

DESCRIPTION OF TWO NEW SPECIES OF INDO-PACIFIC *THYLACOPLETHUS* AND A NEW RECORD OF *THOMPSONIA JAPONICA* (RHIZOCEPHALA: AKENTROGONIDA: THOMPSONIIDAE) FROM HERMIT, PORCELAIN, AND MUD CRABS (DECAPODA) BASED ON MORPHOLOGICAL AND MOLECULAR DATA

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A B S T R A C T

Rhizocephalans of the order Akentrogonida are parasitic barnacles that infest decapods, stomatopods, peracarids, and other cirripedes. Within this order, Thompsoniidae is found in decapods and stomatopods, and is a family comprised of species characterized by having multiple globular reproductive bodies (externae) erupting from the host's extremities and abdominal surface, and connected internally by a root-like system. Two of the four genera currently accepted within Thompsoniidae, *Thompsonia* and *Thylacoplethus*, contain perhaps the most morphologically derived species within Akentrogonida. Herein we describe two new species of *Thylacoplethus*, *T. porcellanus* and *T. umanguvatus*, from the porcellanid and hermit crabs *Petrolisthes scabriculus* (Dana, 1852) and *Calcinus morgani* Rahayu and Forest, 1999, respectively. We also redescribe *Thompsonia japonica* Häfele, 1911 from a xanthid brachyuran crab based on morphological characters and DNA sequences of the nuclear 18S rDNA gene. The new species from the porcellanid crab comprises the first record of an akentrogonid rhizocephalan parasitizing a species of Porcellanidae. We reconstruct a molecular phylogeny of Akentrogonida using new and published DNA sequences, and we discuss our findings within an evolutionary context of host speciation. All species in the four thompsoniid genera are briefly reviewed, and a replacement name is proposed for the preoccupied *Pottsia* Høeg and Lützen, 1993.

KEY WORDS: Anomura, Brachyura, Cirripedia, Porcellanidae, *Pottsia*, Rhizocephala

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INTRODUCTION

Rhizocephala (Thecostraca: Cirripedia) is a group of parasitic barnacles containing more than 260 species highly specialized to infest mostly decapod crustaceans (Caridea, Brachyura, and Anomura) but also peracarids (Isopoda), stomatopods, and other barnacles (Høeg, 1995; Walker, 2001; Boyko and Williams, 2009; Pérez-Losada et al., 2009; Glenner et al., 2010). These parasites are interesting from an evolutionary perspective, as their extreme adaptation to parasitic life has resulted in the adults losing almost all morphological characters normally found in Crustacea. In fact, their affinities with other cirripedes were discovered through study of their larval stages (Thompson, 1836; Delage, 1884; Martin et al., 2014).

Rhizocephala is divided into two orders, Kentrogonida (three families) and Akentrogonida (six families), based on the presence or absence in the reproductive cycle of a post-settlement stage (kentrogon) responsible for infestation of the host (Høeg, 1995; Walker, 2001; Glenner et al., 2010; Yoshida et al., 2011). Glenner et al. (2010) provided molecular evidence that akentrogonids exhibit a derived

loss of the kentrogonid stage because this group is nested within a paraphyletic Kentrogonida. Kentrogonids are only known from decapod hosts whereas akentrogonids have a wider diversity of hosts, and exhibit variation in aspects of their life history (Glenner et al., 2010). Coloniality has evolved independently in both orders of rhizocephalans, e.g., Kentrogonida: *Peltogasterella* spp.; Akentrogonida: *Thompsonia* spp. (Høeg and Lützen, 1995; McDermott et al., 2010).

Rhizocephalans have a direct life cycle (only one host) and produce larvae of separate sexes (genetically or environmentally determined) (Yamaguchi et al., 2014). Female cyprid larvae attach to an unsclerotized cuticular surface of the host, and inject an infective stage that forms a nutrient-absorbing system of rootlets called the interna. After a period of development, the female adult-stage forms an external reproductive body called the externa. Male cyprids are attracted to the virgin female externa on the infested host, and fertilize it through invasion of the mantle aperture by a trichogon (kentrogonids), or via implantation of male material through the cyprid antennule (akentrogonids) (Høeg, 1995; Walker, 2001). Rhizocephalans eventually come to

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control aspects of their host's biology (e.g., physiology and behavior) and can modify their morphology (feminization) (Ritchie and Høeg, 1981; Høeg, 1995). Host specificity seems to vary considerably (see review in Boyko and Williams, 2009), with some species, e.g., *Sacculina carcini* Thompson, 1836, being known from multiple host species (Thresher et al., 2000).

Species of akentrogonid barnacles within Thompsoniidae belonging to *Diplothylacus* Høeg and Lützen, 1993, *Pottsia* Høeg and Lützen, 1993, *Thompsonia* Kossmann, 1872, and *Thylacoplethus* Coutière, 1902, are characterized by globular externae erupting colonially on the body surfaces of decapods (Fig. 1) such as shrimp (Caridea), true crabs (Brachyura), hermit crabs, and squat lobsters (Anomura: Paguroidea, Chirostyloidea, and Galatheoidea), as well as more distantly related mantis shrimps (Stomatopoda) (Høeg and Lützen, 1993; Walker, 2001; Boyko and Williams, 2009). *Diplothylacus* and *Pottsia* contain two species each,

Thompsonia contains five species, while *Thylacoplethus* includes 11 species (Boxshall and Boyko, 2014) plus two new species described herein (see Table 3 below).

Note that *Pottsia* Høeg and Lützen is a homonym of *Pottsia* Chatton and Lwoff, 1927, and is here replaced by *Jensia* Boyko and Williams, nom. nov. in the Appendix; *Jensia* is used as the correct name for the genus in the remainder of this paper. Thompsoniid species are among the most derived of akentrogonids (Glenner and Hebsgaard, 2006; Pérez-Losada et al., 2009; this study); they are most noteworthy for a remarkable simplification of morphology and loss of characters.

Examination of porcellanids recently collected in Australia revealed that a male *Petrolisthes scabriculus* (Dana, 1852) was parasitized by a thompsoniid rhizocephalan (Fig. 1B). Although several species of kentrogonids in Lernaediscidae Müller, 1862, have been described from porcelain crab hosts (Boyko and Harvey, 2000), this is the first

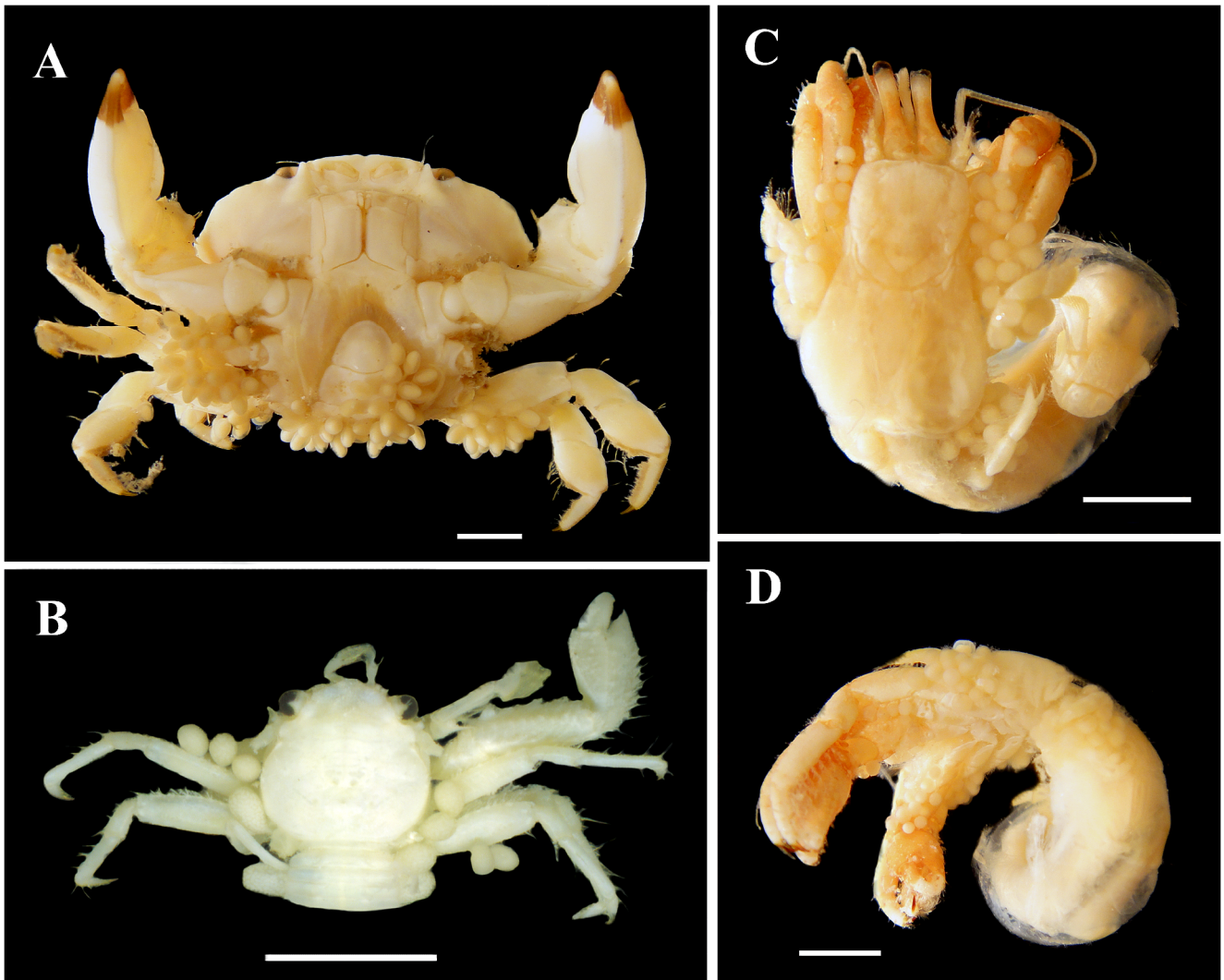


Fig. 1. Rhizocephalans and their hosts. A, *Thompsonia japonica* (USNM1268865) gross view of externae *in situ* on host, *Lophozozymus dodone* (ventral view of host); B, *Thylacoplethus porcellanus* n. sp. (holotype, UF34625) gross view of externae *in situ* on host, *Petrolisthes scabriculus* (dorsal view of host); C, D, *Thylacoplethus umanguvatus* n. sp. (paratype, USNM1268854) (C, D), C, gross view of externae *in situ* on host, *Calcinus morgani* (dorsal view of host), D, gross view of externae *in situ* on host, *Calcinus morgani* (lateral view of host). Scale bars = 3 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

record of any akentrogonid parasitizing a porcellanid crab. In order to determine whether this parasite belongs to *Thylacoplethus* or *Thompsonia* we did the following: 1) characterized the morphology of the externae and compared it to that of other species in these genera; and 2) obtained a DNA sequence of a fragment of the nuclear 18S rDNA gene, compared it to other sequences available in GenBank, and reconstructed the phylogeny of Akentrogonida, which was shown by Glenner et al. (2010) to be monophyletic. In order to have a reference value of 18S rDNA sequence divergence between crustacean sister taxa sharing a relatively recent common ancestor, we estimated the 18S rDNA distance between Caribbean and Pacific individuals of the amphio-American porcellanid *Petrolisthes armatus* (Gibbes, 1850), and of the geminate pair *P. glasselli* Haig, 1957 (eastern Pacific) and *P. rosariensis* Werding, 1982 (western Atlantic). Populations of *P. armatus* on both American coasts were probably separated 2.8 million years ago when emergence of the Central American Isthmus was completed (Lessios, 2008). The geminate pair seems to have diverged before the isthmus closed completely (Hiller et al., 2006).

Morphological and molecular information indicates that the species infesting *P. scabriculus* is a new species of *Thylacoplethus*. We describe this new species and discuss its origin within a phylogenetic context of host speciation. Additionally, we report on the morphology and 18S rDNA sequence of akentrogonids from a xanthid crab collected in Bali, Indonesia, which are morphologically indistinguishable from both *Thompsonia littoralis* Lützen and Jespersen, 1990 and *Thompsonia japonica* Häfele, 1911, and discuss the problems in assigning them to species. Finally, we report on a new species of *Thylacoplethus* from hermit crabs of the genus *Calcinus* Dana, 1851, from Bali, Indonesia, from which we were unable to obtain DNA sequences, but which is morphologically distinct from all other species in the genus.

MATERIALS AND METHODS

Akentrogonid externae were taken from the dorsal and ventral surfaces of the walking legs and inner surface of the pleon of a *P. scabriculus*, the pereopods of a *Lophozozymus dodone* (Herbst, 1801), and the pereopods of 11 *Calcinus morgani* Rahayu and Forest, 1999. Externae were morphologically characterized, and some were used for molecular analyses. None of the host specimens were collected with the original intent of studying the rhizocephalans, and therefore, none were fixed in a manner conducive to histological examination. Host names have been updated using WoRMS (World Register of Marine Species) to reflect current classifications. Taxonomic authorities and dates for hosts and parasites are provided in Tables 1 and 3.

Specimens were borrowed from or are deposited in the following institutions: the Florida Museum of Natural History (UF), Gainesville, FL, USA; the Smithsonian National Museum of Natural History (USNM), Department of Invertebrate Zoology (Museum Support Center), Suitland, MD, USA; and the Justus-Liebig University (JLU), Department of Animal Ecology and Systematics, Giessen, Germany. As these akentrogonids are colonial organisms, we have designated all externae from each type host specimen as representing a single holotype. Size of host is given as carapace length (CL) × width (CW) for xanthid and porcellanid hosts, or shield length (SL) for hermit crab hosts. All means are reported with ±standard deviation.

Morphological Analysis

Externae of all three species were examined using light and scanning electron microscopy (SEM). Line drawings of externae were made with an

Olympus SZX dissecting microscope with a drawing tube attachment. Original drawings were scanned and traced in Adobe Illustrator. Measurements of externae were made from digital images with Image J. Externae were prepared for SEM by dehydrating in an ascending ethanol series (70% to 95% EtOH), followed by four changes of 100% EtOH. Specimens were critical point dried (Samdri 795 Critical Point Dryer), mounted on aluminum stubs, coated with gold (EMS-550 sputter coater), and viewed with an FEI Quanta 250 SEM.

Molecular Analysis

DNA Extraction, Amplification and Sequencing.—DNA was isolated from externae taken from the three host species, from two specimens of *P. armatus*, and one specimen each of *P. glasselli* and *P. rosariensis* (see Table 1), using the QIAGEN DNeasy® Blood & Tissue Kit following the animal tissue protocol.

An approximately 470-bp fragment of the nuclear 18S rDNA gene was amplified through PCR (polymerase chain reaction; Saiki et al., 1988) using the primers 18SRhizoF2 (5'-GCCAGTAATGATATGCTTGTC-3') and 18SRhizoR3 (5'-CTGCTGCCTTCCTTAGATG-3').

At this point we want to report that we started testing PCR amplifications using different combinations of the primers used by Pérez-Losada et al. (2009) to obtain approximately 2000-bp sequences of different Thecostraca. Failure to obtain PCR products using these primers, probably due to degraded DNA, prompted us to design a series of new, specific primers to amplify fragments between 400 bp and 700 bp using the software Primer Premier 6.12 (PREMIER Biosoft). PCR amplifications (25 µl total volume) were performed using the Platinum® Taq DNA Polymerase Kit (Life Technologies) and 8 mM dNTPs (Promega) following the manufacturer's protocol, using an annealing temperature of 50°C, and 1.3 µl of DNA. PCR products were purified by running them in a 2% TAE electrophoresis, excising the desired band, and incubating it with 1.5 µl GELase™ (Epicentre) at 70°C for 25 min and at 45°C for 3 h. Cycle sequencing reactions were performed in both sequencing directions using the BigDye Terminator Kit (Applied Biosystems) following the manufacturer's protocol, then cleaned using Illustra™ Sephadex® G-50 (GE Healthcare Life Sciences) and the MultiScreen® Assay System 96-well filtration plate (EMD Millipore), and finally electrophoresed in an ABI-PRISM 3130xl Genetic Analyzer (Applied Biosystems).

Sequence Alignment and Phylogenetic Analysis

The BioEdit Sequence Alignment Editor (Hall, 1999) was used for sequence edition. Alignment of sequences obtained in this study, and of those retrieved from GenBank (Table 1) was performed using MAFFT v7.149b (Katoh and Standley, 2013). The Akaike Information Criterion (AIC; Akaike, 1974), implemented in the program jModeltest2 (Guindon and Gascuel, 2003; Darriba et al., 2012), was used to select the model of nucleotide substitution that best fits the data. The model selected was GTR + I + G, with I = 0.297 and G = 0.464. The estimated parameter values were incorporated as priors into a Bayesian analysis performed with MrBayes v3.2.2. (Ronquist et al., 2012). Chains were run for the generations needed for the two parallel runs to converge into stationary distribution (value of the standard deviation of split frequencies < 0.01). The number of samples was set to 10% of the number of generations. Burnin was set to 25% of the samples. Kimura 2-parameter distances (K2P; Kimura, 1980) were estimated between all possible pairs of sequences using MEGA v.6.06 (Tamura et al., 2013) setting the Gamma parameter (alpha) according to the jModeltest2 results.

Table 1 lists the GenBank accession-number codes of the sequences used in the present molecular analyses.

RESULTS

The alignment of 10 partial sequences of the 18S rDNA gene from akentrogonid Rhizocephala, including the new *Petrolisthes* parasite and the xanthid parasite, and from one kentrogonid, *Polyascus polygenea* (Lützen and Takahashi, 1997) used as out-group, was 486 bp long. Sequences from the specimens parasitizing *Calcinus* failed to amplify and were not included in the analysis. The phylogenetic reconstruction obtained through Bayesian inference is shown in Fig. 2. All sequences representing mem-

Table 1. List of akentrogonid rhizocephalans included in the molecular analysis, their host species, sampling localities, museum catalog numbers and GenBank (GB) accession numbers of partial 18S rDNA sequences with respective references. A kentrogonid (*Polyascus polygena*) was used as an outgroup to root the 18S rDNA molecular tree. Two *Petrolisthes armatus* from the Atlantic and Pacific coasts of Panama, and one specimen each of *P. glasselli* (East Pacific) and *P. rosartiensis* (West Atlantic) were sequenced for this gene to estimate sequence divergence in transisthmian and geminate species (see text). UF, Florida Museum of Natural History, Gainesville, FL, USA; USNM, Smithsonian National Museum of Natural History (Museum Support Center), Suitland, MD, USA; JLU, Justus-Liebig University Giessen, Giessen, Germany; N/A, not applicable.

Species	Host	Collection locality	GB accession number with reference/museum catalog number
<i>Thylacoplethus porcellanus</i> n. sp.	<i>Petrolisthes scabriculus</i> (Dana, 1852) (Porcellanidae)	Heron Island, QLD, Australia	KP739771 (this study)/UF34625
<i>Thylacoplethus magellani</i> Høeg and Lützen, 1993	<i>Pagurus forceps</i> H. Milne Edwards, 1836 (Paguridae)	Beagle Island, Argentina	FJ751889 (Pérez-Losada et al., 2009)
<i>Thompsonia japonica</i> Häfele, 1911 (this study)	<i>Lophozozymus dodone</i> (Herbst, 1801) (Xanthidae)	Sanur, Bali, Indonesia	KP739770 (this study)/USNM1268865, 1268866
<i>Thompsonia littoralis</i> Lützen and Jespersen, 1990	<i>Leptodius exaratus</i> (H. Milne Edwards, 1834) (Xanthidae)	Labrador Park Beach, Singapore	DQ826573 (Glenner and Hebsgaard, 2006)
<i>Pottisia serenei</i> Lützen and Du, 1999	<i>Squilla</i> sp. (Squillidae)	Vietnam	DQ826567 (Glenner and Hebsgaard, 2006)
<i>Diplothylacus sinensis</i> (Keppen, 1877)	<i>Portunus pelagicus</i> (Linnaeus, 1758) (Portunidae)	Singapore	DQ826568 (Glenner and Hebsgaard, 2006)
<i>Polyasaccus japonicus</i> Høeg and Lützen, 1993	<i>Nihonotrypaea japonica</i> (Ortmann, 1891) (Callinassidae)	Tomioka, Japan	DQ826565 (Glenner and Hebsgaard, 2006)
<i>Clistosaccus paguri</i> Lilljeborg, 1861	Hermit crabs (Paguridae)	Kristineberg, Sweden	GU190697 (Glenner et al., 2010)
<i>Sylon hippolytes</i> M. Sars, 1870	<i>Pandalus</i> sp. (Pandalidae)	Vancouver Island, Canada	DQ826564 (Glenner and Hebsgaard, 2006)
<i>Boschmaella japonica</i> Deichmann and Høeg, 1990	<i>Chthamalus challengeri</i> Hoek, 1883 (Chthamalidae)	Jogashima, Kanagawa Prefecture, Japan	AY265369 (Glenner et al., 2003)
<i>Polyascus polygena</i> (Lützen and Takahashi, 1997)	<i>Hemigrapsus sanguineus</i> (De Haan, 1835) (Varunidae)	Kyushu, Japan	AY265362 (Glenner et al., 2003)
<i>Petrolisthes armatus</i> (Gibbes, 1850)	N/A	María Chiquita, Panama, Caribbean	KP739767 (this study)/JLU1001
<i>Petrolisthes glasselli</i> Haig, 1957	N/A	Isla Naos, Panama, East Pacific	KP739766 (this study)/JLU1002
<i>Petrolisthes rosartiensis</i> Werding, 1978	N/A	Islas Secas, Panama, East Pacific	KP739768 (this study)/JLU1003
		Bocas del Toro, Panama, Caribbean	KP739769 (this study)/JLU1004

Table 2. Percent genetic distances estimated between all pairs of rhizocephalan 18S rDNA sequences using the Kimura two-parameter (K2P) model.

Species	1	2	3	4	5	6	7	8	9	10
1. <i>Thylacoplethus porcellanus</i> n. sp.	—									
2. <i>Thylacoplethus magellani</i>	7.7	—								
3. <i>Thompsonia japonica</i>	21.0	18.3	—							
4. <i>Thompsonia littoralis</i>	17.3	14.4	12.1	—						
5. <i>Jensia serenei</i>	25.2	25.2	24.2	22.6	—					
6. <i>Diplothylacus sinensis</i>	43.3	38.0	33.8	38.5	42.4	—				
7. <i>Boschmaella japonica</i>	40.2	34.4	34.9	34.4	33.8	33.5	—			
8. <i>Polysaccus japonicus</i>	39.6	39.1	43.6	40.9	40.9	47.8	33.2	—		
9. <i>Clistosaccus paguri</i>	49.6	44.6	50.8	45.3	46.1	54.0	47.3	43.4	—	
10. <i>Sylon hippolytes</i>	58.6	56.8	61.0	60.5	55.8	54.1	43.0	49.2	20.6	—
11. <i>Polyascus polygenea</i>	37.4	35.2	42.0	35.1	37.0	37.3	22.1	26.6	33.5	38.8

bers of Thompsoniidae [*Diplothylacus sinensis* (Keppen, 1877), *Jensia serenei* (Høeg and Lützen, 1993), *Thompsonia littoralis*, *Thylacoplethus magellani* Høeg and Lützen, 1993, and the new sequences from *Thompsonia japonica* and *Thylacoplethus porcellanus* n. sp.] nest monophyletically with a relatively high posterior probability (94%), and show *Boschmaella japonica* Høeg, Kapel, Thor, and Webster, 1990 (Chthamalophilidae) as sister taxon to Thompsoniidae. *Clistosaccus paguri* Lilljeborg, 1861 and *Sylon hippolytes* M. Sars, 1870 (Clistosaccidae) are a monophyletic group with a high posterior probability value (100%), and join *Polysaccus japonicus* Høeg and Lützen, 1993 in forming a polytomy with the thompsoniid clade. *Thylacoplethus* and *Thompsonia* are recovered as sister taxa, sufficiently separated to be considered separate genera, as suggested by Høeg and Lützen (1993), although convincing morphological synapomorphies are still lacking (see below). *Jensia* is the sister taxon to *Thompsonia* + *Thylacoplethus*. The new species parasitizing the porcellanid crab is closely related to *Thylacoplethus magellani*, and the species found on the xanthid crab (*Thompsonia japonica*) is close to, but distinct from, *Thompsonia littoralis*.

The K2P distances estimated between all possible pairs of rhizocephalan sequences are shown in Table 2. The mean distance of pairwise comparisons within the clade containing *Thylacoplethus* and *Thompsonia* is 15.1%, with the lowest distances corresponding to the *Thylacoplethus magellani*-*Thylacoplethus porcellanus* pair (7.7%) and the *Thompsonia littoralis*-*Thompsonia japonica* pair (12.1%). The mean sequence divergence between the two genera is 17.7%. No divergence (0%) in the sequence fragment of the 18S rDNA gene was found between Caribbean and Pacific individuals of the porcellanid *Petrolisthes armatus*. The distance between the geminates *P. glasselli* and *P. rosariensis* is 7.2%. These values are reference indicators that support the conclusion that the species here described are different from their putative sister species.

Data are available from the Dryad (<http://doi.org/10.5061/dryad.6s7p8>) and TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S16937>) digital repositories.

SYSTEMATICS

Rhizocephala Müller, 1862

Akentrogonida Häfele, 1911

Thompsoniidae Høeg and Rybakov, 1992

Thompsonia Kossmann, 1872

Thompsonia japonica Häfele, 1911

(Figs. 1A, 4A, B)

Material Examined.—130 externae on a female *Lophozozymus dodone* (CL = 10.7 mm, CW = 16.1 mm), shallow intertidal, coral rubble, 8°42'5.60"S, 115°15'56.82"E, Sanur, Bali, Indonesia, 6 August 1997, J. D. Williams coll. (USNM1268865 in alcohol, USNM1268866 on SEM stub).

Redescription.—Externae ovoid, immature, 1.2–1.6 mm in length (1.36 ± 0.13 mm, $n = 10$), up to 0.8 mm in diameter (0.76 ± 0.07 mm, $n = 10$), set on short stalk (Figs. 1A, 4A, B). Stalk with single annulus, positioned at base of stalk (Fig. 4A, B). Mantle thin and transparent, filled with ovarian tissue. Mantle aperture lacking.

In total, 130 externae on host (host damaged with left pereopods 2 and 3 detached); 39 externae on ventral abdominal surface, 1–18 externae on pereopods 1–5 (mostly on merus but a few on basis or ischium).

Remarks.—*Thompsonia* and *Thylacoplethus* are purportedly distinguished by the following three characters: stalk annulus number (one in *Thompsonia*, two in *Thylacoplethus*), mantle pore opening (absent in mature *Thompsonia* externae, present in *Thylacoplethus*), and spermatogenic bodies within the mantle (present in *Thompsonia*, absent in *Thylacoplethus*) (Høeg and Lützen, 1993). However, none of these characters is consistent across species within the two genera. Some species of *Thylacoplethus* have a mantle pore in mature externae, no spermatogenic bodies, but only one annulus, e.g., *Thylacoplethus pilodiae* Lützen and Jespersen, 1990, *Thylacoplethus orientalis* Høeg and Lützen, 1993; however, another species, *Thylacoplethus isaevae* Rybakov and Shukalyuk, 2004, has two annuli, a mantle pore (only in the most mature specimens), and spermatogenic bodies; only one of these characters (the number of annuli) has been documented for all five species of *Thompsonia*, but only *Thompsonia littoralis* has been well described.

The present specimens on the xanthid host are morphologically indistinguishable from *Thompsonia globosa* Kossmann, 1872, *Thompsonia japonica*, and *Thompsonia lit-*

Table 3. Alphabetical list of all species of Thompsoniidae with their respective hosts and geographic ranges according to WoRMs (Boxshall and Boyko, 2014), Høeg and Lützen (1993) and the present study.

Parasitic species	Host	Parasite locality (Host's geographic range)
<i>Diplothylacus sinensis</i> (Keppen, 1877)	<i>Portunus pelagicus</i> (Linnaeus, 1758) and possibly <i>P. sanguinolentus</i> (Herbst, 1783) (Brachyura: Portunoidae: Portunidae)	China, Singapore, West Malaysia, Sarawak, Thailand (Indo-Pacific)
<i>Diplothylacus thalamitae</i> (Høeg and Lützen, 1993)	<i>Thalamita prymna</i> (Herbst, 1803) and <i>T. admete</i> (Herbst, 1803) (Brachyura: Portunoidae: Portunidae)	Northeast Australia (Indo-Pacific)
<i>Jensia plesionikae</i> (Høeg and Lützen, 1993)	<i>Plesionika acanthonotus</i> (Smith, 1882) (Caridea: Pandaloidea: Pandalidae)	Off Georgia and Florida, USA (Atlantic Ocean and Mediterranean)
<i>Jensia serenei</i> (Lützen and Du, 1999)	<i>Oratosquilla gravieri</i> (Manning, 1978) (Stomatopoda: Squilloidea: Squillidae)	Vietnam (Vietnam to Philippines, New Caledonia and Australia)
<i>Thompsonia affinis</i> Krüger, 1912	<i>Uropyechus</i> sp. and <i>U. tomentosus</i> Baba, 1974 (Anomura: Uropyechidae: Chirostyliidae)	Japan and New Zealand (specific ID and range unknown for Japan specimen; <i>U. tomentosus</i> – New Zealand)
<i>Thompsonia chuni</i> Häfele, 1911	<i>Parapagurus</i> sp. (Anomura: Paguroidea: Parapaguridae)	Unknown
<i>Thompsonia globosa</i> Kossmann, 1872	<i>Lybia tessellata</i> (Latreille, 1812) (Brachyura: Xanthoidea: Xanthidae)	Philippines (Indo-Pacific)
<i>Thompsonia japonica</i> Häfele, 1911	<i>Pilumnus doffleini</i> Balss, 1933; <i>Actumnus squamosus</i> (De Haan, 1835) (Brachyura: Pilumnoidea: Pilumnidae); <i>Lophozozymus dodone</i> (Herbst, 1801) (Brachyura: Xanthoidea: Xanthidae)	Japan, Indonesia (<i>P. doffleini</i> – Japan; <i>A. squamosus</i> and <i>L. dodone</i> – Indonesia)
<i>Thompsonia littoralis</i> Lützen and Jespersen, 1990	<i>Pilodius granulatus</i> Stimpson, 1858; <i>Cyclocladius granulosus</i> (De Man, 1888); <i>Chlorodiella cytherea</i> (Dana, 1852) (Brachyura: Xanthoidea: Xanthidae)	Philippines, Indonesia (Indo-Pacific)
<i>Thylacoplethus africanus</i> Høeg and Lützen, 1993	<i>Gaillardielius rueppelli</i> (Krauss, 1843) (Brachyura: Xanthoidea: Xanthidae)	South Africa (Indo-Pacific)
<i>Thylacoplethus cubensis</i> (Reinhard and Stewart, 1956)	<i>Munida stimpsoni</i> A. Milne Edwards, 1880 (Anomura: Galatheoidea: Munididae)	Cuba (Caribbean)
<i>Thylacoplethus edwardsi</i> Coutière, 1902	<i>Alpheus malleodigitus</i> (Bate, 1888), <i>A. edwardsii</i> (Audouin, 1826), <i>A. strenuus</i> Dana, 1852, “ <i>A. sulcatus</i> ” Kingsley, 1878 (Caridea: Alpheoidea: Alpheidae); <i>Lysmata kempi</i> Chace, 1997 (Caridea: Alpheoidea: Hippolytidae)	Fiji, Australia, Taiwan (Indo-Pacific); <i>A. sulcatus</i> is an eastern Pacific species and this record is from an Indo-Pacific member of the <i>sulcatus</i> species group
<i>Thylacoplethus isaevae</i> Rybakov and Shukalyuk, 2004	<i>Pagurus trigonocheirus</i> (Stimpson, 1858) (Anomura: Paguroidea: Paguridae)	Sakhalin (Arctic coasts of Alaska and Siberia to Bering Sea, Aleutian Islands, and Kamchatka)
<i>Thylacoplethus magellani</i> Høeg and Lützen, 1993	<i>Pagurus foreeps</i> H. Milne Edwards, 1836 (Anomura: Paguroidea: Paguridae)	Chile (Chile, Argentina)
<i>Thylacoplethus minutus</i> Lützen and Nagasawa, 1998	<i>Synalpheus stimpsonii</i> (De Man, 1888) (Caridea: Alpheoidea: Alpheidae)	Australia (Indo-Pacific)
<i>Thylacoplethus novaezealandiae</i> Lützen, Glenner and Lörz, 2009	<i>Uropyechodes epigaster</i> Baba, 2004 (Anomura: Chirostyloidea: Chirostyliidae)	New Zealand (New Caledonia, New Zealand)
<i>Thylacoplethus orientalis</i> Høeg and Lützen, 1993	<i>Dardanus impressus</i> (De Haan, 1849); <i>D. arrossor</i> (Herbst, 1796) (Anomura: Paguroidea: Diogenidae)	Japan (Indo-Pacific)
<i>Thylacoplethus pilodiae</i> (Lützen and Jespersen, 1990)	<i>Pilodius nigrocrinitus</i> Stimpson, 1859 (Brachyura: Xanthoidea: Xanthidae)	Singapore (Indo-Pacific)
<i>Thylacoplethus porcellanus</i> n. sp.	<i>Petrolisthes scabriculus</i> (Dana, 1852) (Anomura: Galatheoidea: Porcellanidae)	Australia (Indo-Pacific)
<i>Thylacoplethus reinhardi</i> (Lützen, 1992)	<i>Discorsopagurus schmitti</i> (Stevens, 1925); possibly <i>Pagurus capitatus</i> (Benedict, 1892) (Anomura: Paguroidea: Paguridae)	Washington, USA (northeast Pacific, Japan – <i>D. schmitti</i> only)
<i>Thylacoplethus squillae</i> Høeg and Lützen, 1993	<i>Oratosquilla oratoria</i> (De Haan, 1844), <i>Harpisquilla harpax</i> (De Haan, 1844) (Stomatopoda: Squilloidea: Squillidae)	Japan, Vietnam (Indo-Pacific)
<i>Thylacoplethus umanguvatus</i> n. sp.	<i>Calcinus morgani</i> Rahayu and Forest, 1999 (Anomura: Paguroidea: Diogenidae)	Bali, Indonesia (Indo-Pacific)

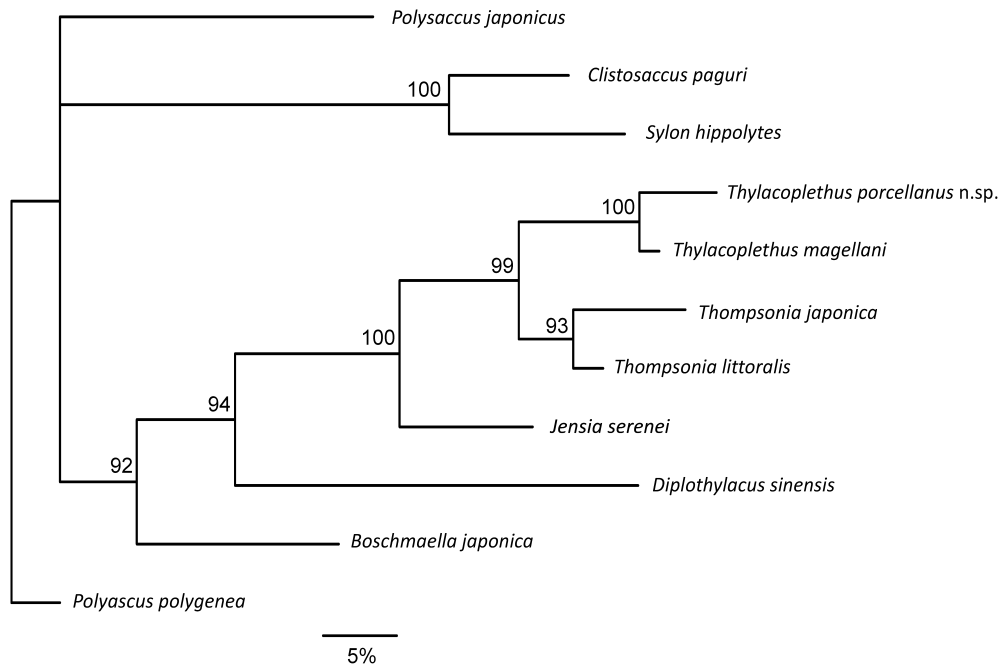


Fig. 2. Bayesian phylogenetic tree reconstructed with partial sequences of the nuclear 18S rDNA gene from 10 akentrogonid rhizocephalans including the two new species, and using the parameters of the GTR + I + G model ($-\ln L = 2.789$) with $I = 0.297$ and $G = 0.464$. Values on nodes correspond to posterior probabilities (%).

toralis. However, *Thompsonia globosa* is extremely poorly described and cannot be convincingly identified without collection of topotypic material (see Table 3). According to Lützen and Jespersen (1990), *Thompsonia japonica* and *Thompsonia littoralis* can only be distinguished based on the carapace length of the cyprid larvae. No molecular data exists for *Thompsonia japonica*, but an 18S rDNA sequence exists for *Thompsonia littoralis* (Glennner and Hebsgaard, 2006) that was derived from either paratypic or topotypic material (which one is not clear). Based on molecular data, our specimens are close to, but distinct from *Thompsonia littoralis* (Table 2). Because there are no characters in our specimens to differentiate them from *Thompsonia japonica*, we have conservatively identified them with the latter species. *Thompsonia japonica* is also known from two other xanthid crabs (see Table 3). The single record from a hermit crab (*Pagurus striatus* Latreille, 1802 = *Dardanus arrosor* (Herbst, 1796)) given by Krüger (1912) is considered by Høeg and Lützen (1993) to represent *Thylacoplethus orientalis*.

Thylacoplethus Coutière, 1902
***Thylacoplethus porcellanus* n. sp.**
 (Figs. 1B, 3A, 4C, D)

Material Examined.—13 externae (UF34625, holotype) on one male *Petrolisthes scabriculus* (UF25638; CL = 2.85 mm, CW = 2.85 mm), in rubble, 23°27'15.48"S, 151°52'1.56"E, north Wistari, Heron Island, Queensland, Australia, 23 November 2009, L. Avery, K. Schnabel, N. Bruce coll.

Description.—Externae ovoid, mature, 0.7 to 1.5 mm in length (1.0 ± 0.3 mm, $n = 13$), up to 0.6 mm in diameter, set on short stalk (Figs. 1B, 3A, 4C). Stalk with

single, conspicuous annulus approximately at its mid-length (Figs. 3A, 4D). Mantle thin and transparent, filled with eggs. Mantle aperture lacking.

In total, 17 externae on host; 6 on ventral pleonal surface, not more than 2 per pleomere, symmetrical around medial line of each segment, not found on tail fan or sixth pleomere, 11 on pereopods (mostly on merus but a few on basis or ischium) (Fig. 1B).

Etymology.—The species is named based on the host, a crab of Porcellanidae, and is a noun in apposition; the gender is masculine.

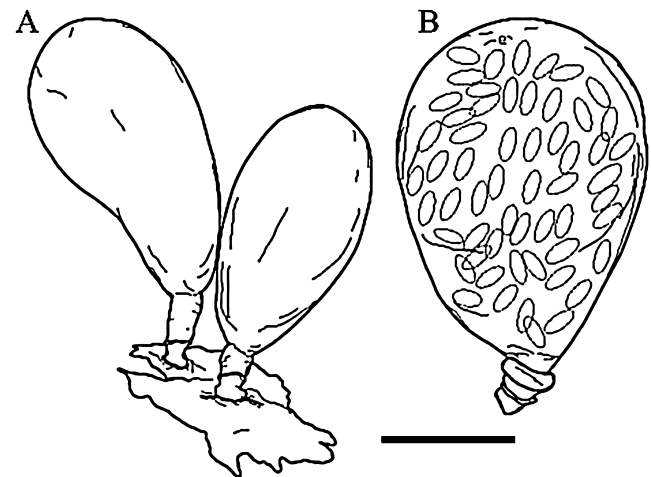


Fig. 3. A, *Thylacoplethus porcellanus* n. sp. (holotype, UF34625), lateral view of individual externae of holotype, two externae with host fragment remaining at base of stalks; B, *Thylacoplethus umanguvatus* n. sp. (holotype, USNM1268852), lateral view of individual externae of holotype; developing cyprids within externa shown. Scale bar = 0.5 mm.

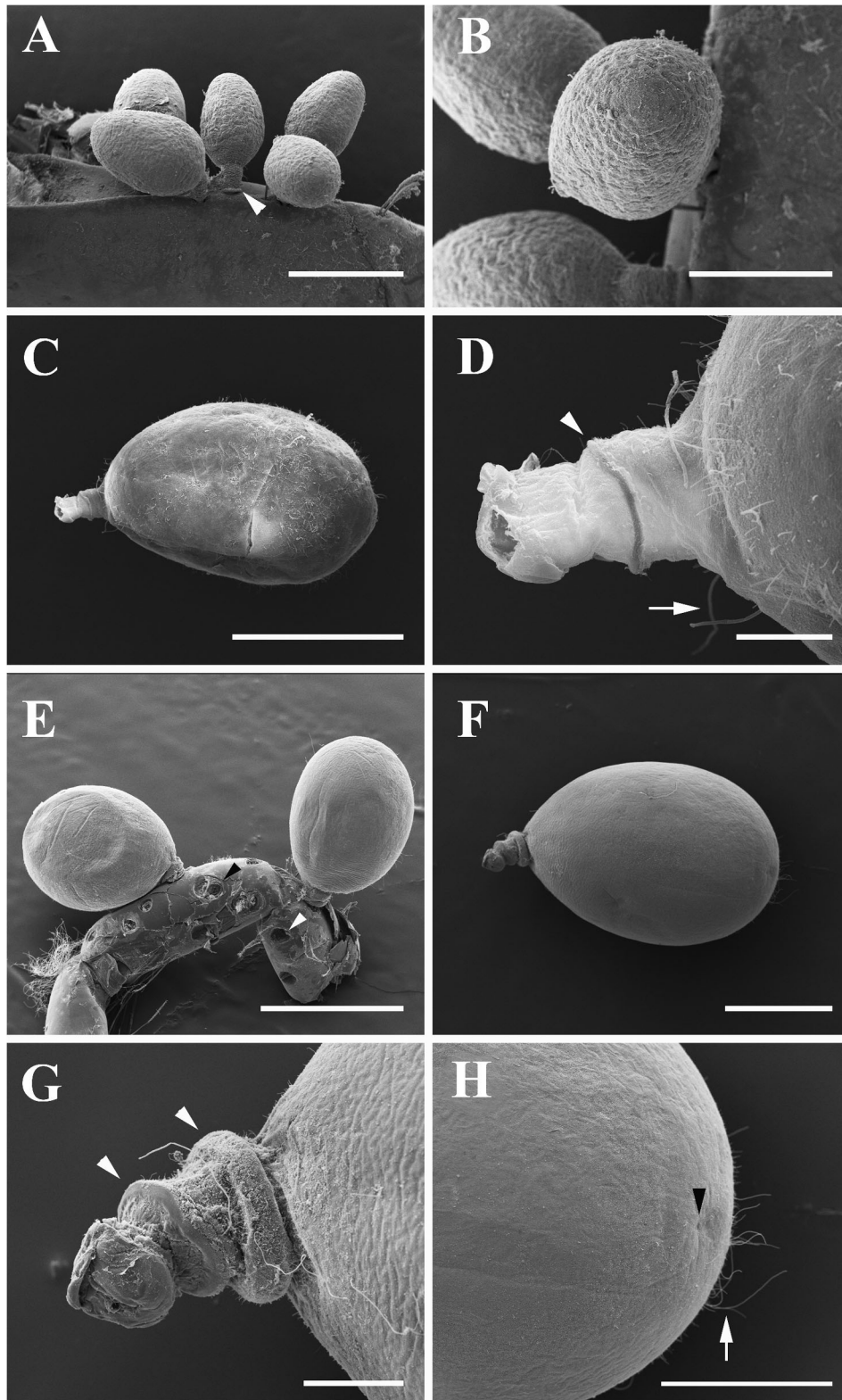


Fig. 4. A, B, *Thompsonia japonica* (USNM1268866); A, five externa *in situ* on fifth leg of host (arrow indicates single cuticular annulus at base of stalk); B, apical view of externa showing lack of pore. C, D, *Thylacoplethus porcellanus* n. sp. (holotype, UF34625); C, whole externa, lateral view; D, stalk of externa, showing single cuticular annulus (arrowhead) and thalli belonging to an unidentified mesomycetozoean (horizontal arrow). E-H, *Thylacoplethus umanguvatus* n. sp. (paratypes, USNM1268863, 1268864), scanning electron micrographs; E, two externa *in situ* on posterior pereiopod of host; several scars of externa are also shown (black arrowhead shows scar where two externa originated, white arrowhead shows scar where single externa originated); F, whole externa, lateral view; G, stalk of externa, showing two cuticular annuli (arrowheads); H, apical view of externa showing presumptive pore (arrowhead) and thalli belonging to an unidentified mesomycetozoean (vertical arrow). Scale bars: A = 400 μ m, B = 50 μ m, C, E = 1 mm, D, F = 500 μ m, G = 100 μ m, H = 300 μ m.

Remarks.—This is the first record of an akentrogonid from a porcelain crab host. The new species presents only a single annulus on the stalk and no mantle pore (although cyprids are not present and the pore may not have developed yet). One annulus and no mantle pore are characteristics of *Thompsonia*, but the molecular data place the new species closest to *Thylacoplethus magellani*, which has two annuli and a mantle pore. Two other species currently placed in *Thylacoplethus* also have only one annulus: *Thylacoplethus pilodiae* and *Thylacoplethus orientalis*. *Thylacoplethus pilodiae* on *Pilodius nigrocrinitus* Stimpson, 1859 (Xanthidae) collected from Singapore was described from specimens that contained cyprid larvae and had a mantle pore (Lützen and Jaspersen, 1990). *Thylacoplethus orientalis* was described from *Dardanus impressus* (De Haan, 1849) and *D. arrosor* (Diogenidae) collected from Japan, and was noted to have a large apical pore (Høeg and Lützen, 1993).

In addition to the clear host differences, *Thylacoplethus porcellanus* differs from *Thylacoplethus orientalis* in lacking a mantle pore (which may correlate with larval development) and in having a conspicuous annulus (as compared to the inconspicuous annulus in *Thylacoplethus orientalis*). The new species is similar to *Thylacoplethus pilodiae* in both size and position of the annulus, but it is more tapered proximally (greatest width about 3/4 distance from base of externa vs. halfway from base in *Thylacoplethus pilodiae*), and lacks a mantle pore. Based on the molecular data, our specimens are distinct from *Thylacoplethus magellani* (Table 2), but this is the only species of *Thylacoplethus* from which molecular data is known. *Thylacoplethus magellani* Høeg and Lützen (1993) was cited as *Thompsonia magellana* (sic) by Pérez-Losada et al. (2009), but the species had originally been described within *Thylacoplethus*.

The externae of *Thylacoplethus porcellanus* were covered with thin extensions on the surface that match the morphology of members of the mesomycetozoean group Eccrinales (Fig. 4D), similar to those found on other hermit crab parasites (Williams and Madad, 2010). “Hair-like microcuticular projections” have been reported from other akentrogonid externae, e.g., *Thylacoplethus isaevae* (see Rybakov and Shukalyuk, 2004). These should be re-examined with SEM to determine whether they also represent Eccrinales. In any case, these structures are distinct from the “excrescences” of Boschma (1955).

***Thylacoplethus umanguvatus* n. sp.**
(Figs. 1C, D, 3B, 4E-H)

Material Examined.—All specimens from *Calcinus morgani*. 15 externae on male host (SL = 3.0 mm) (USNM 1268852, holotype), 56 externae on male host (SL = 2.5 mm), 46 externae on male host (SL = 3.5 mm), 32 externae on female host (SL = 3.5 mm), ~105 externae on female host (SL = 3.2 mm), 35 externae on male host (SL = 3.3 mm), 13 externae on female host (SL = 4.8 mm), 28 externae on male host (SL = 4.8 mm), 85 externae on male host (SL = 3.4 mm), 30 externae on female host (SL = 4.2 mm), 91 externae on male host (SL = 3.2 mm) (USNM1268853-1268862, paratypes in alcohol; USNM1268863, 1268864, paratypes on SEM stubs), shallow intertidal, coral rubble, 8°42'5.60"S, 115°15'56.82"E, Sanur, Bali, Indonesia, 6 Aug 1997, J. D. Williams coll.

Description.—Immature externae ovoid (0.33 ± 0.02 mm by 0.30 ± 0.04 , $n = 10$), mature externae elongate, up to 1.7 mm in length, 1.1 mm in diameter (1.46 ± 0.13 by 0.97 ± 0.10 , $n = 10$), set on short stalk (Fig. 4E, F). Stalk with two conspicuous annuli (Figs. 3B, 4F, G), basal annulus thinner, distal annulus broad, rounded (Fig. 3B). Mantle thin and transparent, filled with eggs or developing cyprids (Fig. 3B). Spermatogenic bodies in mantle. Minute mantle aperture present subapically in externae with developing cyprids (Fig. 4H), lacking in those with eggs.

In total, up to 100+ externae on carpus, merus, and ischium of pereopods 1-5 (Fig. 1C, D); larger numbers of externae on pereopods 4 and 5, some being attached laterally, whereas on pereopods 1-3 externae are restricted mostly to dorsal and ventral surfaces, and found there in rows.

Remarks.—Five species of *Thylacoplethus* are now known from hermit crab hosts: *Thylacoplethus isaevae*, *Thylacoplethus magellani*, *Thylacoplethus orientalis* Høeg and Lützen, 1993, *Thylacoplethus reinhardi* Lützen, 1992, and the new *Thylacoplethus umanguvatus* (see Table 3). *Thylacoplethus orientalis* has only a single annulus, while the other four species have two annuli on the stalk (although very young externae of *Thylacoplethus reinhardi* have only a single annulus; see Lützen, 1992). The mantle pore is subapical and unadorned in *Thylacoplethus isaevae* and *Thylacoplethus umanguvatus* n. sp., subapical with raised “lips” surrounding it in *Thylacoplethus magellani*, and apical in *Thylacoplethus reinhardi*. Externae are found on the abdomen only in *Thylacoplethus magellani* and *Thylacoplethus reinhardi*, on the pereopods and abdomen of *Thylacoplethus isaevae*, and almost entirely on the pereopods of *Thylacoplethus umanguvatus*. Spermatogenic bodies are found in the mantle in *Thylacoplethus isaevae* and *Thylacoplethus umanguvatus* (easily seen through the thin cuticle in the mature externae) but are absent in *Thylacoplethus magellani* and *Thylacoplethus reinhardi* as well as in all other species of this genus. In sum, *Thylacoplethus umanguvatus* is most similar to *Thylacoplethus isaevae*; the two species can be distinguished by host choice, the predominant location of the externae on the body, and the much larger size of externae of *Thylacoplethus isaevae* (up to 4.9 mm vs. 1.7 mm for *Thylacoplethus umanguvatus*). For a review of the impacts of rhizocephalans on hermit crab hosts see McDermott et al. (2010).

Williams and Boyko (1999) described a new species of bopyrid isopod, *Pseudostegias macdermotti* Williams and Boyko, 1999, associated with the same collection of hermit crabs from Bali. The host hermit crabs were then identified as *Calcinus gaimardii* (H. Milne Edwards, 1848). However, that same year *C. gaimardii* was shown to be a species complex and *C. morgani* was described (Rahayu and Forest, 1999). *Calcinus gaimardii* and *C. morgani* are very similar morphologically and can only be distinguished based on shield coloration or molecular data (McLaughlin et al., 2007; Malay and Paulay, 2009). Upon re-examination of the hosts, we have identified them as *C. morgani* based on coloration of the shield (lacking the red-brown coloration on the anterior portion characteristic of *C. gaimardii*). Additionally, 16S rDNA was 100% similar to *C. morgani* when preliminary

attempts were made to generate sequences of mitochondrial genes for *Thylacoplethus umanguvatus*.

As reported for *Thylacoplethus porcellanus* (see above), many externae bore thin extensions from the cuticle that appear to be Eccrinales rather than cuticular extensions of the externae.

Ecology.—Of 34 *C. morgani* sampled in Bali, 11 (32.4%) harbored *Thylacoplethus umanguvatus*. Parasitized hosts harbored up to 105 externae per host (48.7 ± 31.6 externae/host, $n = 11$). Numerous scars left from previous externae or those dislodged during handling were observed on pereopods 1-5 of all specimens. Some scars represented the point of origination of one externa, whereas others represented two externae that erupted from the same point (Fig. 4E). In one specimen, two externae were found to erupt from the anterior portion of the pleon, just below the fifth pereopods; all other externae were recorded on pereopods 1-5.

Etymology.—The specific name *umanguvatus* is an adjective and refers to the grape-like appearance of clustered externae on the host: *umang* (Bahasa Indonesia for hermit crab) plus *uva* (Latin for grape or berry).

DISCUSSION

Three species (including two new to science) of Thompsoniidae are described herein based on morphology and, for two of them, partial sequences of the nuclear 18S rDNA gene. Høeg and Lützen (1993) revised Thompsoniidae, while describing three new genera and seven new species, and revived the genus *Thylacoplethus*, previously considered a junior synonym of *Thompsonia*. We provide a review (Table 3) of all currently recognized species in the two genera with their respective hosts and geographic ranges (five species of *Thompsonia* and 13 species of *Thylacoplethus*). The relatively high sequence divergence (14.4-21%) between these two genera suggests that *Thylacoplethus* merits its genus status despite the problems that still exist in placing species within the genera based on morphology. Until such time as more taxa of *Thompsonia* and *Thylacoplethus* are added to the phylogeny, and the morphology is known in greater detail for more species, the tree is equivocal as to whether these taxa should be considered two genera or only two clades of species within a single genus.

A close relationship between *Thompsonia* and *Thylacoplethus* was also supported by Pérez-Losada et al. (2009), who reconstructed the phylogeny of Thecostraca, the taxon that contains parasitic and suspension-feeding Cirripedia among others, using DNA sequences of three nuclear genes including 18S rDNA, as well as larval characters. These authors were the first to include a species of *Thylacoplethus* in a cirripede phylogeny, although they mistakenly cited *Thylacoplethus magellani* [as *Thompsonia magellana* (sic)] and submitted the GenBank sequence as such. In addition, Pérez-Losada et al. (2009) claimed that their akentrogonid species did not form a monophyletic clade because they incorrectly considered *Sylon hippolytes* as a kentrogonid (as shown in their supplementary material file); this is incorrect morphologically as there is no kentrogon stage in *Sylon* (Høeg and Rybakov, 1992), and it also contradicts Glen-

ner and Hebsgaard's (2006) molecular study, which had already shown *Sylon* to group with the Akentrogonida. In our study, we included all akentrogonid sequences available in GenBank, except that of *Chthamalophilus delagei* Bocquet-Védrine, 1957. This sequence is evidently not reliable, as it showed too many differences in the conservative parts of a preliminary alignment that included all akentrogonid taxa as well as the kentrogonid *Polyascus polygenea*. Our phylogeny recovered two well-supported clades, one containing *Thompsonia*, *Thylacoplethus*, *Jensia*, *Diplothy-lacus* and *Boschmaella* (92% posterior probability), and the other containing *Clistosaccus* and *Sylon* (100% posterior probability). *Polysaccus japonicus* does not nest in either of these clades but instead forms a polytomy with them. Glenner et al. (2010) supported a monophyletic Akentrogonida using 18S rDNA and 28S rDNA sequences with results very similar to ours. However, they did include *C. delagei*, which grouped with *Boschmaella japonica*, forming a monophyletic Chthamalophilidae as a sister taxon to Thompsoniidae. They did not include *Thylacoplethus magellani*, probably because it was not yet available in GenBank from the study by Pérez-Losada et al. (2009).

The new *Thylacoplethus* is the first record of an akentrogonid rhizocephalan parasitizing a porcellanid crab. Of the 13 species of *Thylacoplethus*, 8 parasitize anomurans. *Thylacoplethus cubensis* Reinhard and Stewart, 1956 parasitizes a species of the Munidiidae (Galatheoidea), the family most closely related to Porcellanidae (Bracken-Grissom et al., 2013) also known to be infested with *Thylacoplethus*. The externae of *Thylacoplethus cubensis* and *Thylacoplethus porcellanus* are quite different; those of *Thylacoplethus cubensis* bear two annuli, whereas those of *Thylacoplethus porcellanus* only bear a single annulus.

Our findings of a new host group record for *Thylacoplethus* support previous work showing that Thompsoniidae is the rhizocephalan family with the widest range of hosts infesting most major groups of decapods, and also two species of Stomatopoda (Høeg and Lützen, 1993; Lützen and Du, 1999; Walker, 2001; Boyko and Williams, 2009; Glenner et al., 2010). The hosts, so far reported for the clade containing *Thylacoplethus*, *Thompsonia* and *Jensia* (= Thompsoniidae) (see Tables 2 and 3), include caridean shrimps, brachyuran and anomuran crabs, and stomatopods. Considering this diverse group of hosts it seems reasonable to assume that the common ancestor of these thompsoniid genera was a generalist parasite, and that speciation was probably triggered by accidental infestation of new host lineages.

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REFERENCES

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions of Automatic Control* AC-19: 716-723.
- Audouin, V. 1826. Explication sommaire des planches de crustacés de l'Égypte et de la Syrie, publiées par Jules-César Savigny, membre de l'Inst.; offrant un exposé des caractères naturels des genres avec la distinction des espèces. *Description de l'Égypte. Histoire naturelle* 1(4): 77-98.
- Baba, K. 1974. *Munida brucei* sp. nov., a new galatheid (Decapoda, Anomura) from the East Coast of Africa. *Zoological Society of Japan* 47: 55-60.
- . 2004. *Uroptychodes*, new genus of Chirostylidae (Crustacea: Decapoda: Anomura), with description of three new species. *Scientia Marina* 68: 97-116.
- Balss, H. 1933. Beiträge zur Kenntnis der Gattungen *Pilumnus* (Crustacea Dekapoda) und verwandter Gattungen. *Capita Zoologica* 4: 1-47, pls. 1-7.
- Bate, C. 1888. Report on the Crustacea Macrura collected by the Challenger during the years 1873-76. Report on the Scientific Results of the Voyage of H.M.S. "Challenger" during the years 1873-76 24: i-xc, 1-942, Plates 1-157.
- Benedict, J. E. 1892. Preliminary descriptions of thirty-seven new species of hermit crabs of the genus *Eupagurus* in the U.S. National Museum. *Proceedings of the United States National Museum*, Washington 15: 1-36.
- Bocquet-Védrine, J. 1957. *Chthamalophilus delagei* nov. gen., nov. sp., rhizocephale nouveau parasite de *Chthamalus stellatus*. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 244: 1545-1548.
- Boschma, H. 1955. The described species of the family Sacculinidae. *Zoologische Verhandlungen* 27: 1-76.
- Boxshall, G., and C. B. Boyko. 2014. Thompsoniidae Høeg & Rybakov, 1992. In: M. Schotte, C. B. Boyko, N. L. Bruce, G. C. B. Poore, S. Taiti, and G. D. F. Wilson (eds.), *World Marine, Freshwater and Terrestrial Isopod Crustaceans database*. Available online at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=293297> (accessed 22 May 2014).
- Boyko, C. B., and A. W. Harvey. 2000. A review of the family Lernaediscidae (Cirripedia: Rhizocephala). I. The genus *Lernaediscus* Müller, 1862: new synonymy, hosts, range extensions, and the description of a new species. *Journal of Crustacean Biology* 20: 663-673.
- , and J. D. Williams. 2009. Crustacean parasites as phylogenetic indicators in decapod evolution, pp. 197-220. In: J. W. Martin, K. A. Crandall, and D. L. Felder (eds.), *Decapod Crustacean Phylogenetics*. Crustacean Issues 18. CRC Press, Boca Raton, FL.
- Bracken-Grissom, H. D., M. E. Cannon, P. Cabezas, R. M. Feldmann, C. E. Schweitzer, S. T. Ahyong, D. L. Felder, R. Lemaitre, and K. A. Crandall. 2013. A comprehensive and integrative reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). *BMC Biology* 13: 128.
- Chace, F. A. 1997. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine expedition, 1907-1910, Part 7: families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae. *Smithsonian Contributions to Zoology* 587: 1-106.
- Chatton, E., and A. Lwoff. 1927. *Pottisia infusoriorum* n. g., n. sp., acinetin parasite des folliculines et des cothurnies. *Bulletin de l'Institut océanographique de Monaco* 489: 1-12.
- Coutière, H. 1902. Sur un nouveau type de Rhizocephale gregaires parasite des Alpheidae (Deuxième note). *Comptes Rendus des Séances de la Société de Biologie et de Ses Filiales* 54: 625-626.
- Dana, J. D. 1851. *Conspectus crustaceorum quae in orbis terrarum circumnavi gatione, Carolo Wilkes e classe reipublicae foederatae duce, lexit et descripsit*. (Preprint from) *Proceedings of the Academy of Natural Sciences of Philadelphia* 5: 267-272.
- . 1852a. *Conspectus Crustaceorum &c. Conspectus of the Crustacea of the exploring expedition under Capt. C. Wilkes, U.S.N. Macroura*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 6: 10-28.
- . 1852b. *Conspectus Crustaceorum &c. Conspectus of the Crustacea of the exploring expedition under Capt. Wilkes, U.S.N., including the Crustacea Cancroidea Corystoidea*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 6: 73-86.
- . 1852c. *Crustacea. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U. S. N.* 13: 1-685.
- Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
- De Haan, W. 1833-1849. Crustacea. In: von Siebold, P. F. (ed.), *Fauna Japonica sive Descriptio Animalium, Quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepit, Annis 1823-1830 Collegit, Noitis, Observationibus et Adumbrationibus Illustravit*. Leiden: Lugduni-Batavorum. Fasc. 1-8: 1-243, Plates 1-55.
- De Man, J. G. 1887-1888. Report on the podophthalmous Crustacea of the Mergui Archipelago collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F. R. S., Superintendent of the Museum. *Journal of the Linnean Society, Zoology* 22: 1-312, pls. 1-19.
- . 1888. Bericht über die von Herrn Dr. J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte* 53: 289-600, plates 11-22.
- Deichmann, M., and J. T. Høeg. 1990. *Boschmaella japonica*, new species, a parasite on the barnacles *Chthamalus challenger* and *Balanus amphitrite amphitrite* from Japan (Crustacea: Cirripedia: Rhizocephala: Chthamalophilidae). *Acta Zoologica* 71: 173-175.
- Delage, Y. 1884. Evolution de la sacculine (*Sacculina carcini* Thomps.) crustacé endoparasite de l'ordre nouveau des kentronogonides. *Archives de Zoologie Expérimentale et Générale*, 2nd sér. 2: 417-736, pls. 22-30.
- Gibbes, L. R. 1850. On the carcinological collections of the cabinets of natural history in the United States with an enumeration of the species contained therein, and description of new species. *Proceedings of the American Association for the Advancement of Science* 3rd meeting, pp. 167-201.
- Glenner, H., and M. B. Hebsgaard. 2006. Phylogeny and evolution of life history strategies of the parasitic barnacles (Crustacea, Cirripedia, Rhizocephala). *Molecular Phylogenetics and Evolution* 41: 528-538.
- , J. T. Høeg, J. Stenderup, and A. V. Rybakov. 2010. The monophyletic origin of a remarkable sexual system in akentrogonid rhizocephalan parasites: a molecular and larval structural study. *Experimental Parasitology* 125: 3-12.
- , J. Lützen, and T. Takahashi. 2003. Molecular and morphological evidence for a monophyletic clade of asexually reproducing Rhizocephala: *Polyascus*, new genus (Cirripedia). *Journal of Crustacean Biology* 23: 548-557.
- Guindon, S., and O. Gascuel. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology* 52: 696-704.
- Häfele, F. 1911. Notizen über phylogenetisch interessanten Rhizocephalen. *Zoologischer Anzeiger* 38: 180-185.
- Haig, J. 1957. Four new porcellan crabs from the eastern Pacific. *Bulletin of the Southern California Academy of Sciences* 56: 31-41.
- Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- Herbst, J. F. W. 1782-1804. Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten, 1-3: 1-515, Plates 1-62.
- Hiller, A., H. Krauss, M. Almon, and B. Werding. 2006. The *Petrolithes galathinus* complex: species boundaries based on color pattern, morphology and molecules, and evolutionary interrelationships between this complex and other Porcellanidae (Crustacea: Decapoda: Anomura). *Molecular Phylogenetics and Evolution* 40: 547-569.
- Høeg, J. T. 1995. The biology and life cycle of the Cirripedia Rhizocephala. *Journal of the Marine Biological Association of the United Kingdom* 75: 517-550.
- , C. M. Kapel, P. Thor, and P. Webster. 1990. The anatomy and sexual biology of *Boschmaella japonica*, an akentrogonid rhizocephalan parasite on barnacles from Japan (Crustacea: Cirripedia: Rhizocephala). *Acta Zoologica* 71: 177-188.
- , and J. Lützen. 1993. Comparative morphology and phylogeny of the family Thompsoniidae (Cirripedia, Rhizocephala, Akentrogonida), with descriptions of three new genera and seven new species. *Zoologica Scripta* 22: 363-386.
- , and A. V. Rybakov. 1992. Revision of the Rhizocephala Akentrogonida (Cirripedia), with a list of all the species and a key to the identification of families. *Journal of Crustacean Biology* 12: 600-609.
- Hoek, P. P. C. 1883. Report on the Cirripedia collected by Challenger during the years 1873-1876. Reports of Science Research Voyage of H.M.S. Challenger. *Zoology* 8: 1-169.

- Katoh, K., and M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772-780.
- Keppen, N. A. 1877. *Thompsonia sinensis*, a new species of Suctorina. *Zapiski Novorossiyskago Obschestva Estestvoispytateley*, Odessa 4: 1-15 (in Russian).
- Kimura, M. 1980. A simple method of estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111-120.
- Kingsley, J. S. 1878. A synopsis of North American species of the genus *Alpheus*, VII. *Bulletin of the United States Geological and Geographical Survey* 4: 189-199.
- Kossmann, R. 1872. Beiträge zur Anatomie der Schmarotzenden Rankenfüssler. *Verhandlungen der Physikalisch-Medizinischen Gesellschaft zu Würzburg* 3: 296-335, pls. 216-218.
- Krauss, F. 1843. Die Südafrikanischen Crustaceen. Eine Zusammenstellung aller bekannten Malacostraca, Bemerkungen über deren Lebensweise und geographische Verbreitung, nebst Beschreibung und Abbildung mehrerer neuen Arten. Stuttgart, pp. 1-68, pls. 1-4.
- Krüger, P. 1912. Über ostasiatische Rhizocephalen. *Abhandlungen der mathematisch-physischen Klasse der Königlich Bayerischen Akademie von Wissenschaft* 2, Suppl.-Bd., 8 Abhandlg.: 1-16, pls. 1-3.
- Latreille, P. A. 1802. *Histoire Naturelle, Générale et Particulière, des Crustacés et des Insectes*. Vol. 3. Paris.
- . 1812. Crustacés et insectes, pp. 270-280. In: J. Milbert (ed.). *Voyage pittoresque à l'Île-de-France, au cap de Bonne-Espérance et à l'Île de Ténériffe*, par M. J. Milbert. Peintre embarqué sur la corvette le Géographe, et Directeur des gravures de la partie historique du Voyage aux Terres-Australes. Vol. 2. Crustacés. A. Nepveu, Paris.
- Lessios, H. A. 2008. The great American schism: divergence of marine organisms after the rise of the Central American isthmus. *Annual Review of Ecology, Evolution and Systematics* 39: 63-91.
- Lilljeborg, W. 1861. Supplément au mémoire sur les genres *Liriope* et *Peltogaster*, H. Rathke. *Nova Acta Regiae Societatis Scientiarum Upsaliensis, Seriei Tertiae* 3: 74-102, pl. 106.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. 10th Edition: 1-824.
- Lützen, J. 1992. Morphology of *Thompsonia reinhardi*, new species (Cirripedia: Rhizocephala), parasitic on the northeast Pacific hermit crab *Discorsopagurus schmitti* (Stevens). *Journal of Crustacean Biology* 12: 83-93.
- , and P. T. Du. 1999. Three colonial rhizocephalans from mantis shrimps and a crab in Vietnam, including *Pottisia serenei*, new species (Cirripedia: Rhizocephala: Thompsoniidae). *Journal of Crustacean Biology* 19: 902-907.
- , H. Glenner, and A.-N. Lörz. 2009. Parasitic barnacles (Cirripedia: Rhizocephala) from New Zealand off-shore waters. *New Zealand Journal of Marine and Freshwater Research* 43: 613-621.
- , and Å. Jespersen. 1990. Records of *Thompsonia* (Crustacea: Cirripedia: Rhizocephala) from Singapore, including description of two new species, *T. littoralis* and *T. pilodiae*. *The Raffles Bulletin of Zoology* 38: 241-249.
- , and K. Nagasawa. 1998. Two akentrogonid rhizocephalans (Crustacea, Cirripedia) parasitic on shrimps, *Thylacoplethus edwardsi* Coutière from Japan and *T. minutus* sp. nov. from Australia. *Bulletin of the National Science Museum of Tokyo, Series A* 24: 177-184.
- , and T. Takahashi. 1997. *Sacculina polygenea*, a new species of Rhizocephalan (Cirripedia: Rhizocephala) from Japan, parasitic on the intertidal crab *Hemigrapsus sanguineus* (De Haan, 1835) (Decapoda: Brachyura: Grapsidae). *Crustacean Research* 26: 103-108.
- Malay, M. C., and G. Paulay. 2010. Peripatric speciation drives diversification and distributional pattern of reef hermit crabs (Decapoda: Diogenidae: *Calcinus*). *Evolution* 64: 634-662.
- Manning, R. B. 1978. Further observations on *Oratosquilla*, with accounts of two new genera and nine new species (Crustacea: Stomatopoda: Squillidae). *Smithsonian Contributions to Zoology* 272: 1-44.
- Martin, J. W., J. Olesen, and J. T. Høeg. 2014. *Atlas of Crustacean Larvae*. Johns Hopkins University Press, Baltimore, MD.
- McDermott, J. J., J. D. Williams, and C. B. Boyko. 2010. The unwanted guests of hermits: a worldwide review of the diversity and natural history of hermit crab parasites. *Journal of Experimental Marine Biology* 394: 2-44.
- McLaughlin, P. A., D. L. Rahayu, T. Komai, and T. Y. Chan. 2007. A Catalog of the Hermit Crabs (Paguroidea) of Taiwan. National Taiwan Ocean University, Keelung.
- Milne Edwards, H. 1836. Observations zoologiques sur les Pagures et description d'un nouveau genre de la tribu des Paguriens. *Annales des Sciences Naturelles*, 2^e série 6: 257-288, Plates 13-14.
- . 1834-1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. Librairie Encyclopédique de Roret, Paris, 1-3: 1-468. Plates 1-42.
- . 1848. Note sur quelques nouvelles espèces du genre Pagure. *Annales des Sciences Naturelles Zoologie*, Paris 10: 59-64.
- Milne-Edwards, A. 1880. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea, etc. VIII. Études préliminaires sur les Crustacés. *Bulletin of the Museum of Comparative Zoology at Harvard College* 8: 1-68, 2 pls.
- Müller, F. 1862. Die Rhizocephalen, eine neue Gruppe Schmarotzender Kruster. *Archiv für Naturgeschichte* 29: 1-9, pl. 1.
- Ortmann, A. E. 1891. Die Decapoden-Krebse des Strassburger Museums mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und z. Z. im Strassburger Museum aufbewahrten Formen. III. Theil. Die Abtheilungen der Reptantia Boas: Homaridae, Loricata und Thalassinidea. *Zoologische Jahrbücher. Abteilung für Systematik* 6: 1-58.
- Pérez-Losada, M., J. T. Høeg, and K. A. Crandall. 2009. Remarkable convergent evolution in specialized parasitic Thecostraca (Crustacea). *BMC Biology* 7: 15.
- Rahayu, D. L., and J. Forest. 1999. Sur le statut *Calcinus gaimardii* (H. Milne Edwards, 1848) (Decapoda, Anomura, Diogenidae) et description de deux espèces nouvelles apparentées. *Zoosystema* 21: 461-472.
- Reinhard, E. G., and T. Stewart. 1956. The hermaphroditic nature of *Thompsonia* (Crustacea: Rhizocephala) with description of *Thompsonia cubensis* n. sp. *Proceedings of the Helminthological Society of Washington* 23: 162-168.
- Ritchie, L. E., and J. T. Høeg. 1981. The life history of *Lernaediscus porcellanae* (Cirripedia: Rhizocephala) and co-evolution with its porcellanid host. *Journal of Crustacean Biology* 1: 334-347.
- Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539-542.
- Rybakov, A. V., and A. I. Shukalyuk. 2004. *Thylacoplethus isaevae* sp. nov., a new colonial rhizocephalan (Crustacea: Rhizocephala: Thompsoniidae) parasitic on a north-west Pacific hermit crab *Pagurus trigonocheirus*. *Journal of the Marine Biological Association of the United Kingdom* 84: 1009-1017.
- Saiki, R. K., D. H. Gelfand, S. Stoffel, S. J. Scharf, R. Higuchi, G. T. Horn, K. B. Mullis, and H. A. Erlich. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science* 239: 487-491.
- Sars, M. 1870. Bidrag til Kundskab om Christianiafjordens Fauna. II. Crustacea. *Nyt Magazin for Naturvidenskaberne* 17: 113-126.
- Smith, S. I. 1882. Reports on the results of dredging under the supervision of Alexander Agassiz, on the east coast of the United States during the summer of 1880, by the U.S. Coast Survey Steamer "Blake", Commander J.R. Bartlett, U.S.N., commanding. *Bulletin of the Museum of Comparative Zoology at Harvard College* 10: 1-108, plates 1-16.
- Stevens, B. A. 1925. Hermit crabs of Friday Harbor, Washington. *Publications of the Puget Sound Marine Biological Station* 3: 273-309.
- Stimpson, W. 1858a. Prodröm descriptionis animalium evertetatorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit. Pars IV. Crustacea Cancroidea et Corystoidea. *Proceedings of the Academy of Natural Sciences of Philadelphia* 10: 31-40.
- . 1858b. Prodröm descriptionis animalium evertetatorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit. Pars VII. Crustacea Anomura. *Proceedings of the Academy of Natural Sciences of Philadelphia* 10: 225-252.
- . 1859. Untitled report (A remarkable new form of brachyurous crustacean in the coral reefs at Hawaii: *Hapalocarcinus marsupialis*). *Proceedings of the Boston Society of Natural History* 6: 412-413.

- Tamura, K., G. Stecher, D. Peterson, A. Filipowski, and S. Kumar. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2725-2729.
- Thompson, J. V. 1836. Natural history and metamorphosis of an anomalous crustacean parasite of *Carcinus maenas*, the *Sacculina carcini*. *Entomological Magazine*, London 3: 452-456.
- Thresher, R., M. Werner, J. Høeg, I. Svane, H. Glenner, N. Murphy, and C. Wittwer. 2000. Developing the options for managing marine pests: specificity trials on the parasitic castrator, *Sacculina carcini*, against the European crab, *Carcinus maenas*, and related species. *Journal of Experimental Marine Biology and Ecology* 254: 37-51.
- Walker, G. 2001. Introduction to the Rhizocephala (Crustacea: Cirripedia). *Journal of Morphology* 249: 1-8.
- Werding, B. 1982. Porcellanid crabs of the Islas del Rosario, Caribbean coast of Colombia, with a description of *Petrolisthes rosariensis* new species (Crustacea: Anomura). *Bulletin of Marine Sciences* 32: 439-447.
- Williams, J. D., and C. B. Boyko. 1999. A new species of *Pseudostegias* Shiino, 1933 (Crustacea: Isopoda: Bopyridae: Athelginae) parasitic on hermit crabs from Bali. *Proceedings of the Biological Society of Washington* 112: 714-721.
- , and A. Z. Madad. 2010. A new species and record of branchial parasitic isopods (Crustacea: Isopoda: Bopyridae: Pseudioninae) of porcellanid crabs from the Philippines. *Experimental Parasitology* 125: 23-29.
- Yamaguchi, S., J. T. Høeg, and Y. Iwasa. 2014. Evolution of sex determination and sexually dimorphic larval sizes in parasitic barnacles. *Journal of Theoretical Biology* 347: 7-16.
- Yoshida, R., M. Osawa, M. Hirose, and E. Hirose. 2011. A new genus and two new species of Peltogastridae (Crustacea: Cirripedia: Rhizocephala) parasitizing hermit crabs from Okinawa Island (Ryukyu Archipelago, Japan), and their DNA-barcodes. *Zoological Science* 28: 853-862.

APPENDIX

HISTORICAL HOMONYMY OF *POTTSIA* RYDER, 1885 (CNIDARIA), *POTTSIA* CHATTON AND LWOFF, 1927 (CILIOPHORA) AND *POTTSIA* HØEG AND LÜTZEN, 1993 (CRUSTACEA) WITH *JENSIA* BOYKO AND WILLIAMS NOM. NOV. AS A REPLACEMENT NAME FOR THE RHIZOCEPHALAN *POTTSIA*

The genus-group name *Pottisia* has been introduced three times in the zoological literature, once each in Cnidaria, Ciliophora, and Crustacea (it is also a genus of plant in Apocynaceae, but that name does not compete in homonymy with any of the zoological names). We review the history of this popular name and clarify the status of each usage following the International Code of Zoological Nomenclature (ICZN).

Pottisia Ryder, 1885 (Cnidaria: Hydrozoa)

Potts (1885) described *Microhydra* as a monotypic genus of hydrozoan with the type species *Microhydra ryderi* Potts, 1885. This description was based solely on the hydroid stage and it took 12 more years for Potts to discover the corresponding medusa form (see Potts, 1906). Ryder (1885) stated “that if *Microhydra* should turn out to be only the hydroid stage of a mature medusa-form the latter will be found to be generically distinct from *Limnocoodium*, in which case it might be called *Pottisia*.” Ryder’s logic was based on the then-common practice of providing a double nomenclature for polyps and medusae when the connection between the forms was not known (see Altuna, 2008). Although Ryder (1885) made a conditional proposal of the generic name *Pottisia*, this by itself does not make the name unavailable as it was proposed before 1961 (see ICZN Article 15). Thus, Ryder (1885) unequivocally

introduced *Pottisia* as a conditional name for the (then unknown) medusa form of the polyp called *Microhydra ryderi*. As such, *Pottisia* Ryder, 1885 must have as its type species *Microhydra ryderi*. Because the two genera have the same type species, *Pottisia* Ryder, 1885 was de facto introduced as an objective synonym of *Microhydra* Potts, 1885. Although names introduced in synonymy are not usually available, Corliss (1960) treated *Pottisia* Ryder, 1885 as an available name before 1961 (see below) and this satisfies the requirements of ICZN Article 11.6.1. *Pottisia* Ryder, 1885, is therefore an available name, although it has always been a synonym of *Microhydra*. *Microhydra ryderi* is now regarded as a synonym of *Craspedacusta sowerbii* Lankester, 1880 (Fritz et al., 2007).

Pottisia Chatton and Lwoff, 1927 (Ciliophora)

Chatton and Lwoff (1927) described the monotypic ciliophoran genus and species *Pottisia infusorium*. Because of the assumed homonymy between *Pottisia* Chatton and Lwoff and *Pottisia* Ryder, Corliss (1960) proposed the replacement name *Pottsiocles* for *Pottisia* Chatton and Lwoff. Corliss (1960) could have, and probably should have, considered *Pottisia* Ryder as a name introduced in synonymy and therefore an unavailable name. However, he did not and Corliss’ (1960) action in erecting a replacement name for *Pottisia* Chatton and Lwoff made *Pottisia* Ryder, 1885 available. The correct name for this ciliophoran taxon is therefore *Pottsiocles infusorium* (Chatton and Lwoff, 1927). *Pottsiodes* (sic) Edwards and Vevers, 1975 is a spelling error.

Pottisia Høeg and Lützen, 1993

Høeg and Lützen (1993) were unaware of the two prior usages of *Pottisia* when they erected the rhizocephalan genus and species *Pottisia plesionikae*. As this name is a homonym of both *Pottisia* Ryder and *Pottisia* Chatton and Lwoff, we propose the replacement name *Jensia* Boyko and Williams, **nom. nov.**, to honor Jens T. Høeg, the preeminent rhizocephalan biologist of the 20th and 21st centuries. As with *Pottisia*, *Jensia* is also a genus of plant (Asteraceae) but that name does not enter into homonymy with the present zoological replacement name.

REFERENCES

- Altuna, A. 2008. The life cycle of *Eucheilota medusifera* (Torrey, 1902), comb. nov. [= *Campalecium medusifera*] (Cnidaria: Hydrozoa: Lovenellidae) from the Bay of Biscay (northeastern Atlantic), including a description of the adult medusa. *Zootaxa* 1856: 1-15.
- Chatton, E., and A. Lwoff. 1927. *Pottisia infusorium* n. g., n. sp., acinetin parasite des folliculines et des cothurnies. *Bulletin de l’Institut océanographique de Monaco* 489: 1-12.
- Corliss, J. O. 1960. The problem of homonyms among generic names of ciliated protozoa, with proposal of several new names. *Journal of Protozoology* 7: 269-278.
- Edwards, M. A., and H. G. Vevers (eds.). 1975. *Nomenclator Zoologicus*. Vol. 7 (1956-1965). Zoological Society of London, London.
- Fritz, G. B., R. O. Schill, M. Pfannkuchen, and F. Brümmer. 2007. The freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 (Limnomedusa: Olindiidae) in Germany, with a brief note on its nomenclature. *Journal of Limnology* 66: 54-59.
- Høeg, J. T., and J. Lützen. 1993. Comparative morphology and phylogeny of the family Thompsoniidae (Cirripedia, Rhizocephala, Akentrogonida), with descriptions of three new genera and seven new species. *Zoologica Scripta* 22: 363-386.

- International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. 4th Edition. International Trust for Zoological Nomenclature, London.
- Lankester, E. R. 1880. On a new jellyfish of the order Trachomedusae, living in freshwater. *Nature* 22: 147-148.
- Potts, E. 1885. *Microhydra ryderi*. *Science Bulletin*, supplement to *Science* 5: v.
- . 1906. On the medusa of *Microhydra ryderi* and on the known forms of medusae inhabiting fresh water. *Quarterly Journal of Microscopical Science* 50: 623-633, pls. 35, 36.
- Ryder, J. A. 1885. The development and structure of *Microhydra ryderi* Potts. *The American Naturalist* 19: 1232-1236.

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