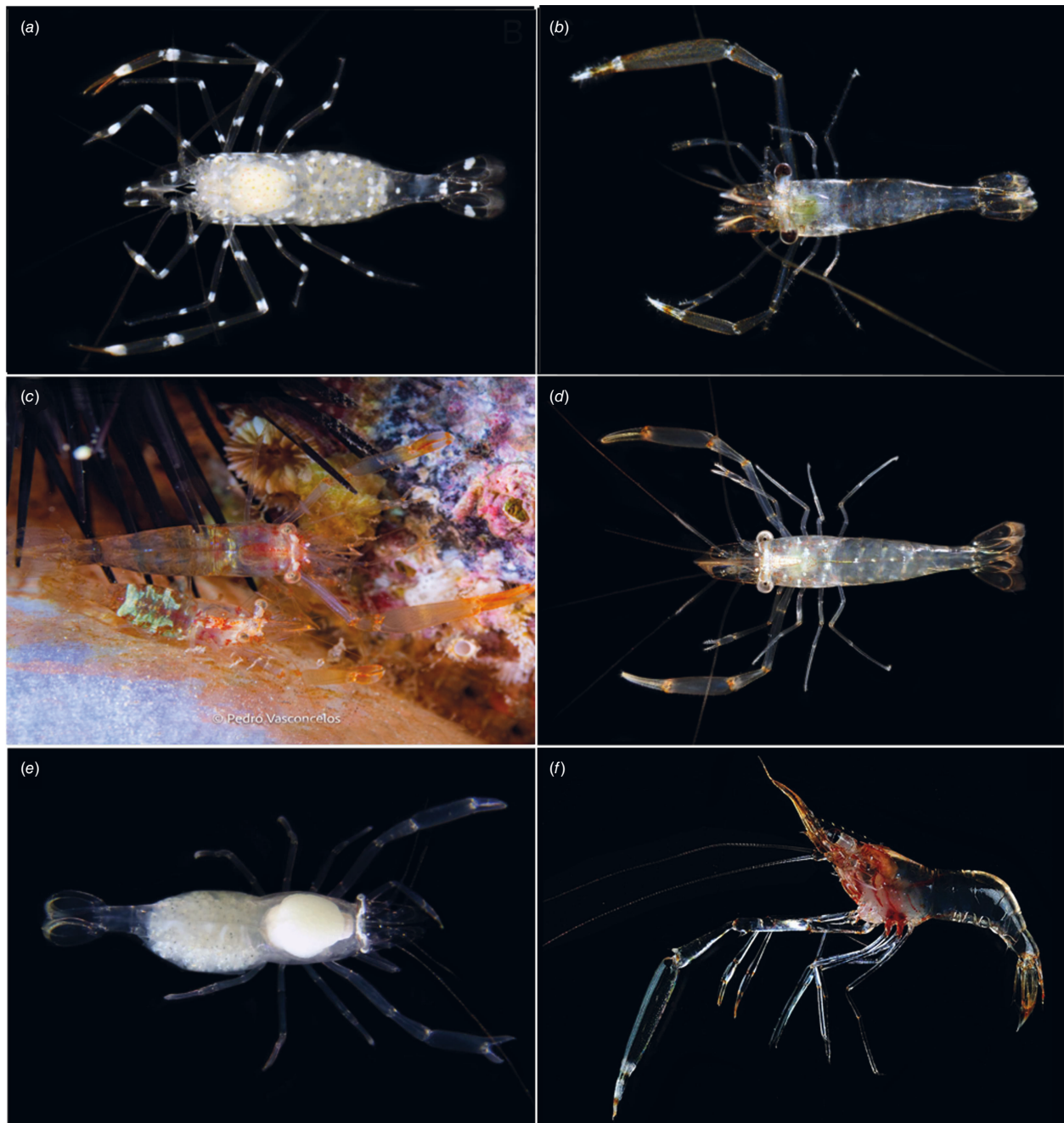


Fig. 3. Examples of species of *Palaemonella*. (a) *P. aliska* Marin, 2008, MNHN-IU-2019-3493, New Caledonia. (b) *P. americana* (Kingsley, 1878) comb. nov., MNHN-IU-2016-4076, Martinique. (c) *P. atlantica* Holthuis, 1951, Madeira. (d) *P. burnsi* Holthuis, 1973, NMMBCD6109, Taiwan. (e) *P. colemani* (Bruce, 2003) comb. nov., MNHN-IU-2013-10614, Papua New Guinea. (f) *P. disalvoi* Fransen, 1987, NMMBCD4117, Taiwan. Photographs: (a, b, d–e) Z. Ďuriš; (c) P. Vasconcelos; (f) C.-W. Lin.

members of the previous *Eupontonia*, i.e. *P. gracilipes*, *P. noctalbata* and *P. oahu* (Bruce 1971, 2010b; Komai and Minemizu 2014; Marin 2014).

Depth range

2–4 m.

Habitat

Mangrove littoral (original report); backreef, under stone.

Host

Inquilinistic association in burrow with *Alpheus* aff. *bellulus* (Marin 2008; Anker and De Grave 2019; present study).

Distribution

Indo-West Pacific: Vietnam, South China Sea (type locality); Solomon Islands (Anker and De Grave 2019); Madang area, Papua New Guinea and Koumac, New Caledonia (new records from our study).

Palaemonella americana (Kingsley, 1878), comb. nov.

(Fig. 3b, 4, 5.)

Anchistia americana Kingsley, 1878, p. 96. [Key West, Florida].

Periclimenes americanus. – Borradaile (1898), p. 383.

Kemponia americanus. – Bruce (2004), p. 11.

Cuapetes americanus. – Okuno (2009), p. 67.

Cuapetes americanus A. – Frolová *et al.* (2022), fig. 3, 4.

Material examined

Belize: 1 ovig. female, UO.S1b-Be06, Belize: Tobacco Caye, backreef, in or on sponge *Hyrtios violaceus*, depth 0.1 m, 6 Jun. 2006, leg. Z. Ďuriš, I. Horká. **USA, Florida:** 1 spm, OUMNH.2009-05-0001, USA: SMS dock, Fort Pierce, Florida, 27°27.376'N, 80°18.588'W, seagrass, depth 0.5 m, 21 Aug. 2008, leg. S. De Grave. **Martinique:** 1 spm, MNHN-IU-2016-1633, MADIBENTHOS Expedition, AB177, Martinique: Banc du Diamant, 14°26.4'N, 61°01.7'W, depth 18 m, 15 Sep. 2016, leg. Z. Ďuriš, A. Šobáňová. 1 male, pocl 2.8 mm, MNHN-IU-2016-4076, MADIBENTHOS Expedition, AD208, Martinique: Anse Noire, sortie rivièrè, côté gauche, 14°31.7'N, 61°05.3'W, seagrass, depth 5–10 m, 7 Sep. 2016, leg. Z. Ďuriš, A. Šobáňová. 1 ovig. female, pocl 2.6 mm, MNHN-IU-2016-4077, MADIBENTHOS Expedition, AD208, Martinique: Anse Noire, sortie rivièrè, côté gauche, 14°31.7'N, 61°05.3'W, seagrass, depth 5–10 m, 7 Sep. 2016, leg. Z. Ďuriš, A. Šobáňová. 1 ovig. female, pocl 2.2 mm, 2 males pocl 1.7 and 2.5 mm, MNHN-IU-2016-4399, MADIBENTHOS Expedition, AR137, Martinique: Baie du François, Pointe René, 14°37.3'N, 60°53'W, depth 2 m, 18 SEP 2016, leg. Z. Ďuriš, A. Šobáňová.

Remarks

The presence of the finger-like median process on the fourth thoracic sternite and simple ambulatory dactyli confirm the inclusion of *Palaemonella americana* in the *Palaemonella*–*Cuapetes* complex of palaemonid genera by Frolová *et al.* (2022) (= 'Pon-I group' by Chow *et al.* 2020, 2021). The lack of the mandibular palp had directly distinguished this species from *Palaemonella* that was therefore placed in *Periclimenes* O.G. Costa, 1844 by Rathbun (1902) (see: Bruce 2004). Bruce (2004) separated the *Periclimenes grandis* group of species (already indicated by Kemp 1922) into the new genus *Kemponia* Bruce, 2004 as closely related to *Palaemonella*, based on the sternal process but differing in the lack of the mandibular palp. Okuno (2009) subsequently replaced the generic name *Kemponia* by *Cuapetes* Clark, 1919 as the senior synonym. Species in the genus *Cuapetes*

are predominantly distributed in the IWP but have contained *Palaemonella americana* as the single representative in the Atlantic waters. Based on the current phylogenetic analysis (Frolová *et al.* 2022; present report: Fig. 1), the species is well nested in a wide clade of *Palaemonella* species, positioned in a group of the eastern Pacific and Atlantic representatives basally separated from the IWP species. This is therefore also *Palaemonella*. The position within *Palaemonella* is only partially surprising as the previous affiliation with *Cuapetes* was based only on the lack of the mandibular palp. This feature was widely regarded as an important key character for classification of shrimps (Holthuis 1955, 1993), nevertheless the infraspecific variability was known even in palaemonids, e.g. in species of the genera *Palaemon* and *Leander* (Fujino and Miyake 1968; Carvacho 1977). *Palaemonella americana* is therefore a unique species in the genus that lost the mandibular palp in the process of evolution. The subsequent reduction of the palp is also well illustrated in the nearest related species, another western Atlantic species *P. rhizophorae*, that possesses a greatly reduced, minute unisegmented mandibular palp (see below).

The current placement of *Cuapetes americanus* in *Palaemonella* seemingly leads to a loss of the single known Atlantic representative of the genus. Nevertheless, the recent discovery of a new species of the genus in the eastern Atlantic by Fransén *et al.* (2022b) permits the retention of *Cuapetes* as a taxon with a pantropical distribution.

Depth range

From waterline to 18 m.

Habitat

Free-living, on coral reef and seagrass; occasionally in coral rubble and external cavities of sponges.

Distribution

Western Atlantic: USA: Florida (from our study), St Eustatius, Aruba (Rathbun 1920), St Thomas (Schmitt 1935), Bonaire (Schmitt 1936), St Thomas, St Croix, St Eustatius, Tobago, Trinidad, Cubagua, Aruba (Holthuis 1951b), St John (Peter Is.), Tortola (Guana Is.), Virgin Gorda, Anguilla, Barbuda, St Kitts (St Christopher), Antigua, Guadeloupe, St Lucia, St Vincent (Mustique, Tobago Cays), Grenada (Carriacou), Tobago (Chace 1972), Guadeloupe (Carvacho 1979; Vaslet *et al.* 2013), Los Roques (Grajal and Laughlin 1984), Aruba (Abele and Kim 1986), Los Roques (Rodríguez 1986), Tortuga (Lira 2004), Cubagua (Hernández-Ávila *et al.* 2007), Curaçao (Horká *et al.* 2016), St Maarten (Poupin 2018), south-eastern Brazil (Moraes *et al.* 2021); and Martinique (new record from our study). Some of the older records may refer to *Palaemonella rhizophorae* (Lebour, 1949).

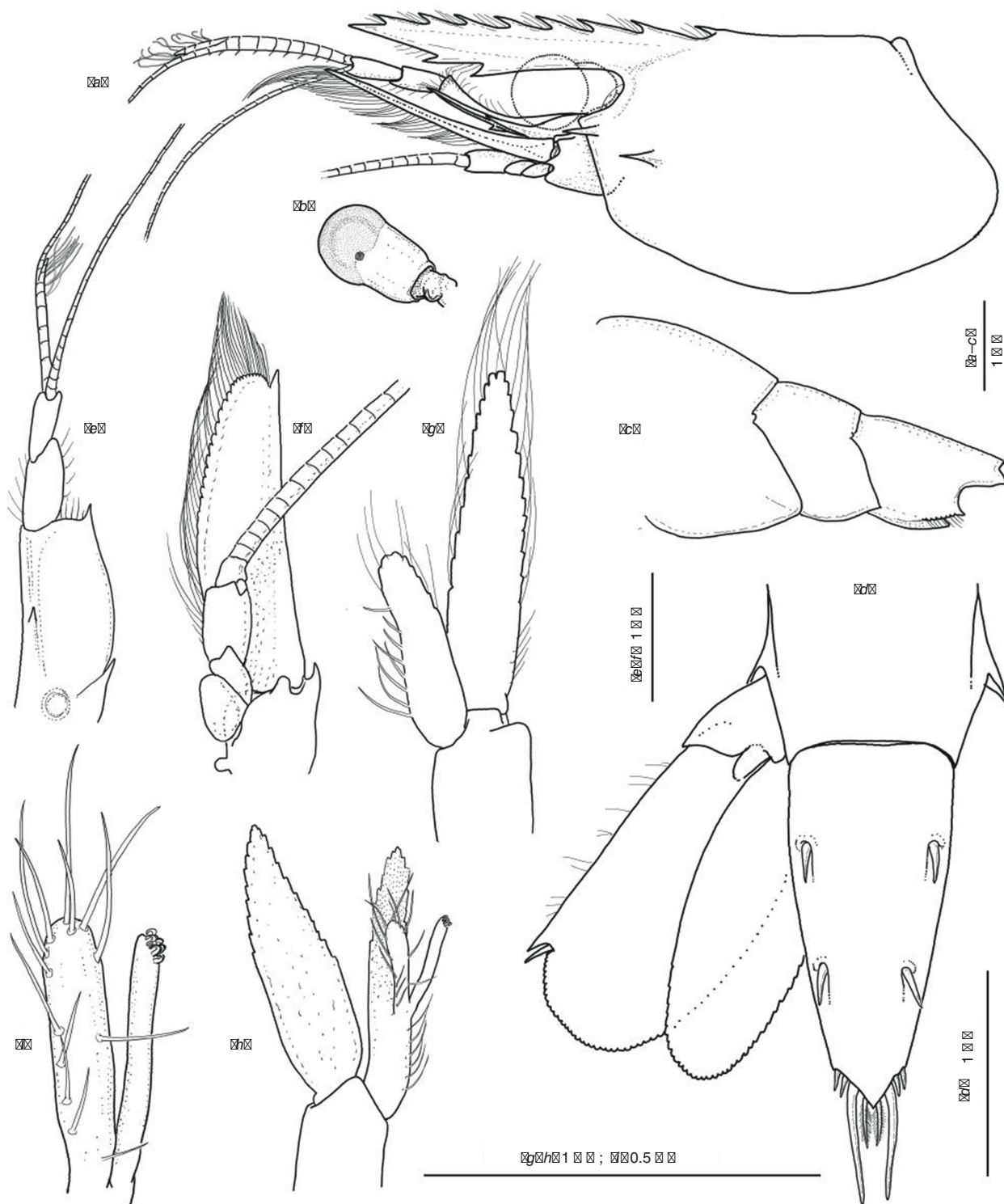


Fig. 4. *Palaemonella americana* (Kingsley, 1878) comb. nov., male pochl 3.2 mm, MNMHN-IU-2016-7369, MADIBENTHOS, Martinique, 2016. (a) Carapace with antennae, lateral view (eye indicated). (b) Right eye, dorsal view. (c) Posterior pleomeres, left lateral view. (d) Sixth pleomere, telson and uropod, dorsal view. (e) Left antennula, ventral view. (f) Left antenna, ventral view. (g) First male pleopod. (h) Second male pleopod. (i) Second male pleopod, appendices interna and masculina. Image credit: Z. Ďuriš.

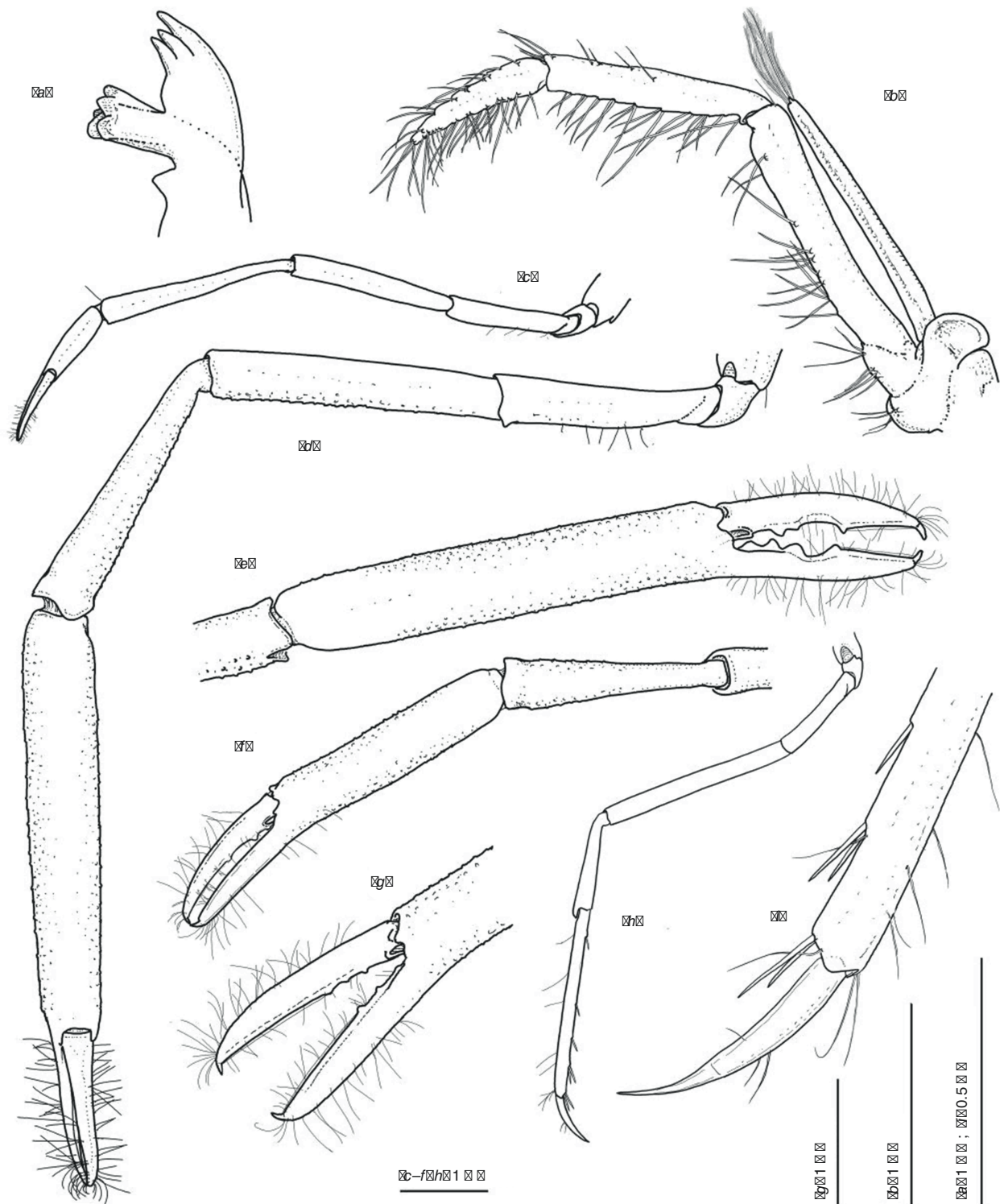


Fig. 5. *Palaemonella americana* (Kingsley, 1878) comb. nov., male pochl 3.2 mm, MNMHN-IU-2016-7369, MADIBENTHOS, Martinique, 2016. (a) Mandible, lateral view. (b) Third maxilliped, lateral view. (c) First pereopod, lateral view. (d) Major second pereopod, lateral view. (e) Major second pereopod, chela, medial view. (f) Minor second pereopod, distal segments, medial view. (g) Minor second pereopod, distal segments, fingers. (h) Third pereopod, lateral view. (i) Third pereopod, dactylus and distal propodus, medial view. Image credit: Z. Ďuriš.

Palaemonella asymmetrica Holthuis, 1951

Palaemonella asymmetrica Holthuis, 1951b, p. 19, pl. 5. [Sullivan Bay, James Island].

Material examined

E. Pacific, Clipperton Island: 1 male, pocl 2.3 mm, MNHN-U-2016-8898 [=Na.15977; macerated, lost], CLIPPERTON Expedition, Stn 46, 10°17.49'N, 109°13.52'W, depth 33 m, 6 Feb. 2003; [id.: X.Z. Li, 2007]. 1 male, pocl 2.9 mm, MNHN-IU-2016-8899 [=Na.16019; macerated, lost; some appendages preserved in extra microtube], CLIPPERTON Expedition, stn 6, 10°18.49'N, 109°14.1'W, depth 17 m, seagrass, coral rubble, 11 Jan. 2005; [id.: X.Z. Li, 2007]. 1 male, pocl 1.9 mm, 1 ovig. female, 1.6 mm, MNHN-IU-2016-8900 [=Na.16028; macerated, lost], CLIPPERTON Expedition, Stn 45, 3 Feb. 2005, 10°17.49'N, 109°13.52'W, brushing, depth 22 m, coral wall, leg. J.-M. Bouchard, L. Albenga, L. Dugrais; [id.: X.Z. Li, 2007]. 11 spms (3 males pocl 1.5–2.4 mm; 3 non-ovig. females; 3 ovig. females 1.8–2.1 mm), MNHN-IU-2016-8901 [=Na.16036; macerated, 10 spm lost, 1 spm preserved in extra microtube], CLIPPERTON Expedition, Stn 46, 6 Feb. 2005, 10°17.49'N, 109°13.52'W, depth 22 m, coral wall, leg. J.-M. Bouchard, L. Albenga, L. Dugrais; [ID: X.Z. Li, 2007].

Remarks

All specimens are congruent with the original description by Holthuis (1951b). If unbroken, the rostra are distinctly longer than pocl, with $RF = (1 - 2) + (4 - 6) \div (2 - 3)$. The second pereopods are long and held with dactyli down. The major chela has the typical heavier dactylus, with several prominent obtuse proximal teeth, a narrow dorsolateral flange and slight concavity on the mesial side. The major and minor chelae share some similarities with those of *Palaemonella atlantica*, and with the shrimps of the genera *Exoclimenella* and *Periclimenella* (Holthuis 1951b; Ďuriš and Bruce 1995). The endopod of the second male pleopod bears a well-developed *appendix masculina* with a series of setae on distal and lateral margins; the length is subequal to the *appendix interna*. All lots were accidentally damaged after examination, macerated and lost for further re-examination due to a leaky container, except a single specimen and some appendages that were preserved in additional tubes. Prior to this, the DNA from selected specimens was analysed for our phylogenetic study.

Palaemonella asymmetrica is one of two currently known eastern Pacific species of the genus; the second is *P. holmesi* (below). In our phylogenetic reconstruction, *P. asymmetrica* forms the most basally separated lineage and is sister to all other *Palaemonella* species.

Colour

Debelius (1999), p. 192 – unnumbered top photograph.

Depth range

From littoral zone to depth of 33 m.

Habitat

Coastal waters, living on rocky, sandy bottom or seagrass.

Distribution

Eastern Pacific: Galapagos Archipelago (original report); Clipperton Island (Li and Poupin 2009).

Palaemonella atlantica Holthuis, 1951

(Fig. 3c.)

Palaemonella atlantica Holthuis, 1951a, p. 152, fig. 31. [São Pedro Bay, São Vicente, Cape Verde Islands, 16°50'N, 25°04'W].

Material examined

Madeira: 1 male, pocl 4.1 mm, OUMNH.ZC.2006-17-0001, Canico, 10 Aug. 2006, leg. P. Wirtz; det. S. De Grave. **St Helena Is.:** 1 male, pocl 2.7 mm, 1 ovig. female, 2.2 mm, OUMNH 131224-55-04. 1 spm, OUMNH 140115-61-08. **Canary Islands:** 1 ovig. female, pocl 3.9 mm, RMNH.CRUS.D.45626, Spain, Canary Islands, SW Tenerife, Playa Paraiso, ~25 km NE of Los Christianos, Jul. 1994, depth 25 m, from sea anemone *Telmatactis cricoides*, collected by P. Wirtz. **Azores:** 1 spm, RMNH.CRUS.D.48798, Azores, Monte da Guia, 8 Aug. 1995, collected by P. Wirtz. **Gabon:** 1 juv. female, pocl 1.7 mm, MNHN-IU-2016-8893 [=Na 7765], INVMAR, N. of Libreville, depth 50 m, Jul. 1960; det. A. Crosnier. 1 female, pocl 4.7 mm, MNHN-IU-2016-8894 [=Na 7766], INVMAR, between Nyanga and Pointe Panga, 25 Jul. 1960, depth 65–70 m, collected by Rossignol and Blache; det. Rossignol. 2 males, pocl 1.7, 2.1 mm, MNHN-IU-2016-8895 [=Na 7767], INVMAR, Pointe Panga, depth 70 m; det. A. Crosnier. 5 spms (2 males pocl 2.8, 2.9 mm, 2 ovig. females 2.3, 2.6 mm, 1 female 2.5 mm), MNHN-IU-2016-8896 [=Na 7768], INVMAR, W. of Pointe Sante Clara, depth 45–57 m, 1 Jul. 1960, collected by Rossignol and Blache; det. Rossignol. 1 female, pocl 2.0 mm, MNHN-IU-2016-8897 [=Na 7769], INVMAR, near Libreville, depth 50 m, Jul. 1960.

Remarks

Palaemonella atlantica is one of three currently known Atlantic species of the genus (the others are *P. americana* and *P. rhizophorae*) and the only species known from the eastern Atlantic. All specimens are congruent with descriptions in the original report by Holthuis (1951a). Minor variability was observed in the rostral dentition $(2-3) + (4-7) \div (2-3)$ (v. two type specimens: $2 + 7 \div 3$) and stoutness of the chelipeds. The first pereopods are more slender in the Madeira, Canary Island and St Helena Island specimens, with the chela shorter than the carpus (v. longer in types). The second pereopods are also more slender in these specimens, but typically stout in adult Gabon specimens. In the latter, a slight subdistal constriction of the second pereopod carpus is present, as is typical for most *Palaemonella* species. The second pereopods are distinctly asymmetrical with strong cutting teeth and a deep dactylus on the major chela, and these features are remarkably similar to those in related genera (*sensu* Frolová et al. 2022) *Exoclimenella* Bruce, 1995 and *Periclimenella* Bruce, 1995 (Ďuriš and Bruce 1995). In our phylogenetic analysis, *P. atlantica* is sister to *P. americana* and *P. rhizophorae*, with which the species forms a separate clade of the Atlantic species within *Palaemonella*.

Depth range

Original report 40 m; present records: Gabon 45–70 m. Canary Is. (RMNH) 25 m. One specimen observed 1 m below sea level in a submarine cave of Madeira (Z. Ďuriš, unpubl. data).

Habitat and host

The observed Madeiran specimen (above) hides in crevices behind antipatharian *Tanacetipathes cavernicola* Opresko. The examined MNHN specimens were dredged from a hard bottom with stones, gravel and corals. The RMNH specimen from the Canary Islands was collected from the stem of a *Telmatactis cricoides* (Duchassaing) sea anemone. The species was also frequently observed on this sea anemone at Madeira (P. Wirtz, pers. obs.).

Distribution

Eastern Atlantic: Cape Verde Islands (type locality) (Holthuis 1951a; Türkay 1982; Wirtz and d'Udekem d'Acoz 2001); Azores, Madeira, Canary Islands (Fransen and Wirtz 1997; Wirtz 1997), Gabon (Rossignol 1962); St Helena Island (new records from our study).

Palaemonella burnsi Holthuis, 1973

(Fig. 3d.)

Palaemonella burnsi Holthuis, 1973, p. 24, fig. 8, 9. [Cape Kinau Peninsula, Maui, Hawaiian Islands; small lava pool near coast of Keoneoio (=La Pérouse) Bay, at the extreme eastern end of the Cape.]

Material examined

Hawaii: 1 ovig. female holotype, pocl 4.7 mm, RMNH.CRUS.D.28955, and 2 ovig. females paratypes, pocl 4.3, 5.0 mm, RMNH.CRUS.D.28957, Hawaii, type locality (see above), 12 Jun. 1972, leg. J.A. Maciolek (no. K-dc-1,4). **Taiwan:** 1 male, pocl 3.5 mm, NMMBCD6109, Pingtung, Kenting, rocky shore near NMMBA, tidal pool, at night, collected by Z. Ďuriš (fcn UO.36-Tw17). 2 spms, NMMBCD6110, same locality, at night, collected by Z. Ďuriš and A. Šobáňová (fcn UO.37-Tw17).

Remarks

The species is recognisable because of a pair of subequal, obtusely subtriangular lobes situated distally on the carpus of the second pereopods, of which margins are orange–brown. The Taiwanese specimens were collected from tidal pools on the rocky coastal platform and this habitat is in accordance with the originally reported habitat (below). The rostrum dentition of the Hawaiian type (Holthuis 1973) was $2 + 6 \div 2$ and that of the Taiwanese specimen examined matches this rostrum formula. In our phylogenetic analysis, *P. burnsi* is sister to *P. aliska* and *P. nudirostris*, both of which

are suggested to be species inquiline with burrowing animals (see Remarks for these species).

Habitat

Originally located in landlocked saltwater pools of Hawaii (Holthuis 1973); in rocky tidal pools in SW Taiwan (current report), specimens active in night.

Distribution

Indo-West Pacific: Hawaii (type locality); Taiwan (new record from our study).

Palaemonella colemani (Bruce, 2003), comb. nov.

(Fig. 3e.)

Vir colemani Bruce, 2003a, p. 119, fig. 1–6. [Loloata Island, Papua New Guinea, depth 15 m.]

Vir philippinensis. – Bruce and Svoboda (1984), p. 87 [partim; non *Vir philippinensis* Bruce & Svoboda, 1984].

Material examined

Papua New Guinea: ovigerous female holotype, NTM Cr13446, AMPI 1349, Loloata Island, depth 15 m, on coral, 2 Dec. 2002, collected by N. Coleman. 1 ovig. female, MNHN-IU-2013-10543, PAPUA NIUGINI, PR02, Madang area, Kranket Is., 05°12.01'S, 145°49.3'E, reef slope, depth 17.1 m, from coral *Fimbriaphyllia ancora*, 6 Nov. 2012, collected by Z. Ďuriš (fcn 09-Png12). MNHN-IU-2013-10614, PAPUA NIUGINI, PR13, Madang area, S. Kranket Is., 05°12.3'S, 145°48.8'E, depth 3 m, from coral cf. *F. divisa*, 9 Nov. 2012, collected by Z. Ďuriš (fcn 86-Png12). 1 spm, MNHN-IU-2013-10999, PAPUA NIUGINI, PR171, Madang area, S. Sek Is., 05°07'S, 145°49.4'E, depth 10–15 m, from euphylliid coral, 4 Dec. 2012, collected by C.-W. Lin and P.-H. Kuo (fcn.575C-Png12). **West Papua, Raja Ampat:** 2 ovigerous females, pocl. 2.3 and 3.5 mm, RMNH.CRUS.D.53094, stn RAJ.08, Mioskon Island, 00°29.808'S, 130°43.623'E, 21 Nov. 2007, depth 17.6 m, on *Fimbriaphyllia ancora*, collected by E. van der Veer. 1 ovigerous female pocl. 3.5 mm, 1 male pocl. 2.2 mm, RMNH.CRUS.D.53096, stn RAJ.11, SE Gam, Friwen Wonda, 00°28.499'S, 130°41.913'E, 22 Nov. 2007, depth unknown, on *Fimbriaphyllia ancora*; collected by E. van der Veer.

Remarks

Our 16S analysis (Fig. 2) includes the holotype of *Palaemonella colemani* (Bruce, 2003) that was described as being associated with the scleractinian coral *Plerogyra sinuosa* (Dana, 1846). The holotype is nested in the clade together with parts of specimens identified by morphology, colouration and host as *Vir euphyllius* described by Marin and Anker (2005) and associated with euphylliid scleractinians of the genus *Fimbriaphyllia* Veron & Pichon, 1980. The sister clade contains the remaining *Vir euphyllius* specimens, together with the *V. philippinensis* paratype, however, the analysed RMNH paratype 16S gene marker of *V. philippinensis* differs from the conspecifics and therefore most likely belongs to

V. colemani or *V. euphyllius* but this has not yet been clarified. The morphological distinctions between these shrimp species are small, and variation of the specific characters reported by Bruce and Svoboda (1984) and Marin and Anker (2005) may overlap among specimens of these two clades.

These specimens are most likely conspecifics. In the four-marker analyses however, two distinct paraphyletic clades with specimens identified as *P. euphyllius* can be recognised. As no morphological differences or differences in colouration have been detected between these clades, Fransen *et al.* (2023) write, 'As tissue of the holotype of *P. euphyllius* is not available for DNA analyses, it is not clear which of the two paraphyletic clades includes the real *P. euphyllius*. For the time being, it is thus not possible to draw conclusions on the taxonomic status of *P. euphyllius*; whether it is a valid species or if it has to be synonymized with *P. colemani*.' Although both clades are presented as '*P. colemani/euphyllius*' in the latter study, we provisionally keep these two taxa separate (Fig. 2), with an as yet unresolved status for *P. euphyllius*.

Recent taxonomic confusion with species identification had also been caused by the evident mixed state of the type material of *V. colemani*, and an erroneous colour description and photograph provided by Bruce (2003a, p. 123, fig. 6) showing one of the colour varieties of *V. philippinensis*, instead of *V. colemani*. The colour photograph does not belong to the *V. colemani* holotype. Also, the host coral *Plerogyra sinuosa* on the photograph is typical for *V. philippinensis*, but the colouration and the host coral of the holotype were evidently other than that reported, as currently reviewed for '*Palaemonella colemani/euphyllius*' by Fransen *et al.* (2023). Nevertheless, the colouration of *P. colemani* may be clarified only after resolving the taxonomic state of both of these species.

Habitat, host

Associated with scleractinian corals of *Fimbriaphyllia*: *F. ancora* (Veron & Pichon), *F. parancora* (Veron), *F. divisa* (Veron & Pichon) and *F. yaeyamensis* (Shirai) [Cnidaria: Scleractinia: Euphyllidae].

Depth range

3–17.6 m (current data).

Distribution

Indo-West Pacific: Loloata Island, south-eastern Papua New Guinea (Bruce 2003a); Nhatrang Bay, Vietnam; south-western Taiwan; Philippines, Indonesia, West Papua, Lembah strait, Malaysia, Vanuatu (Fransen *et al.* 2023); Papua New Guinea (new records from our study).

Palaemonella crosnieri Bruce, 1978

Palaemonella crosnieri Bruce, 1978, p. 210, fig. 2–4. [Iles Glorieuses, 11°28.1'S, 27°[sic, 'S'] 21.1'E, depth 20 m.]

Material examined

No specimen examined.

Remarks

See below for *P. disalvoi*.

Habitat, host

Coral reefs. Bruce (1978) observed no evidence to suggest any symbiotic associations of *P. crosnieri*; based on general similarities with most congeners in the form of chelae of the second pereopods and the third maxillipeds, a micropredatory mode of life was suggested.

Depth range

Low tide to 26 m.

Distribution

Indo-West Pacific: Kenya, Madagascar (Bruce 1976, 1978).

Palaemonella dijonesae Bruce, 2010

Palaemonella dijonesae Bruce, 2010a, p. 151, fig. 1 [Rocky Head, Enderby Island, Dampier Archipelago, 20°40'14"S, 116°27'96"E, depth 12.5 m].

Material examined

Western Australia (only tissues for DNA): 1 male paratype, WAM C.28094, Nelson Rocks, Dampier Archipelago, DA3/99/68, 20°27.998'S, 116°39.707'E, depth 6.3 m, 7 Jul. 1999. 1 ov. female holotype, WAM C.29308, Rocky Head, Enderby Island, Dampier Archipelago, stn DA2/99/73, 20°40'14"S, 116°27'96"E, depth 12.5 m, 24 July 1999.

Remarks

Owing to close similarity of *P. dijonesae* with *P. spinulata*, most of the Pacific reports on the latter species need to be revised (see Bruce 2010a). No DNA sequences were obtained for the study.

Depth range

6.3–12.5 m (Bruce 2010a).

Host and habitat

No data.

Distribution

Indo-West Pacific: Dampier Archipelago, Western Australia (type locality).

***Palaemonella disalvoi* Fransen, 1987**

(Fig. 3f.)

Palaemonella disalvoi Fransen, 1987, p. 511, fig. 7–12. [Tahai, west coast of Easter Island, depth 35 m, in substrate of dead coral].

Material examined

Chile, Easter Island: 1 ovig. female holotype, pocl. 2.4 mm, RMNH.CRUS.D.37160, Tahai, W. of Easter Island. 1 male paratype, pocl. 2.5 mm, RMNH.CRUS.D.37161, off Hanga Rao, depth 60 m, in dead coral. **Papua New Guinea:** 1 spm, MNHN-IU-2013-10803, PAPUA NIUGINI, PS23, N. Sek Is., 05°04.6'S, 145°49.2'E, depth 21 m, 23 Nov. 2012, lgt. Z. Đuriš and A. Anker (fcn UO.341i-Png12). **New Caledonia:** 1 spm, MNHN-IU-2019-2994, KOUMAC 2.3, KL39, Koumac Barrier Reef, 20°45.1'S, 164°14'E, depth 26 m, 10 Nov. 2019. **Taiwan:** 1 spm, pocl. 2.9 mm, NMMBCD4117, Pingtung, Hojie, depth 10–20 m, 03 Apr. 2013, collected by C.-W. Lin (fcn 20130403-04). 1 spm, NMMBCD6106, Pingtung, Hojie, depth 10–20 m, 18 Feb. 2017, Hojie, collected by C.-W. Lin (fcn 20170218-nn).

Remarks

The species closely resembles *P. crosnieri* from the western Indian Ocean (Bruce 1978) and is distinguishable from the former only by a lower number of rostral teeth (Fransen 1987). The current New Caledonia specimens are genetically congruent with RMNH.CRUS.D.37161, the paratype of *P. disalvoi*, whereas the specimens from Taiwan and Papua New Guinea seem to be somewhat divergent but possibly conspecific with *P. disalvoi*. Molecular comparison of specimens from the western Indian Ocean (not yet available) with those of the Pacific Ocean are necessary for a final conclusion on the taxonomic status of both taxa. Specimens of *P. disalvoi* we analysed are sister to *P. rotumana*. Both those species, together with *P. crosnieri*, have an elongated, well dentate rostrum, a supraorbital tooth or acute tubercle on the carapace, distally tapering scaphocerite with the distolateral tooth far overreaching the lamella and a strong distoventral tooth on the second pereopod merus (also on the ischium in *P. disalvoi* and *P. crosnieri*) (Bruce 1978, 1991; Fransen 1987).

Depth range

33–60 m (Fransen 1987), 20–26 m (current data).

Host, habitat

Free-living, on substrate of dead coral (Fransen 1987; Gan *et al.* 2015, Fransen *et al.* 2022).

Distribution

Indo-West Pacific: Easter Islands (type locality); Taiwan (Gan *et al.* 2015, Fransen *et al.* 2022); Madang area, Papua New Guinea and Kavieng, New Caledonia (new records from our study).

***Palaemonella dolichodactylus* Bruce, 1991**

Palaemonella dolichodactylus Bruce, 1991, p. 232, fig. 6F–L, 7. [New Caledonia, Ouen Is., Prony Bay, Lagoon East, 22°14.5'S, 167°02.0'E, 65–70 m].

Material examined

Vanuatu: 1 spm, MNHN-IU-2014-12007, SANTO 2006, AT55, N. Urélapa Is., 15°36.2'S, 167°02.5'E, depth 80–82 m, 2 Oct. 2006; det. X.-Z. Li. **New Caledonia:** 1 spm, MNHN-IU-2019-3470, KOUMAC 2.3, KB635, lagoon, drop-off of large coral platform, 20°38.4'S, 164°16.5'E, depth 16 m, 11 Nov. 2019.

Remarks

Palaemonella dolichodactylus is typical for the group of predominantly deep water (lower part of continental shelf and upper slope) species but with the current species and *P. okunoi* collected in shallow sublittoral depths; further species are *P. hachijo*, *P. meteorae* and *P. komaii*. Species of the '*P. dolichodactylus* group' (after Bruce 2008) are remarkable for the unusually long, slender ambulatory pereopods with slender dactyli more than 8× longer than the basal depth. The uniquely subsegmented ambulatory propodi are notable for *P. dolichodactylus* but these are less distinctive than the true segmentation known variably on certain pereopods of, e.g. alpheid, hippolytid, pandalid or processid shrimps. This propodal subdivision may be confused with accidental damages of propodi on legs of preserved specimens, therefore molecular and morphological revisions of a wider series of such shrimps is needed to confirm the specific state of the present and other specimens with *P. dolichodactylus*. *Palaemonella dolichodactylus* and *P. okunoi* also constitute a sister pair in our phylogenetic tree, not forming a natural group with a cluster of *P. komaii* or with *P. hachijo*. The *dolichodactylus* group is therefore not supported by our phylogenetic analysis.

Depth range

44–80 m (Bruce 1991); 80–82 m (Vanuatu, present report); 16 m (New Caledonia, present report).

Distribution

Indo-West Pacific: New Caledonia (type locality); Vanuatu (new records from our study).

***Palaemonella euphyllius* (Marin & Anker, 2005),
comb. nov.**

(Fig. 6a.)

Vir euphyllius Marin & Anker, 2005, p. 118, fig. 1–5. [Vietnam, Nha Trang Bay, Tre Island, southern bay, near lighthouse, depth 15 m, on *Euphyllia* cf. *divisa*.]

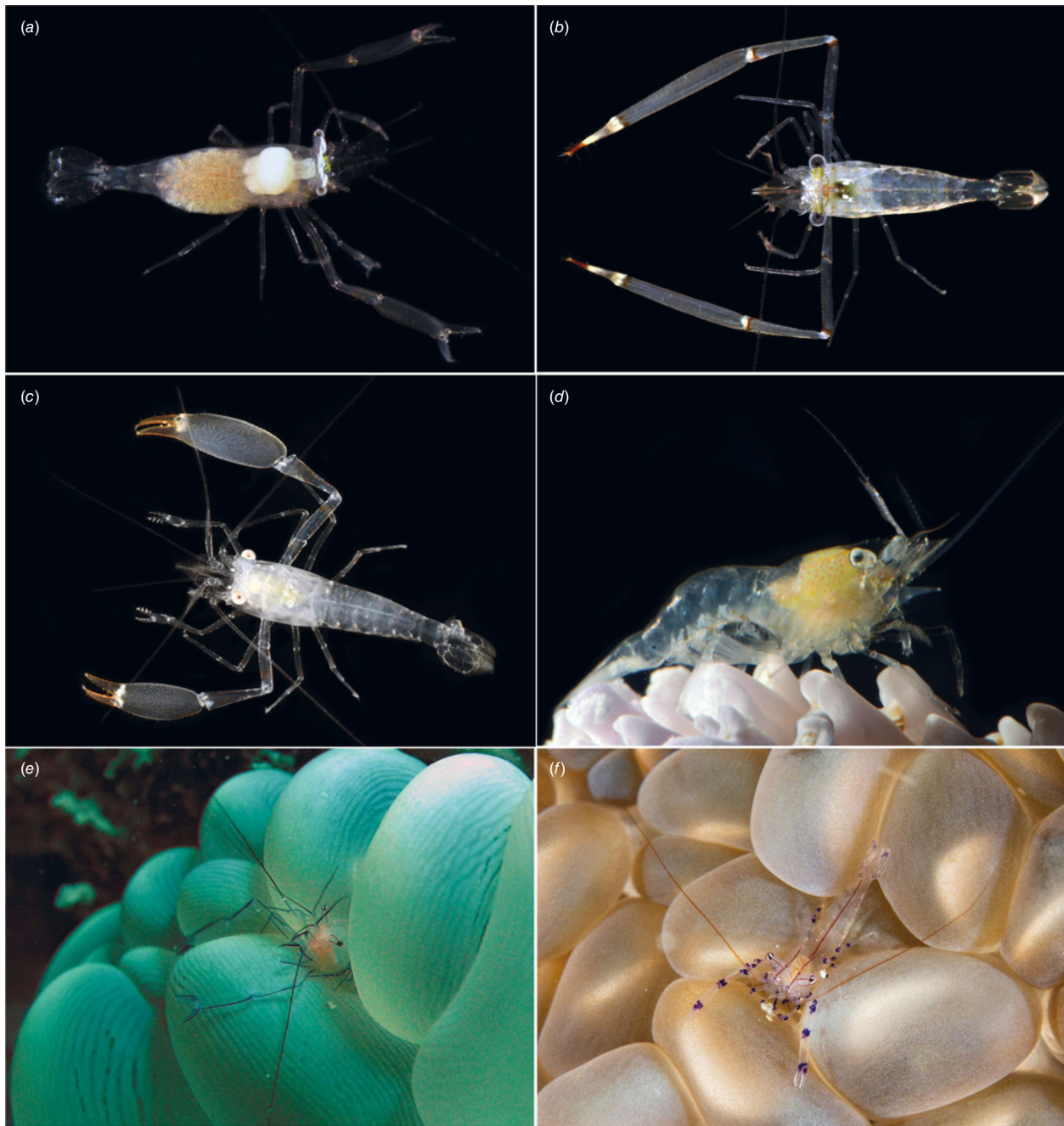


Fig. 6. Examples of species of *Palaemonella*. (a) *P. euphyllius* (Marin & Anker, 2005) comb. nov., 46-Vn10, Vietnam. (b) *P. holmesi* (Nobili, 1907), MZUSP 33965, Las Perlas Archipelago, Panama. (c) *P. nudirostris* (Marin, 2014) comb. nov., OUMNH. ZC. 2018-06-01, Solomon Islands. (d) *P. orientalis* Dana, 1852, MNMHN-IU-2018-844 (specimen with second chelipeds regenerating), New Caledonia. (e) *P. philippinensis* (Bruce & Svoboda, 1984) comb. nov., UO.83-Vn08, Vietnam. (f) *P. philippinensis*, Papua New Guinea. Photographs: (a, d, e) Z. Ďuriš; (b, c) A. Anker; (f) A. Berberian.

Vir euphyllius Marin & Anker, 2005, p. 123, fig. 6–8. [Vietnam, Nha Trang Bay, Tre Island, northern ‘Bay Tre’, depth 7 m, on *Euphyllia* cf. *parancora*.]

Material examined

Philippines: 1 spm, RMNH.CRUS.D.35559 (*V. philippinensis* paratype; see below). **Vietnam:** 1 spm, UO.90-Vn07, N. off Nhatrang, Whale Is.,

12°34′54.6″N, 107°23′54″E, scuba, depth 5.6 m, from euphylliid coral *Euphyllia glabrescens*, 17 Sep. 2007, collected by Z. Ďuriš. 1 male, 1 ovig. female, UO.46-Vn10, Nhatrang Bay, Mun Is., Pipefish Bay, scuba, depth 15.2 m, from euphylliid coral *E. glabrescens*, 13 Aug., 2010, collected by Z. Ďuriš. **Indonesia:** 1 ovigerous female, pochl. 3.6 mm, RMNH.CRUS.D.53055, stn BER.02, Kalimantan, Derawan Island, W-side, Mangalase, 02°16′52.5″N, 118°13′39.4″E, 4 Oct. 2003, depth 10 m, on *Fimbriaphyllia divisa*, collected by C.H.J.M. Franssen. 1

ovigerous female, pochl. 2.2 mm, RMNH.CRUS.D.53056, stn BER.30, Kalimantan, Berau Islands, lighthouse-1 reef, N-side (S of Derawan Isl.), 02°16'02.1"N, 118°14'22.6"E, 18 Oct. 2003, depth 20 m, on *Fimbriaphyllia ancora*, collected by C.H.J.M. Fransen. 1 male, pochl. 2.0 mm, RMNH.CRUS.D.49851, stn BAL.15, Bali, NE-side Pulau Serangan, 08°44'03"S, 115°15'05"E, slowly declining reef slope, sandy base, scuba-diving, depth 20 m, 7 Apr. 2001, on *Fimbriaphyllia ancora*, collected by C.H.J.M. Fransen. 1 ovigerous female, pochl. 1.9 mm, purple-banded colour variety, RMNH.CRUS.D.50403, stn BAL.18, Bali, Padang Bai, E-side Tanjung Sari, 08°31'11"S, 115°30'37"E, shallow reef flat and slope, sandy slope, scuba-diving, depth 20 m, 8 Apr. 2001, on *Fimbriaphyllia ancora* or *F. parancora*, collected by C.H.J.M. Fransen. 1 ovigerous female, pochl. 2.5 mm, RMNH.CRUS.D.53054, stn SER.15, Java Sea, Kepulauan Seribu, Kelapa Island, NW-side, 5°39'16"S, 106°33'32"E, 13 Sept. 2005, depth 18 m, on *Fimbriaphyllia divisa*, collected by C.H.J.M. Fransen. 1 ovigerous female, pochl. 3.7 mm, RMNH.CRUS.D.53053, stn SER.23, Java Sea, Kepulauan Seribu, Jukung Island, NW-side, 5°34'01"S, 106°31'38"E, 15 Sept. 2005, depth 20 m, on *Fimbriaphyllia divisa*, collected by C.H.J.M. Fransen. 1 male, pochl. 2.8 mm, RMNH.CRUS.D.53069, stn RAJ.70, West Papua, Raja Ampat, NW Batanta, cape, 00°47.408'S, 130°29.223'E, 14 Dec. 2007, depth 9.5 m, on *Fimbriaphyllia divisa*, collected by E. van der Veer. 1 ovigerous female, pochl. 3.0 mm, RMNH.CRUS.D.53095, stn RAJ.11, West Papua, Raja Ampat, SE Gam, Friwen Wonda, 00°28.499'S, 130°41.913'E, 22 Nov. 2007, depth 18.7 m, on *Fimbriaphyllia ancora*, collected by C.H.J.M. Fransen, CF041. **SW Taiwan:** 1 male pochl. 1.3 mm, 1 female pochl. 1.7 mm, NMMBCD6102, Pingtung, Sanjiaoting, collected by C.-W. Lin (fcn 20140909-08). **Philippines:** ovig. female ('paratype of *Vir philippinensis*' – see below), pochl. 3.0 mm, RMNH.CRUS.D.35559.

Remarks

See taxonomic status under *P. colemani* (Bruce, 2003). In our 16S phylogenetic reconstruction (Fig. 2), the paratype of *Vir philippinensis* is clustered with specimens identified as *E. euphyllius*. The latter are close to *P. colemani* in our four-gene analysis but remotely positioned outside of the *V. philippinensis* clade. The paratype therefore more likely belongs to *P. euphyllius*. Unfortunately the gene sequences of the types of *P. euphyllius* remain unavailable for comparison, therefore the specific status of the *Vir philippinensis* paratype has not yet been resolved.

Our specimens are morphologically similar to those of both *P. colemani* and *P. euphyllius* though these may vary in details of rostrum length and dentition, mandibular palp segmentation and development of the ambulatory propodal distoventral spines or the walking dactyli stoutness (see Bruce and Svoboda 1984; Bruce 2003a; Marin and Anker 2005).

Depth range

7–20 m.

Host

Associated with the scleractinian euphylliid corals *Euphyllia glabrescens* (Chamisso & Eysenhardt) and *Fimbriaphyllia ancora* [Scleractinia: Euphylliidae].

Distribution

Nhatrang Bay, Vietnam (type locality); Raja Ampat, Indonesia (Fransen 2008); Sabah, Malaysia (Fransen 2012); Vietnam and Taiwan (new records from our study), possibly also Philippines (see *Vir philippinensis* paratype).

Palaemonella foresti Bruce, 2002

Palaemonella foresti Bruce, 2002a, p. 279, fig. 1–4. [BP Oil Refinery Jetty, Cockburn Sound, Western Australia, 32°13.9'S, 115°45.14'E, depth 7 m.]

Material examined

Australia: 1 male, pochl. 4.6 mm, WAM C 43684, Woodside Kimberley Survey, 17/K09-Adhoc, N. West Australia, Montgomery Is., 15°35.323'S, 124°18.876'E, 20 Oct. 2009, collected by L. Patterson, leg. P. Hosie; det. A.J. Bruce, 2009.

Remarks

The Western Australian specimen of *P. foresti* is clustered with *P. longidactylus* Hayashi, 2009 and the crinoid-ectobiotic *P. pottsi* in our molecular analysis and all three species are sister to *P. spinulata*. A closer relation of *P. foresti* and *P. pottsi* had already been reported by Bruce (2002a), indicating the lack of the supraorbital armature, the presence of a two-segmented mandibular palp, the second pereopod ischium being unarmed, the merus distoventrally armed and the carpus without a preterminal tooth. *Palaemonella foresti* can be distinguished by, for example, having four ventral rostral teeth, numerous small spines distally on the third maxilliped ischiomerus and the distoventral spines of the ambulatory propodi being longer than the propodal depth Bruce (2002a).

Depth

7 m.

Habitat

Originally recorded from harbour piles, with mixed sessile invertebrates, without evidence of any symbiotic association.

Distribution

Indo-West Pacific: Western Australia.

Palaemonella gracilipes (Komai & Minemizu, 2014)

Eupontonia gracilipes Komai & Minemizu, 2014, p. 172, fig. 1–4. [Off Osaka, Ishigaki Island, Yaeyama Islands, Ryukyu Islands.]

Material examined

Not examined.

Remarks

Formerly a member of the genus *Eupontonia*, distinguishable from *Palaemonella* by the lack of the hepatic tooth, considered to be a free-living species. Although *P. noctalbata*, the type species of the ‘*Eupontonia* complex’ of the genus *Palaemonella* is considered free-living, for the other 2 species, *P. oahu* and *P. nudirostris*, the symbioses with scleractinian corals or burrowing worms respectively, were repeatedly reported (Bruce 2010b; Marin 2014; Anker and De Grave 2019). As the reduction of the hepatic tooth on the carapace and a shortened rostrum could be regarded as adaptive characters to symbioses, the other 2 species may also be predicted to be symbiotic. Nevertheless, as even the 2 symbiotic species of ‘*Eupontonia*’, are not sister-positioned in the present phylogenetic tree, the whole ‘*Eupontonia* complex’ is polyphyletic. The absence of the hepatic tooth thus could be the result of its multiple independent evolutionary loss within the genus *Palaemonella*.

Habitat

Under coral rubble.

Depth

5 m.

Host

Symbiotic association is unknown. Komai and Minemizu (2014) considered *E. gracilipes* to be a free-living species.

Distribution

Indo-West Pacific: Japan, Ryukyu Islands.

Palaemonella hachijo Okuno, 1999

Palaemonella hachijo Okuno, 1999, p. 739, fig. 1–3. [33°03.5'N, 139°47.9'E, southern Japan, Izu Islands, Hachijo-jima Island, Occhogahama, submarine cave, depth 20 m.]

Material examined

Salomon Sea: 1 male, pocl 3.6 mm, MNHN-IU-2015-556, MADEEP, DW4313, N. Normanby I., d'Entrecasteaux Islands, 09°49'S, 151°34'E, depth 105–175 m, 3 May 2014.

Remarks

The species is a member of the *P. dolichodactylus* species group (see paragraphs on *P. dolichodactylus* and *P. komaii*) and most closely resembles *P. dolichodactylus* (see Okuno 1999). The single specimen in our molecular analysis is separately placed between most core *Palaemonella* species and members of the former *Vir* complex.

Depth range

15–45 m (submarine cave, Japan) (Okuno 1999, 2001); 105–175 m (dredged, Salomon Sea; present report).

Habitat

Deeper than 100 m (current data); submarine caves in shallower waters; considered a free-living species, without symbiotic association (Okuno 1999, 2001).

Distribution

Indo-West Pacific: southern Japan, Izu Islands; Salomon Sea (our study).

Palaemonella holmesi (Nobili, 1907)

(Fig. 6b.)

Anchista tenuipes Holmes, 1900, p. 216. [Santa Catalina Island.]

Periclimenes Holmesi Nobili, 1907, p. 5. [Replacement name for *Anchista tenuipes* Holmes, 1900.]

Palaemonella holmesi. – Holthuis (1951b), p. 13.

Material examined

Panama (Pacific): 1 spm, MZUSP 33965, Las Perlas Archipelago, Nov. 2018, collected by A. Anker.

Remarks

One of two currently known eastern Pacific species of the genus; the second is *P. asymmetrica* (above). As indicated by Holthuis (1951b), formerly partly confused with the IWP species *Cuapetes tenuipes* (Borradaile, 1898). In our phylogeny, *P. holmesi* is basally separated from the trio of Atlantic species, thereby forming a monophyly with the latter, whereas the other eastern Pacific congener, *P. asymmetrica*, forms the most basally positioned lineage, sister to all other *Palaemonella* species.

Depth range

Littoral to 90 m.

Habitat

Usually shallow coastal waters, sandy or on rocky bottom with vegetation (Müller 1993).

Distribution

Eastern Pacific: California, Mexico, Costa Rica, Panama, Colombia, Ecuador, Galapagos Archipelago (Holthuis 1951b; Müller 1993).

Palaemonella jamila Anker & Benzoni, 2023

Palaemonella jamila Anker & Benzoni, 2023, p. 79, fig. 1–4. [Saudi Arabia, Makkah Province, Thuwal, King Abdullah University of Science and Technology (KAUST), near King Abdullah Monument, 22°20'26.2"N, 39°05'15.1"E, shallow sand-rubble flat between small mangrove and deeper channel, in burrow of *Alpheus* sp., depth 1 m.]

Material examined

Not examined.

Remarks

As indicated by Anker and Benzoni (2023), *P. jamila* is morphologically and ecologically close to *P. aliska* and *P. shirakawai*. These 3 species are symbiotically associated with burrowing animals, the snapping shrimps *Alpheus* or opistognathid fish. The species differs from *P. shirakawai*, among other characters, in the broader scaphocerite that is 3× longer than broad, with the lateral margin almost straight (v. 4.5× longer with concave margin in the latter), more numerous dorsal rostral teeth, the ventral rostral tooth not subterminal and the second pereopod carpus distinctly shorter than 1.5× the pocl (v. distinctly longer). Although *P. shirakawai* is reported as symbiotic with burrowing fish (Okuno 2017), *P. aliska* and *P. jamila* live in burrows with *Alpheus* spp. (Marin 2008; Anker and De Grave 2019; Anker and Benzoni 2023). The latter can be easily distinguished from *P. aliska* by the distinctly more slender second pereopods, with the carpus 1.5 to 2× the palm length (v. subequal). These 3 species may be evolutionarily closely related based on morphological and ecological evidence and of these, only *P. aliska* was DNA-analysed within this study. In our phylogenetic analysis, *P. aliska* is clustered with *P. nudirostris* (previously *Eupontonia*), living with a burrowing echiurid worm and the more basally separated free-living *P. burnsi*.

Habitat, host

Shallow sand-rubble flat near mangrove and a deeper channel, in burrows of *Alpheus* sp. (Anker and Benzoni 2023).

Distribution

Known only from the type locality in Saudi Arabia, the Red Sea.

Palaemonella komaii Li & Bruce, 2006

Palaemonella komaii Li & Bruce, 2006, p. 657, fig. 9–11. [Tonga, Vava'u group, 18°37'S, 174°03'W, depth 327–360 m.]

Material examined

Philippines: 1 spm, NTOU 2004.08.06, PANGLAO, T4, trawled. **New Caledonia:** 1 female, pocl 3.7 mm, MNHN-IU-2017-2771, KANADEEP,

DW4978, Chesterfield Bank, N/O 'Alis', depth 310–335 m, 9 Sep. 2017. **Fiji:** 1 paratype, MNHN-IU-2013-16387, BORDAU 1, Ride de Lau, Vanua Balavu, N/O 'Alis', depth 350–365 m, 03 Mar. 1999. **French Guiana:** 1 ovig. female, pocl 2.7 mm, MNHN-IU-2013-19827, PROTEUS-GUYANE, DW5071, 6°15.5'N, 52°06.4'W, depth 125–129 m, 1 Dec. 2017, leg. M. Castelin and C. Chambard.

Remarks

As indicated by Li and Bruce (2006), *P. komaii* is a member of a group of species with very long, slender ambulatory pereopods with the dactyli more than 8× longer than the basal depth and with several long setae on the dorsal dactylar margin. Bruce (2008) applied the term '*P. dolichodactylus* species complex' to this group of species and listed *P. dolichodactylus*, *P. komaii*, *P. hachijo* Okuno, 1999 and *P. meteorae* Bruce, 2008, and mentioned 2 other as yet unnamed species previously reported by Bruce (2003b) and Li *et al.* (2008). The complex comprises predominantly deepwater species living at depths over 100 m, usually 250–500 m (see Remarks for *P. dolichodactylus*). The 4 specimens we analysed showed distinct genetic diversity, whereas the specimen from the Philippines was deeply divergent from the 3 remaining specimens, and therefore needs re-examination for the species affiliation. The New Caledonian specimen is closer to the pair composed of a type from Japan and, surprisingly (see below), a specimen from French Guiana (western Atlantic). Generally, *P. komaii* is separately positioned on a polytomy with the *P. pusilla*–*P. oahu* pair and the major clade of the remaining IWP congeners. No sister species is indicated here.

Depth range

Tonga, 327–360 m (original report); Fiji, 335–350 m; French Guiana, 125–129 m (current report).

Habitat

Deep water, lower shelf and upper continental slope.

Distribution

Indo-West Pacific: Tonga, south Pacific (type locality). Reported here for the first time from the Philippines and New Caledonia. The current report from French Guiana is either a surprising range extension to the Atlantic Ocean or the consequence of a mislabelled museum specimen.

Palaemonella lata Kemp, 1922

Palaemonella lata Kemp, 1922, p. 127, fig. 3–6. [Aberdeen, Port Blair, Andamans, rock pool at low tide.]

Material examined

Not examined.

Remarks

The species belongs to the group of congeners without the supraorbital tooth on the carapace, with the ambulatory dactyli not unusually slender, i.e. less than 8× longer than the basal width and with a disoventrally unarmed merus of the second pereopod. The carpus of the second pereopod bears 2 acute teeth in the medial margin (Holthuis 1952; Bruce 2010a; Komai and Yamada 2015).

Depth range

Intertidal zone.

Habitat

Rock pools and coral reef flats.

Host

Unidentified large sponge in reef pool (Müller 1993).

Distribution

Indo-West Pacific: Zanzibar; Andaman Islands; Indonesia; Hawaii.

***Palaemonella longidactylus* Hayashi, 2009**

Palaemonella longidactylus Hayashi, 2009, p. 97, fig. 5–7 [non *Vir longidactylus* Marin, 2008; = *Palaemonella smiti* (Fransen & Holthuis, 2007)]. [Beppu Bay, Ooita Prefecture.]

Material examined

Papua New Guinea: 1 ovig. female, pocl 2.8 mm, MNHN-2015-1344, KAVIENG 2014, CP445, New Ireland, N/O 'Alis', depth 133–178 m, 2 Sep. 2014. **Philippines:** 1 spm, NTOU, PANGLAO, T29, Panglao Is., Biking, 0°43.5'N, 123°50.6'E, depth 77–84 m, mud, 1 Jul. 2004.

Remarks

The current synonymisation of *Vir* with *Palaemonella* (also see Discussion) would result in *P. longidactylus* Hayashi becoming an objective junior homonym of *Vir longidactylus* Marin, 2008. This would be enacted because of molecular results showing the holotype of *V. longidactylus* to be conspecific with 'Vir smiti Fransen & Holthuis, 2007' (now *Palaemonella smiti*; see below). Marin's (2008) species is therefore synonymised with *P. smiti* and *P. longidactylus* Hayashi, 2009 remains a valid name. The 2 specimens from which DNA was analysed show a closer genetic relationship to *P. foresti* and *P. pottsii*.

Habitat

No data.

Depth range

84–133 m (PNG – present report).

Distribution

Indo-West Pacific: Japan (type locality). Papua New Guinea, Philippines (our study).

***Palaemonella maziwi* Bruce, 2002**

Palaemonella maziwi Bruce, 2002b, p. 15, fig. 1. [Maziwi Island, Pangani, Tanganyika, 5°30.6'S, 39°04.06'E, depth 2 m.]

Palaemonella spinulata. – Bruce (1975), p. 177–183, fig. 6, 7; Bruce (1978), p. 209, fig. 1 [non *Palaemonella spinulata* Yokoya, 1936, p. 135–136, fig. 4].

Material examined

Kenya: 1 female paratype, RMNH.CRUS.D.50023, Fort Jesus, Mombasa, Kenya, stn AJB-205, #2185, scuba, depth 10 m, 21 Aug. 1974, collected by J. Wood.

Remarks

Previously misidentified with *P. spinulata* Yokoya, 1936 (e.g. Bruce 1975, p. 177, 1976, p. 471, 1978, p. 209). No DNA sequence was obtained from the single available specimen examined, the RMNH paratype.

Depth range

From 0.5 to 40 m.

Habitat

Sublittoral – lagoon, reef edge.

Distribution

Indo-West Pacific: Maziwi (Island) reef (type locality), Tanzania, Kenya (Bruce 1975).

***Palaemonella meteorae* Bruce, 2008**

Palaemonella meteorae Bruce, 2008, p. 64, fig. 1, 2. [Red Sea, off Port Sudan, 19°33.3'N, 37°16.4'E–19°33.9'N, 37°16.2'E.]

Material examined

Not examined.

Remarks

This species belongs to the *P. dolichodactylus* species complex (see paragraphs on *P. dolichodactylus* and *P. komaii*). *Palaemonella meteorae* and *P. komaii* are remarkable because of the branchiostegal position of the hepatic tooth on the sides of the carapace. This position was also reported by Li *et al.*

(2008) for an undescribed species. Apart from *P. meteorae*, the only congeners recorded from the Red Sea are *P. tenuipes* Dana (see Bruce 2008), *P. pottsi* and *P. rotumana* (see Āuriš 2017).

Depth range

519–544 m.

Habitat

Deepwater; bathyal slope.

Distribution

Indo-West Pacific: Red Sea, off Port Sudan (Bruce 2008).

Palaemonella noctalbata (Bruce, 1971), comb. nov.

Eupontonia noctalbata Bruce, 1971, p. 308, fig. 1–5. [Wasini Channel, Kenya, 4°39.4'S, 39°22.2'E, depth 6 fms, ~11 m.]

Material examined

Not examined.

Remarks

The type species of the 'Eupontonia complex' of the genus *Palaemonella*. See also remarks for *P. gracilipes* and Discussion.

Depth

11 m.

Host, habitat

The type specimen was discovered on the coral *Galaxea fascicularis* (L.) by examination. Bruce (1971, p. 235) considered *E. noctalbata* a free-living species without symbiotic relationships. The other 3 known species were reported as associates of corals, burrowing worms or of unknown association (see following 2 species and *P. gracilipes*).

Distribution

Indo-West Pacific: known only from the type locality, Kenya, western Indian Ocean.

Palaemonella nudirostris (Marin, 2014), comb. nov.

(Fig. 6c.)

Eupontonia nudirostris Marin, 2014, p. 556, fig. 1–4, 5a, b. [Pacific Ocean, South China Sea, Vietnam, Nhatrang Bay, south-east of Tre

Island, Dam Bay, 12°12'19.53"N, 109°18'11.12"E, mangrove littoral, depth 0.5 m.]

Material examined

Solomon Islands: 1 male, pochl 2.2 mm, OUMNH.ZC.2018-06-01, New Georgia, near Munda, Hopei Island, shallow sandflat near seagrass bed, depth 0.5–1.0 m, in burrow of unidentified echiuran (Thalassematidae), suction (yabby) pump, 14 Sep. 2016, leg. A. Anker (fcn SOL-107).

Remarks

A species of the former genus *Eupontonia* (see Discussion) with a remarkable full reduction of the rostral dorsal and ventral teeth and with non-acute, rounded apex. This unusual morphology, the full reduction of the hepatic tooth and partially the reduced eye cornea (see Remarks for *P. aliska*) are evidently evolutionary adaptations to the inquiline association with a burrowing host worm. Based on our molecular analysis, *P. nudirostris* is closely related to another suggested inquiline, *P. aliska* and to *P. burnsi* occurring in tidal or landlocked saltwater pools (see paragraphs for the latter species).

Depth range

0.5–1 m.

Host, habitat

Muddy sand bottom or shallow sandflat near seagrass bed, in burrow of a thalassematid spoon worm; *Listriolobus* sp. [Echiura] (Marin 2014; Anker and De Grave 2019).

Distribution

Indo-West Pacific: South China Sea, Vietnam (type locality). Solomon Islands (Anker and De Grave 2019).

Palaemonella oahu (Bruce, 2010), comb. nov.

Eupontonia oahu Bruce, 2010b, p. 405, fig. 1–5. [Kahe Point, Oahu, Hawai'an Islands.]

Material examined

S. Pacific, Marquesas Archipelago: 4 spms (1 male pochl 1.4 mm, 1 female 1.3 mm, 2 ovig. females 1.3, 1.6 mm), MNHN-IU-2013-16342, PAKAIHI I TE MOANA, Stn MQ15-GR, Fatu Hiva, Grotte Matautu, 10°28.31'S, 138°40.68'W, N/O 'Braveheart', depth 0–28 m, 17–18 Jan. 2012.

Remarks

Palaemonella oahu is a species of the former genus *Eupontonia* (see remarks for *P. gracilipes* and Discussion). In our molecular phylogeny, the species is nested in a pair with *P. pusilla*. Both species are small-sized representatives

of *Palaemonella* possessing a very short rostrum with a few dorsal teeth (with 1 postrostral) and a single small distoventral tooth; eye cornea diameter is smaller than the swollen eyestalk; the third maxilliped bears 2 spinules distolaterally on the antepenultimate segment; the *appendix masculina* is relatively stout, short and not noticeably overreaching the distal end of the endopodite of the second male pleopod (Bruce 1975, 2010b; Li and Bruce 2006).

Depth range

In shallow waters, 0–28 m (current report).

Host, habitat

The species is a coral associate living on *Pocillopora* colonies, *P. meandrina* Dana [Pocilloporidae: Scleractinia] (Bruce 2010b).

Distribution

Indo-West Pacific: Hawaii (original report). Marquesas (our study).

Palaemonella okunoi Komai & Yamada, 2015

Palaemonella okunoi Komai & Yamada, 2015, p. 353, fig. 1–5. [Cape Maeda, Onna Village, Okinawa Island, Ryukyu Islands, depth 30 m, coral rubble.]

Material examined

Japan: 1 ovig. female paratype, pocl 3.7 mm, CBM-ZC-13082, Awa, Nago, Okinawa Island, depth 5–10 m, coral rubble, 25 Apr. 2013, collected by N. Shirakawa and S. Komai.

Remarks

As indicated in the original description of the species by Komai and Yamada (2015), *Palaemonella okunoi* is highly similar to *P. hachijo*. A unique character of the former is the presence of a pair of submedian teeth flanking the spiniform median process on the fourth thoracic sternite. A similar, even more projecting ‘trispinose’ thoracic sternum was observed by one of the authors (Z. Ďuriš) in a specimen of *Palaemonella* sp. from the South China Sea, Vietnam (deposited in IO VAST, Nhatrang). The only current type specimen of *P. okunoi* that has undergone DNA analysis is genetically sister to *P. dolichodactylus* (see the Remarks for the latter species).

Depth range

5–30 m.

Habitat

Coral rubble.

Distribution

Indo-West Pacific: Okinawa Island, Ryukyu Islands, Japan (type locality).

Palaemonella orientalis Dana, 1852

(Fig. 6d.)

Palaemonella orientalis Dana, 1852, p. 26. [*in mari Suluensi.*]

Vir orientalis. – Holthuis, 1952, p. 30.

Palaemonella orientalis. – Fransen *et al.* (2022a), p. 568, fig. 9–16.

Material examined

Great Barrier Reef, Australia: 1 male, pocl 2.1 mm, MTQ W 33130, CReefs Lizard Island Expedition 2010, LI10-024, Channel, 14°41.222'S, 145°27.905'E, from *Pocillopora* sp., depth 8 m, 28 Aug. 2010, collected by I. Marin, leg. Z. Ďuriš. **New Caledonia:** 1 male, pocl 1.9 mm, 1 ovig. female, 2.9 mm, MNHN-IU-2018-844, KOUMAC 2.1, KM308, Koumac Barrier Reef, seagrass beds, corals, sand, 20°33.5'S, 164°05.8'E, depth 0 m, 16 Sep. 2018. **Vanuatu:** 2 males, pocl 2.0 and 2.2 mm; 1 damaged specimen, pocl 1.9 mm, MNHN-IU-2022-2001, stn FR18, Santo, NW Tutuba Island, 15°19'47.892"S, 167°10'1.128"E, 18 Sept. 2006, depth unknown, steep reef slope, leg. C.H.J.M. Fransen. **Maldives:** 1 ovigerous female, pocl 2.3 mm, RMNH.CRUS.D.58034, stn MAL.19.068, N Nilandhe Atoll, Magoodhoo Island, lagoon in front of station, 3°4'51.92"N, 72°57'57.74"E, 15 May 2014, depth 0–2 m, among *Pocillopora* spec. and *Acropora* spec., leg. C.H.J.M. Fransen. **Indonesia:** 1 ovig. female pocl 1.9 mm, RMNH.CRUS.D.58035, stn LEM.25, NE Sulawesi, Lembeh Strait, N Pulau Dua, 1°23'28.6434"N, 125°12'58.7154"E, 13 Feb. 2012, depth 11 m, on *Acropora* spec., leg. Zoi Farenzena.

Remarks

Type species of the former genus *Vir*, distinguished from *Palaemonella* by the lack of the hepatic tooth and living in symbiosis with scleractinian corals. *Palaemonella orientalis* is distinguishable from other currently recognised species of the *Vir*-complex by the presence of distinct brushes of long distoventral setae on the ambulatory propodi. The setae are evidently an adaptation to diminish the harmful effect of dactyli from shrimp climbing on the fine live tissues of the host coral. The species has recently been redescribed by Fransen *et al.* (2022a). *Palaemonella orientalis* is the most basally positioned among the species of the ‘*Vir*’ complex of the genus (including the recently described *P. rubrolineata* and *P. sandyi* – see the respective paragraphs for these species).

Depth range

0–8 m (current data).

Habitat and host

Seagrass beds, sandy bottom with corals. Associated with scleractinian corals *Acropora* and *Pocillopora*.

Distribution

Indo-West Pacific: Sulu Sea (type locality); widely distributed in the IWP, from eastern Africa to the Mariana Islands and Hawaii. Queensland, Australia (Fransen *et al.* 2022a); New Caledonia (new record from our study).

Palaemonella philippinensis (Bruce & Svoboda, 1984), comb. nov.

(Fig. 6e, f.)

Vir philippinensis Bruce & Svoboda, 1984 (partim), pp. 87–93, fig. 1–3. [Cebu, Philippines, on *Plerogyra sinuosa*.]

Vir colemani. – Bruce (2003a) (partim). p. 119, fig. 1–6.

Material examined

2 spms, **Great Barrier Reef, Australia:** MTQ W.33131, CReefs Lizard Island 2010, LI10-001, Channel bommies, 14°41.317'S, 145°27.835'E, depth 11 m, 25 Aug. 2010, collected by I. Marin, leg. Z. Ďuriš (fcn UO.45-Au10). **Papua New Guinea:** 1 spm, MNHN-IU-2013-10718, PAPUA NIUGINI, PR48, S. Sek Is., Malamal Passage, 05°07.2'S, 145°49.4'E, depth 13 m., from coral *Plerogyra sinuosa*, 17 Nov. 2012, collected by C.-W. Lin (fcn UO.216-Png12). 1 spm, MNHN-IU-2013-10723, PAPUA NIUGINI, PR48, Madang area, S. Sek Is., Malamal Passage, 05°07.2'S, 145°49.4'E, depth 25 m, from *Plerogyra sinuosa*, 17 Nov. 2012 collected by Heok Hui (fcn UO.220-Png12). 1 spm, MNHN-IU-2013-10955, PAPUA NIUGINI, PR175, Madang area, Yabob, depth 9 m, from ephylliid coral *Physogyra lichtensteini*, 4 Dec. 2012, collected by A. Berberian (fcn UO.537C-Png12). 1 spm, MNHN-IU-2013-10956, PAPUA NIUGINI, PR170, Madang area, Kranket, depth 15 m, from *Plerogyra sinuosa*, 4 Dec. 2012, collected by A. Berberian (fcn UO.538-Png12). **Taiwan:** 1 ovig. female, pocl 3.1 mm, NMMBCD6103, Pingtung, Hojie, depth 10–20 m, 26 Sep. 2014, collected by C.-W. Lin (fcn 20140926-13). **Vietnam:** 1 ovig. female, UO.91-Vn07, N. off Nhatrang, Whale Is., 12°34'54.6"N, 107°23'54"E, scuba, depth 7.2 m, from coral *P. sinuosa*, 17 Sep. 2007, collected by Z. Ďuriš. 1 ovig. female, UO.48-Vn10, Nhatrang Bay, Mun Is., Pipefish Bay, scuba, depth 15.2 m, 12 Aug. 2010, collected by Z. Ďuriš. **Indonesia:** 1 male pocl 2.4 mm, RF = 1 + 6 ÷ 2, RMNH.CRUS.D.53080, stn RAJ.08, Raja Ampat Islands, West Papua, Mioskon Island, 00°29.808'S, 130°43.623'E, 21 Nov. 2007, depth 16.4 m, on *Physogyra lichtensteini*, collected by E. van der Veer. 1 male pocl 1.7 mm, RF = 2 + 5 ÷ 2, RMNH.CRUS.D.53086, stn RAJ.11, Raja Ampat Islands, West Papua, SE Gam, Friwen Wonda, 00°28.499'S, 130°41.913'E, 22 Nov. 2007, depth 15.3 m, on *Physogyra lichtensteini*, leg. E. van der Veer. 1 male pocl 1.8 mm, RF = 2 + 5 ÷ 1, RMNH.CRUS.D.53082, stn RAJ.25, Raja Ampat Islands, West Papua, S. Gam, E entrance Besir Bay, Cape Besir, 00°30.859'S, 130°34.191'E, 27 Nov. 2007, depth 8 m, on *Plerogyra sinuosa*, leg. E. van der Veer. 1 male pocl 2.4 mm, RF = 2 + 6 ÷ 2, 1 non ovig. female pocl 2.2 mm, RF = 1 + 6 ÷ 2, RMNH.CRUS.D.53083, stn RAJ.28, Raja Ampat Islands, West Papua, N Batanta, N pulau Yarifi; 00°46.779'S, 130°42.711'E, 28.xi.2007, depth 15.5 m, on *Plerogyra sinuosa*, collected by C.H.J.M. Fransen. 1 male pocl 2.0 mm, RF = 2 + 6 ÷ 2, RMNH.CRUS.D.53085, stn RAJ.08, Indonesia, Raja Ampat Islands, West Papua, Mioskon Island, 00°29.808'S, 130°43.623'E, 21 Nov. 2007, depth 16.2 m, on *Physogyra lichtensteini*, leg. E. van der Veer. 1 ovig. female pocl 2.1 mm, RF = 2 + 5 ÷ 1, RMNH.CRUS.D.53081, stn RAJ.19, Indonesia, Raja Ampat Islands, West Papua, Maya's mimpi, 00°30.456'S, 130°39.919'E, 25 Nov. 2007, depth 14.3 m, on *Physogyra*

lichtensteini, leg. E. van der Veer. 1 male pocl 2.1 mm, RF = 2 + 5 ÷ 2, 1 non ovig. female pocl 2.6 mm, RF = 2 + (4–5) ÷ 2 tip broken, RMNH.CRUS.D.53084, stn RAJ.46, Indonesia, Raja Ampat Islands, West Papua, Yenweres Bay, 00°29.216'S, 130°40.394'E, 5. Dec. 2007, depth 18 m, on *Physogyra lichtensteini*, leg. E. van der Veer. 1 ovig. female pocl 2.9 mm, RF = 2 + 5 ÷ 1, RMNH.CRUS.D.53087, stn RAJ.55, Indonesia, Raja Ampat Islands, West Papua, S Friwin Isl., 00°28.909'S, 130°41.901'E, 7. Dec. 2007, depth 15 m, on *Plerogyra sinuosa*, leg. E. van der Veer. 2 males, pocl 2.1 and 2.2 mm, RMNH.CRUS.D.53091, stn SER.15, Java Sea, Kepulauan Seribu (Thousand Islands), off Jakarta, Kelapa Island, NW-side, 5°39'16"S, 106°33'32"E, 13 Sept. 2005, depth 18 m, on *Physogyra lichtensteini*, leg. C.H.J.M. Fransen – 1 ovig. female pocl 2.6 mm, RMNH.CRUS.D.53092, stn SER.23, Java Sea, Kepulauan Seribu (Thousand Islands), off Jakarta, Jukung Island, NW-side, 5°34'01"S, 106°31'38"E 15 Sept. 2005, depth 15 m, on *Plerogyra/Physogyra* spec; leg. C.H.J.M. Fransen. 1 ovig. female, pocl 3.4 mm, RMNH.CRUS.D.51745, stn SER.29, Indonesia, Java Sea, Kepulauan Seribu (Thousand Islands), off Jakarta, Tikus Island, N-side, 5°51'13"S, 106°34'43"E, 18 Sept. 2005, depth 12 m, on *Plerogyra sinuosa* leg. C.H.J.M. Fransen. 1 male, pocl 2.8 mm, RMNH.CRUS.D.53089, stn SER.42, Indonesia, Java Sea, Kepulauan Seribu (Thousand Islands), off Jakarta, Peniki Island, NW-side, 5°41'48"S, 106°42'56"E, 25 Sept. 2005; depth 15 m, on *Plerogyra* spec., leg. C.H.J.M. Fransen. 1 ovig. female, pocl 3.6 mm, RMNH.CRUS.D.53090, stn SER.42, Indonesia, Java Sea, Kepulauan Seribu (Thousand Islands), off Jakarta, Peniki Island, NW-side, 5°41'48"S, 106°42'56"E, 25 Sept. 2005, depth 15 m, on *Plerogyra* spec., leg. C.H.J.M. Fransen. 2 ovig. females, pocl 3.2 and 3.3 mm, RMNH.CRUS.D.53093, stn BER.02, NE Kalimantan, Berau Islands, Derawan Island, W-side, Mangakalase, 02°16'52.5"N, 118°13'39.4"E, 4 Oct. 2003, depth 10 m, on *Plerogyra sinuosa*, leg. C.H.J.M. Fransen. **Philippines:** 1 male, pocl 2.5 mm, 1 ovig. female, pocl 2.8 mm, RMNH.CRUS.D.48528, stn CEB.10, Philippines, Cebu Strait, W of Bohol, SE side of Cabilao Island, SW of Talisay, 9°52.28'N, 123°46.76'E, gentle slope, low coral density, much rubble, scuba, 13 Nov. 1999, depth 20 m, on *Plerogyra sinuosa*, leg. C.H.J.M. Fransen. **Maldives:** 1 juv. pocl 1.3 mm, RF = 1 + 5 ÷ 1, RMNH.CRUS.D. 59348, stn MAL.04; Maldives, N Nilandhe Atoll, Magoodho island, Wall Street, 3°07'14.2"N, 72°58'46.9"E; 7 May 2014, depth 20 m, on *Plerogyra* spec., leg. C.H.J.M. Fransen.

Remarks

A species of the former genus *Vir*. The species is readily recognisable by longitudinal purple lines or purple rings in articulations of segments in each cheliped and ambulatory leg in live state, and uncoloured statocyst, eyestalk without bright white line. Similar but slightly feebler pattern may be in one of two colour forms of *P. colemani* but usually with a distinct purple ring outlining statocysts, and a bright white uninterrupted line inside and between eyestalks (see also Fransen *et al.* 2023 and remarks for *P. colemani*). The RMNH *Vir colemani* paratype belongs to *P. colemani* or *P. euphyllius* (also see Discussion) based on our 16S analysis (Fig. 2).

Depth range

7.2–25 m (current report).

Host

Associated with corals *Physogyra lichtensteini* (Milne Edwards & Haime) and *Plerogyra sinuosa* (Dana) [Scleractinia: Plerogyridae].

Distribution

Indo-West Pacific: Philippines (type locality); Indonesia (Fransen and Holthuis 2007); Vietnam, Maldives (Fransen et al. 2022a).

Palaemonella pottsi (Borradaile, 1915)

(Fig. 7a, b.)

Periclimenes (Falciger) pottsi Borradaile, 1915, p. 212. [Torres Straits, on *Comanthus*.]

Material examined

SW Taiwan, Pingtung, Hojie: 1 ovig. female, pocl 2.4 mm, NMMBCD5637, depth 10–20 m, 25 Feb. 2011, collected by C.-W. Lin (fcn 20110225-nn). 1 male, pocl 3.5 mm, NMMBCD5614, depth 10–20 m, 16 Dec. 2013, collected by C.-W. Lin (fcn 20131216-05). 1 ovig. female, pocl 3.9 mm, NMMBCD5639, depth 10–20 m, 17 Mar. 2013, collected by C.-W. Lin (fcn 20130317-05). 1 ovig. female, pocl 3.9 mm, NMMBCD6100, depth 10–20 m, 21 Mar. 2013, collected by C.-W. Lin (fcn 20130321-10). 1 spm, NMMBCD6105, depth 10–20 m, 12.09.2015, collected by C.-W. Lin (fcn 20150912-11). 2 spms, UO.38-Tw17, depth 11.6 m, 2 Oct. 2017, collected by Z. Ďuriš and A. Šobáňová (crinoid host photographed by Z. Ďuriš). **S Taiwan, South Bay:** 1 spm, UO.51-Tw12, depth 8.5 m, 10 Sep. 2012, from black crinoid, collected by Z. Ďuriš. **NE Taiwan:** 1 male, pocl 2.9 mm, NTOU (fcn 20170808-Dav), Keelung, NE Taiwan, Aug. 2017, collected by W.-Ch. 'David' Lin. **New Caledonia:** 1 spm, MNHN-IU-2018-1246, KOUMAC 2.1, KR407, Koumac Barrier Reef, pool, sandy bottom with coral pebbles, 20°34.4'S, 164°05.7'E, depth 5 m, 26 Sep. 2018, collected by Z. Ďuriš and A. Šobáňová.

Remarks

The only species of the genus associated with echinoderms and crinoids. Morphologically close to the most common congener, free-living *P. rotumana*, from which this differs in the slightly sinuate ventral outline of the ambulatory dactyli (v. smoothly concave in the latter). The variation of the rostral dentition in the specimens examined is $RF = (1-2) + (5-9) \div (2-3)$. In our phylogeny, *P. pottsi* clusters with *P. longidactylus* and *P. foresti* and all three are sister to *P. spinulata*.

Colour

Deeply red or purple, almost black on dark crinoids. In captivity this species may change colour to light brown on a semi-transparent body.

Depth range

2–29 m, coral reefs.

Host

The ecto-symbiosis on crinoids has been widely recorded in *P. pottsi* (e.g. Bruce 1970; Minemizu 2000, 2013; Kato and Okuno 2001 Kawamoto and Okuno 2003; present report). Host Echinodermata: Crinoidea (see Müller 1993); also observed among long spines on body of the sea urchin

Diadema setosum (Leske) (Echinoidea) in Vietnam, South China Sea (Z. Ďuriš, pers. obs.).

Distribution

Indo-West Pacific: the species is known from eastern Africa, the Red Sea and throughout the Indian Ocean to the western Pacific, including the Philippines, Great Barrier Reef, New Caledonia and Marshall Islands (Ďuriš 2017).

Palaemonella pusilla Bruce, 1975

Palaemonella pusilla Bruce, 1975, p. 169, fig. 1–5. [Kisiti Island, near Wasin, Kenya, 4°43.3'S, 39°22.15'E, on sheltered coral reef at LWS.]

Material examined

Papua New Guinea: 1 spm, MNHN-IU-2015-623, PAPUA NIUGINI, PB45, Sinub I., 05°07.9'S, 145°48.9'E, depth 8 m, 8 Dec. 2012. 1 male, pocl 1.7 mm, 1 ovig. female, 1.3 mm, MNHN-IU-2015-1568, PAPUA NIUGINI, PB33, Rasch passage, 05°09.1'S, 145°49.7'E, depth 30 m, 1 Dec. 2012. **Great Barrier Reef, Australia:** 1 ovig. female, pocl 1.4 mm, MTQ W.33321, Lizard Island 2010, LI10-077, Bay Reef (outer barrier), 14°28.227'S, 145°31.707'E, depth 17 m, 5 Sep. 2010, leg. Ch. Buxton, (fcn UO.133E-Au10).

Remarks

One of the smallest species of the genus, with pocl 1.3–1.7 mm in current specimens. The rostrum in the specimens examined is shorter than the antennular peduncle and bears a dentition $RF = (1-2) + (3-5) \div 1$ (matching the state in the holotype ovigerous female, with $RF = 2 + 4 \div 1$ Bruce 1975), except the ovigerous female (pocl 1.3 mm), MNHN-IU-2015-1568, with 4 ventral rostral teeth ($RF = 1 + 6 \div 4$). The Australian specimen, another ovigerous female with pocl 1.4 mm, had only 9 eggs 0.58×0.52 mm in size, with eyespots; these eggs fully occupied the compartment of the females' marsupium beneath the pleon. The PNG specimen MNHN-IU-2015-1568 (only well preserved exuvium present) has the second pereopods somewhat unequal, the major cheliped is stouter than illustrated for the holotype (Bruce 1975, fig. 4D, 5B), with stronger cutting teeth and the minor pereopod has a smaller chela with feeble dentition. The closer phylogenetic relationship with *P. oahu* is commented on above (see paragraph for *P. oahu*).

Habitat

Occurs in sheltered coral reef locations, where the species was found on the non-living base of a coral colony at low tide level.

Depth range

From littoral to 30 m.

Distribution

Indo-West Pacific: Kenya (Kisiti Island, near Wasin). Great Barrier Reef, Australia and Papua New Guinea (new records from our study).

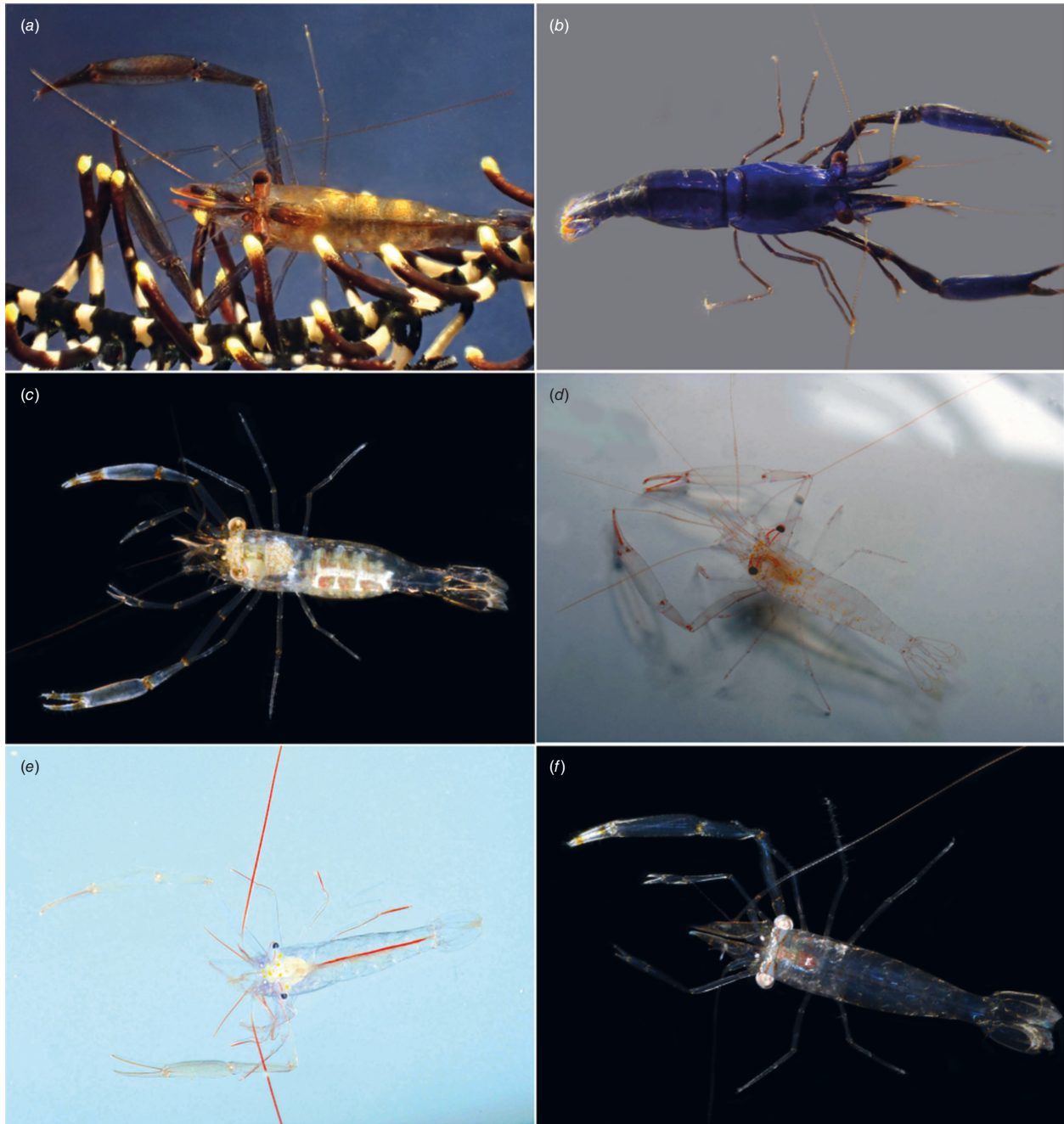


Fig. 7. Examples of species of *Palaemonella*. (a) *P. pottsii* (Borradaile, 1915), UO.38-Tw17, Taiwan. (b) *P. pottsii*, UO.51-Tw12, Taiwan. (c) *P. rotumana* (Borradaile, 1898), IU-2018-473, New Caledonia. (d) *P. rubrolineata* Fransen, van der Veer & Frolová, 2022, RAJ.02, Raja Ampat. (e) *P. smiti* (Fransen & Holthuis, 2007) comb. nov., MNHN-IU-2013-10827, Papua New Guinea. (f) *P. tenuipes* Dana, 1852, MNHN-IU-2018-1286 (left second cheliped lost), New Caledonia. Photographs: (a–c, f) Z. Ďuriš; (d) C. H. J. M. Fransen; (e) A. Anker.

***Palaemonella rhizophorae* (Lebour, 1949),
comb. nov.**

(Fig. 8, 9.)

Periclimenes (Ancylocaris) bermudensis Lebour, 1949a, p. 1115, fig. 6.
[Mangrove Lake, Bermuda.]

Periclimenes (Ancylocaris) rhizophorae Lebour, 1949b, p. 605.
[Replacement name for *Periclimenes (Ancylocaris) bermudensis* Lebour, 1949a (nec *Periclimenes (Periclimenaeus) bermudensis* Armstrong, 1940).]

Periclimenes americanus. – Holthuis (1951b), p. 66 [partim].

Cuapetes americanus B. – Frolová et al. (2022), pp. 4–7.

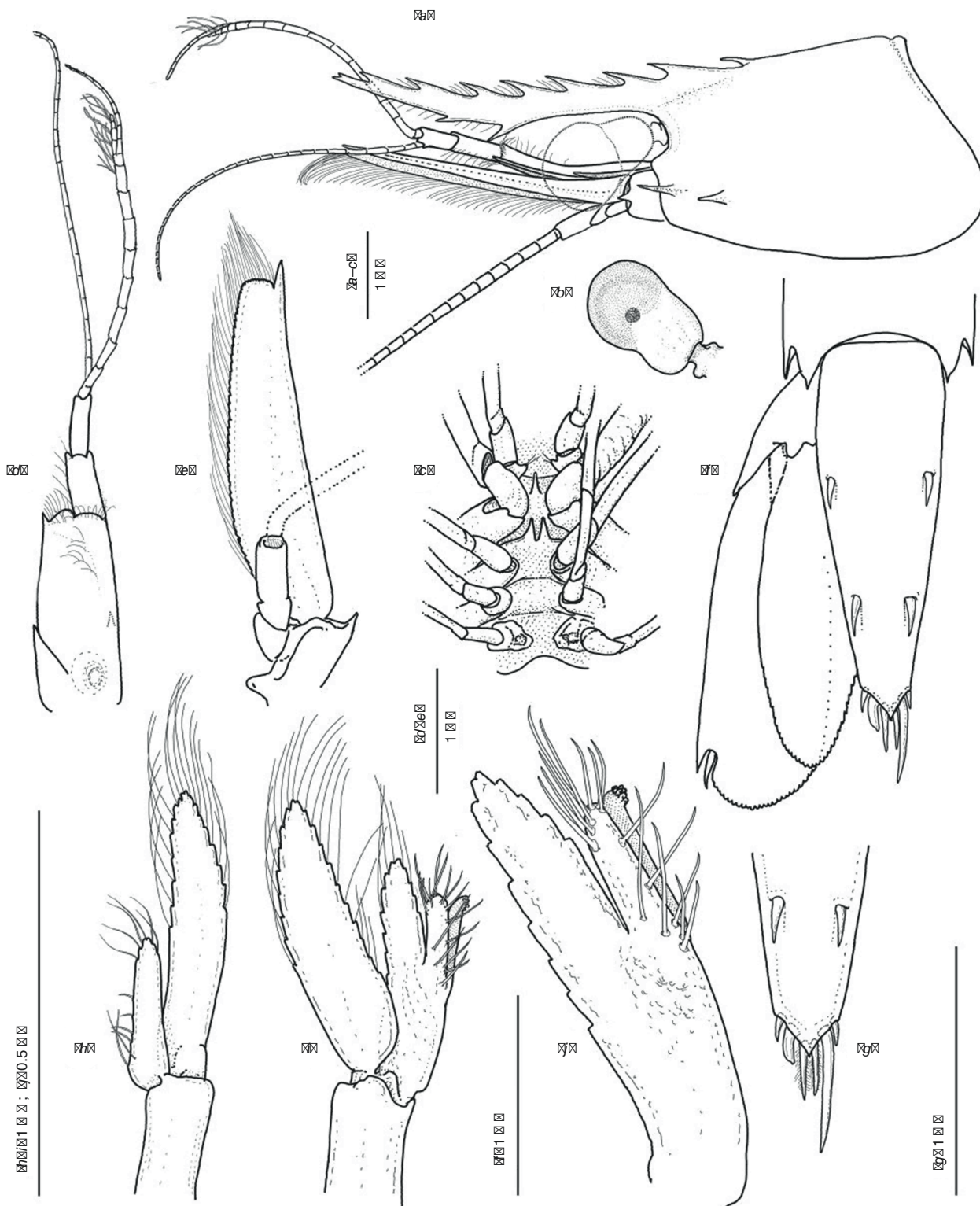


Fig. 8. *Palaemonella rhizophorae* (Lebour, 1949) comb. nov., male pochl 2.7 mm, MNMHN-IU-2016-7568, Martinique, 2016. (a) Carapace with antennae, lateral view (eye indicated). (b) Right eye, dorsal view. (c) Fourth to seventh thoracic sterna with proximal segments of pereiopods 1–5. (d) Left antennula, ventral view. (e) Left antenna, ventral view. (f) Sixth pleomere, telson and uropod, dorsal view. (g) Telson apex. (h) First male pleopod. (i) Second male pleopod, *appendices interna* and *masculina*. Image credit: Z. Ďuriš.

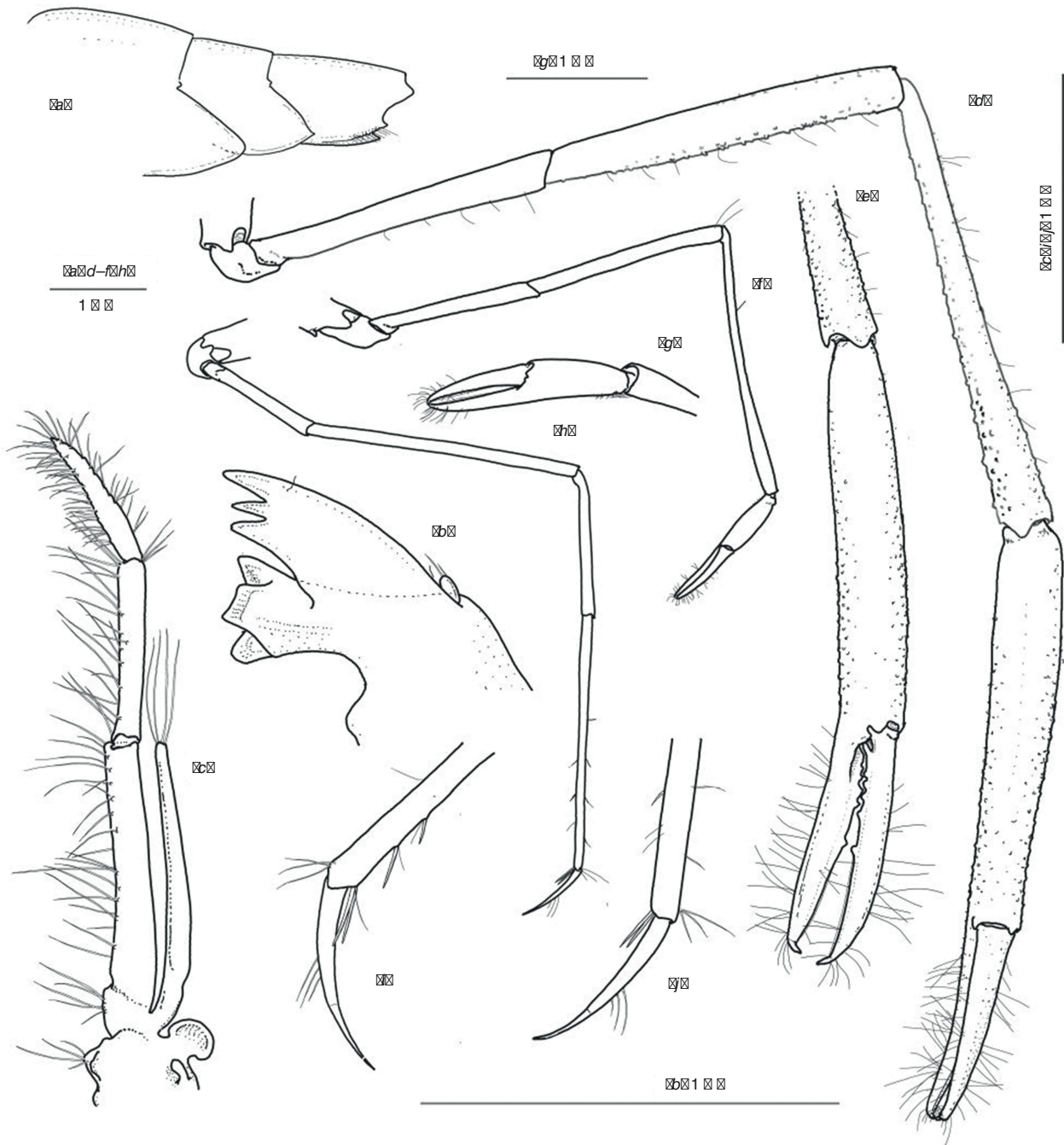


Fig. 9. *Palaemonella rhizophorae* (Lebour, 1949) comb. nov., male pochl 3.2 mm, MNHN-IU-2016-7369, Martinique, 2016. (a) Posterior pleomeres, left lateral view. (b) Mandible, lateral view. (c) Third maxilliped, lateral view. (d) Second pereiopod, lateral view. (e) Second pereiopod, chela, lateral view. (f) First pereiopod, lateral view. (g) First pereiopod, chela, medial view. (h) Third pereiopod, lateral view. (i) Third pereiopod, dactylus and distal propodus, medial view. (j) Third pereiopod, dactylus and distal propodus, lateral view. Image credit: Z. Ďuriš.

Material examined

Martinique, MADIBENTHOS Expedition: 1 male, pochl 2.3 mm, MNHN-IU-2016-1699, AS66, Pase du Marin, Pointe Borguesse, 14°26.9'N, 60°54'W, depth 15 m, 11 Sep. 2016. 1 female, pochl 1.7 mm, MNHN-IU-2016-1769, AD263, Macouba, on large, 14°55'N, 62°08.9'W, depth 76–80 m, 24 Sep. 2016. 22 spms (1 male, pochl 2.4, 9 males, 1.7–3.0 mm,

7 ovig. females), MNHN-IU-2016-1950, AB394, Baie de Fort-de-France, Monsigny, 14°34.3'N, 61°02.7'W, depth 7 m, 7 Oct. 2016. 1 male, pochl 2.2 mm (MNHN-IU-2016-7456), AD248, N. Caravelle Peninsula, 14°52.5'N, 60°51.1'W, depth 58 m, 19 Sep. 2016. 3 spms (2 males, pochl 2.7, 2.1 mm, 1 ovig. female, 2.3 mm), MNHN-IU-2016-7568, AB398, Baie de Fort-de-France, E. Grande Sèche, 14°34.6'N, 61°03.3'W, depth 6 m, 9 Oct. 2016. 3 males, pochl 1.6–2.0 mm, MNHN

MNHN-IU-2016-7584, AD264, Macouba, on large, 14°55'N, 62°08.8'W, depth 77 m, 25 Sep. 2016.

Diagnosis

Body slender. Carapace with rostrum longer than pocl, rostral dentition (1–2) + (4–7) ÷ (2–3), most frequently 2 + (5–6) ÷ 2, posteriormost dorsal tooth epigastric, supra-orbital tooth lacking, hepatic and antennal teeth present, 4th thoracic sternum with median finger-like process, fifth sternite with pair of acute submedian projections. Mandible with minute unisegmented palp. Third maxilliped with reduced unilamelled arthrobranch. Antennal scaphocerite with distolateral tooth overreaching distal margin of blade. Pereiopods long and slender. First pereiopods with carpus subequal to pocl and 2× as long as chela in adults. Second pereiopods with carpus distinctly longer than pocl or palm. Fifth pleomere with posteroventral angle pointed; telson with anterior pair of dorsal spines on approximately anterior third of segment length.

Remarks

Examining the early taxonomic history of the species, Holthuis (1951b, p. 66) noted:

In 1949 Lebour described a new species of *Periclimenes* from Bermuda under the name *Periclimenes (Ancylocaris) bermudensis*. In the same year Lebour (1949b) changed this name, which is preoccupied by the name *Periclimenes (Periclimenaeus) bermudensis* Armstrong, 1940, into *Periclimenes (Ancylocaris) rhizophorae*. Through Dr. Lebour's kindness I was able to examine the type specimen of her species, which now is preserved in the Laboratory of the Marine Biological Association at Plymouth, England. The specimen in my opinion is nothing else but a female of *Periclimenes americanus* (Kingsley) in which the rostrum has been damaged and is regenerated. Actual comparison with specimens of Kingsley's species did not bring forth differences between the two forms. The large cheliped indeed is very slender, but it wholly falls within the range of variation shown by this species (cf. Gurney's 1943, table with measurements of the various joints of the chelipeds of females of this species).

The affiliation of the current species to *Palaemonella* has not yet been suggested because the key diagnostic characters were not originally observed; Lebour (1949a, p. 1115), by describing the species, had directly indicated that 'the mandible is without palp', but no comment was provided on the thoracic sterna. Holthuis (1951b) also did not report on these but synonymised Lebour's (1949) species with *Periclimenes americanus*. Later, Chace (1972, p. 29) re-examined available western Atlantic *Periclimenes* species and observed the median process on the fourth thoracic sternite in *P. americanus*. Our closer examination of

available specimens of '*P. americanus*' revealed the presence of a very small unisegmented mandibular palp in some specimens with more slender pereiopods and the median spiniform process on the fourth thoracic sternite in these, and also confirmed the process in *P. americanus* (currently *Cuapetes americanus*). The current molecular analyses (Frolová *et al.* 2022; as '*Cuapetes americanus* B'; our study) have confirmed the independent status of the more slender specimens corresponding with the descriptions of *Periclimenes rhizophorae* by Lebour (1949a, 1949b) and separation from *C. americanus*. Our molecular analysis affiliated both taxa with the wider clade of *Palaemonella* species but showed these to be more closely related to the eastern Atlantic congener, *P. atlantica* and the eastern Pacific *P. holmesi*. In the both western Atlantic species, the evolutionary reduction of the mandibular palp was fully completed and the feature is currently completely lacking. Also, the arthrobranch, strongly reduced in *P. rhizophorae*, was not recorded in *P. americana* during our examinations.

Palaemonella rhizophorae therefore differs from *P. americana* in the presence of a small mandibular palp (v. missing in *P. americana*), distinctly more slender chelipeds with carpi longer than the chela on the first pereiopods and longer than the palm on the second chelipeds (v. shorter and stout), and distinctly more slender ambulatory legs.

Habitat and depth

Lebour (1949a, p. 1117) reported 'a lake without known access to the sea'. Chace (1972) reported the depth range and habitat from 0.3 to 9 m on mud or sand flats and coral [rubble?]; current specimens were collected from 6 to 77 m.

Distribution

Western Atlantic: previously reported only from the original locality, the Mangrove Lake, Bermuda. Currently also known from Martinique, the Caribbean Sea (new record from our study).

Palaemonella rotumana (Borradaile, 1898)

(Fig. 7c.)

Periclimenes rotumanus Borradaile, 1898, p. 383 [Rotuma]. – Borradaile (1899), p. 1005, pl. 63, fig. 5b.

Palaemonella vestigialis Kemp, 1922, p. 123, fig. 1–2, pl. 3 fig. 2. [Port Blair, Andamans.]

Material examined

Red Sea, Jordan: 1 male, UO.43B-Aq09, Aqaba, near Marine Science station, depth 2 m, washed from dead coral, 27 Jun. 2009, collected by Z. Ďuriš. **Madagascar:** 1 small, pocl 2.8 mm, MNHN-IU-2010-3946, ATIMO VATAE, TP24, south Madagascar: Port d'Ehoala, fine sand

with *Clypeaster* sea urchins, 25°03.7–03.8'S, 46°57.6–57.7'E, depth 2–7 m, 14–15 May 2010. **Taiwan:** 1 ovig. female, pocl 3.2 mm, NMMBCD6104, Longdon, Northeast core, NE Taiwan, 14 Nov. 2014, collected by C.-W. Lin (fcn 20141114-01). 1 male, NMMBCD6107, Hojie, Pingtung, SW Taiwan, depth 10–20 m, 9 Sep. 2017, collected by C.-W. Lin (fcn 20170909-30). **Vietnam:** 1 spm, UO.15D-Vn10, Diamond Bay, S. off Nhatrang, washed from dead corals, depth 1 m, 7 Aug. 2010; collected by Z. Ďuriš. **Great Barrier Reef, Australia:** 1 ovig. female, pocl 2.6 mm, 1 female, 2.8 mm, MTQ W 33178, 2010, CREEFS LIZARD ISLAND 2010, LI10-037, lagoon, 14°41.202'S, 145°27.307'E, depth 1.5 m, 30 Aug. 2010, collected by I. Marin, leg. Z. Ďuriš. **New Caledonia:** 4 ovig. females, pocl 1.9–2.8 mm, MNHN-IU-2018-473, KOUMAC 2.1, KR403, Ilôt Rat, platform with sand and coral rubble, 20°33.5'S, 164°10.9'E, depth 0 m, 5 Sep. 2018, collected by Z. Ďuriš and A. Šobánová.

Remarks

Common, mainly shallow water Indo-West Pacific palaemonid shrimp. Our specimens are congruent with described characters (Bruce 2002a). The specimens examined have the rostral dentition $RF = (1-2) + (5-6) \div (2-3)$ that matches Bruce's (2002a) data on 2 postorbital and 5–6 dorsal teeth on the rostrum. In our phylogenetic study, *P. rotumana* is sister to *P. disalvoi* (see Remarks for the latter).

Depth range

0.5–107 m (Müller 1993).

Habitat

Coral reefs; most specimens were found among corals in shallow water or flat reef pools; sometimes on muddy shores and pearl banks (Müller 1993).

Host

Though often found on corals, the species is considered to be free-living (Müller 1993).

Distribution

Indo-West Pacific: the species is common throughout the whole Indo-West Pacific area, from the Red Sea and eastern Africa to Hong Kong and Hawaii (Ďuriš 2017). Also known from the eastern Mediterranean as a Lessepsian migrant from the Red Sea (d'Udekem d'Acoz 1999).

Palaemonella rubrolineata Fransen, van der Veer & Frolová, 2022

(Fig. 7d.)

Palaemonella rubrolineata Fransen, van der Veer & Frolová, 2022a, p. 558, fig. 1–8. [Indonesia, Raja Ampat Islands, West Papua, SE Gam, Desa Besir, 00°27.802'S, 130°41.243'E, 2.xii.2007, depth 5 m, on *Pocillopora damicornis*.]

Material examined

See original report (Fransen *et al.* 2022a).

Remarks

This species is remarkable in the presence of numerous setae distoventrally on the ambulatory propodi, distinctive colouration and symbiotic habit. The setae and ectosymbiosis on corals engender high similarity to *P. orientalis*, a member of the former *Vir*-complex of species. *P. rubrolineata* differs from the latter complex and particularly *P. orientalis* in the presence of a minute hepatic tooth on the carapace. Genetically, *P. rubrolineata* also belongs to the *Vir* clade, confirming a closer phylogenetic relationship with *P. orientalis*. This illustrates the possible gradual evolutionary reduction of the hepatic tooth in the series, from well developed in most *Palaemonella* spp. to minute in *P. rubrolineata* to lacking in the previous 'Vir' species.

Depth range

5–15 m.

Habitat and hosts

Coral reef. Associated with corals of Scleractinia: Pocilloporidae: *Pocillopora damicornis* (Linnaeus) and *Seriatopora hystrix* Dana (see Fransen *et al.* 2022a).

Distribution

Indo-West Pacific: the species has been recorded from Ambon and Raja Ampat, Indonesia, and Santo, Vanuatu.

Palaemonella sandyi Fransen, van der Veer & Ďuriš, 2023

Vir euphyllius. – Marin and Savinkin (2007), fig. 95B; Marin (2007), fig. 1D, 3. [non *Vir euphyllius* Marin & Anker, 2005.]

Palaemonella sandyi Fransen, van der Veer & Ďuriš, 2023, p. 348, fig. 1–10, 13, 16E, 17A. [Indonesia, NE Kalimantan, Berau Islands, Kakaban Island, N-side, 02°09'47.1"N, 118°32'03.3"E, depth 15 m, on *Euphyllia glabrescens*.]

Material examined

See original report (Fransen *et al.* 2023).

Additional material

Taiwan: 1 male pocl 3.7 mm, NMMBCD4106, Soft Coral Area, South Bay, Pingtung, collected by C.-W. Lin (fcn 20100720-11). 1 male pocl 1.8 mm, NMMBCD5638, Green Island, collected by C.-W. Lin (fcn 20120401-104). 1 male pocl 2.2 mm, NMMBCD6111, Pingtung, South Bay, 8.5 m, from *Euphyllia glabrescens*, collected by Z. Ďuriš (fcn UO.53-Tw12).

Remarks

A new species of the 'Vir complex' within the genus *Palaemonella*, described in a separate study (Fransen et al. 2023). This species lacks the hepatic tooth on the carapace, similarly to the species of the previous *Vir*. Genetically, this clusters with most previous *Vir* species, except *V. orientalis* and *P. rubrolineata*.

Colour

The species is recognisable in live form by the densely red-dotted body, irregular white line inside and between eyestalks, and colourless statosysts (Fransen et al. 2023).

Host

Euphyllia cristata Chevalier, *E. glabrescens* [Cnidaria: Scleractinia: Euphylliidae].

Depth

2–30 m (Fransen et al. 2023).

Distribution

Maldives, Indonesia, Malaysia, Philippines (Fransen et al. 2023); Taiwan (current report).

Palaemonella shirakawai Okuno, 2017

Palaemonella shirakawai Okuno, 2017, p. 522, fig. 1–4. [Off Touma Beach, Zamami-jima Islet, Kerama Group, Ryukyu Islands, Japan, 26°13'51"N, 127°19'41.7"E, depth 16 m.]

Material examined

Not examined.

Remarks

Previously erroneously identified as or similar to *P. lata* (cf. Debelius 1999, p. 192) or *P. aliska* (cf. Kuitert and Debelius 2009, p. 101; Humann and DeLoach 2010, p. 130; Minemizu 2013, p. 42). These misidentifications and similarity of *P. shirakawai* to *P. aliska* are remarkable because both species were reported as cohabiting with burrowing animals, i.e. opistognathid fish or alpheid shrimp (Okuno 2017, and Marin 2008; Anker and De Grave 2019, resp.). Also see Remarks under *P. jamila*. *P. shirakawai* differs from the other suggested inquilinists in the unusually long, slender carpi of the second pereopods, eyestalk that is not swollen and the eye cornea subequal in diameter to the stalk (see Remarks for *P. aliska*).

Colour

Debelius (1999), p. 192, unnumbered photograph in centre of page (under name *P. lata*).

Depth

16 m.

Host and habitat

Inquilinist living in burrow with unidentified opistognathid fish.

Distribution

Indo-West Pacific: Ryukyu Islands, southern Japan (type locality); Philippines (Minemizu 2013), Thailand (Debelius 1999) and Indonesia (Kuitert and Debelius 2009).

Palaemonella smiti (Fransen & Holthuis, 2007), comb. nov.

(Fig. 7e.)

Vir smiti Fransen & Holthuis, 2007, p. 101, fig. 1–27, 32–34. [Philippines, Cebu Strait, W of Bohol, N side of Cabilao Island, NE of Looc, 9°53.59'N, 123°46.92'E, 15 m, on *Physogyra lichtensteini*.]

Vir longidactylus Marin, 2008, p. 383, fig. 6–8, 9c [non *Palaemonella longidactylus* Hayashi, 2009]. [South China Sea, Vietnam, Nhatrang Bay, Tré Island, Tré Bay, on *Physogyra lichtensteini*, 5 m.]

Material examined

Philippines: 1 ovig. female holotype, pocl 3.9 mm, RMNH.CRUS.D.48539, CEB.09, Cebu Strait, W. of Bohol, N. side of Cabilao Island, NE of Looc, 9°53.59'N, 123°46.92'E, overhanging wall with caves, scuba, depth 15 m, on *Physogyra lichtensteini*, 13 Nov. 1999, leg. C.H.J.M. Fransen. **Indonesia:** 1 ovig. female, pocl 2.8, RMNH.CRUS.D.49854, BAL.20, Bali, Tulamben beach, 'Coral Garden' off hotel area, 08°16'36"S, 115°35'37"E, shallow reef flat and slope, sandy slope, depth 20 m, 13 Apr. 2001, on *Physogyra lichtensteini*, leg. C.H.J.M. Fransen. 1 male pocl. 1.6 mm, RF = 1 + 7 ÷ 2, RMNH.CRUS.D.53076, stn RAJ.14, Raja Ampat Islands, West Papua, Akber Reef, 00°34.253'S, 130°39.561'E, 23 Nov. 2007, depth unknown, on *Physogyra lichtensteini*, leg. E. van der Veer. 1 ovig. female pocl. 2.2 mm, rostrum broken, RMNH.CRUS.D.53077, stn RAJ.15, Raja Ampat Islands, West Papua, SW Kri, Kuburan, 00°33.713'S, 130°39.673'E, 23 Nov. 2007, depth unknown, on *Physogyra lichtensteini*, leg. C.H.J.M. Fransen, CF059. 1 male pocl. 1.6 mm, RF = 1 + 7 ÷ 2, RMNH.CRUS.D.53078, stn RAJ.19, Raja Ampat Islands, West Papua, Maya's mimpí, 00°30.456'S, 130°39.919'E, 25 Nov. 2007, depth 16.2 m, on *Physogyra lichtensteini*, leg. E. van der Veer. 1 ovig. female pocl. 3.4 mm, RF = 2 + 5 ÷ 2, RMNH.CRUS.D.53079, stn RAJ.21, Raja Ampat Islands, West Papua, SE Manuar, Nikson new, 00°34.857'S, 130°38.527'E, 26 Nov. 2007, depth 18.5 m, on *Physogyra lichtensteini*, leg. C.H.J.M. Fransen, CF080. 1 ovig. female pocl 3.2 mm, RF = 1 + 6 ÷ 2, RMNH.CRUS.D.51742, stn BER.13, NE Kalimantan, Berau Islands, Sangalaki Island, reef, S-side, 02°04'46.9"N, 118°23'47.3"E; 8 Oct. 2003, depth 15 m, on *Physogyra lichtensteini*, leg. C.H.J.M. Fransen. 1 ovig.

female pochl 3.8 mm, RF = 2 + 5 ÷ 2, RMNH.CRUS.D.51743, stn BER.36, NE Kalimantan, Berau Islands, Kakaban Island, SE-side, 02°07'56.6"N 118°32'39.8"E, 21 Oct. 2003, depth 5 m, on *Physogyra lichtensteini*, leg. C.H.J.M. Fransen. **Taiwan:** 1 ovig. female pochl 3.3 mm, NMMBCD5619, Pingtung, Hojje, depth 10–20 m, 8 Jul. 2013, leg. C.-W. Lin (fcn 20130720-08). 1 spm, NMMBCD6101, Pingtung, Hojje, depth 10–20 m, 29 Jul. 2013, leg. C.-W. Lin (fcn 2013.07.29-nn). **Papua New Guinea:** 1 spm, MNHN-IU-2013-10769, PAPUA NIUGINI, PR69, Rempia Area, south of lagoon inside bay, 05°01.6'S, 145°48.1'E, depth 10 m, on *Physogyra lichtensteini*, 20 Nov. 2012, leg. Z. Đuriš (fcn UO.286-Png12). 2 spms, MNHN-IU-2013-10827, PAPUA NIUGINI, PR105, N. Tab I., 05°10'S, 145°50.4'E, depth 3–30 m, 26 Nov. 2012, collected by A. Berberian, lgt. Z. Đuriš (fcn UO.391-Png12). 1 spm, MNHN-IU-2013-10982, PAPUA NIUGINI, PR183, S. Sek I. S. Malamal Passage, 05 Dec. 2012, depth 17 m, collected by A. Berberian, lgt. Z. Đuriš (fcn UO.561-Png12). **Vietnam, *Vir longidactylus* Marin, 2008,** p. 1 ovig. female holotype, pochl 3.2 mm, 1 male allotype, pochl 2.1 mm, RMNH.CRUS.D.51919, South China Sea, Nhatrang Bay, Tré Island, Tré Bay, rocks, on caryophyllid [sic] coral *Physogyra lichtensteini*, depth 5 m, 3 Jul. 2006, collected by I.N. Marin.

Remarks

Our molecular comparison revealed the conspecificity of *Vir longidactylus* Marin, 2008 type specimens with the present species; the former name is therefore the junior synonym of *Vir smiti* Fransen & Holthuis, 2007, with the latter transferred to *Palaemonella* as *P. smiti* (Fransen & Holthuis, 2007) comb. nov.

Colour

Rather distinct from other species of the 'Vir complex' in having red antennal flagella, never purple; ambulatory pereopods have longitudinal red lines (indistinct or absent in juveniles); eyestalks with few small white chromatophores; statocysts purple, less distinct than in *P. colemani* or *P. euphyllius* (see Fransen and Holthuis 2007; Fransen *et al.* 2023; current report, Fig. 7e).

Depth range

4–20 m.

Host, habitat

Coral reefs; associated with the coral *Physogyra lichtensteini* [Scleractinia: Plerogyridae].

Distribution

Indo-West Pacific: Philippines (type locality); Vietnam (Marin 2008); Taiwan, Indonesia, Papua New Guinea (new records from our study).

Palaemonella spinulata Yokoya, 1936

Palaemonella spinulata Yokoya, 1936, p. 135, fig. 4. [Sagami Bay, off Misaki to Yokosuka, Miura Peninsula, 35°10.53'N, 139°34.56'E to

39°10.53'N, 139°34.53'E, depth 73–62 m; neotype designation by Hayashi, 2009.]

Material examined

Sagami Bay, Japan: 1 spm, CBM-ZC 9515, Sagami Bay, off Misaki to Yokosuka, Miura Peninsula, 35°10.53'N, 139°34.56'E–39°10.53'N, 139°34.53'E, depth 73–62 m, oyster beds, 8 Mar. 2002, gill net, FB *Aoki-maru No. 2*, collected by T. Komai. **New Caledonia:** 1 spm, MNHN-IU-2018-528A, KOUMAC 2.1, KM300, Infernet Reef, 20°36.3'S, 164°14.2'E, seagrass beds, corals and sandy bottoms on flats, depth 0 m, 6 Sep. 2018.

Remarks

Some previous records may belong to *P. maziwi* (see above). Our specimens identifiable as *P. spinulata* all have the rostrum dentition RF = 2 + (5–6) ÷ 2, postorbital ridge on the carapace distinct, dorsally with a slender acute supraorbital tooth, the second pereopod ischium distoventrally unarmed and moderately stout ambulatory dactyli as reported by Hayashi (2009). Instead of the supraorbital tooth, a minute acute tubercle may be present, as also shown by Hayashi (2009, fig. 1, 2a–c). In our molecular analysis, *P. spinulata* is basally separated from the subclade formed by *P. foresti*, *P. longidactylus* and *P. pottsii*.

Depth range

Subtidal, to 32 m.

Host, habitat

Free-living on coral reefs, among dead corals.

Distribution

Indo-West Pacific: Japan, near Misaki (type locality); Seychelles, Kenya, Tanzania, Réunion, eastern Australia (Müller 1993); China (Li *et al.* 2007).

Palaemonella tenuipes Dana, 1852

(Fig. 7f.)

Palaemonella tenuipes Dana, 1852, p. 25. [in mari Suluensi.]

Palaemonella tridentata Borradaile, 1899, p. 1007, pl. 64 fig. 8–8c. [Funafuti.]

Palaemonella elegans Borradaile, 1915, p. 210. [Salomon Island.]

Material examined

New Caledonia: 1 male, pochl 2.4 mm, MNHN-IU-2018-1286, KOUMAC 2.1, KR408, Grand Récif de Koumac, lagoon, sand and coral rubble, 20°34.2'S, 164°06.3'E, depth 6 m, 27 Sep. 2018. **SW Taiwan:** 1 ovig. female, pochl 3.6 mm, NMMBCD5615, Wanlitong, tidal pools, 09.03.2014, collected by C.-W. Lin (fcn 20140309-01).

Remarks

This species is easily recognisable, among the majority of congeners lacking the supraorbital tooth and with moderately slender ambulatory dactyli, by the distinctly subterminal distoventral tooth on the second pereopod and the merus with a conspicuous distoventral tooth. The rostrum dentition of the specimens examined, $RF = 1 + (4-5) \div 2$, slightly modifies the formula provided in the identification key by Bruce (2002a) to the form $RF = 1 + (4-7) \div 2$. *Palaemonella tenuipes* is morphologically similar to the crinoid associated *P. pottsi* but differs in the generally transparent body (v. intensely dark red colour) and characters mentioned above (see also Jose *et al.* 2021). In our molecular analysis, *P. tenuipes* diverges basally from a wider clade composed of *P. disalvoi*, *P. foresti*, *P. longidactylus*, *P. pottsi*, *P. rotumana* and *P. spinulata*.

Depth range

Intertidal, to 6 m.

Habitat

Sheltered coral reef locations, reef flat and pools, lagoon with sand and coral rubble. Found on *Millepora tenera* Boschma, *Acropora* spp., *Pocillopora damicornis* (L.) and *Seriatopora hystrix* but considered to be free-living (Müller 1993).

Distribution

Indo-West Pacific: Known from the Red Sea and Comoros to Japan, Palmyra Islands and Hawaii (Bruce and Svoboda 1983; Bruce 2008; Jose *et al.* 2021). Papua New Guinea, New Britain (new record from our study).

Palaemonella yalla Anker & Assayie, 2023

Palaemonella yalla Anker & Assayie, 2023, p. 428, fig. 1–3. [Saudi Arabia, Makkah Province, Thuwal, King Abdullah University of Science and Technology (KAUST), near King Abdullah Monument, 22°20'26.2"N, 39°05'15.1"E, shallow sandflat between small mangrove and deeper channel, some coral rubble and seagrass present, in burrow, suction (yabby) pump, depth 0.3–1 m.]

Material examined

Not examined.

Remarks

As indicated by Anker and Assayie (2023), this species shows a distinct similarity to *P. okunoi* from Japan, sharing, for example, the lack of a supraorbital tooth, presence of a hepatic spine, a short rostrum, the presence of a postorbital ridge and general colouration, but differing mainly in the

presence of a distoventral tooth on the second pereopod merus and the more slender ambulatory dactyli (see: Komai and Yamada 2015). Among the possibly closely related species, *P. foresti* Bruce, 2002, *P. hachijo* Okuno, 1999, *P. lata* Kemp, 1922, *P. pottsi* (Borradaile, 1915), *P. rotumana* (Borradaile, 1898) and *P. tenuipes* Dana, 1852 were mentioned. However, the closest similarity is to *Palaemonella* sp. reported by Bruce (2003b), which is morphologically almost identical, as indicated by Anker and Assayie (2023), differing only in the ventral rostral dentition and spinulation on the antepenultimate segment of the third maxilliped. Bruce's (1982, p. 241, fig. 4B) specimen also lacks the ventral spinulation on the ambulatory propodi proximally to a single distoventral spine, but the spinules and distoventral pair are present in *P. yalla*. Future molecular analysis of the latter species would clarify the relationship with currently valid congeners.

Depth range

0.3–1 m.

Habitat

Shallow near-shore sandflat with patchy seagrass and fragmented coral rubble, near mangrove stands; silty sandflat dominated by living, mostly massive corals, near large rocky outcrops; suggested dwelling inside a type of burrow excavated by a larger animal such as a pair of snapping shrimps or a ghost-shrimp (Anker and Assayie 2023).

Distribution

Known only from Saudi Arabian coast of the Red Sea near Thuwal (type locality) and Masirah Island, eastern Oman (Anker and Assayie 2023).

Discussion

The palaemonid shrimp genus *Palaemonella* Dana, 1852 (*type species*: *P. tenuipes* Dana, 1852) has been represented by 27 species (De Grave and Fransen 2011; Komai and Yamada 2015; Anker and Assayie 2023; Fransen *et al.* 2022a, 2023). *Palaemonella* belongs to a separate group of palaemonid genera with unresolved taxonomic status, the '*Palaemonella–Cuapetes* group', as named in Frolová *et al.* (2022 – see review of the group). The generic complex currently comprises almost 90 predominantly free-living species belonging to 11 genera from which the most species-rich have been *Cuapetes* (29 spp.) and *Palaemonella* (27 spp.). All genera of the complex share two diagnostic symplesiomorphic characters: (1) the finger-like median process on the fourth thoracic sternite, and (2) the simple ambulatory dactyli (Frolová *et al.* 2022). *Palaemonella* has been distinguished from most genera of

the group by having a mandibular palp, a hepatic tooth on the carapace and unarmed cutting edges on the first pereopod fingers (Chace and Bruce 1993; Bruce 1995, 2002a; Komai and Yamada 2015; Okuno 2017). The three valid genera, *Exoclimenella*, *Eupontonia* and *Vir* share the mandibular palp with *Palaemonella* but differ in the subspatulate first pereopod chelae with denticulate cutting edges and strongly unequal second pereopod chelae (*Exoclimenella*; see Āuriš and Bruce 1995) or in the lack of the hepatic tooth on the sides of the carapace (other two genera). The distinctions between *Eupontonia* and *Vir* were quite feeble as the characters highlighted by Bruce (1995, 2010b), for example, the postorbital rostral teeth, supraorbital ridges, submedian sternal teeth on the fifth thoracic somite (not the fourth, as given by Bruce 2010b, p. 413), or number of terminal exopodal setae on the maxillipeds, may be variably present in both genera. However, stout eyestalks with reduced corneas, the presence of spinulation posteriorly on the ambulatory propodi and dorsally on the telson, seemed to be more useful for formally distinguishing *Eupontonia* from *Vir* (Bruce 2010b, p. 413 – key).

Our multigene phylogenetic reconstruction has revealed the paraphyletic nature of the whole assemblage of *Palaemonella* species due to the inclusion of the six currently known species of the genus *Vir*, two analysed (of four known) species of *Eupontonia*, one western Atlantic species of *Cuapetes* (*C. americanus*) and another western Atlantic species, currently reinstated (*Periclimenes rhizophorae*). To rectify the taxonomy of *Palaemonella* concerning the resulting monophyletic state, all species mentioned (also including two non-analysed *Eupontonia* spp.) are incorporated into the genus *Palaemonella* in this study.

As indicated above, *Eupontonia* was distinguishable from *Palaemonella* virtually exclusively by the lack of the hepatic tooth. Among the four current species, *E. noctalbata* (type species) and *E. gracilipes* are regarded as free-living, an association with a scleractinian coral was reported for *E. oahu* (Bruce 2010) and inquilinism with burrowing worms was repeatedly observed in *P. nudirostris* (Bruce 2010; Marin 2014; Anker and De Grave 2019). Although the reduction of the hepatic tooth on the carapace and a shorter rostrum could be regarded as adaptive characters to symbioses, the former two species with unknown associations may also be predicted to be symbiotic. Nevertheless, as even the two symbiotic species, the only DNA-analysed representatives of the genus in this study, are not sister-related in our phylogenetic tree, these species indicate the overall polyphyletic state of *Eupontonia*. The loss of the hepatic tooth on the carapace could therefore result from multiple independent and different evolutionary processes that had led to the direct taxonomic affiliation of such ‘aberrant’ *Palaemonella* species as members of a separate genus, *Eupontonia*. All four species are highly similar to *Palaemonella* and therefore evidently evolved from *Palaemonella* ancestors. Future molecular comparison of

E. noctalbata and *E. gracilipes* will clarify the taxonomic status but we provisionally transferred these species to *Palaemonella* following the state of the two analysed congeners.

The current genus ‘*Vir*’ was analysed within our phylogenetic studies with the full set of six currently known coral-associated species, i.e. *V. colemani*, *V. euphyllius*, *V. longidactylus*, *V. orientalis*, *V. philippinensis* and *V. smiti*. However, our phylogenies (Fig. 1, 2) have revealed seven genetic lineages with different species compositions comprising six respective to the previous *Vir* (excluding *V. longidactylus* – synonym of *P. smiti* but including one recently described species *P. sandyi*; Fransen et al. 2023). The seventh lineage, positioned inside the *Vir* clade, comprises a species recently directly affiliated with *Palaemonella* (*P. rubrolineata*; Fransen et al. 2022a) due to the presence of a small hepatic tooth on the carapace (Fransen et al. 2022a). The lack of the hepatic tooth was regarded as an important diagnostic character of the genus *Vir* (see Holthuis 1952; Bruce 1995). *Palaemonella rubrolineata* (with a small tooth), nested among traditional *Vir* species, illustrates the evolutionary loss of the hepatic tooth within a partial group of related species and therefore serves as additional proof of the true affiliation of all *Vir* species with *Palaemonella*. Similarly, the hepatic tooth was lost in the *Palaemonella* species previously affiliated with the genus *Eupontonia* (above).

A similar case of evolutionary loss of an important diagnostic character is observed in another group of species composed of non-IWP representatives. The presence or absence of the mandibular palp is often the only practical tool to distinguish species of *Palaemonella* from *Cuapetes*. The eastern Pacific (EP) *P. asymmetrica* and *P. holmesi* bear a reduced, unisegmented palp, whereas most of the IWP congeners have a small two-segmented palp. The only current Atlantic representative of the genus, *P. atlantica*, also has a similar small unisegmented palp. Based on the study by Frolová et al. (2022) and our analysis, two more species, most closely related to the two EP congeners, occur in the tropical western Atlantic (WA), both as a pair of the sister genetic lineages of specimens identifiable as *Cuapetes americanus* (lineages *C. americanus* A and B – see Frolová et al. 2022). One of these, more stoutly built, completely lacks the palp (relative to *C. americanus*), whereas the other has a minute unisegmented palp, and slender elongated chelipeds and ambulatory legs (i.e. relative to the former *Periclimenes rhizophorae*, later synonymised with *C. americanus*; see Holthuis 1951b and Okuno 2009). Both species are therefore valid, genetically distinct and also belong to *Palaemonella*. The former, *P. americana* comb. nov., had developed from IWP and subsequently EP *Palaemonella* ancestors (as indicated by Frolová et al. 2022) but lost the palp and was therefore formally correctly described as a member of *Periclimenes* (later transferred to *Kemponia* Bruce, 2004 and subsequently to *Cuapetes* Clark, 1919; Lebour 1949a, 1949b; Holthuis 1951b; Bruce 2004; Okuno 2009). Together with *P. atlantica* and *P. rhizophorae* comb.

nov., these show a full, or almost full, evolutionary reduction of the mandibular palp and likely a paleohistorical dispersal from the Pacific into the Atlantic Oceans (Frolová et al. 2022).

Except for *Palaemonella sandyi* and *P. rubrolineata*, the remaining five genetic lineages of the ‘Vir’ group of species are however not in line with current taxonomy in which six species are recognised. Our results (Fig. 2) revealed the type specimen of *Vir longidactylus* Marin, 2008 being nested among specimens of *Vir smiti* Fransen & Holthuis, 2007, also comprising one paratype (RMNH.CRUS.D.49854). Both species, *Vir smiti* and *V. longidactylus*, were described recently with *Vir smiti* being described earlier (Fransen and Holthuis 2007; Marin 2008). *Vir longidactylus* differed formally from the latter in the full lack of the distoventral spinules on the ambulatory propodi. During the recent re-examination of the holotype and allotype of *V. longidactylus* by one of the authors (Z. Đuriš) in NBC, Leiden, very minute distoventral spinules on the ambulatory propodi were recognised among long setae under high magnification by the transmitting microscope. ‘Two very small blunt ventrodistal spines’ on the ambulatory propodi were described by Fransen and Holthuis (2007, p. 112) for *V. smiti*. *Vir longidactylus* is therefore stated as the primary junior synonym of *V. smiti*. This act prevents the appearance of the secondary homonym of *Palaemonella longidactylus* Hayashi, 2009 because of the transfer of *Vir longidactylus* to *Palaemonella*.

Remaining species of the traditional ‘Vir’ include the following: *V. colemani*, *V. euphyllius*, *V. orientalis* and *V. philippinensis* (see Dana 1852; Bruce and Svoboda 1984; Bruce 2003a; Marin and Anker 2005; Marin 2007). Although *V. orientalis* is distinguishable by a distinct brush of long distoventral setae on the ambulatory propodi, the other three species together with *V. smiti* seemed, to the present, to be distinguishable by the colour pattern and coral hosts (Fransen and Holthuis 2007; Marin 2008). In our phylogenetic tree of the *Vir*-species complex, shrimps of the typical ‘*philippinensis*’ colouration (longitudinal purple lines in pereopods – e.g. Debelius 1999, p. 191; our Fig. 6e) and ‘*colemani*’ colouration (purple rings or spots on pereopod articulations – photographs, e.g. Minemizu 2013, p. 63; our Fig. 6f) are nested in the same genetic clade; in addition, specimens with the colouration of both ‘species’ combined (purple lines and rings) had already been photographed (e.g. Ryanskiy 2010, p. 13, unnumbered right bottom photograph; Fransen et al. 2023, fig. 19D), thereby illustrating that these are all representatives of *V. philippinensis*.

However, the analysed paratype of ‘*V. philippinensis*’ (RMNH.CRUS.D.35559) is nested in one lineage of the wider genetic clade of specimens distinguishable (also by the host) as *V. euphyllius*. This paratype is therefore not *P. philippinensis*, also having not been collected from *Plerogyra* but *Fungia* or an unidentified solitary coral (see Bruce and Svoboda 1984, p. 93). The features and relative length of the rostrum compared to the carapace in Bruce and

Svoboda (1984, fig. 4D) are within the range of *P. colemani/euphyllius* and outside the range of *P. philippinensis*, *P. smiti* and *P. sandyi* (see Fransen et al. 2023).

The second lineage of specimens identifiable as *V. euphyllius* however also contains the analysed holotype of *V. colemani*. This clade is therefore affiliated with *V. colemani* as the earlier described taxon. The host affiliation is not useful as specimens of both lineages are associated with *Fimbriaphyllia* corals. We therefore provisionally leave the name ‘*euphyllius*’ after the former clade, whereas the second clade is currently rectified as *P. colemani*. According to the four-marker analysis (Fig. 1), we retain the two taxa until more information becomes available regarding the placement of sequences of the type of *P. euphyllius*.

The cause of the ‘taxonomic puzzle’ of the previous *Vir* taxa has been raised mainly because of the close morphological similarity of the latter four species, and in accidentally misplaced specimens and live photographs of the types of *V. philippinensis* and *V. colemani*. Nevertheless, these species may differ in colouration and host affiliations to a broader extent. Marin and Anker (2005, p. 127) stated:

We have serious doubts that Bruce and Svoboda’s (1984) material from *Fungia* identified as *V. philippinensis* actually refers to this species. For instance, the *V. philippinensis* female paratype differs in several important features from the holotype and allotype, including the much lower number of dorsal teeth on the rostrum (5 v. 8 in the holotype), the telson with much broader posterior margin and also bearing more spines, and the better developed distal segment of the mandibular palp (Bruce and Svoboda 1984, fig. 4). These differences appear to be beyond the normal intraspecific variation, and in our opinion the paratypes of *V. philippinensis* associated with *Fungia* probably belong to another, possibly undescribed, species. Similarly, the material from *Euphyllia* (Bruce 1994 [sic, Bruce 1995]) could refer to *V. euphyllius*, sp. n., *V. pareuphyllius*, sp. n., or yet another species.

Indeed, in our 16S analysis (Fig. 2), the RMNH.CRUS.D.35559 paratype of *V. philippinensis* clusters with specimens identifiable (and *Fimbriaphyllia* coral-associated) as *P. euphyllius* or *P. colemani*.

Nevertheless, although the morphological identification of museum or dead colourless individuals remains difficult because of very subtle differences and overlapping variabilities, most previous *Vir* species seem to be easily recognisable by live colouration (Fransen and Holthuis 2007). The confusion with the types, colour photograph and coral hosts in Bruce (2003a) led to erroneous field identifications at least among *V. colemani*, *V. euphyllius* and *V. philippinensis*. The colouration of these species of *Palaemonella* to the current extent is partially rectified in colour photographs in our study (also see Fransen et al. 2023). The only unresolved question in this species group remains in the

true phylogenetic position of *Vir euphyllius* because of the lack of gene sequences from the types.

Our synonymising of a series of taxa, i.e. *Cuapetes americanus*, reinstated *Periclimenes rhizophorae*, and the genera *Eupontonia* (4 spp.) and *Vir* (5 spp.) have added 11 further species to *Palaemonella*. We report that 33 of the 38 valid species occur in the Indo-West Pacific (IWP) region (e.g. Bruce 1970, 1975, 2002a, 2002b, 2008, 2010a, 2010b; Hayashi 2001, 2009; Li and Bruce 2006; Marin 2008; Komai and Yamada 2015; Okuno 2017), two in the eastern Pacific (Holthuis 1951b) and three in the Atlantic (Holthuis 1951a, 1951b; our study). In addition, at least three further unnamed IWP species have been recognised (e.g. Bruce 2003b, 2010; Li *et al.* 2008; Minemizu 2013), thereby indicating undescribed diversity of species of *Palaemonella*.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data used to generate the results in this paper, i.e. the gene sequences, are available at GenBank.

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