Zootaxa 3635 (3): 286–296
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3635.3.8
http://zoobank.org/urn:lsid:zoobank.org:pub:8E0F6CBE-54AA-4932-850B-73545A19BD49

Hamodactylus macrophthalmus spec. nov., a new coral-associated pontoniine shrimp (Decapoda, Caridea, Palaemonidae) from Indonesia

CHARLES H.J.M. FRANSEN[1] & CESSA RAUCH[2]
Department of Marine Zoology, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands.
E-mail: [1]charles.fransen@naturalis.nl; [2]cessarauch@gmail.com

Abstract

A new coral-associated species of the genus *Hamodactylus* is described from Lembeh Strait, NE Sulawesi, Indonesia. The three other known species in the genus have been recorded in association with octocorals. The single ovigerous female specimen of the new species was collected from a scleractinian host. It can be easily separated from its congeners by the very long eyestalks and the chela of the second pereiopods having blunt tips of the fingers with tufts of long simple setae giving it an atyid-like appearance.

Key words: Crustacea, Decapoda, Palaemonidae, Pontoniinae, *Hamodactylus macrophthalmus* new species, taxonomy, phylogeny

Introduction

The pontoniine genus *Hamodactylus* Holthuis, 1952, at present contains three named species (De Grave & Fransen 2011), all known from the Indo-West Pacific and associated with Octocorallia: *H. aqabai* Bruce & Svoboda, 1983; *H. boschmai* Holthuis, 1952; and *H. noumeae* Bruce, 1970.

A faunal survey for shallow-water pontoniine shrimps associated with mushroom corals (Scleractinia: Fungiidae) during fieldwork near Lembeh Island, NE Sulawesi, Indonesia, revealed a fourth hitherto unknown species in the genus associated with the fungiid scleractinian *Herpolitha limax* (Esper, 1797). The species is herein described and illustrated, with its systematic position discussed, based on morphological and molecular (COI) data. The holotype is deposited in the Crustacea collection (RMNH.CRUS.) of Naturalis Biodiversity Center, Leiden, the Netherlands, formerly known as Rijksmuseum van Natuurlijke Historie. Abbreviation: pocl., postorbital carapace length.

Material and methods

Sample collection. Specimens were collected during field surveys in northern Sulawesi, Indonesia (2012), and East Sabah, Malaysia (2010), representing all species within the genus *Hamodactylus* known to date. Specimens were preserved in 95% ethanol. Representatives of the pontoniine genus *Palaemonella* were selected as outgroup for the molecular work. Data for specimens studied are given in Table 1. Tissue samples, derived from eggs or pleopods, were preserved in ethanol before DNA extraction. Voucher specimens are stored in the Crustacea collection of Naturalis Biodiversity Center (RMNH.CRUS).

Molecular analysis. Total genomic DNA was extracted from eggs or pleopods using the DNeasy Blood &Tissue Kit (QIAGEN, Hilden, Germany). Incubation lasted overnight for approx. 16 hours. The volume in the elution step was decreased to 120 µL to increase the final DNA concentration. For amplifying mitochondrial COI sequences with a polymerase chain reaction (PCR), the universal primers LCO1490 and HCO2198 (Folmer *et al*. 1994) were used: 5'-GGTCAACAAATCATAAAGATATTGG-3' and 5'-TAAACTTCAGGGTGACCAAAAAATCA-3'. The PCR conditions were as follows: 3 min. at 95°C for initial denaturing, followed by 39 cycles of 15 sec. at 95°C, 30 sec. at 49°C, 40 sec. at 72°C with a final extension for 5 min. at 72°C. Each PCR consisted of 2.5 µL CoralLoad PCR buffer (10x; containing 15mM MgCl2) (QIAGEN), 0.5 µL dNTP's (2.5mM), 1.0 µL of each primer, 0.3 µL Taq DNA polymerase (5 units/µL) (QIAGEN). PCR reactions were performed in volumes of 25 µl. Sequences were generated on an Automatic Sequencer 3730xl at Macrogen, Amsterdam. The obtained sequences were edited in Sequencher (vers. 4.10.1) and aligned with the aid of ClustalW Multiple alignment (vers. 1.4, Thompson *et al.* 1994) incorporated in Bioedit (vers. 5.09, Hall 2001). Of 648 total aligned sites, 197 were variable and informative for maximum parsimony (MP). When sequences were translated to amino acids, 14 of the 216 amino acids were variable and informative for maximum parsimony. Sequences were deposited in GenBank (accession nos. given in Table 1).

TABLE 1. Taxa sampled for molecular analyses with reference to collection registration numbers of voucher specimens, location data, host, and GenBank accession numbers. *Sequences obtained from GenBank.

Taxa	Voucher spec. reg. Nr.	Location
Hamodactylus macrophthalmus **spec. nov.**	RMNH.CRUS.D.55048	Indonesia, NE Sulawesi, Strait Lembeh
Hamodactylus aqabai Bruce & Svoboda, 1983	RMNH.CRUS.D.53969	Malaysia, Sabah, Semporna area, Ligitan Reef
Hamodactylus noumeae Bruce, 1970	RMNH.CRUS.D.53812	Malaysia, Sabah, Semporna area, Creach Reef
Hamodactylus boschmai Holthuis, 1952	RMNH.CRUS.D.53786	Malaysia, Sabah, Semporna area, Larapan Isl.
Hamodactylus boschmai Holthuis, 1952	RMNH.CRUS.D.53814	Malaysia, Sabah, Semporna area, Larapan Isl.
Hamodactylus boschmai Holthuis, 1952	RMNH.CRUS.D.53831	Malaysia, Sabah, Semporna area, Ligitan Reef
Palaemonella rotumana (Borradaile, 1898)	RMNH.CRUS.D.53973	Malaysia, Sabah, Semporna area, Sipanggau Isl.
Palaemonella pottsi (Borradaile, 1915)	RMNH.CRUS.D.53928	Malaysia, Sabah, Semporna area, Ligitan Isl.
Palaemonella pottsi (Borradaile, 1915)	RMNH.CRUS.D.53933	Malaysia, Sabah, Semporna area, Ligitan Isl.

continued.

Taxa	Host class: subclass: order: species	GenBank accession #
Hamodactylus macrophthalmus spec. nov.	Anthozoa: Hexacorallia: Scleractinia: *Herpolitha limax*	KC633177
Hamodactylus aqabai Bruce & Svoboda, 1983	Anthozoa: Octocorallia: Alcyonacea: Nephtheidae	KC633175
Hamodactylus noumeae Bruce, 1970	Anthozoa: Octocorallia: Alcyonacea: *Ellisella* spec.	KC633176
Hamodactylus boschmai Holthuis, 1952	Anthozoa: Octocorallia: Alcyonacea: indet.	KC633174
Hamodactylus boschmai Holthuis, 1952	Anthozoa: Octocorallia: Alcyonacea: *Ellisella* spec.	KC633173
Hamodactylus boschmai Holthuis, 1952	Anthozoa: Octocorallia: Alcyonacea: *Melithea* spec.	KC633172
Palaemonella rotumana (Borradaile, 1898)	Anthozoa: Hexacorallia: Scleractinia: *Pectinia paeonia*	JX85715*
Palaemonella pottsi (Borradaile, 1915)	Crinozoa: Articulata: Comatulida: *Comaster* spec.	JX85713*
Palaemonella pottsi (Borradaile, 1915)	Crinozoa: Articulata: Comatulida: *Comaster* spec.	JX85714*

Data analysis. The best-fitting model for sequence evolution (TIM2+I+G) of the COI dataset was determined by jModelTest (vers. 0.1.1., Posada 2008), selected by the AIC (Akaike Information Criterion), and was subsequently applied to the maximum likelihood (ML) analyses with PAUP* (vers. 4.0b10, Swofford 2003) with 2000 bootstrap reiterations. A maximum parsimony (MP) tree based on sequences translated to amino acids was constructed using PAUP* with 2000 bootstrap reiterations of a simple heuristic search, TBR (tree bisection-reconnection) branch-swapping, and 10 randomly added sequence replications.

Results

Palaemonidae Rafinesque, 1815

Pontoniinae Kingsley, 1879

Hamodactylus Holthuis, 1952

Hamodactylus macrophthalmus spec. nov.
(figs. 1–4)

Material examined. 1 ovigerous female holotype (pocl. 1.5 mm) RMNH.CRUS.D.55048, stn LEM.23, Indonesia, N Sulawesi, Lembeh Strait, Tanjung Kuning, 1º23'10.788"N 125º10'23.2314"E, 11.ii.2012, depth 23.4 m, on *Herpolitha limax* (Esper, 1797), collected by C. Rauch, field collection number S.172.

Comparative material examined. *Hamodactylus aqabai* Bruce & Svoboda, 1983: 1 ovigerous female holotype (pocl. 2.5 mm), RMNH.CRUS.D.33233, Aqaba, Jordan, depth 6 m, 24.ii.1976, on *Litophyton arboreum* Forskål, 1775, collected by A. Svoboda (no. 2398). 1 ovigerous female (pocl. 2.2 mm) RMNH.CRUS.D.53969, stn SEM.09b, Malaysia, Semporna area, Ligitan reef N2, 04º14'57.5"N 118º37'54.0"E, depth 10 m, 1.xii.2010, on nephtheid alcyonarian, collected by Nina Ho. *Hamodactylus boschmai* Holthuis, 1952: 1 ovigerous female (pocl. 1.8) syntype, RMNH.CRUS.D.8999, Snellius Expedition, Indonesia, Ternate, depth 2–4 m, 6.vi.1930, divinghood. 1 ovigerous female (pocl. 3.1 mm), RMNH.CRUS.D.53786, stn SEM.47, Malaysia, Semporna area, Larapan Isl., 04º34'27.5"N 118º36'15.0"E, depth 18 m, 13.xii.2010, on red gorgonarian, collected by Bastian T. Reijnen. 1 female (pocl. 3.1 mm), RMNH.CRUS.D.53814, stn SEM.47, Malaysia, Semporna area, Larapan Isl., 04º34'27.5"N 118º36'15.0"E, depth 20 m, 13.xii.2010, on *Ellisella* spec., collected by C.H.J.M. Fransen. 1 female (pocl. 1.0 mm), RMNH.CRUS.D.53831, stn SEM.09, Malaysia, Semporna area, Ligitan Reef 1 S / Yoshi Point, 04º14'05.8"N 118º33'26.7"E, depth 20 m, 1.xii.2010, on red melitheid, collected by Bastian T. Reijnen. *Hamodactylus noumeae* Bruce, 1970: 1 ovigerous female (pocl. 2.2 mm), RMNH.CRUS.D.53812, stn SEM.20, Malaysia, Semporna area, Creach Reef, 04º18'58.8"N 118º36'17.3"E, depth 5 m, 5.xii.2010, on *Ellisella* spec., collected by Nina Ho.

Description. Very small sized, rather slender pontoniine shrimp (fig. 1A), with slender pereiopods.

Carapace smooth (fig. 1A). Rostrum short (fig. 1B), reaching to middle of basal segment of antennular peduncle; lamina deep, lateral carina indistinct, ventral margin slightly convex, toothless, proximally setose; dorsal margin convex, elevated, strongly compressed, with four subequal teeth, of which first situated above level of posterior margin of orbit. Supra-orbital and epi-gastric spines absent. Orbit obsolescent. Inferior orbital angle feebly produced, rounded in lateral view. Antennal tooth of moderate size, submarginal, situated below inferior orbital angle. Hepatic tooth as large as antennal tooth, situated well behind level of posterior orbital margin and slightly above level of antennal tooth. Antero-lateral angle of carapace blunt, not produced.

Abdominal segments smooth (fig. 1A). Third segment not produced posterodorsally. Pleura all broadly rounded. Posteroventral angle of sixth segment feebly produced, posterolateral angle feebly acute.

Telson 0.9 of length of sixth abdominal segment and 2.4 times longer than maximum width (fig. 1D); lateral margins converge posteriorly; two pairs of moderately sized submarginal dorsal spines present at 0.45 and 0.70 of telson length; posterior margin rounded, about half of anterior width, with three pairs of spines. Lateral spines short, about as long as dorsal spines. Intermediate spines about 0.13 of telson length, 1.3 times length of submedian spines.

Eyes twice as long as rostrum (fig. 1B, C). Cornea globular, obliquely set on stalks, with distinct accessory pigment spot posterodorsally. Eyestalks slightly more than twice as long as proximal width, slightly swollen proximally.

Antennular peduncle normal (fig. 1B, C), exceeding tip of rostrum by half length of proximal segment. Proximal segment long, slender, 2.8 times longer than wide; stylocerite slender, acute, reaching almost to middle of segment; disto-lateral margin straight, anterolateral margin slightly produced, with one distolateral tooth and row of setae; medial ventral margin with distinct acute tooth just before mid length of segment. Statocyst normally developed containing a granular statolith. Intermediate and distal segments short, together equal to 0.36 of proximal segment length. Upper flagellum biramous, with first 4–6 segments fused. Shorter free ramus uni-segmented, longer rami incomplete. Few aesthetascs present. Lower flagellum slender.

Antennal basicerite (fig. 1B, C) without lateral tooth. Ischiocerite and merocerite normal. Carpocerite slender, reaching to 2/3 of scaphocerite. Scaphocerite long, rather narrow, with lamella almost reaching distal margin of antennular peduncle. Lateral border broadly convex, ending in an acute distolateral tooth. Lamella extending far beyond distolateral tooth, feebly angulated distomedially, about 2.7 times longer than broad, with greatest width at about one third of its length.

Fourth thoracic sternite unarmed.

Mandible (fig. 2A, B) with cylindrical molar process bearing a few brushes of setae distally. Incisor process rather slender, with four teeth distally, of which lateralmost slightly enlarged. Mandible without palp.

Maxillula lost during dissection.

Maxilla (fig. 2C) with tapering non-setose palp. Basal endite simple, short, stout and blunt, with about six simple setae distally. Coxal endite obsolete medial region slightly convex. Scaphognathite normal, widest centrally, about 2.8 times longer than broad, with marginal plumose setae.

First maxilliped (fig. 2D) with slender, tapering palp with one subdistal long seta. Basal region broad, not distinctly separated from coxal region. Median margin sparsely provided with setulose and slender simple setae. Caridean lobe distinct, with coarsely setulose plumose marginal setae. Flagellum of exopod well developed, with 4 long plumose terminal setae. Epipod small, indistinctly bilobed.

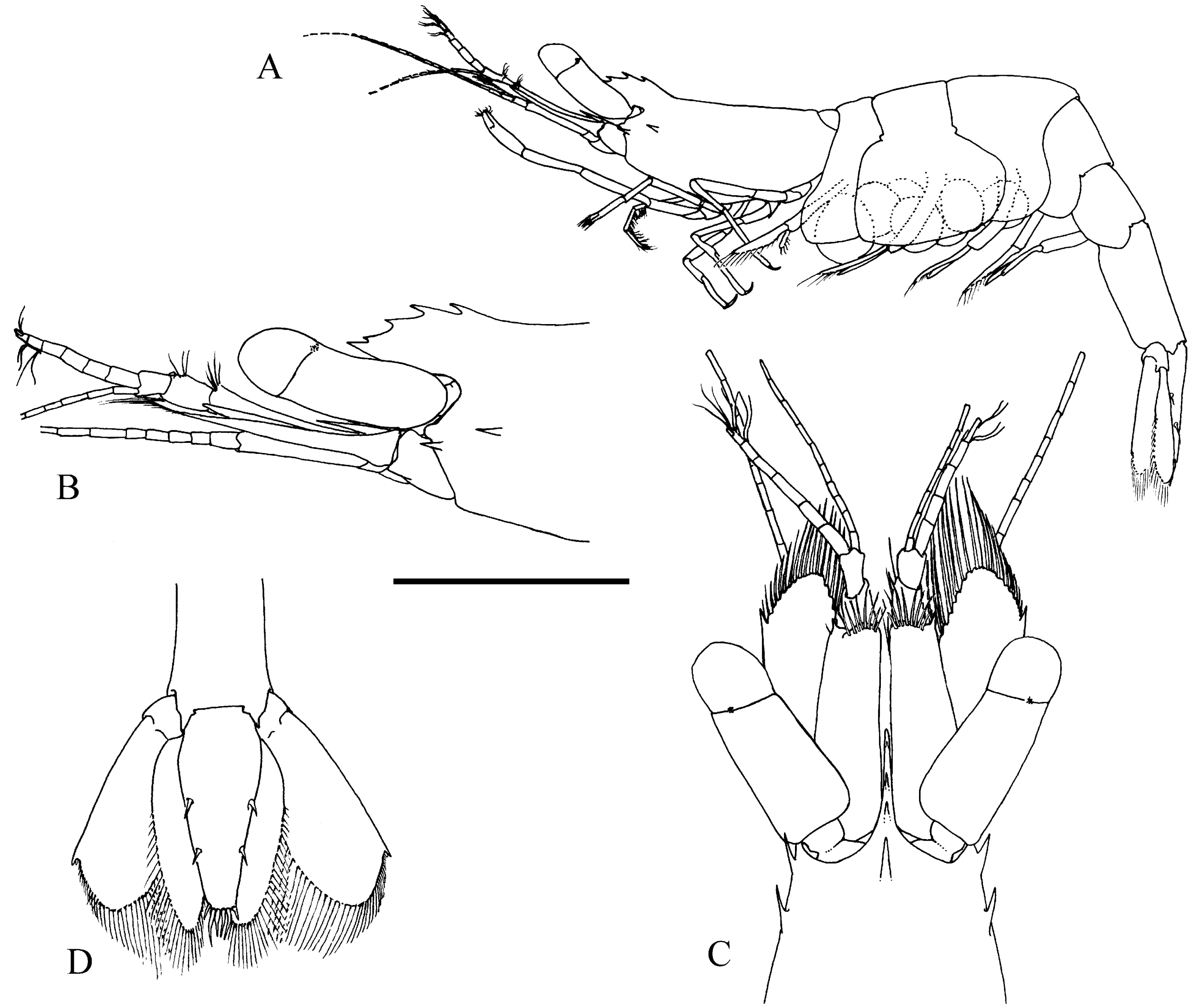

FIGURE 1. *Hamodactylus macrophthalmus* **spec. nov.**, ovigerous female holotype, pocl. 1.5 mm, RMNH.CRUS.D.55048. A, habitus, lateral view; B, anterior carapace and appendages, lateral view; C, anterior carapace and appendages, dorsal view; D, telson and uropods, dorsal view. Scale: A = 2 mm; B–D = 1 mm bar.

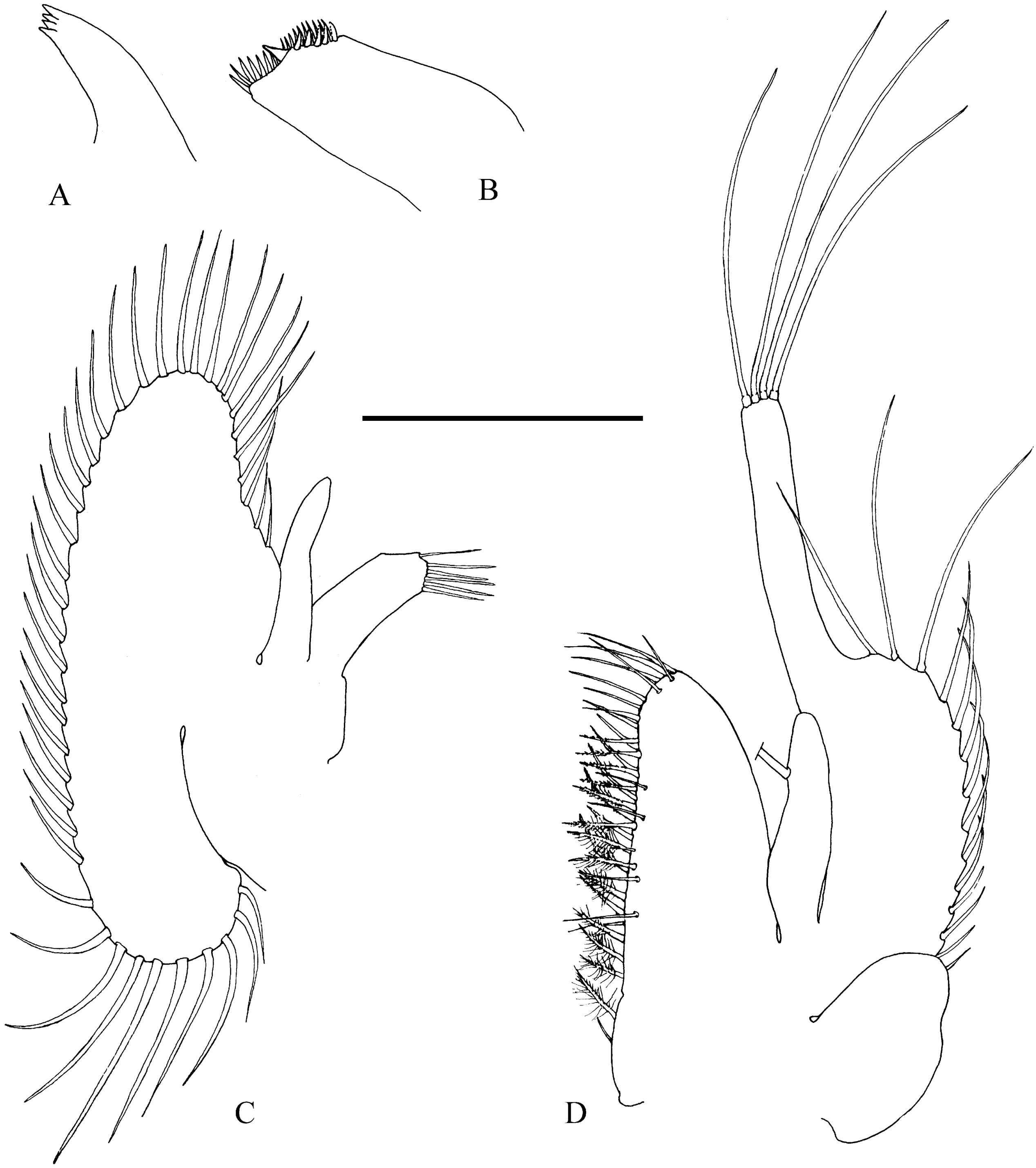

FIGURE 2. *Hamodactylus macrophthalmus* **spec. nov.**, ovigerous female holotype, pocl. 1.5 mm, RMNH.CRUS.D.55048. A, left mandible, incisor process, ventral view; B, idem, molar process, ventral view; C, left maxilla, dorsal view; D, left first maxilliped, ventral view. Scale bar: 0.25 mm.

Second maxilliped (fig. 3A) with broadly triangular dactylar segment, about 3 times broader than long, slightly convex medially, bearing row of stout biserrulate spines. Propodal segment broader than dactylar segment, with subrectangular distomedial angle with few long serrulate setae. Carpus short. Merus partly fused to ischium. Ischium completely fused to basis. Basis without exopod. Coxa not produced medially, with small, rounded epipod laterally.

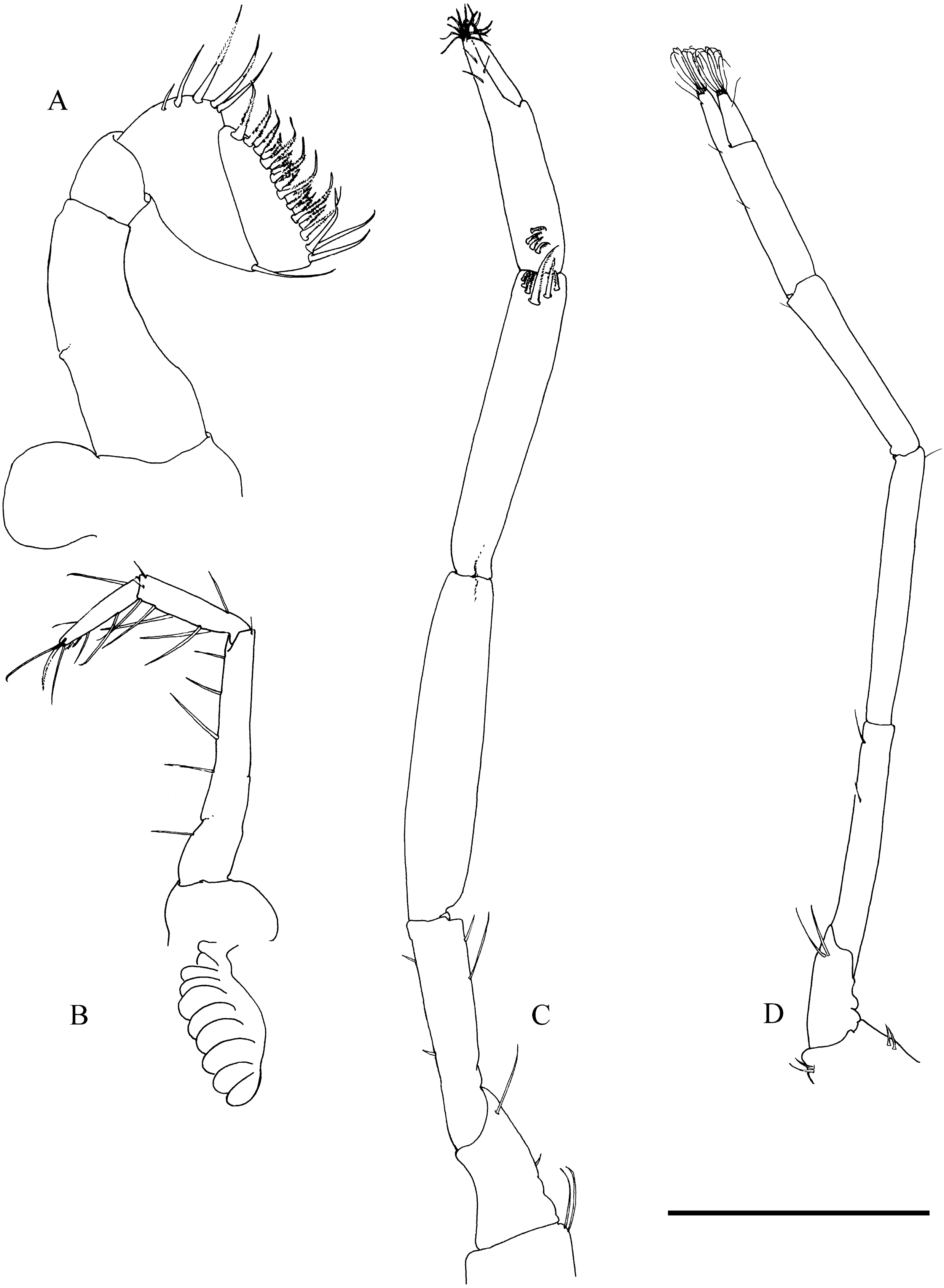

FIGURE 3. *Hamodactylus macrophthalmus* **spec. nov.**, ovigerous female holotype, pocl. 1.5 mm, RMNH.CRUS.D.55048. A, left second maxilliped, dorsal view; B, left third maxilliped, dorsal view; C, left first pereiopod; D, left second pereiopod. Scale bar: A = 0.25 mm; B–D = 0.5 mm.

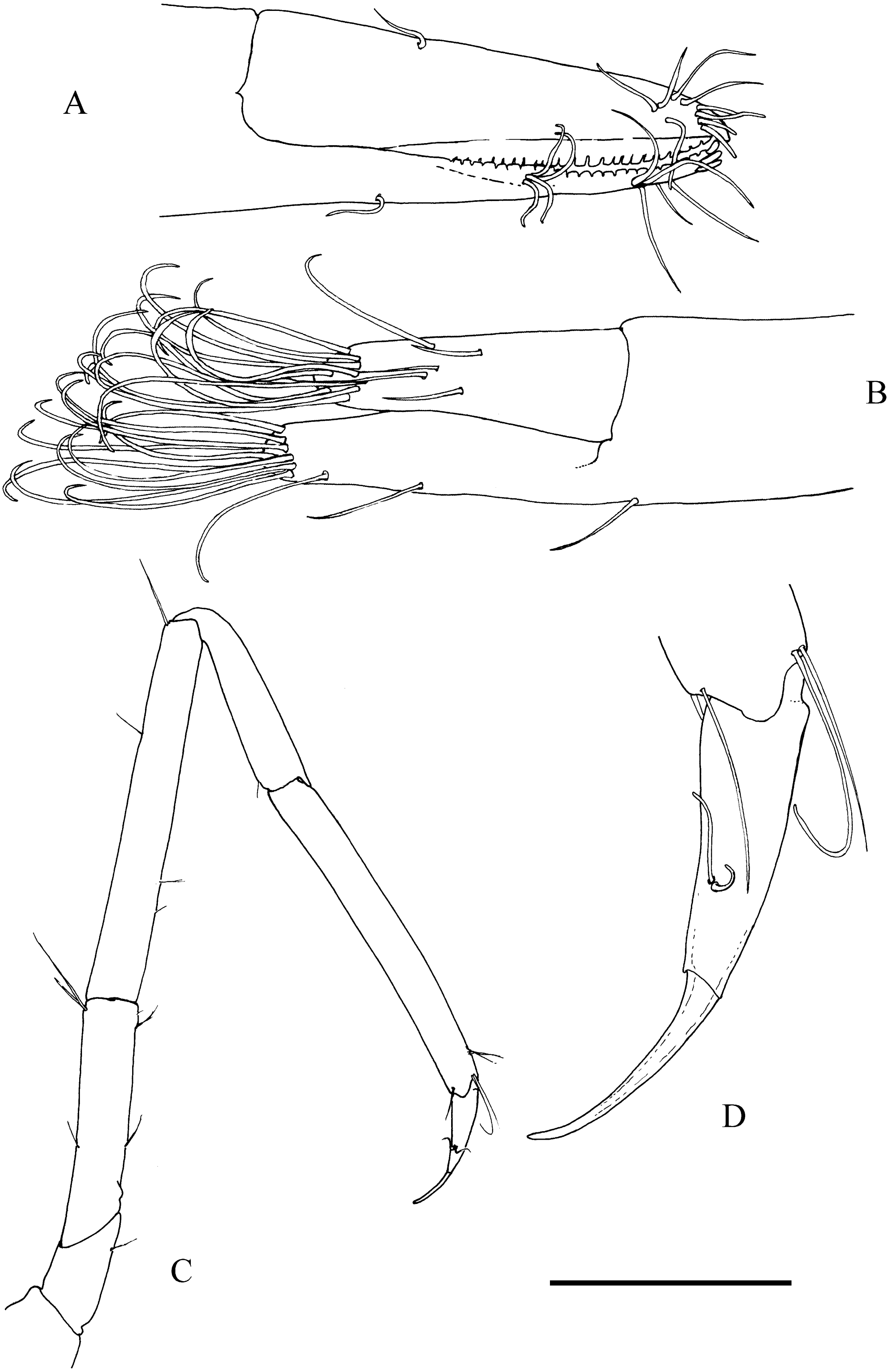

FIGURE 4. *Hamodactylus macrophthalmus* **spec. nov.**, ovigerous female holotype, pocl. 1.5 mm, RMNH.CRUS.D.55048. A, left first pereiopod, fingers; B, left second pereiopod, fingers; C, left third pereiopod; D, idem dactylus. Scale bar: A, B, D = 0.1 mm; C = 0.4 mm.

Third maxilliped (fig. 3B) with slender antepenultimate segment, about 5 times longer than proximal width. Basis completely fused with ischiomerus, junction indicated medially by small knob. Median margin of antepenultimate segment with few simple setae. Penultimate segment slender, 4.5 times longer than wide, 0.44 of length of antepenultimate segment, with few long slender setulose setae on medial border. Terminal segment 4.3 times longer than wide, slightly shorter than penultimate segment, with few serrulate and simple setae medially distally. Exopod absent. Coxa feebly produced medially, with rounded lateral lobe. Multilamellar arthrobranch present laterally.

First pereiopod slender (figs. 3C, 4A), reaching to end of scaphocerite. Chela with palm subcylindrical, slightly bowed, about 3.2 times longer than wide. Fingers 0.58 of palm length, feebly subspatulate with brushes of few setae in distal part. Cutting edges with very thin denticulate lamella laterally in distal 2/3. Tip of dactylus with distinct tooth. Cleaning setae present proximally on palm and distoventral end of carpus. Carpus 1.2 times length of chela, 5.5 times longer than wide. Merus 1.12 times longer than carpus and twice length of ischium. Coxa with very small medial setose process.

Second pereiopods (figs. 3D, 4B) greatly reduced, subequal and similar, only extending slightly beyond carpocerite. Chela atyid-like, with blunt fingers with brushes of distal curled setae, cutting edges not developed. Dactylus distinctly shorter than fixed finger, unguis not developed. Palm subcylindrical, 2.5 times longer than dactylus, 3.8 times longer than wide, unarmed. Carpus, merus and ischium also unarmed, their lengths ratio of 1.3, 1.8 and 1.5 times length of palm. Basis and coxa without special features.

Ambulatory pereiopods (fig. 4C, D) slender, similar, increasing in length from third to fifth. Dactylus slender, uniformly tapering, unarmed, with distinct slender unguis. Total length about five times width near base. Propodus about 9 times longer than wide, 3.6 times length of dactylus, devoid of spines. Carpus, merus and ischium 0.55, 1.1 and 0.65 of propodus length, unarmed.

Pleopods well developed. Marginal plumose setae of exopod and endopod coarsely serrulate.

Uropods (fig. 1D) slender just extending beyond tip of telson. Protopodite unarmed laterally. Exopod about 2.3 times longer than wide, about as long as endopod, with lateral border almost straight, entire, terminating in tooth with small mobile spine medially.

About 30 eggs of ca. 0.5 mm in length present under abdomen.

Colouration. Not recorded.

Etymology. The specific name *macrophthalmus* is a noun composed of the prefix macro- (Gr. makros), = long, and the suffix –opthalmus (Gr. opthalmos), = eye, referring to the eyes with the long eyestalks.

Host. *Herpolitha limax* (Esper, 1797) (Scleractinia), identification confirmed by B.W. Hoeksema, Naturalis Biodiversity Center. The three previously known species of *Hamodactylus* have all been recorded as associated with Octocorallia. The closely related *Hamodactyloides incompletus* is only known from species of the hydrocoral *Millepora* (see Bruce 1976, 1978, 1981, 1983; Fujino 1973 (as *Hamodactyloides ishigakiensis*)). The new species is the first species of the genus *Hamodactylus* recorded in association with a scleractinian coral.

Systematic position

Morphological data. The new species differs from its congeners in (1) having the eyestalks oblong, more than twice their proximal width, versus short, almost as long as wide; (2) possessing an atyid-like chela on the second pereiopods, versus a normal chela with distinct hooked tips or a chela with the fixed finger strongly reduced; (3) having the rostrum very short, not reaching beyond the middle of the basal segment of the antennular peduncle, versus at least reaching the distal margin of the basal segment of the antennular peduncle. It differs from *H. boschmai* in lacking supra-orbital teeth on the carapace. From *H. aqabai* and *H. noumeae*, the new species differs in having the distolateral margin of the basal segment of the antennular peduncle with one tooth, versus multidentate in the above mentioned species.

Molecular data. The hypothesized phylogeny based on COI (fig. 5) shows *Hamodactylus macrophthalmus* to be nested in the *Hamodactylus* clade. The statistical support for its position as sister taxon of *H. boschmai* is, however, low.

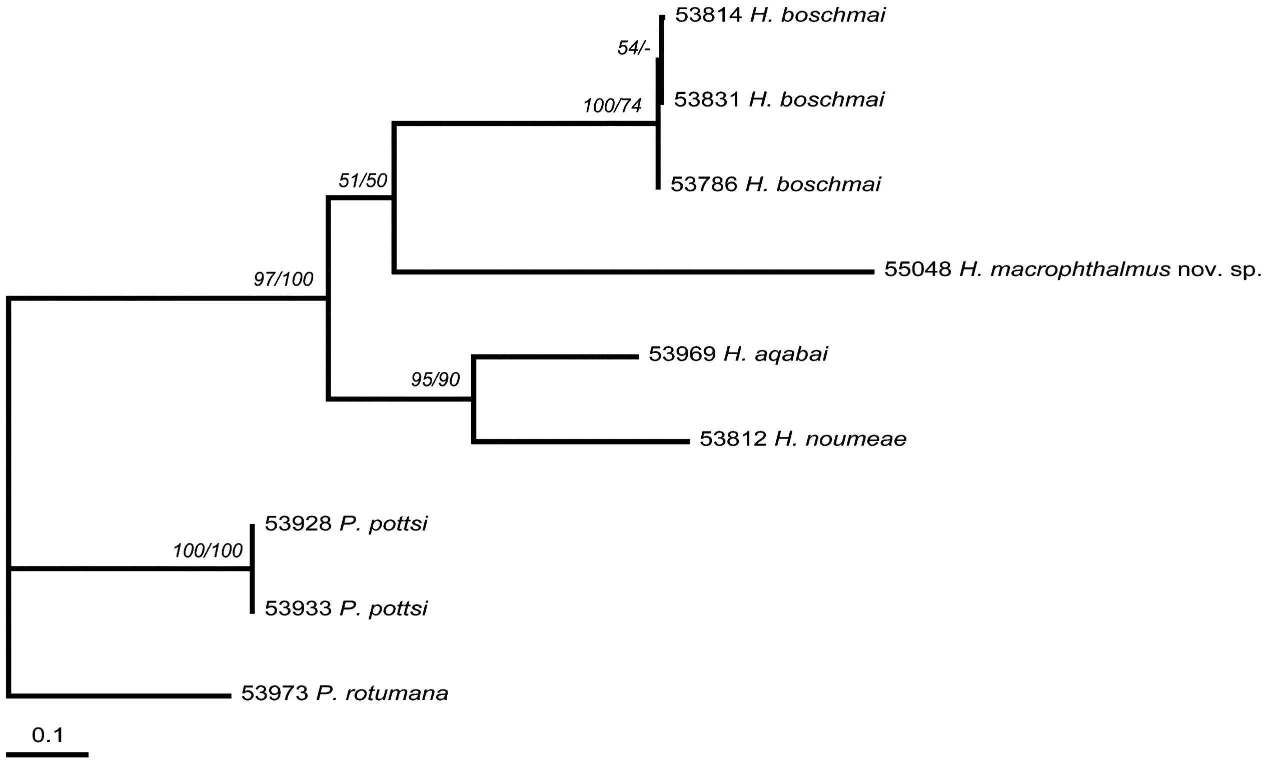

FIGURE 5. Maximum-likelihood tree based on COI sequence data with the TIM2+I+G substitution model; bootstrap values <50% are not shown; bootstrap values are shown in the order ML/MP.

Key to the species of *Hamodactylus* Holthuis, 1952

1. Carapace without supra-orbital tooth 2
- Carapace with supra-orbital tooth . . . . *Hamodactylus boschmai*
2. Second pereiopod non-chelate, fixed finger obsolescent . . . . *Hamodactylus aqabai*
- Second pereiopod with chela, fixed finger about as long as dactylus 3
3. Basal segment of antennular peduncle with multidentate distolateral margin; eyestalk short, about as long as wide . . . .*Hamodactylus noumeae*
- Basal segment of antennular peduncle with one distolateral tooth; eyestalk long, about twice as long as wide . . . .*Hamodactylus macrophthalmus* **spec. nov.**

A new host

The new *Hamodactylus* species is unique in its genus by being associated with a mushroom coral (Anthozoa: Scleractinia) instead of an octocoral (Anthozoa: Alcyonacea). Mushroom corals are known to act as host for a variety of associated animal species, including pontoniinid shrimps (Bos 2012; Hoeksema *et al*. 2012; van der Meij & Hoeksema 2013). A single mushroom coral may even host individuals of various shrimp species (De Grave 1998; Hoeksema & Fransen 2011). The new host, *Herpolitha limax,* is a free-living mushroom coral (Hoeksema 1989), which is so far known to act as the host of three other pontoniine shrimp species (Hoeksema *et al*. 2012). More than 50 species of Fungiidae are recognized, (Gittenberger *et al*. 2011; Benzoni *et al*. 2012) which collectively were known to act as habitat for 18 shrimp species. The new species is therefore the 19th shrimp species recorded so far from mushroom coral hosts.

Acknowledgements

The Marine Biodiversity Workshop at which the new species was collected was organized by Universitas Sam Ratulangi (UNSRAT in Manado) and the Bitung field station of the Research Centre of Oceanography (PPO-LIPI) in cooperation with Naturalis Biodiversity Center. Prof. dr. Suharsono, former director of the Research Centre for Oceanography (PPO-LIPI), is acknowledged for his support. Prof. Dr. Markus T. Lasut (Universitas Sam Ratulangi), Dr. Bert W. Hoeksema (Naturalis) and Ir. Yosephine Tuti (PPO-LIPI) acted as workshop coordinators.

The Semporna Marine Ecological Expedition was jointly organized by WWF-Malaysia, Universiti Malaysia Sabah's Borneo Marine Research Institute, Netherlands Centre for Biodiversity Naturalis and Universiti Malaya's Institute of Biological Sciences. Research permission was granted by Economic Planning Unit, Prime Minister's Department, Economic Planning Unit Sabah, Sabah Parks and Department of Fisheries Sabah. Dr. Bert W. Hoeksema and Ms. Zarinah Waheed acted as expedition leaders for the biodiversity theme.

Fieldwork of the second author was funded by the Jan Joost ter Pelkwijkfonds, the L.B. Holthuis Fonds.

We thank Bastian T. Reijnen and Dick Groenenberg for their help with the molecular analyses. Bert W. Hoeksema is acknowledged for the identification of the host coral. Sammy De Grave (Oxford University Museum of Natural History, Oxford, UK) and Zdeněk Ďuriš (University of Ostrava, Ostrava, Czech Republic) kindly reviewed the manuscript and made a number of useful comments.

Literature cited

Benzoni, F., Arrigoni, R., Stefani, F., Reijnen, B.T., Montano, S. & Hoeksema, B.W. (2012) Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): lost mushroom corals find their way home. *Contributions to Zoology*, 81, 125–146.

Bos, A.R. (2012) Fishes (Gobiidae and Labridae) associated with the mushroom coral *Heliofungia actiniformis* (Scleractinia: Fungiidae) in the Philippines. *Coral Reefs*, 31, 133. http://dx.doi.org/10.1007/s00338-011-0834-3

Bruce, A.J. (1970) Report on some commensal pontoniid shrimps (Crustacea: Palaemonidae) associated with an Indo-Pacific gorgonian host (Coelenterata: Gorgonacea). *Journal of Zoology, London*, 160, 537–544. http://dx.doi.org/10.1111/j.1469-7998.1970.tb03096.x

Bruce, A.J. (1976a) A report on a small collection of shrimps from the Kenya National Marine Parks at Malindi, with notes on selected species. *Zoologische Verhandelingen*, 145, 1–72.

Bruce, A.J. (1976b) A synopsis of the pontoniinid shrimp fauna of Central East Africa. *Journal of the marine biological Association of India*, 16, 462–490.

Bruce, A.J. (1981) Some pontoniine shrimps from the Solomon Islands. *Micronesica*, 17, 261–269.

Bruce, A.J. (1983) The pontoniine shrimp fauna of Australia. *Australian Museum Memoirs*, 18, 195–218. http://dx.doi.org/10.3853/j.0067-1967.18.1984.385

Bruce, A.J. & Svoboda, A. (1983) Observations upon some pontoniine shrimps from Aqaba, Jordan. *Zoologische Verhandelingen*, 205, 1–44.

De Grave, S. (1998) Pontoniinae (Decapoda, Caridea) associated with *Heliofungia actiniformis* (Scleractinia) from Hansa Bay, Papua New Guinea. *Belgian Journal of Zoology*, 128, 13–22.

De Grave, S. & Fransen, C.H.J.M. (2011) Carideorum catalogus: the Recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). *Zoologische Mededelingen*, 85, 195–589.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3(5), 294–299.

Fujino, T. (1973) A new genus of pontoniid shrimp, *Hamodactyloides*, with a description of *H. ishigakiensis* sp. nov. (Decapoda Natantia, Pontoniinae), from the Ryukyu Islands. *Crustaceana*, 25, 171–180. http://dx.doi.org/10.1163/156854073X00812

Gittenberger, A., Reijnen, B.T. & Hoeksema, B.W. (2011) A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contributions to Zoology*, 80, 107–132.

Hall, T.A. (2001) Bioedit: A User-Friendly Biological Sequence Alignment Editor and Analysis, version 5.09. Department of Microbiology, North Carolina State University, North Carolina.

Hoeksema, B.W. (1989) Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zoologische*

Verhandelingen, 254, 1–295.
Hoeksema, B.W. & Fransen, C.H.J.M. (2011) Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. *Coral Reefs*, 30, 519. http://dx.doi.org/10.1007/s00338-011-0736-4
Hoeksema, B.W., Meij, S.E.T. van der & Fransen, C.H.J.M. (2012) The mushroom coral as a habitat. *Journal of the Marine Biological Association of the United Kingdom*, 92, 647–663. http://dx.doi.org/10.1017/S0025315411001445
Holthuis, L.B. (1952) The Decapoda of the Siboga Expedition. Part XI. The Palaemonidae collected by the Siboga and Snellius Expeditions with remarks on other species. II. Subfamily Pontoniinae. *Siboga Expeditie*, 39a10, 1–253.
Kingsley, J.S. (1879) List of the North American Crustacea belonging to the suborder Caridea. *Bulletin of the Essex Institute*, 10(for 1878), 53–71.
Meij, S.E.T. van der & Hoeksema, B.W. (2013) Distribution of gall crabs inhabiting mushroom corals on Semporna reefs, Malaysia. *Marine Biodiversity.* http://dx.doi.org/10.1007/s12526-012-0135-2
Posada, D. (2008) jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution*, 25, 1253–1256. http://dx.doi.org/10.1093/molbev/msn083
Rafinesque, C.S. (1815) Analyse de la nature ou tableau de l'univers et des corps organisés: 1–224. (Palermo).
Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680. http://dx.doi.org/10.1093/nar/22.22.4673