

Four new species and one new genus of zoanthids (Cnidaria, Hexacorallia) from the Galápagos Islands

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Abstract

Recent research has confirmed the presence of several species of undescribed macrocnemic zoanthids (Cnidaria: Hexacorallia: Zoantharia: Macrocnemina) in the Galápagos. In this study four new species, including two belonging to a new genus, are described. Two species, *Terrazoanthus onoi* **sp. n.** and *Terrazoanthus sinnigeri* **sp. n.**, both belong within the recently erected family Hydrozoanthidae to the new genus *Terrazoanthus*, which can be distinguished from the type genus *Hydrozoanthus* by being attached to abiotic substrate as opposed to hydrozoans for *Hydrozoanthus*. Each new species of zoanthid can be clearly distinguished by a number of characters. *Antipathozoanthus hickmani* **sp. n.** is distinguished by its exclusive association with the antipatharian *Antipathes galapagensis*, and has approximately 40 tentacles. *Parazoanthus darwini* **sp. n.** is distinguished by its frequent association with sponges, with approximately 24–30 tentacles and polyps embedded in a well-developed coenenchyme. *T. onoi* **sp. n.** is distinguished by its bright red oral disk color, 32–40 tentacles, and has only basitrichs and mastigophores present in the pharynx. *T. sinnigeri* **sp. n.** is distinguished by usually occurring on the underside of rubble and rocks on sandy bottoms, showing 30–36 tentacles, and numerous nematocyst types in the pharynx. The two *Terrazoanthus* species, although divergent in both morphology and ecology, are apparently very closely related,

with identical mitochondrial 16S ribosomal DNA and cytochrome oxidase subunit I sequences. These two species can be molecularly distinguished by their subtly different yet distinct sequences of internal transcribed spacer of ribosomal DNA (ITS-rDNA).

Keywords

Key words: zoanthid, Galápagos, new genus, new species, ITS-rDNA, mt DNA

Introduction

The Galápagos Archipelago is a group of oceanic islands in the south-east Pacific. The islands are surrounded by warm and cold ocean currents that include upwelling currents. As a result of these currents, the marine ecosystems of the Galápagos islands are isolated from other regions, and there are high levels of diversity and unique fauna (Bustamante et al. 2000, 2002). The marine area of the Galapagos islands was inscribed as a UNSECO natural World Heritage Site in 1978. However, as the Galápagos islands are becoming increasingly famous and numbers of tourist visits rise, environmental pollution and other associated problems have arisen. Since 2007 the Galápagos have been designated as a World Heritage Site in danger.

Recently, the marine fauna of the Galápagos has begun to become more intensively investigated. Some results have been published as the Galápagos Marine Life Series field guides. One of these guides is focused on corals, zoanthids, octocorals and other benthic cnidarians of the Galápagos (Hickman 2008). The results of these investigations have demonstrated that there are many unidentified species in the order Zoantharia in the Galápagos (Reimer et al. 2008a).

However, zoanthids (Cnidaria, Anthozoa, Hexacorallia, Zoantharia) form a taxonomical group for which studies are lacking in general. Zoanthids are an order of benthic cnidarians that are found in most marine ecosystems (Sinniger et al. 2005; Reimer et al. 2007). Distinguishable by their two rows of tentacles, incorporation of sand into their mesoglea, and colonial nature (for most described species) (Sinniger et al. 2005), zoanthids are increasingly becoming a subject of research as they possess unique bioactive compounds and chemicals (Behenna et al. 2008). Despite this increase in research, the classification and identification of many zoanthids remains difficult due to a myriad of problems, including but not limited to morphological variation within species, a lack of research into their species diversity, and difficulty in internal morphological examinations due to the presence of sand and detritus (Reimer et al. 2010). Consequently, the true number of zoanthid species is currently unknown (Reimer et al. 2004).

However, studies using molecular techniques have begun to bring some standardization and reassessment to zoanthid taxonomy. Allozymes (Burnett et al. 1997), mitochondrial DNA (mt DNA) (Reimer et al. 2004; Sinniger et al. 2005) and nuclear DNA phylogenies (Reimer et al. 2007b; Swain 2009) combined with ecological data have resulted in the creation of new taxa (Sinniger and Häussermann 2008; Reimer et al. 2008a; Sinniger et al. 2009) and the merging of other taxa (e.g. Reimer et al. 2006).

With a molecular phylogenetic framework in place, recent research into zoanthids has focused on diversity in insular and previously under-investigated locations, such as New Caledonia (Sinniger 2008), the deep-sea (Reimer et al. 2007a), and the Galápagos (Reimer et al. 2008b, 2009).

Recent investigations into the diversity of zoanthids in the Galápagos revealed the presence of several new zoanthid species groups (Reimer et al. 2008b). In this study, four species and one new genus of zoanthids from the Galápagos are formally described, and the proposed future of zoanthid research in the southeastern Pacific is briefly discussed.

Materials and methods

Sample collection: Specimens were collected by hand intertidally, or by SCUBA or snorkeling from numerous sites at the Galápagos between June 2001 and March 2007. As specimens were collected, in situ digital images were taken to assist in identification and morphological analyses (oral disk/polyp diameter, color, polyp form, etc.). After collection specimens were further examined, photographed, and preserved in 75% ethanol. Specimens in this study consist of specimens initially described as *Parazoanthus* sp. G1, *Parazoanthus* sp. G2, and *Parazoanthus* sp. G3 in Reimer et al. (2008b, 2010).

DNA extraction and PCR amplification: DNA was extracted as described in Reimer et al. (2008a), using a spin-column Dneasy Blood and Tissue Extraction protocol (Qiagen, Santa Clarita, CA, USA). Mitochondrial 16S ribosomal DNA (mt 16S rDNA) was amplified using primers and protocol described in Sinniger et al. (2005), the cytochrome oxidase subunit I (COI) gene was amplified following Reimer et al. (2004, 2007a), and the internal transcribed spacer region of ribosomal DNA (ITS-rDNA) following Reimer et al. (2007b). PCR amplification procedures for each of the molecular markers were as given in the original references above. Amplified products were visualized by 1.5% agarose gel electrophoresis.

Phylogenetic analyses: New sequences obtained in the present study (Table 1) were deposited in DDBJ and GenBank (accession numbers GU357551-GU357567). By using CLUSTAL X version 1.8 (Thompson et al. 1997), the nucleotide sequences of mt 16S rDNA, COI, and ITS-rDNA from samples were aligned with previously published sequences (see Reimer et al. 2008b) from various zoanthid species representing the genera *Zoanthus*, *Savalia*, *Corallizoanthus*, *Mesozoanthus*, *Hydrozoanthus*, and *Parazoanthus*.

The outgroup sequences for both mt 16S rDNA and COI trees were from the genera *Zoanthus* and/or *Palythoa*. The only zoanthid genera not included in both analyses were *Epizoanthus*, previously shown to be basal in the order Zoantharia phylogeny for both mt 16S rDNA and COI (Sinniger et al. 2005; Reimer et al. 2007a); *Abyssozoanthus*, demonstrated to be divergent from other zoanthids for both mt 16S rDNA and COI (Reimer et al. 2007a), and *Sphenopus*, which is in the same family as one of the out-

groups of this study, *Palythoa* (family Sphenopidae). These represent the current full range of described zoanthid genera. New mt 16S rDNA sequences from specimens in this study were clearly divergent when compared with *Mesozoanthus* sequences, but *Mesozoanthus* sequences from Sinniger and Häussermann (2009) were not included in trees presented in this study due to their relatively short length (469 base pairs).

Hydrozoanthidae ITS-rDNA sequences (particularly ITS-1 and ITS-2 spacers) were highly divergent from other obtained ITS-rDNA sequences, and thus initially an ITS-rDNA alignment consisting only of Hydrozoanthidae sequences with sequence AB214161 from *Hydrozoanthus gracilis* Carlgren (Reimer et al. 2007c) plus two new *H. gracilis* specimen sequences as the outgroup was generated. The new Galapagos specimens were shown to form a very well supported monophyletic group, and therefore to improve resolution, subsequently an alignment was created with only these sequences. An ITS-rDNA phylogeny from a previous study shows the monophylies and positions of non-Hydrozoanthidae species discussed in this study (*Parazoanthus* sp. G1, *Parazoanthus* sp. G2; both *sensu* Reimer et al. 2008b; see Figure 7 in Reimer et al. 2008b).

All alignments were inspected by eye and manually edited by removing all ambiguous sites (if present) of the alignments (*e.g.* sites present in either only forward or reverse directions, not seen in any other sequence) from the dataset for phylogenetic analyses, and aligning mt 16S rDNA and ITS-rDNA indels as in previous studies (Reimer et al. 2008b; Sinniger et al. 2009). Consequently, three alignment datasets were generated: 1) 651 sites of 39 sequences (mt 16S rDNA); 2) 280 sites of 45 sequences (COI); and 3) 595 sites of 14 sequences (ITS-rDNA). The alignment data are available on request from the corresponding author.

The alignments of mt 16S rDNA, COI, and ITS-rDNA were tested for optimal fit of various nucleotide substitution models using jModelTest version 0.1.1 (Posada 2008). For the mt 16S rDNA dataset, the general time reversible (GTR) model (Rodriguez et al. 1990) incorporating variable sites and a discrete gamma distribution (GTR + I + G) was suggested by jModelTest under Akaike Information Criterion (AIC), while the Hasegawa, Kishino and Yano model (Hasegawa et al. 1985) incorporating variable sites (HKY + I) was suggested for the COI dataset, and the K80 model (Kimura 1980) was suggested for the ITS-rDNA dataset. The maximum-likelihood (ML) analyses with PhyML (Guindon and Gascuel 2003) of these datasets were independently performed using an input tree generated by BIONJ (Gascuel 1997) with the models selected by jModelTest. PhyML bootstrap trees (1000 replicates) were constructed using the same parameters as the individual ML tree.

Bayesian trees were reconstructed by using the program MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) under the K80 model incorporating variable sites of nucleotide substitution (K80 + I) for the mt DNA 16S rDNA and COI datasets, and under the Jukes and Cantor model (JC69; Jukes and Cantor 1969) for the ITS-rDNA dataset [all models selected by jModelTest under Bayes Information Criterion]. One cold and three heated Markov chain Monte Carlo (MCMC) chains with default-chain temperatures were run for 20 million generations, sampling log-likelihoods (lnLs), and trees at 1000-generation intervals (20,000 lnLs and trees were saved during MCMC). The first

15% of all runs were discarded as “burn-in” for all datasets. The likelihood plots for all three datasets also showed that MCMC reached the stationary phase by this time. Thus, the remaining 17,000 trees (17 million generations) of mt 16S rDNA, COI and ITS-rDNA were used to obtain posterior probabilities and branch-length estimates, respectively.

Morphological analyses: The external morphology of specimens was examined using both preserved specimens and in situ images. Polyp dimensions (oral disk diameter, polyp height) for both in situ and preserved specimens were obtained, as were the following data: tentacle number, color of polyp, color(s) of oral disk, relative amount of sand encrustation, associated/substrate species. Additionally, the relative development of the coenenchyme was examined.

For internal morphological examinations, some specimens underwent initial decalcification followed by desilification as outlined in Reimer et al. (2010). After these treatments, specimens were dehydrated through an ethanol-xylene series. Some specimens in 100% ethanol were placed *in vacuo* for approximately 30 minutes to remove bubbles in the coelenteron. Then, they were embedded in paraffin. Serial sections of 5–10 µm thick were prepared with a rotary microtome and stained with Delafield’s hematoxylin and eosin.

Obtained slides of HF-treated zoanthid specimens were examined with a light microscope (Nikon Express E50i). The following morphological characters and conditions were examined; mesentery condition, number, and form (in particular fifth mesentery from dorsal directive complete or incomplete); presence or absence of drag marks from debris; presence or absence of sand and debris in mesoglea; overall condition of tissue and cells; and in particular ectoderm and endoderm; any other morphological characters of note (e.g. presence of gametes, etc.) (described in Reimer et al. 2010).

Nematocyst observation: Undischarged nematocysts were measured from tentacles, column, actinopharynx, and mesenterial filaments of polyps (specimens examined $n=2-4$; polyp $n=4-8$) for all new species. 400x images of the nematocysts were obtained by optical microscope, and measured using the software ImageJ (National Institutes of Health, USA). Nematocyst nomenclature generally followed England (1991), however both Schmidt (1974) and Hidaka and co-workers (1987; 1992) have previously suggested basitrichs and mastigophores are same type of the nematocyst, and thus in this study, these two types were dealt with as the same type, unless they could be clearly distinguished from one another, in which case they were analyzed separately.

Abbreviations used:

- USNM** National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
CMNH Coastal Branch of Natural History Museum and Institute, Chiba, Japan
MHNG Natural History Museum of Geneva, Switzerland
MISE Molecular Invertebrate Systematics and Ecology Laboratory, University of the Ryukyus, Nishihara, Okinawa, Japan

Systematics

Family Parazoanthidae Delage & Hérourard, 1901

Diagnosis: Macrocnemic zoanths that have an endodermal sphincter muscle. Many species in this family associated with other organisms as substrate.

Genus *Antipathozoanthus* Sinniger, Reimer & Pawlowski, 2009

Type species: *Antipathozoanthus macaronesicus* (Ocaña & Brito, 2004)

Diagnosis (from Sinniger et al. 2009): Unlike other described zoanthid genera, *Antipathozoanthus* is found on living antipatharians (Hexacorallia: Antipatharia), and unlike gorgonian-associated *Savalia*, does not appear to secrete its own scleroproteinous axis. Colonial zoanths, polyps linked together by a basal coenenchyme usually covering all of antipatharian substrate axis, size of expanded oral disks usually between 4–12 mm width and 4–15 mm high. Column lightly incrustated with fine sediments, not completely covering ectoderm. Column and tentacles often yellowish, pinkish, cream or red. Mesenteries follow macrocnemic organisation. Distributed in tropical and subtropical area at depths ranging from 10 m to 45 m.

Antipathozoanthus hickmani sp. n.

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Figures 1, 5, 7, 9, Tables 1, 2, 3

Etymology. Named after Dr. Cleveland Hickman, Jr., who graciously invited the first author to the Galápagos, and collected the first specimens of this new species. Noun in the genitive case.

Material examined. *Type locality:* Ecuador, Galapagos: Floreana I., La Batielle, 1.2904°S 90.4989°W.

Holotype: Specimen number MHNG-INVE-67495. Colony of approximately 40 polyps connected by well-developed coenenchyme on two branches of *Antipathes galapagensis* Diechmann, 1941 branches. Both branches approximately 7 cm long. Polyps approximately 1.5–4.0 mm in diameter, and approximately 1.0–6.0 mm in height from coenenchyme. Coenenchyme covers branches of antipatharian. Polyps and coenenchyme sand encrusted, cream-yellow in color. Collected from La Batielle, Floreana I., Galapagos, Ecuador, at 31.4 m by A. Chiriboga (AC), March 13, 2007. Preserved in 99.5% ethanol.

Paratypes (all from Galapagos, Ecuador):

Paratype 1. Specimen number CMNH-ZG 05883. Collected from Roca Onan, Pinzon I., at 27 m by AC, March 14, 2007.

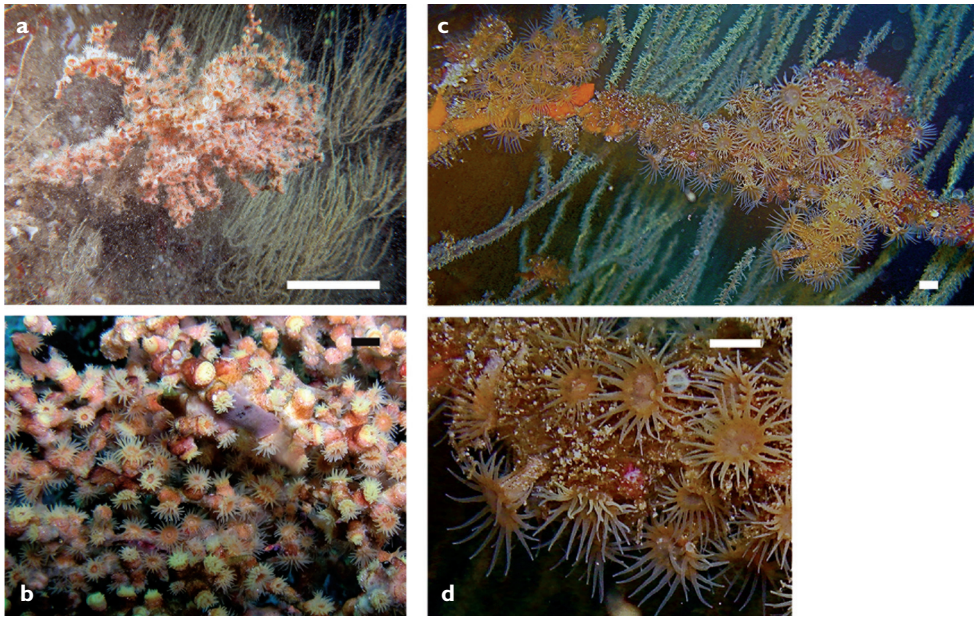


Figure 1. *Antipathozoanthus hickmani* sp. n. in situ in the Galapagos. **a** holotype MHNG-INVE-67495 showing the entire colony covering an *Antipathes galapagensis*, with living antipatharians visible in the background. Image by Angel Chiriboga (AC) **b** specimen MISE 441 at Don Ferdi, Bainbridge Rocks, Santiago I., at 23 m by JDR, March 9, 2007 **c** and **d** specimen MISE 474, Roca Onan. Pinzon I., at 35 m by AC. All scale bars: 1 cm except in **a** (10 cm).

Paratype 2. Specimen number USNM 1134064. Collected from Cousins Rock, at 28 m by James D. Reimer (JDR), March 10, 2007.

Other material (all from Galapagos, Ecuador): MISE 03-221, Cousins Rock, at 12 m by AC on October 9, 2003; MISE 03-539, Cousins Rock, at 20 m by CH on November 11, 2003; MISE 03-549, Cousins Rock, at 23 m by CH on November 11, 2003; MISE 04-341, Elizabeth Bay, Isabela I., at 25 m by G. Edgar (GE) on December 2, 2003; MISE 440, Don Ferdi, Bainbridge Rocks, at 22 m by JDR, March 9, 2007; MISE 441, Don Ferdi, Bainbridge Rocks, at 23 m by JDR, March 9, 2007; MISE 444, Cousins Rock, Galapagos, Ecuador, at 21 m JDR, March 10, 2007; MISE 474, La Batielle, Floreana I., at 35 m by AC, March 14, 2007.

Sequences. See Table 1.

Description. *Size:* Polyps in situ approximately 4–12 mm in diameter when open, and approximately 4–15 mm in height.

Morphology: *Antipathozoanthus hickmani* has approximately 40 bright yellow and/or red tentacles, with long red, yellow, or cream-colored polyps that extend well clear of the coenenchyme (Figure 1). Tentacles are almost always longer than the expanded oral disk diameter.

Cnidae: Basitrichs and microbasic p-mastigophores (often difficult to distinguish), holotrichs (large and medium), spirocysts (see Table 2, Figure 9).

Table 1. Examined zoanthid specimens for new species from the Galapagos Islands, and GenBank Accession Numbers.

Collection no. ^a	Collection locality	Latitude ^b	Longitude ^b	Date collected	Depth (m)	Collected by ^c	Oral disk color	Substrate	COI Accession Number	mt 16S rDNA Accession Number	ITS-rDNA Accession Number	Taxonomic identification
03–221	Cousins Rock	-0.2370	-90.5731	2003.10.9	12	AC	Yellow	<i>Antipathes galapagensis</i>	NA	EU333755	EU333797	<i>Antipathozoanthus hickmani</i>
03–539	Cousins Rock	-0.2370	-90.5731	2003.11.11	20	CH	Cream yellow	<i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>
03–549	Cousins Rock	-0.2370	-90.5731	2003.11.11	23	CH	Yellow	Dead <i>Antipathes galapagensis</i>	EU333783	EU333756	EU333798	<i>Antipathozoanthus hickmani</i>
04–341	Isabela: Elizabeth Bay	-0.5996	-91.09059	2004.12.2	25	GE	NA	Dead <i>Antipathes galapagensis</i>	EU333790, EU333796	EU333757	NA	<i>Antipathozoanthus hickmani</i>
440	Bainbridge Rocks: Don Ferdi	-0.2100	-90.567	2007.3.9	22	JDR	Red	<i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>
441	Bainbridge Rocks: Don Ferdi	-0.2100	-90.567	2007.3.9	23	JDR	Red	<i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>
USNM 1134064	Cousins Rock	-0.2370	-90.5731	2007.3.10	28	JDR	Red	<i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>
444	Cousins Rock	-0.2370	-90.5731	2007.3.10	21	JDR	Red	Dead <i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>
MHNG 67495	Floreana: La Borella	-1.2904	-90.4989	2007.3.13	31	AC	Pale yellow	<i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>
474	Pinzon: Roca Onan	-0.5909	-90.6860	2007.3.14	35	CH, RP, AC	Red	<i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>
CMNH ZG05883	Pinzon: Roca Onan	-0.5909	-90.6860	2007.3.14	27	AC	Red	<i>Antipathes galapagensis</i>	NA	NA	NA	<i>Antipathozoanthus hickmani</i>

Collection no. ^a	Collection locality	Latitude ^b	Longitude ^b	Date collected	Depth (m)	Collected by ^c	Oral disk color	Substrate	COI Accession Number	mt 16S rDNA Accession Number	ITS-rDNA Accession Number	Taxonomic identification
03–47	Isabela: Punta Vicente Roca	-0.0558	-91.5604	2003.1.16	2	CH	Pink	Lava rock	EU333778	EU333749	EU333801	<i>Panzoanthus darwini</i>
03–177	Gordon Rocks	-0.5660	-90.1406	2003.1.22	18	CH	Pink	Lava rock	EU333781	EU333753	EU333799	<i>Panzoanthus darwini</i>
03–290	Fernandina: Cape Douglas	-0.30037	-91.6483	2003.8.25	6	AC	Red-yellow	Rock/debris	EU333782	EU333748	EU333800	<i>Panzoanthus darwini</i>
03–652	Isabela: Tagus Cove	-0.2677	-91.3723	2003.1.16	13	CH	NA	Live red sponge	EU333786	EU333752	NA	<i>Panzoanthus darwini</i>
04–155	Floreana: La Borella	-1.2904	-90.4989	2004.5.25	12	AC	Cream yellow	Lava rock	EU333788	EU333754	NA	<i>Panzoanthus darwini</i>
04–184	Isabela: Las Marietas	-0.5996	-91.0906	2004.12.2	6	AC	Pink-red	Live sponge & rock	GU357559	NA	NA	<i>Panzoanthus darwini</i>
04–328	Isabela: Las Marietas	-0.5996	-91.0906	2004.12.2	3	AC	NA	Live sponge	EU333789	EU333750	NA	<i>Panzoanthus darwini</i>
04–348	Isabela: Caleta Iguala	-0.9945	-91.4454	2004.12.3	9	CH	NA	Rock	EU333795	EU333751	EU333802	<i>Panzoanthus darwini</i>
412	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	6	JDR, CH, FL	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
413	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	7	JDR, CH, FL	Yellow	Rock	NA	NA	NA	<i>Panzoanthus darwini</i>
USNM 1134065	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	8	JDR, CH, FL	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
CMNH ZG05884	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	8	JDR, CH, FL	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
MHNG 67497	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	8	JDR, CH, FL	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
417	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	NA	JDR, CH, FL	Yellow	Rock	NA	NA	NA	<i>Panzoanthus darwini</i>

Collection no. ^a	Collection locality	Latitude ^b	Longitude ^b	Date collected	Depth (m)	Collected by ^c	Oral disk color	Substrate	COI Accession Number	mt 16S rDNA Accession Number	ITS-rDNA Accession Number	Taxonomic identification
424	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	9	JDR, FL, BR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
425	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	9	JDR, FL, BR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
428	Wolf: El Elefante	1.3726	-91.8249	2007.3.5	24	DR, FR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
429	Wolf: El Elefante	1.3726	-91.8249	2007.3.5	21	DR, FR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
430	Wolf: El Elefante	1.3726	-91.8249	2007.3.5	22	JDR, OB, BR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
431	Wolf: El Elefante	1.3726	-91.8249	2007.3.5	21	JDR, OB, BR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
450	Gordon Rocks	-0.5660	-90.1406	2007.3.11	17	JDR	Tan	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
451	Gordon Rocks	-0.5660	-90.1406	2007.3.11	21	JDR	Tan	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
452	Gordon Rocks	-0.5660	-90.1406	2007.3.11	17	AC	Tan	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
456	San Cristobel: Whale Rock	-0.8868	-89.6308	2007.3.12	17	JDR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
458	San Cristobel: Kicker Rock	-0.7797	-89.5219	2007.3.12	15	JDR	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
461	Espanola: Baho Garden	-1.3646	-89.6353	2007.3.12	10	MV	NA	Rock	NA	NA	NA	<i>Panzoanthus darwini</i>
466	Floreana: Gardner	-1.3329	-90.2953	2007.3.13	15	JDR, AC	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>
468	Floreana: Gardner	-1.3329	-90.2953	2007.3.13	14	JDR, CH	Yellow	Sponge	NA	NA	NA	<i>Panzoanthus darwini</i>

Collection no. ^a	Collection locality	Latitude ^b	Longitude ^b	Date collected	Depth (m)	Collected by ^c	Oral disk color	Substrate	COI Accession Number	mt 16S rDNA Accession Number	ITS-rDNA Accession Number	Taxonomic identification
470	Floreana: Devil's Crown	-1.2144	-90.4238	2007.3.13	9	JDR, MV	Yellow	Sponge	NA	NA	NA	<i>Parazoanthus daruini</i>
01–61	Isabela: Punta Vicente Roca	-0.0558	-91.5604	2001.6.19	6	CH	Red	Dead giant barnacle	EU333770	EU333761	EU333803	<i>Terrazoanthus onoi</i>
02–27	Darwin: Arch	1.6725	-91.9900	2002.5.18	6–8	CH	Red	Dead coral	EU333774	EU333760	EU333810	<i>Terrazoanthus onoi</i>
02–59	Isabela: Punta Vicente Roca	-0.0558	-91.5604	2002.5.20	9	CH	Red	Lava rock	EU333775	EU333758	EU333806	<i>Terrazoanthus onoi</i>
03–46	Isabela: Punta Vicente Roca	-0.0558	-91.5604	2003.1.16	2	CH	Red	Lava rock	EU333777	NA	NA	<i>Terrazoanthus onoi</i>
03–135	Pinzon: Roca Onan	-0.5909	-90.6860	2003.1.20	NA	LV	Red	Rock	EU333780	EU333762	EU333809	<i>Terrazoanthus onoi</i>
03–566	Marchena: Punta Espejo	0.3113	-90.3984	2003.1.12	9	CH	Red	Rock and shells	EU333784	EU333767	EU333808	<i>Terrazoanthus onoi</i>
03–641	Isabela: Punta Vicente Roca	-0.0558	-91.5604	2003.11.15	NA	CH	Red	Lava rock	EU333785	EU333759	EU333805	<i>Terrazoanthus onoi</i>
04–140	Floreana: La Botella	-1.2904	-90.4989	2004.2.8	8	AC	Red	Dead giant barnacle	GU357558	NA	NA	<i>Terrazoanthus onoi</i>
04–343	Isabela: Caleta Iguana	-0.9945	-91.4454	2004.12.3	NA	GE	Red	Dead antipatharian	EU333791	EU333768	NA	<i>Terrazoanthus onoi</i>
04–345	Isabela: Caleta Iguana	-0.9945	-91.4454	2004.12.3	8	CH	Red	Rock	EU333792	EU333766	NA	<i>Terrazoanthus onoi</i>
04–346	Isabela: Elizabeth Bay	-0.5996	-91.09059	2004.12.2	25	GE	Red	Dead antipatharian	EU333793	EU333763	EU333804	<i>Terrazoanthus onoi</i>
04–347	Isabela: Elizabeth Bay	-0.5996	-91.09059	2004.12.2	2	CH	Red	Rock	EU333794	EU333764	EU333807	<i>Terrazoanthus onoi</i>
04–641	Isabela: Punta Vicente Roca	-0.0558	-91.5604	2004	NA	NA	Red	Rock	GU357557	NA	NA	<i>Terrazoanthus onoi</i>
CMNH ZG05885	Darwin: Glynn's Reef	1.6731	-91.9981	2007.3.8	13	FL, AC	Red	Rock	NA	NA	NA	<i>Terrazoanthus onoi</i>

Collection no. ^a	Collection locality	Latitude ^b	Longitude ^b	Date collected	Depth (m)	Collected by ^c	Oral disk color	Substrate	COI Accession Number	mt 16S rDNA Accession Number	ITS-rDNA Accession Number	Taxonomic identification
USNM 1134066	San Cristobel: Whale Rock	-0.8868	-89.6308	2007.3.12	21	JDR	Red	Rock	NA	NA	NA	<i>Terrazoanthus onoi</i>
MHNG 67496	Espanola: Anchorage	-1.3646	-89.6353	2007.3.12	Inter-tidal	AC	Red	Rock	NA	NA	NA	<i>Terrazoanthus onoi</i>
467	Floreana: Gardner	-1.3329	-90.2953	2007.3.13	14	JDR, CH	Red	Rock	NA	NA	NA	<i>Terrazoanthus onoi</i>
469	Floreana: Devil's Crown	-1.2144	-90.4238	2007.3.13	12	JDR, MV	Red	Rock	NA	NA	NA	<i>Terrazoanthus onoi</i>
473	Floreana: La Borella	-1.2904	-90.4989	2007.3.13	12–15	AC	Red	NA	NA	NA	NA	<i>Terrazoanthus onoi</i>
475	Pinzon: Roca Onan	-0.5909	-90.6860	2007.3.14	8	AC	Red	Rock	NA	NA	NA	<i>Terrazoanthus onoi</i>
02–09	Genovesa: Entrance	0.3019	-89.9440	2002.5.13	9	CH	White	Empty mollusk shell facing downwards	EU333773	EU333765	NA	<i>Terrazoanthus sinnigeri</i>
03–560	Marchena: Punta Espejo	0.3113	-90.3984	2003.11.12	7	CH	White	Under rock	NA	NA	NA	<i>Terrazoanthus sinnigeri</i>
418	Marchena: Punta Espejo	0.3113	-90.3984	2007.3.3	7	JDR, CH, FL	Brown/clear	Under rock	GU357567	NA	GU357553	<i>Terrazoanthus sinnigeri</i>
MHNG 67498	Marchena: Roca Espejo	0.3125	-90.4012	2007.3.3	9	JDR, FL, BR	White	Under rock	GU357564	NA	GU357551	<i>Terrazoanthus sinnigeri</i>
CMNH ZG05886	Darwin: Glynn's Reef	1.6731	-91.9981	2007.3.7	13	AC, FL	Brown	Under rock	GU357562	NA	NA	<i>Terrazoanthus sinnigeri</i>
434	Darwin: Glynn's Reef	1.6731	-91.9981	2007.3.7	13	AC, FL	White	Under rock	GU357560	NA	NA	<i>Terrazoanthus sinnigeri</i>
438	Darwin: Glynn's Reef	1.6731	-91.9981	2007.3.7	10	JDR, CH, FL	Brown/clear	Under rock	NA	NA	NA	<i>Terrazoanthus sinnigeri</i>
USNM 1134067	Darwin: Glynn's Reef	1.6731	-91.9981	2007.3.7	10	JDR, CH, FL	Brown/clear	Under rock	GU357565	NA	NA	<i>Terrazoanthus sinnigeri</i>

Collection no. ^a	Collection locality	Latitude ^b	Longitude ^b	Date collected	Depth (m)	Collected by ^c	Oral disk color	Substrate	COI Accession Number	mt 16S rDNA Accession Number	ITS-rDNA Accession Number	Taxonomic identification
442	Bainbridge Rocks: Don Ferdi	-0.2100	-90.567	2007.3.9	25	AC	Brown	Rock	GU357561	NA	GU357555	<i>Terrazoanthus sinnigeri</i>
445	North Seymour	-0.4118	-90.2871	2007.3.10	15	MV	Brown	Rock, bottom of ledge	NA	NA	GU357556	<i>Terrazoanthus sinnigeri</i>
464	Floreana: Gardner	-1.3329	-90.2953	2007.3.13	27	JDR, AC	Brown	Under rock	GU357563	NA	GU357554	<i>Terrazoanthus sinnigeri</i>
471	Floreana: Devil's Crown	-1.2144	-90.4238	2007.3.13	7	JDR, AC	Brown	Under rock	GU357566	NA	GU357552	<i>Terrazoanthus sinnigeri</i>

NA = not available or data not acquired.

^aSpecimens with the designations such as 03-560 are from 2001-2004 surveys (see Reimer et al. 2008b). Other specimens are from 2007 and have either specimen numbers (e.g. 471) in JDR's collection, or museum type specimen numbers as given. Abbreviations: USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA, CMNH: Chiba Prefectural Natural History Museum, Japan, MHNG: Natural History Museum of Geneva, Switzerland, MISE: Molecular Invertebrate Systematics and Ecology Laboratory, University of the Ryukyus, Nishihara, Okinawa, Japan.

^bLatitude and longitude values that are negative represent South and West values respectively, while positive values (latitude only) represent North values.

^cCollector abbreviations: CH = C. Hickman, Jr., LV = L. Vinuesa, AC = A. Chiriboga, GE = G. Edgar, JDR = JD Reimer, RP = R. Pepolas, FL = F. Liss, BR = B. Riegl, DR = D. Ruiz, FR = F. Riveira, OB = O. Breedy, MV = M. Vera.

Differential diagnosis. Differs from *Antipathozoanthus macaronesicus* (Ocaña & Brito, 2004) (with regards to distribution; Galapagos as opposed to Cape Verde), coloration (no red or cream colors observed in *A. macaronesicus*), substrate (*Antipathes galapagensis* as opposed to *Tanacetipathes cavernicola* Opresko, 2001).

Other morphologically similar and undescribed zoanthids (epizoic on antipatharians, similar sizes, yellowish in color) have been recorded from Madagascar and Japan (specimens in JDR's collection), although these other specimens were found on different antipatharian species than *Antipathozoanthus hickmani*, and were never red or cream in color.

Antipathozoanthus hickmani is the only zoanthid in the Galápagos found on living *Antipathes galapagensis* (Table 3).

Habitat and distribution. All collected samples from Galapagos were on the black coral *Antipathes galapagensis*, at depths of 12 m to 35 m. Although *A. galapagensis* is found throughout the archipelago, *Antipathozoanthus hickmani* colonies were observed only at Santiago, Floreana, Isabela and Pinzon Islands, and it may be that this genus has a patchy distribution in the Galápagos. *A. hickmani* is potentially also found at Isla del Coco (Costa Rica) on the same antipatharian species, based on Museo de Zoología, University of Costa Rica specimen UCR 827, although this has yet to be confirmed with detailed examinations.

Biology and associated species. *Antipathozoanthus hickmani* may cover only a portion of a living *Antipathes galapagensis* black coral colony, or cover the entire colony, suggesting this species may be parasitic. Some *A. hickmani* specimens were found on completely dead *A. galapagensis* colonies or branches.

Notes. Previously mentioned in Reimer et al. (2008b, 2010) and Hickman (2008) as *Parazoanthus* sp. G1.

Genus *Parazoanthus* Haddon & Shackleton, 1891

Type species: *Parazoanthus axinellae* Schmidt, 1862

Diagnosis. Colonial zoanthids characterised by a mesogleal lacuna and by canals forming a 'ring sinus' in distal part of polyp. Fine mineral particles incorporated in polyps.

Parazoanthus darwini sp. n.

urn:lsid:zoobank.org:act:9CE65167-B6F8-4CF7-BCF2-BCAF277F9AAC

Figures 2, 5, 9, Tables 1, 2, 3

Etymology. Named after Charles Darwin, whose 200th birthday was celebrated in 2009. Noun in the genitive case.

Material examined. *Type locality:* Ecuador, Galapagos: Marchena I., Roca Espejo, 0.3125°N 90.4012°W.

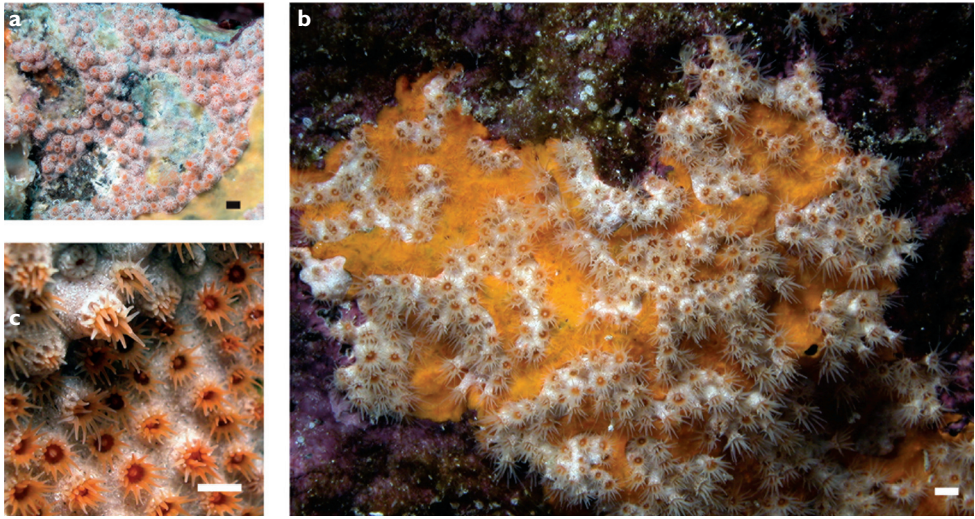


Figure 2. *Parazoanthus darwini* sp. n. in situ in the Galapagos. **a** specimen MISE 451 at Gordon Rocks, depth 21 m, by JDR, March 11, 2007 **b** specimen 456 on orange sponge at Whale Rock, San Cristobel I., depth 17 m, by JDR, March 12, 2007 **c** close up of specimen 03-290, Cape Douglas, Fernandina Island, 6 m, by Angel Chiriboga, August 8, 2003. All scale bars: 1 cm.

Holotype. MHNG-INVE-67497. Colony divided into three pieces, on rocks of approximately 1.5×2.0 cm, with heights of approximately 1.0 cm. Total of approximately 90 polyps connected by very well-developed coenenchyme on top of a white sponge. Polyps approximately 1.0–3.0 mm in diameter, and completely embedded in coenenchyme to 2.0 mm in height from coenenchyme. Polyps and coenenchyme encrusted with black sand, which appear as specks, tissue of polyps and coenenchyme light brown in color. Collected from Roca Espejo, Marchena I., Galapagos, Ecuador, at 8 m, collected by JDR and C. Hickman, Jr. (CH), March 3, 2007. Preserved in 99.5% ethanol.

Paratypes (all from Galapagos, Ecuador):

Paratype 1. Specimen number CMNH-ZG 05884. Roca Espejo, Marchena I., at 8 m, collected by JDR and CH, March 3, 2007.

Paratype 2. Specimen number USNM 1134065. Roca Espejo, Marchena I., at 8 m, collected by JDR and CH, March 3, 2007.

Other material (all from Galapagos, Ecuador): MISE03-47, Punta Vicente Roca, Isabela I., at 2 m, collected by CH, January 16, 2003; MISE03-177, Gordon Rocks, at 18 m, collected by CH, January 22, 2003; MISE03-290, Cape Douglas, Fernandina I., at 6 m, collected by AC, August 25, 2003; MISE03-652, Tagus Cove, Isabela I., at 13 m, collected by CH, November 16, 2003; MISE04-155, La Botella, Floreana I., at 12 m, collected by AC, May 25, 2004; MISE04-184, Las Marielas, Isabela I., at 6 m, collected by AC, December 2, 2004; MISE04-328, Las Marielas, Isabela I., at 3 m, collected by AC, December 2, 2004; MISE04-348, Caleta Iguana, Isabela I., at 9 m, collected by CH, December 3, 2004; MISE 412, Roca Espejo,

Table 2. Nematocyst types and sizes of different areas of polyps of new zoanthid species in this study.

Location	Zoanthid species	Nematocyst Type(s)	Length (max-min) (µm)	Width (max-min) (µm)	Frequency within samples ^a (number of specimens found in/total specimens examined)
tentacles	<i>P. darwini</i>	Basitrich & Mastigophores	13–23	3–5	Common (2/2)
		Holotrich M	15–22	7–9	Occasional (1/2)
		Spirocysts	8–18	2–3	Numerous (2/2)
	<i>A. hickmani</i>	Basitrich & Mastigophores	14–20	3–4	Occasional (2/2)
		Holotrich M	11–21	6–10	Numerous (2/2)
		Spirocysts	12–22	2–4	Numerous (2/2)
	<i>T. sinnigeri</i>	Basitrich & Mastigophores	7–15	2–3	Common (3/3)
		Holotrich M	17–31	7–14	Rare (2/3)
		Spirocysts	10–17	1–4	Numerous (3/3)
	<i>T. onoi</i>	Basitrich& Mastigophores	8–16	2–4	Numerous (2/2)
Holotrich L		37–43	14–18	Rare (1/2)	
Holotrich M		17–19	6–7	Rare (1/2)	
Spirocysts		10–18	2–3	Numerous (2/2)	
Basitrich & Mastigophores		13–25	3–6	Numerous (2/2)	
pharynx	<i>P. darwini</i>	Holotrich M	28	11	Rare (1/2)
		Holotrich S	12	5	Rare (1/2)
		Spirocysts	13–24	2–4	Occasional (2/2)
	<i>A. hickmani</i>	Basitrich & Mastigophores	14–22	3–5	Common (2/2)
		Holotrich M	13–26	5–10	Numerous (2/2)
		Spirocysts	13–23	2–4	Common (2/2)
	<i>T. sinnigeri</i>	Basitrich & Mastigophores	11–17	2–4	Numerous (3/3)
		Holotrich L	23–40	7–15	Occasional (2/3)
		Holotrichs M	10–16	4–8	Rare (1/3)
		Holotrich S	7–14	3–7	Occasional (2/3)
	Spirocysts	10–18	2–4	Occasional (2/3)	

Location	Zoanthid species	Nematocyst Type(s)	Length (max-min) (µm)	Width (max-min) (µm)	Frequency within samples ^a (number of specimens found in/total specimens examined)
filament	<i>T. onoi</i>	Basitrich & Mastigophores	13–17	2–4	Numerous (2/2)
		Holotrichs M	24	7–8	Rare (1/2)
		Spirocysts	10–15	2–3	Occasional (1/2)
	<i>P. darwini</i>	Basitrich & Mastigophores	8–21	2–5	Numerous (2/2)
		Holotrich M	12–25	5–12	Occasional (2/2)
		Holotrich S	5–7	2–4	Occasional (1/2)
		Spirocysts	7–18	1–3	Occasional (2/2)
		Basitrich & Mastigophores	14–18	3–5	Occasional (2/2)
	<i>A. hickmani</i>	Holotrich L	24–32	9–12	Numerous (2/2)
		Holotrich M	12–22	5–10	Numerous (2/2)
		Spirocysts	15–21	3–4	Occasional (1/2)
		Holotrich L	27–45	11–19	Common (2/3)
		Holotrich M	9–20	6–10	Common (3/3)
column	<i>T. sinnigeri</i>	Holotrich S	8–13	3–6	Numerous (1/3)
		Mastigophores	8–20	4–6	Numerous (2/3)
		Spirocysts	9–24	2–4	Rare (2/2)
		Holotrich L	32–43	12–16	Numerous (1/2)
		Basitrich & Mastigophores	9–17	2–5	Numerous (2/2)
	<i>P. darwini</i>	Holotrich M	10–27	5–26	Numerous (2/2)
		Holotrich S	4–10	2–5	Occasional (2/2)
		Basitrich & Mastigophores	13–17	4–5	Occasional (1/2)
		Holotrich M	10–18	5–10	Common (2/2)
		Holotrich L	14–48	5–16	Occasional (3/3)
	<i>A. hickmani</i>	Holotrich M	13–18	6–9	Common (2/3)
		Holotrich S	6–12	3–7	Numerous (1/3)
		Holotrich L	36–45	14–19	Occasional (2/2)
		Holotrich M	11–24	6–20	Common (2/2)
	<i>T. onoi</i>				

^aFrequency, in decreasing order; Numerous, Common, Occasional, Rare.

Marchena I., 6 m, collected by JDR and CH, March 3, 2007; MISE413, Roca Espejo, Marchena I., 7 m, collected by JDR and CH, March 3, 2007; MISE417, Roca Espejo, Marchena I., no depth given, collected by CH, March 3, 2007; MISE 424, Roca Espejo, Marchena I., 9 m, collected by JDR, F. Liss (FL), B. Riegl (BR), March 3, 2007; MISE425 Roca Espejo, Marchena I., 9 m, JDR, FL, BR, March 3, 2007; MISE428 El Elefante, Wolf I., 24 m, collected by D. Ruiz (DR) and F. Riveira (FR), March 5, 2007; MISE429 El Elefante, Wolf I., 21 m, collected by DR and FR, March 5, 2007; MISE430 El Elefante, Wolf I., 22 m, collected by JDR, O. Breedy (OB), BR (FR), March 5, 2007; MISE431 El Elefante, Wolf I., 22 m, collected by JDR, OB, BR, March 5, 2007; MISE450 Crater at Gordon's Rock, 17 m, collected by JDR, March 11, 2007; MISE451 Crater at Gordon's Rock, 21 m, collected by JDR, March 11, 2007; MISE452 Crater at Gordon's Rock, 17 m, collected by AC, March 11, 2007; MISE456 Whale Rock, San Cristobel I., 17 m, collected by JDR, March 12, 2007; MISE458 Kicker Rock, San Cristobel I., 15 m, collected by JDR, March 12, 2007; MISE461 Baho Garden, Espanola I., 10 m, collected by M. Vera (MV), March 12, 2007; MISE466 Gardner, Floreana I., 15 m, collected by JDR and AC, March 13, 2007; MISE468 Gardner, Floreana I., 14 m, collected by JDR and CH, March 13, 2007; MISE470 Devil's Crown, Floreana I., 9 m, collected by JDR and MV, March 13, 2007.

Sequences. See Table 1.

Description. *Size:* Polyps are approximately 3–6 mm in diameter when open, and approximately 2–6 mm in height. Colonies may be very small (a few cm² in area), or extend to cover large areas over a square meter in area.

Morphology: *Parazoanthus darwini* polyps have yellow, orange, or cream tentacles, and a red, yellow, or light yellow oral disk, with a light tan, light pink, or cream coenenchyme. Polyps have between 24 and 30 tentacles that are usually longer than expanded oral disk diameter. Although polyps extend clear of the coenenchyme, when contracted the polyps are mere bumps on the surface of the coenenchyme.

Cnidae: Basitrichs and microbasic p-mastigophores (often difficult to distinguish), holotrichs (medium and small), spirocysts (see Table 2, Figure 9).

Differential diagnosis. In *P. darwini*, the polyps are much more embedded in the coenenchyme than those of both *A. hickmani* and Hydrozoanthidae species of the Galápagos (Table 3). Whereas many *Parazoanthus* species from other areas of the world are epizoid on sponges, none are morphologically similar (color, size, polyp shape; see below) to *P. darwini*. *Parazoanthus axinellae* and *P. catenularis* Duchassaing de Fonbressin & Michelotti 1860 from the Caribbean are found on clearly different host sponges from *P. darwini*. *Parazoanthus swiftii* Duchassaing de Fonbressin & Michelotti, 1860 and *P. parasiticus* Duchassaing de Fonbressin & Michelotti, 1860 are somewhat similar to *Parazoanthus darwini* in both polyp and coenenchyme color, but have fewer tentacles (maximum to 28; *sensu* Swain 2009) than *P. darwini*, and clearly different mitochondrial 16S ribosomal DNA (Reimer et al. 2008b).

Table 3. Differences between four new species of zoanthids from the Galapagos.

Species	Polyp length (mm)	Oral disk diameter (mm)	Number of tentacles	Color	Substrate, microhabitat	Other distinguishing features
<i>Antipathozoanthus hickmani</i>	6–15	6–12	Approx. 40	Cream, yellow, or red	<i>Antipathes galapagensis</i>	
<i>Parazoanthus darwini</i>	2–6	3–6	24–30	Cream, yellow, light pink, or light red	(Usually) sponges	Polyps embedded in well-developed coenenchyme
<i>Terrazoanthus onoi</i>	Up to 20	4–12	32–40	Bright red	Upper surfaces of rock, non-living substrate	Only basitrichs and mastigophores in pharynx; unique ITS-rDNA from <i>T. sinnigeri</i> .
<i>Terrazoanthus sinnigeri</i>	<10	2–8	30–36	Brown, white, or transparent	Undersides of rocks or other non-living substrate	Many types of nematocysts in pharynx; unique ITS-rDNA from <i>T. onoi</i>

Habitat and distribution. Similar to *Terrazoanthus onoi* sp. n. (below), specimens of *Parazoanthus darwini* are found on rock walls, in crevices, or at the base of rocks, and were found from depths of 2 m to ~30 m, and may extend deeper. Colonies of *P. darwini* were seen at Wolf, Marchena, Isabela, Fernandina, Santa Cruz, San Cristobal, Española and Floreana Islands, and its range is likely throughout the archipelago.

Biology and associated species. Collected *Parazoanthus darwini* specimens from Galapagos are often (but not always) associated with different species of bright yellow-orange or red sponges, possibly in the groups Poecilosclerida and/or Hadromerida (T. Swain, personal communication). *P. darwini* colonies often grow in patches over the sponge, or may even cover it entirely, and often extend to surrounding rock substrate. Despite being covered by *P. darwini*, the sponge is always alive, suggesting this association may be symbiotic.

Notes. Despite COI and mt 16S rDNA sequences of this species being identical to sequences from *Parazoanthus swiftii* from the Caribbean (Figures 5a, 5b), slightly longer mt 16S rDNA sequences (Figure 2 in Reimer et al. 2007) were not identical. Additionally, due to the morphology of *P. swiftii* (rarely not on sponges, relatively shorter tentacles, large [6 mm] diameter polyps that often extend well out from coenenchyme) and large geographic distances between *P. swiftii* and *P. darwini* localities, it is clear that these are two different species.

Previously mentioned in Reimer et al. (2008b) and Hickman (2008) as *Parazoanthus* sp. G2.

Family Hydrozoanthidae Sinniger, Reimer & Pawlowski, 2009

Diagnosis (from Sinniger et al. 2009):

Tropical and sub-tropical macrocnemic zoanthids associated with hydrozoans or associated with non-living substrate. Includes former Parazoanthidae species sharing

specific insertions and deletions in mt 16S rDNA, especially in the V5 region (as defined in Sinniger et al. 2005) of this gene. Phylogenetically species are more closely related to brachycnemic zoanthids (especially from the genus *Palythoa* Lamouroux 1816) than to other parazoanthids.

Genus *Terrazoanthus* gen. n.

urn:lsid:zoobank.org:act:BFED371E-2284-4B8A-82F1-0D53A5AE0B5F

Type species: (present designation): *Terrazoanthus onoi* sp. n.

Diagnosis. Sub-tropical to tropical Hydrozoanthidae that are found on rocky substrates, (e.g., not obligate symbionts with hydrozoans). Some species in this genus are brightly colored.

Etymology. Named for the latin “terra” meaning “rock”, the substrate on which species of this genus are commonly found on, with ending in concordance to other zoanthid genera. Gender neuter, as with other zoanthid genera ending in “-zoanthus”.

***Terrazoanthus onoi* sp. n.**

urn:lsid:zoobank.org:act:429212C7-BC17-4ECC-BC66-85465AFE7C83

Figures 3, 5, 6, 8, 9, Tables 1, 2, 3

Etymology. This species is named in honor of Dr. Shusuke Ono, who introduced the first author to zoanthids and has played a major role in zoanthid research in Japan. Noun in the genitive case.

Material examined. *Type locality:* Ecuador, Galapagos: Espanola I., Anchorage, 1.3646°S 90.2953°W.

Holotype: MHNG-INVE-67496. Colony on rock, approximately 3.0 × 6.0 cm. Total of approximately 130 polyps connected by well-developed coenenchyme. Polyps approximately 1.0–3.0 mm in diameter, and approximately 0.5–2.0 mm in height from coenenchyme. Polyps and coenenchyme encrusted with sand, tissue of polyps and coenenchyme dark brown in color. Collected from Anchorage, Espanola I., Galapagos, Ecuador, at low tide line, collected by AC, March 12, 2007. Preserved in 99.5% ethanol.

Paratypes (all from Galapagos, Ecuador):

Paratype 1. Specimen number CMNH-ZG 05885. Glynn’s Reef, Darwin I., at 13 m, collected by FL and AC, March 8, 2007.

Paratype 2. Specimen number USNM 1134066. Whale Rock, San Cristobel I., at 21 m, collected by JDR, March 12, 2007.

Other material (all from Galapagos, Ecuador): MISE 02-59, Punta Vincente Roca, Isabela I., at 9 m, collected by CH, May 20, 2002; MISE 03-46, Punta Vincente Roca, Isabela I., at 2 m, collected by CH, January 16, 2003; MISE 03-135, Roca Onan, Pinzon I., depth not available, collected by L. Vinuesa (LV), January 20, 2003; MISE 03-566, Punta Espejo, Marchena I., at 9 m, collected by CH, November 12, 2003; MISE 03-641,

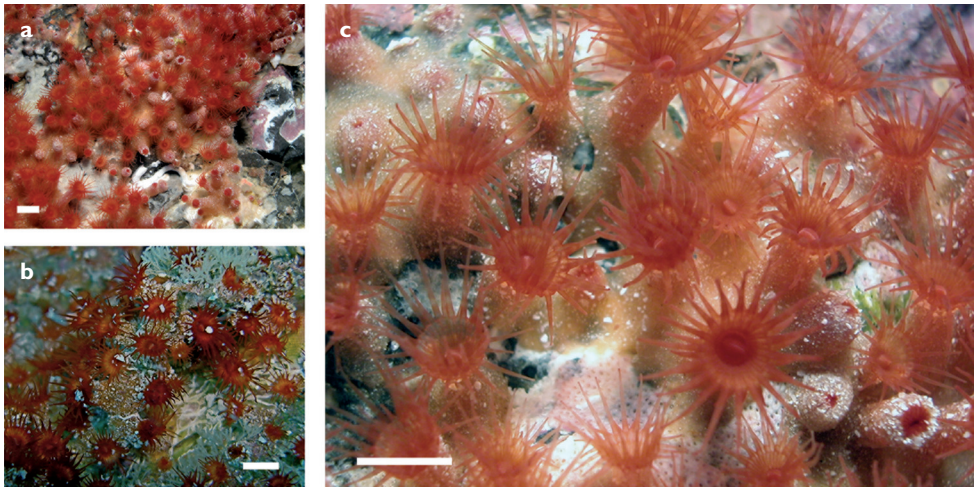


Figure 3. *Terrazoanthus onoi* sp. n. in situ in the Galapagos. **a** and **c** paratype USNM 1134066, at Whale Rock, San Cristobel I., depth 21 m, by JDR, March 12, 2007 **b** paratype CMNH-ZG 05885, Glynn's Reef, Darwin I., depth 13 m, by Fred Liss, March 8, 2007. All scale bars: 1 cm.

Punta Vincente Roca, Isabela I., depth not available, collected by CH, November 15, 2003; MISE 04-140, La Botella, Floreana I., at 8 m, collected by AC, February 8, 2004; MISE 04-343, Caleta Iguana, Isabela I., depth not available, collected by GE, December 3, 2004; MISE 04-345, Caleta Iguana, Isabela I., at 8 m, collected by CH, December 3, 2004; MISE 04-346, Elizabeth Bay, Isabela I., at 25 m, collected by GE, December 2, 2004; MISE 04-347, Elizabeth Bay, Isabela I., at 13 m, collected by CH, December 2, 2004; MISE 467, Gardner, Floreana I., 14 m, collected by JDR and CH, March 13, 2007; MISE 469, Devil's Crown, Floreana I., 12 m, collected by JDR and MV, March 13, 2007; MISE 473, La Botella, Floreana I., at 12–15 m, collected by AC, March 13, 2007; MISE 475, Roca Onan, Pinzon I., 8 m, collected by AC, March 14, 2007

Sequences. See Table 1.

Description. *Size:*

Polyps are approximately 4–12 mm in diameter when open, and rarely more than 20 mm in height. Colonies may reach sizes of over a meter in diameter.

Morphology: *Terrazoanthus onoi* has bright red or red-brown oral disks and the outer surface of polyps is tan to dark brown, with polyps relatively clear of the coenenchyme. *T. onoi* has 32 to 40 tentacles that are almost as long as the diameter of the expanded oral disk (Figure 3).

Cnidae: Basitrichs and microbasic p-mastigophores (often difficult to distinguish), holotrichs (large, medium, and small), spirocysts (see Table 2, Figure 9).

Differential diagnosis. In the Galápagos, *Terrazoanthus onoi* differs from *Parazoanthus darwini* and *Antipathozoanthus hickmani* by substrate preference (rock as opposed to sponges and anthipatharians, respectively), as well as from *Terrazoanthus sinigeri* sp. n. (below) by both color (bright red as opposed to brown, white or transparent) and habitat ecology (exposed rock surfaces as opposed to under rocks and rubble).

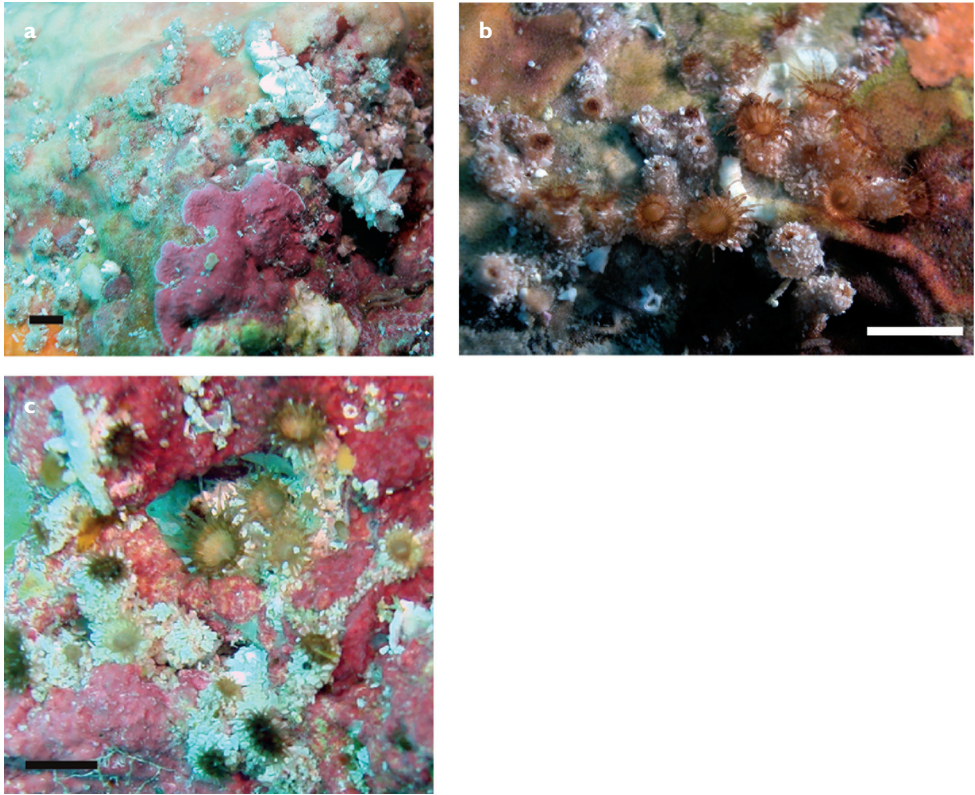


Figure 4. *Terrazoanthus sinnigeri* sp. n. in situ in the Galapagos. **a** specimen MISE 442, depth 25 m, Don Ferdi, Bainbridge Rocks, Santiago I., by Angel Chiriboga, on March 9, 2007 **b** specimen MISE 445, Gardner, Floreana I., depth 15 m, by Mariana Vera, on March 10, 2007 **c** specimen MISE 438, Glynn's Reef, Darwin I., depth 10 m, by JDR, March 7, 2007. All scale bars: 1 cm.

In addition, *T. onoi* is bigger (oral disk diameter and polyp height) than *T. sinnigeri*, and forms much larger colonies (Table 3). *T. onoi* commonly has only basitrichs and microbasic p-mastigophores in its pharynx, and no large or small holotrichs at all, unlike *T. sinnigeri* (Table 2).

Phylogenetically, *Terrazoanthus onoi* is very closely related to *T. sinnigeri*, with identical COI and mt 16S rDNA sequences, but consistently differs by four base pairs in ITS-rDNA, and forms a clade separate from *T. sinnigeri*.

An extensive literature search revealed no other described Parazoanthidae species from the Pacific that are non-epizoic and bright red in color. An undescribed zoanthid species inhabiting rock and coral reef substrata from Indonesia often referred to as “yellow polyps” (*sensu* Sinniger et al. 2005) is likely also a *Terrazoanthus* sp., but is distinct from *T. onoi* in terms of color and distribution, and is phylogenetically different.

Habitat and distribution. Specimens of *Terrazoanthus onoi* were found on rock substrate in areas of high current (i.e., the base of large rocks, rock walls, etc.). Colonies were found at Darwin, Marchena, Genovesa, Isabela, Pinzon, Española, and Floreana

Islands, and it is likely *T. onoi* is found throughout the archipelago. This species has been found from the low infra-littoral to depths of over 35 m, and is likely to be at even deeper depths.

Biology and associated species. Found on the top surfaces of rocks and biogenic non-living substrate, *Terrazoanthus onoi* is often found close to sponges, seaweed, and other benthos, but is not epizoic and does not have an association with any particular species.

Notes. Previously mentioned in Reimer et al. (2008b, 2010) and Hickman (2008) as *Parazoanthus* sp. G3, except for specimen MISE 02-27 mentioned below.

It should be noted that specimen MISE 02-27 was found to have an ITS-rDNA sequence inconsistent with other *Terrazoanthus onoi* specimens (Figure 6), although other data (morphology, mt 16S rDNA and COI data) fit well with *T. onoi*. For these reasons, this specimen has not been conclusively assigned to *T. onoi* or to the other new *Terrazoanthus* species below. These results indicate there may be other *Terrazoanthus* species in the Galápagos that await discovery and description.

***Terrazoanthus sinnigeri*, sp. n.**

urn:lsid:zoobank.org:act:2B865570-1FD7-4FB6-BF86-81B5DEDA2289

Figures 4, 5, 6, 9, Tables 1, 2, 3

Etymology. This species is named for Dr. Frederic Sinniger, who has greatly helped spur the recent phylogenetic reexamination of zoanthid taxonomy. Noun in the genitive case.

Material examined. *Type locality:* Ecuador, Galapagos: Marchena I., Roca Espejo, 0.3125°N 90.4012°W.

Holotype: MHNG-INVE-67498. Colony divided into three pieces, on rocks of approximately 2.5 × 2.5 cm, 2.5 × 1.0 cm, and 2.0 × 1.5 cm, with heights of approximately 1.0 cm. Total of approximately 40 polyps connected by stolons. Polyps approximately 1.5–2.0 mm in diameter, and approximately 1.0–2.0 mm in height from coenenchyme. Polyps and coenenchyme encrusted with relatively large pieces of sand clearly visible to the naked eye, tissue of polyps and coenenchyme light brown/grey in color. In situ, colony was on bottom of rock. Collected from Roca Espejo, Marchena I., Galapagos, Ecuador, at 9.1 m, collected by JDR, FL, and BR, March 3, 2007. Preserved in 99.5% ethanol.

Paratypes (all from Galapagos, Ecuador):

Paratype 1. Specimen number CMNH-ZG 05886. Glynn's Reef, Darwin I., at 13 m, collected by FL and AC, March 7, 2007.

Paratype 2. Specimen number USNM 1134067. Glynn's Reef, Darwin I., at 10 m, collected by JDR, FL, CH, March 7, 2007.

Other material (all from Galapagos, Ecuador):

MISE 464, Gardner, Floreana I., 27 m, collected by JDR and AC, March 13, 2007; MISE 471, Devil's Crown, Floreana I., 7 m, collected by JDR and AC, March 13, 2007; MISE 418, Punta Espejo, Marchena I., 7 m, collected by JDR, FL, CH,

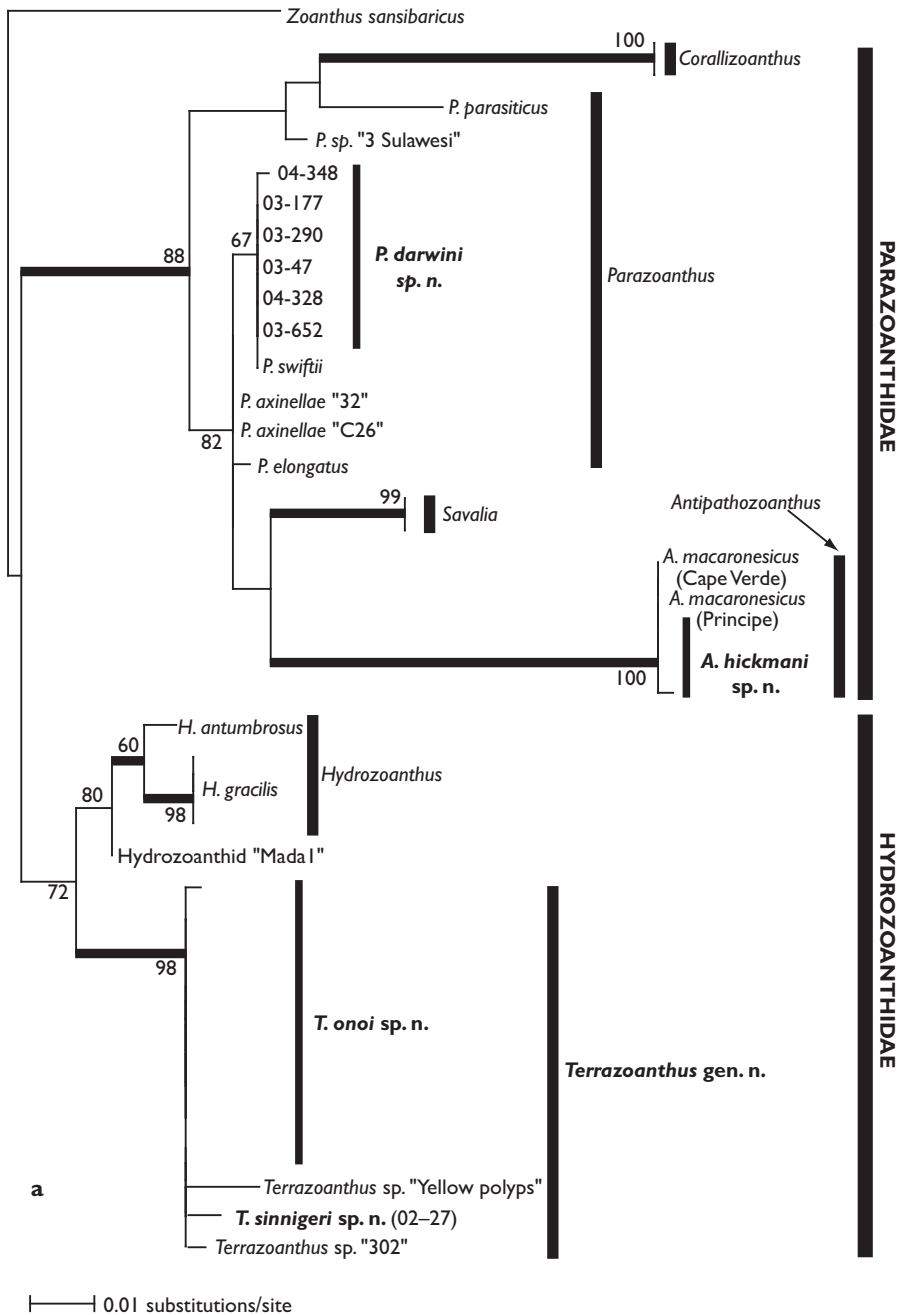
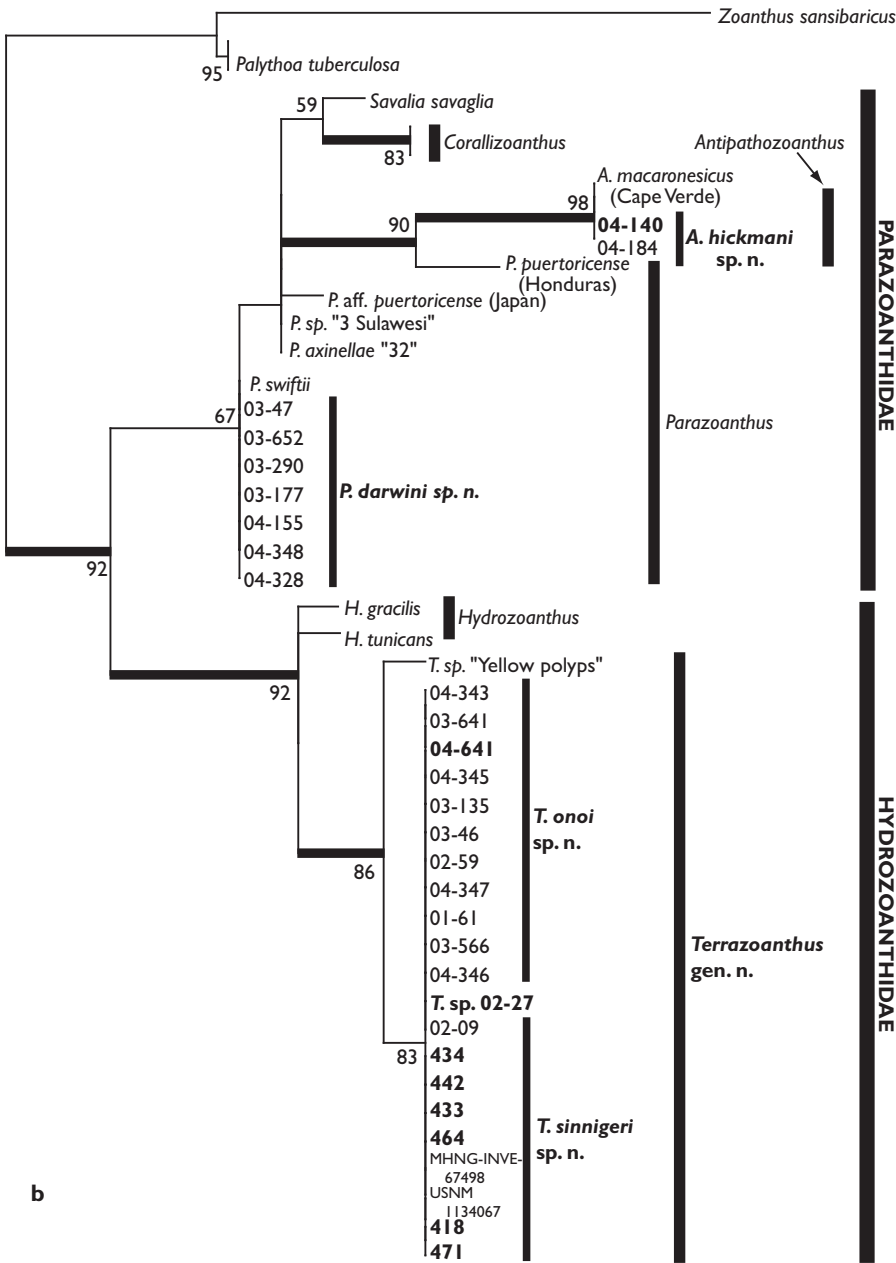


Figure 5. Maximum likelihood (ML) trees of **a** mitochondrial 16S ribosomal DNA, and **b** cytochrome oxidase subunit I (COI) sequences for zoanthid specimens. Values at branches represent ML probabilities (>50%). Monophyly with more than 95% Bayesian posterior probabilities are shown by thick branches. Sequences for new species in this study in larger font; sequences newly obtained in this study and new taxa described in this study in bold. Sequences/species names from previous studies in regular font. For specimen information see Table 1.



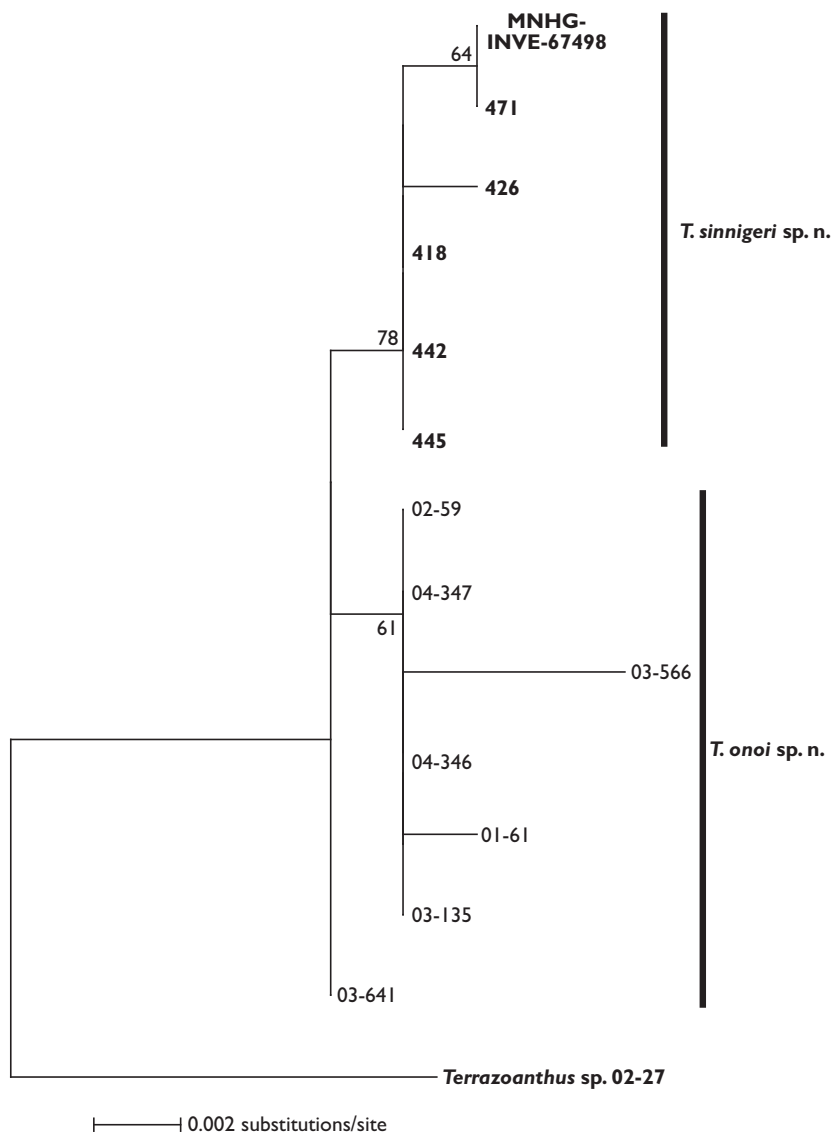


Figure 6. Maximum likelihood (ML) tree of internal transcribed spacer of ribosomal DNA (ITS-rDNA) for *Terrazoanthus* specimen sequences. Values at branches represent ML probabilities (>50%). Monophyly with more than 95% Bayesian posterior probabilities are shown by thick branches. For specimen information see Table 1.

March 3, 2007; MISE 02-09, Entrance, Genovesa I., at 9 m, collected by CH, May 13, 2002; MISE 03-560, Punta Espago, Marchena I., 7 m, collected by CH, November 12, 2003; MISE 434, Glynn's Reef, Darwin I., 13 m, collected by AC and FL, March 7, 2007; MISE 442, Don Ferdi, Bainbridge Rocks, 25 m, collected by AC, March 9, 2007; MISE 445, North Seymour I., 15 m, collected by MV, March 10, 2007.

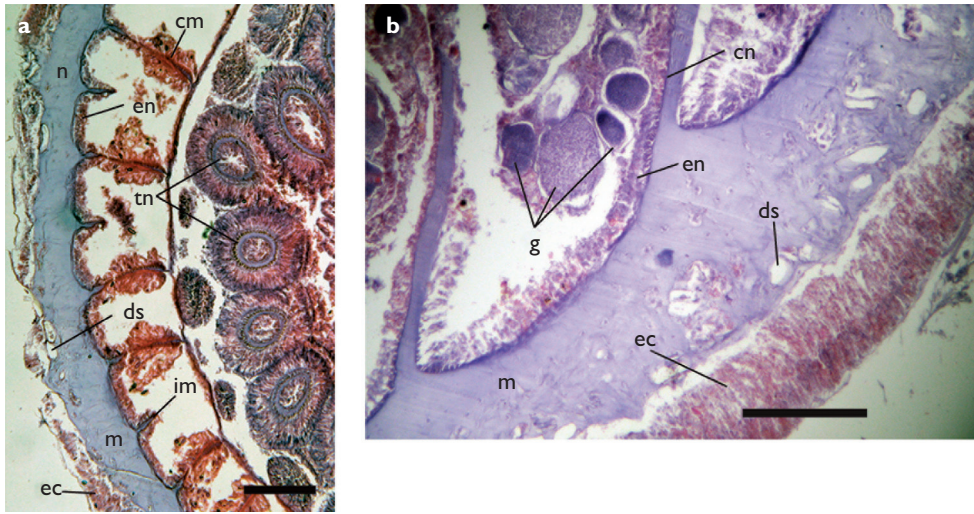


Figure 7. a–b Cross sections of *Antipathozoanthus hickmani* sp. n., MISE specimen 04-345 (details in Table 1) at the actinopharynx region showing preserved histological features. Abbreviations: cm=complete mesentery, ds=dissolved sand “holes”, ec=ectoderm, en=endoderm, g=gonads, im=incomplete mesentery, m=mesoglea, tn=tentacles. Scales = a) 100 μ m; b) 50 μ m.

Sequences: See Table 1.

Description. *Size:* Polyps are approximately 2–8 mm in diameter when open, and rarely more than 10 mm in height. Colonies small, consisting of one polyp (unitary) to less than 50 polyps.

Morphology: *Terrazoanthus sinnigeri* has dull brown, white, or clear oral disks and the outer surface of polyps is heavily encrusted with large particles, with polyps clear of the stolon. Stolons are also heavily encrusted, and approximately the width of polyp diameters. *T. sinnigeri* has 30 to 36 tentacles that are almost as long or sometimes longer as the diameter of the expanded oral disk (Figure 4). Tentacles often much more transparent than oral disks (when colored).

Cnidae: Basitrichs and microbasic p-mastigophores (often difficult to distinguish from each other), holotrichs (large, medium), spirocysts (Table 2, Figure 9).

Differential diagnosis. In the Galápagos, *Terrazoanthus sinnigeri* differs from *Parazoanthus darwini* and *Antipathozoanthus hickmani* by substrate preference (rock as opposed to sponges and anthipatharians, respectively), as well as from *Terrazoanthus onoi* sp. n. (above) by both color (brown, white or transparent as opposed to bright red) and microhabitat (under rocks and rubble as opposed to exposed rock surfaces). In addition, *T. sinnigeri* is smaller (oral disk diameter and polyp height) than congener *T. onoi*. *T. sinnigeri* colonies are stoloniferous and generally much smaller than colonies of *T. onoi* (Table 3). *Terrazoanthus sinnigeri* can be further distinguished from *T. onoi* by the presence of many types of nematocysts in the pharynx, unlike *T. onoi*, which only commonly possesses basitrichs and microbasic p-mastigophores with rare medium-sized holotrichs in the pharynx (Table 2). *Terrazoanthus sinnigeri* also has small holot-

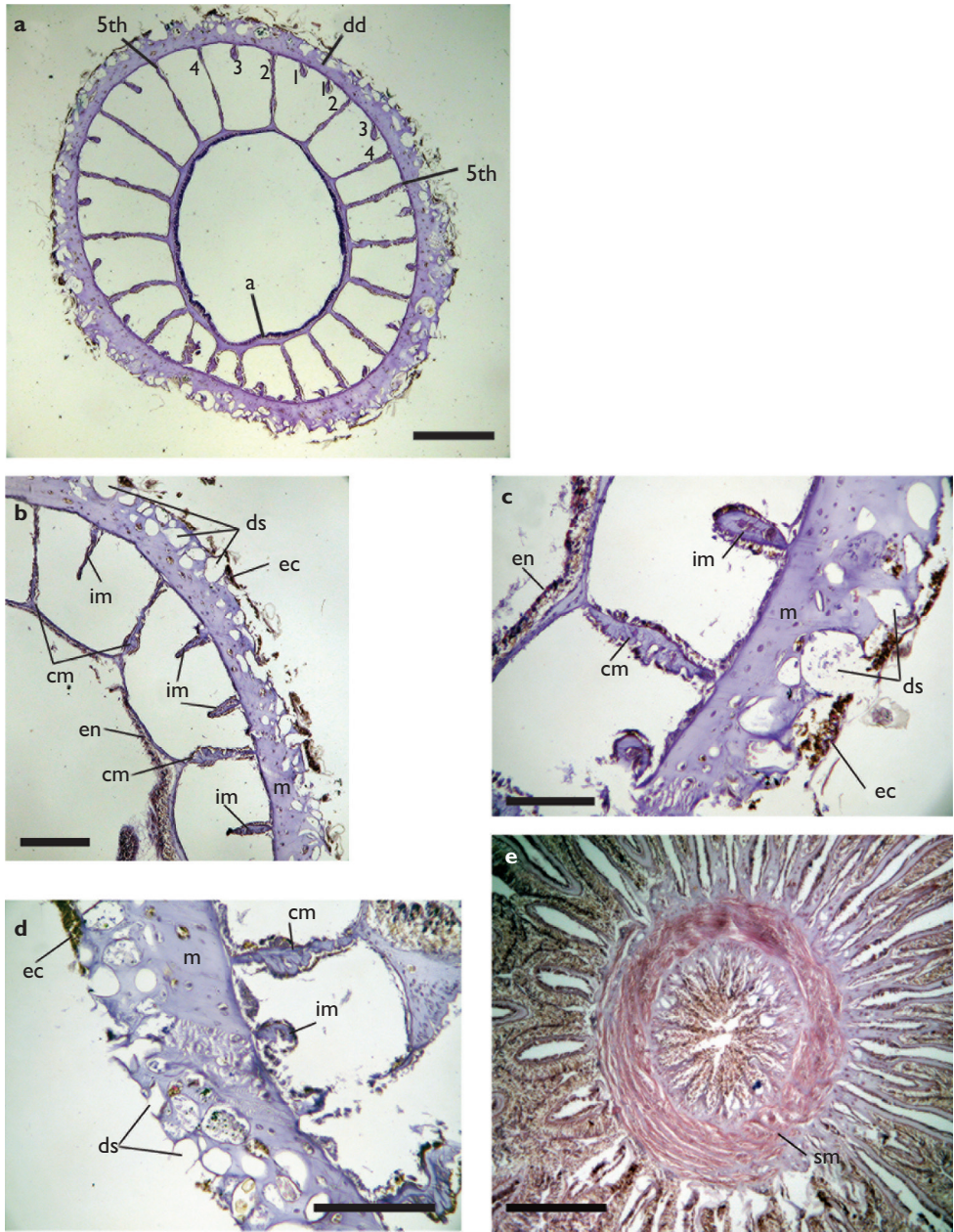


Figure 8. Cross-sections of *Terrazoanthus onoi* sp. n., MISE specimen 03-539 (details in Table 1) **a** Cross-section at the actinopharynx region demonstrating some major features of zoanthids. Note fifth mesentery is complete and therefore specimen is in the suborder Macrocnemina **b** to **e** various cross sections of *T. onoi* at the actinopharynx region showing preserved histological features. Abbreviations: **a**=actinopharynx, **cm**=complete mesentery, **dd**=dorsal directives, **ds**=dissolved sand “holes”, **ec**=ectoderm, **en**=endoderm, **im**=incomplete mesentery, **m**=mesoglea, **numbers**=mesentery numbers from the dorsal directive, **sm**=sphincter muscle, **5th**=fifth mesentery. Scales = a) 500 µm, b) and e) 100 µm, c) and d) 50 µm.

richs, while *T. onoi* does not (Table 2). Encrustations on the scapus of *T. sinnigeri* are generally much larger than on *T. onoi* (compare Figures 3 and 4).

Terrazoanthus sinnigeri is phylogenetically very closely related to *T. onoi*, but has different and unique ITS-rDNA (see *T. onoi* description; Figure 6).

Similar to *Terrazoanthus sinnigeri*, there have been reports of other small zoanthids inhabiting cryptic habitats under coral rubble and rock from the Galápagos, Singapore and Japan (J.D. Reimer, T. Fujii, personal observation), but these zoanthids are clearly different in DNA sequence from all known Hydrozoanthidae and Parazoanthidae, and will be described elsewhere. Morphologically, these undescribed zoanthids look very similar to *T. sinnigeri*, but are often unitary (not colonial), are encrusted with very large pieces of sand, have very little coloring (usually lacking any color asides from around the oral opening) and have fewer tentacles (<26, usually 20–22; data not shown) than *T. sinnigeri*.

Habitat and distribution. Specimens located at depths of 7 to over 27 meters at Floreana, Marchena, Darwin, North Seymour Islands, and Bainbridge Rocks, with other potential specimens observed at other islands. It is likely that this species is widely distributed throughout the Galápagos, and its distribution may extend into deeper waters as it was often found at the lowest depth searched during collection dives. Generally found on the underside of rocks, rubble, or dead shells, often in small cracks or crevices.

Biology and associated species. Found under rocks and rubble, *Terrazoanthus sinnigeri* is often found nearby bryozoans and coralline algae, but appears to not be epizoic on any particular organism.

Notes. In Reimer et al. (2008b) it was originally thought that *Terrazoanthus sinnigeri* (specimens 02-09, 03-560) was a different, white morphotype of *T. onoi* (mentioned in the paper and Hickman (2008) as *Parazoanthus* sp. G3) based on COI and mt 16S rDNA sequence data, but given the species' divergent morphologies, cnidae, and ecologies, as well as different ITS-rDNA sequences, we describe them as closely related but distinct species. It is likely that these two sibling species have recently diverged from one another.



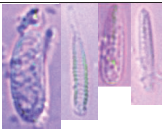
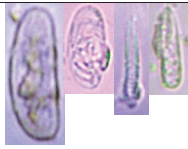
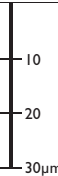
Although speculative, it may be that *Terrazoanthus sinnigeri*'s preferred habitat under rocks has resulted in its lack of bright pigmentation or occasional total lack of pigments compared to bright red *T. onoi*, which is found in areas more exposed to light, similar as to seen in subterranean invertebrates (e.g. Leys et al. 2003), and this should be investigated in the future.

Phylogenetic results





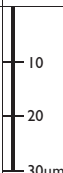
mt 16S rDNA

The phylogenetic tree from analyses of mt 16S rDNA showed two large clades; one consisting of Parazoanthidae specimens, and another of Hydrozoanthidae specimens

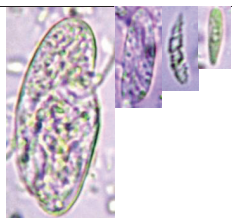
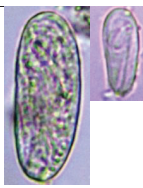
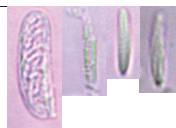
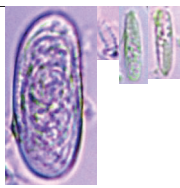

Antipathozoanthus hickmani sp. n.

Tentacles	Column	Pharinx	Filaments	
HM S O	HM O	HM S O O	HL HM S O	
				

Parazoanthus darwini sp. n.

Tentacles	Column	Pharinx	Filaments	
HM S O	HM HS	HM HS S O O	HM HS S O O O	
				

Terrazoanthus onoi sp. n.

Tentacles	Column	Pharinx	Filaments	
HL HM S O	HL HM	HM S O O	HL S O O	
				

Terrazoanthus sinnigeri sp. n.


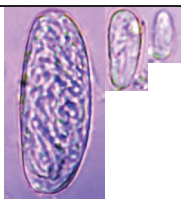
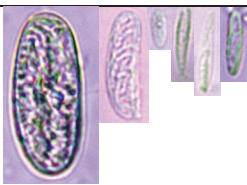
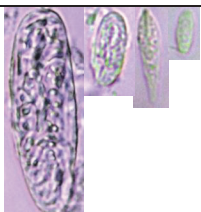
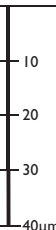
Tentacles	Column	Pharinx	Filaments	
HM S O O	HL HM HS	HL HM HS S O O	HL HM O O	
				

Figure 9. Cnidae in the tentacles, column, pharynx and filament of *Antipathozoanthus hickmani* sp. n., *Parazoanthus darwini* sp. n., *Terrazoanthus onoi* sp. n., and *Terrazoanthus sinnigeri* sp. n., respectively. Abbreviations: **HL**: large holotrich, **HM**: medium holotrich, **HS**: small holotrich, **O**: basitrichs or mas-tigophores, **S**: spirocysts.

(Figure 5a). Antipatharian-associated specimens previously referred to as *Parazoanthus* sp. G1 (04-140, 03-549, 04-341) formed a very well supported (ML=100%, Bayes=1.00) clade together with *Antipathozoanthus* specimens from Principe and from Cape Verde. This clade was sister to the genus *Savalia* Nardo 1814.

Sponge-associated specimens previously referred to as *Parazoanthus* sp. G2 (03-290, 03-47, 04-328, 03-652, 03-177) formed a moderately supported monophyletic group (ML=70%, Bayes=0.80) that also included *Parazoanthus swiftii*. This clade was derived from *Parazoanthus axinellae* (two specimens from Europe) and *P. elongatus* McMurrich 1904 from Chile.

Specimens previously designated *Parazoanthus* sp. G3 (03-566, 04-346, 02-59, 03-641, 02-27, 02-09, 01-61, 03-135, 04-345, 04-347, as well as 02-09) were within the large Hydrozoanthidae clade, within a subclade separate from *Hydrozoanthus* spp. sequences. The sequences formed a very well supported monophyletic group (ML=98%, Bayes=1.00) that also included “yellow polyps” *sensu* Sinniger et al. (2005) and “*Parazoanthus*” sp. 302, which both had slightly divergent sequences.

COI

COI phylogenetic results are shown in Figure 5b. The phylogenetic tree showed two large clades: one consisting of Parazoanthidae specimens, and another of Hydrozoanthidae specimens. Antipatharian-associated specimens previously informally described as *Parazoanthus* sp. G1 (04-140, 04-184) formed a well-supported (ML=98%, Bayes=1.00) clade together with an *Antipathozoanthus macaronesicus* specimen from Cape Verde. This clade was sister to *Parazoanthus puertoricense* West 1979 from Honduras.

Sponge-associated specimens previously informally described as *Parazoanthus* sp. G2 (03-290, Ang155, 03-47, 04-328, 04-348, 03-652, 03-177) formed a moderately supported monophyletic group (ML=67%, Bayes=0.92) that also included *Parazoanthus swiftii*. This clade was basal to all other Parazoanthidae.

Specimens previously designated *Parazoanthus* sp. G3 (04-343, 03-641, 04-461, 04-345, 03-46, 02-59, 04-347, 01-61, 03-566, 04-346, 02-09, 02-27) as well as new specimens (434, 442, 464, 426, 439, 418, 471) were within the large Hydrozoanthidae clade, within a subclade separate from *Hydrozoanthus* spp. sequences. The sequences formed a moderately well supported monophyletic group (ML=83%, Bayes=<0.50) sister to “yellow polyps” *sensu* Sinniger et al. (2005), which together formed a well-supported monophyletic group (ML=86%, Bayes=1.00).

ITS-rDNA

ITS-rDNA phylogenetic results are shown in Figure 6. The ITS-rDNA sequence from 02-27 is divergent from other sequences. Most sequences from brightly red-colored

specimens previously designated *Parazoanthus* sp. G3 (02-59, 04-347, 01-61, 04-346, 03-566, 03-135) formed a poorly supported monophyletic group (ML=64%, Bayes=0.70). Basal to this was one sequence from specimen 03-641. Many specimens from 2007 collection trips (471, 464, 426, 418, 442, 445) that were similar morphologically to earlier specimens 02-09 and 03-560, being brown, white, or clear in color, and found on the undersides of rocks, formed a separate moderately supported monophyletic group (ML=76%, Bayes=0.78) sister to the red-colored specimen sequences. These 2007 sequences had four base pairs unique from the “red clade” sequences.

Discussion

“Parazoanthid” diversity

Traditionally, the higher-level taxonomy of zoanthids has relied on a wide variety of diagnostic characteristics, including mesenterial arrangement (Haddon and Shackleton 1891) and nematocysts (Schmidt 1974). Although suborders are organized based on the position of the sphincter muscle (mesodermal or endodermal), genera have been historically designated based on not only morphology, but also ecology and species associations. Thus, the recent reexamination and reclassification of zoanthid taxa utilizing DNA sequences along with their ecology as diagnostic characters is not without historical precedent. From the results of this study along with data in Sinniger et al. (2009), Sinniger and Häussermann (2009) and Reimer et al. (2008a) the “parazoanthids” (the family Parazoanthidae as it formerly existed) are now divided into two families and eight genera (Parazoanthidae, including *Parazoanthus* Haddon & Shackleton, 1891, *Savalia* Nardo, 1814, *Isozoanthus* Chun, 1903, *Corallizoanthus* Reimer et al., 2008, *Mesozoanthus* Sinniger & Häussermann, 2009, *Antipathozoanthus* Sinniger et al., 2009; and Hydrozoanthidae, including *Hydrozoanthus* Sinniger et al., 2009 and *Terrazoanthus* gen. n.), reflecting the formerly unknown levels of generic and family diversity that are present in this zoanthid group. It is apparent that Parazoanthidae as it formally existed was clearly a “catch-all” for many different zoanthid species, as previously hypothesized (Reimer et al. 2008a).

It is also becoming increasingly apparent that zoanthid diversity is higher than previously thought in “ignored” or understudied regions, ecosystems (Reimer et al. 2007a) or even microhabitats (Reimer et al. 2008b, this study). This is clearly demonstrated by *Terrazoanthus sinnigeri*, which inhabits the underside of rocks and dead coral, a very common yet relatively understudied microhabitat. In subtropical seas, biological studies of zoanthids have focused mainly on coral reef areas, and in contrast studies of boulder/rubble areas have been neglected. This microhabitat has also recently been shown to host other previously undescribed invertebrate species, such as the comatulid *Dorametra sesokonis* Obuchi, Kogo & Fujita, 2009 in southern Japan (Obuchi et al. 2009). Additional specimens collected from the Galápagos also found

from the undersides of rocks (specimen 03-103 in Reimer et al. 2008b; specimens 427, 455, 460 in JDR's collection from the 2007 expedition) apparently belong to one or more other undescribed zoanthid taxa, and will be described elsewhere. Until the discovery of such zoanthids (Reimer et al. 2008b), no information on zoanthids found in such a cryptic microenvironment had been reported, and it may be that this and other understudied microhabitats also harbor zoanthid species new to science.

Proposed future zoanthid research in the southeastern Pacific

Despite a few reports, zoanthid diversity over the entire southeastern Pacific remains understudied. This study and recent investigations from Chile (Sinniger and Häussermann 2009) demonstrate that undescribed zoanthid diversity exists in this region. In particular, very little data exist for the Pacific coast of South and Central America, and efforts should be made to promote investigations in this area. With more knowledge of zoanthid diversity and distribution in the southeastern Pacific, more accurate biogeographical discussions of the evolution of parazoanthids and hydrozoanthids will become possible.

Conclusions

As shown by this research and other recent investigations (Sinniger et al. 2009), the levels of higher level (e.g. >genus) diversity of zoanthids are much higher than has previously been thought.

Insular and relatively unexplored marine regions of the world such as the Galapagos likely harbor many undiscovered and undescribed zoanthid species.

Phylogenetic analyses as performed here provide a powerful identification tool that can determine relative levels of relationships between zoanthids that would not be possible with only morphological and ecological data. This is most strongly demonstrated by the very close evolutionary relationship between the two new *Terrazoanthus* species, which are genetically very close and morphologically and ecologically quite distinct.

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Description of a new coccid (Hemiptera, Coccidae) on avocado (*Persea americana* Mill.) from Colombia, South America

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Abstract

A new soft scale insect, *Bombacoccus aguacatae* Kondo, **gen. n.** and **sp. n.** (Hemiptera: Coccidae) collected on the branches and twigs of avocado, *Persea americana* Mill. (Lauraceae) in Colombia, is described and illustrated based on the adult female. An updated taxonomic key to closely related genera of the *Toumeyella*-group is provided.

Keywords

soft scale insect, coccid, taxonomy, new genus, new species

Introduction

In the last 10 years, nineteen species of scale insects have been described for Colombia. Two of these species, *Laurencella colombiana* Foldi and Watson (2001) (Monophlebidae) and *Akermes colombiensis* Kondo and Williams (2004) (Coccidae) were reported on avocados. *Laurencella colombiana* is a giant monophlebid collected in the municipality of Villamaría, in the State of Caldas, Colombia, where it is regarded as a pest of avocado because it causes dieback of branches and a significant reduction in produc-

tivity and fruit quality (Foldi and Watson 2001). *Akermes colombiensis* is a polyphagous soft scale insect recorded on avocado (Lauraceae), guava (Myrtaceae), a shrub of the family Melastomataceae and *Ocotea* sp. (Lauraceae) in Valle del Cauca, Colombia (Kondo and Williams 2004). The avocado tree on which *A. colombiensis* was collected has been cut down, and this species has not been collected on avocados since (T. Kondo, personal observation).

On April 2007, an interesting soft scale insect that produces a cottony wax cover was reported in Anserma, Caldas, Colombia, on avocados (A.A. Ramos-Portilla, pers. comm.). The author was able to visit the farm where the insect was originally collected and obtained specimens of this coccid on April 2, 2009. During this visit, the author noted that the avocado trees were affected by sooty moulds which grew on the coccids' honeydew. After studying the microscopic features of this coccid, it was determined that it was a species new to science and belonged to the *Toumeyella*-group, a group currently included in the subfamily Myzolecaniinae (Kondo and Williams 2009). The new species does not fit into any known genus, and thus a new genus is erected here in order to accommodate it.

Materials and methods

Specimens were slide mounted and examined under a compound microscope. Descriptions of the body shape of the adult female is described both as unmounted and as mounted on a microscope slide. The body length and width of the adult female was measured in millimeters (mm) as mounted on the slide; other measurements are in microns (μm). Length was measured from the farthest point of the head to the posterior end of the body; width was the greatest width. Description of the adult female of the new species is based on multiple slide-mounted specimens. The number of specimens measured for the description is represented as: n = number of specimens studied. The slide-mounting technique follows that of Williams and Granara de Willink (1992). The material studied is represented by the number of slides and the number of specimens on each slide, e.g., 1(2) means 1 slide with 2 adult specimens. The growth stage and sex of the specimen is listed only for non-adult females. The depository in parentheses is given for each lot of material studied (see abbreviation of depositories below). Each drawing is a generalization of several specimens and was made with the assistance of a *camera lucida* attached to a phase contrast compound microscope. An updated taxonomic key to the adult females of the coccid genera of Myzolecaniinae that occur in the New World was modified from Kondo and Williams (2009).

Abbreviations for the depositories are as follows: Colección de Insectos, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia (UNCB); The National Museum of Natural History, Coccoidea Collection, Beltsville, Maryland, U.S.A. (USNM).

Taxonomy

Key to genera of New World Myzolecaniinae based on adult females

(Adapted from Kondo and Williams 2009)

1. Anal plates located submedially; anterior spiracular pore band incomplete, not extending to margin (posterior spiracular pore band extending to margin); marginal setae cylindrical, peg-like..... ***Cyclolecanium* Morrison**
- Anal plates not located submedially, usually found at about 1/5 of body length from posterior margin; anterior spiracular pore band complete, extending to margin or extending as far as posterior spiracular pore band; marginal setae variable, not peg-like..... **2**
2. Stigmatic clefts deep; dorsal sclerotized plates associated with each spiracle..
.....***Cryptostigma* Ferris**
- Stigmatic clefts shallow or absent, or rarely deep; without dorsal sclerotized plates associated with each spiracle..... **3**
3. Dorsal microducts around body margin conspicuously larger than rest of microducts on dorsum.....***Octolecanium* Kondo**
- Dorsal microducts around body margin not conspicuously larger than rest of microducts on dorsum..... **4**
4. Large bilocular pores (probably macroducts), present in 1 or 2 small groups anterior to anal plates; marginal setae slender, sharply spinose, with tips mostly pointed, but some with lanceolate, or bifurcate apex, arranged in 1 or 2 rows, numerous (distance between each marginal seta less than half the length of a seta).....***Aztecalecanium* Kondo & Williams**
- Groups of large bilocular pores or macroducts absent from area anterior to anal plates; marginal setae variable, arranged in 1 row, not as numerous (distance between each marginal seta more than the length of a seta)..... **5**
6. Preopercular pores absent; dorsum with dense pattern of invaginated bilocular microducts; stigmatic setae absent.....***Pseudophilippia* Cockerell**
- Preopercular pores present; dorsal microducts variable, generally without dense pattern of invaginated bilocular microducts; stigmatic setae present, rarely absent..... **8**
8. Ventral tubular ducts absent..... **9**
- Ventral tubular ducts present at least around perivulvar area **10**
9. Dorsum of slide-mounted specimens with a dense pattern of microducts. Young adult females in life covered by a white cottony to powdery wax, although this powdery wax disappears in old specimens. Perivulvar pores mostly with 5 loculi and one central loculus***Bombacoccus* Kondo**
- Dorsum of slide-mounted specimens without a dense pattern of microducts. Adult females in life covered by a thin layer of glassy wax. Perivulvar pores mostly with 7 or 8 loculi and with 2 or 3 central loculi....***Akermes* Cockerell**

10. Ventral tubular ducts present at least in a submarginal band on abdominal region and reaching area around posterior spiracular pore band *Neotoumeyella* Kondo & Williams
- Ventral tubular ducts not distributed as above..... 11
11. Ventral tubular ducts located around vulva and mediolaterally on abdomen; dorsal setae lanceolate; stigmatic clefts deep *Megasaissetia* Cockerell
- Ventral tubular ducts located around vulva and often also on posterior abdominal segments, but absent mediolaterally on abdomen; dorsal setae generally sharply spinose, rarely lanceolate; stigmatic clefts shallow or absent
..... *Toumeyella* Cockerell

***Bombacoccus* Kondo gen. n.**

urn:lsid:zoobank.org:act:60134B68-1040-47ED-8D20-C7622A1E0E21

Type species. *Bombacoccus aguacatae* Kondo. By present designation.

Proposed common name. English: Cottony avocado scale. Spanish: Escama blanca algodonosa del aguacate.

Generic description, adult female. Body of adult female convex, young adult females covered by a cottony to powdery white wax; old specimens lacking wax. *Dorsum.* Derm membranous but becoming heavily sclerotized at maturity. Dorsal tubercles absent. Body setae sharply spinose, straight or with bent tips. Preopercular pores oval in shape, convex, present in a group anterior to anal plates and extending onto mid-dorsum. Simple pores present. Dorsal microducts present, with well-developed septa, and a long terminal filament, distributed evenly throughout dorsum. Anal plates with 5 or 6 apical setae, with about 4 subapical setae, 2 fringe and 12 hypopygial setae. Anal ring with 10 setae. In older specimens, a sclerotized area about half the width or less of the anal plates is formed around anal plates. Anal ring with 10 setae, translucent pores in 2 irregular rows. *Margin.* Marginal setae sharply spinose, straight or with bent tips. Stigmatic spines totaling 3; median spine often longest. Eyespots not detected. *Venter.* Ventral derm membranous. Ventral body setae sharply spinose, with 3 pairs of long prevulvar setae. Submarginal setae in one row, similar to rest of ventral body setae. Interantennal setae totaling 6. Antennae reduced, each 4–6 segmented. Mouthparts well developed; labium with 4 pairs of setae. Legs all reduced; prothoracic legs generally shortest. Tarsal digitules each pointed; claw digitules each knobbed; claw without a denticle. Spiracles large, posterior spiracle largest and larger than hind leg. Spiracular pores with 5 loculi; each pore band broad, reaching margins. Tubular ducts absent. Perivulvar pores with 5 loculi, present in a small group on each side of anal lobes present ventrad to anal plates. Ventral microducts abundant, scattered throughout venter.

Diagnosis. *Bombacoccus* gen. n. is closest to *Akermes* Cockerell but the two genera can be separated by the following combination of features (morphological features of *Akermes* in parentheses): (i) dorsum with a dense pattern of microducts (dorsum without a dense pattern of microducts); (ii) young insects in life covered by a white cottony

or powdery wax (young insects in life not covered by a white cottony or powdery wax); and (iii) perivulvar pores mostly quinquelocular, with one central loculus (perivulvar pores variable, with 7 or 8 loculi, with 2 or 3 central loculi). Character states of *Akermes* taken from Granara de Willink (1999).

Etymology. The new genus *Bombacoccus* is formed by the combination of the Medieval Latin word “*bombax*” meaning cotton and the Latin word “*coccus*” meaning a berry, and commonly used as an ending of scale insect names.

***Bombacoccus aguacatae* Kondo, sp. n.**

urn:lsid:zoobank.org:act:77590E98-7A9B-4644-A5CF-1C90CE916C31

Figs 1, 2

Description, adult female (measurements based on $n=18$). **Insects in life.** Dorsum of young adult females covered by a white cottony wax, with a broad marginal fringe of cottony wax. The cottony wax is gradually replaced by a powdery white wax in older specimens (Fig. 1A–E), and eventually the wax completely wears out. Insect after removal of wax, yellow-green to greenish brown in color, but older specimens becoming dark brown.

Mounted material. Adult female, oval to elongate oval in outline, 4.2–10.0 mm long, 3.8–8.2 mm wide.

Dorsum. Derm membranous, becoming sclerotized in old specimens. Body setae sharply spinose, straight or slightly bent, each 12.5–20.0 μm long, scattered over dorsum, but abundant on mid-dorsum on area anterior to anal plates. Simple pores each 5.0–6.0 μm wide. Preopercular pores oval in shape, each 6.3–12.5 μm wide, convex, present in a large group anterior to anal plates and extending onto mid-dorsum. Dorsal microducts each 5.0 μm wide, evenly distributed throughout dorsum, densely distributed particularly in younger specimens, but less dense in older specimens due to dilation of derm. Anal plates each triangular in shape, located at about 1/4 of body length from posterior margin, each plate 240–265 μm long, 125–150 μm wide, anterolateral margin 160–175 μm long, posterolateral margin 165–200 μm long. Each plate with 5–7 dorsal apical setae, about 4 ventral subapical setae, 2 fringe setae and 12 hypopygial setae. In older specimens, a sclerotized area about half the width of the anal plates or wider is formed around the anal plates. Anal ring with 10 setae, translucent pores in 2 irregular rows. **Margin.** Marginal setae sharply spinose, straight or with bent tips, each 22.5–42.5 μm long, arranged in an irregular single row around body margin, with 9–14 marginal setae between anterior and posterior stigmatic spines. Stigmatic spines totaling 3; median spine each 22.5–37.5 μm long, lateral spines each 15.0–32.5 μm long; median seta often longest. Eyespots not detected. **Venter.** Ventral derm membranous. Ventral body setae sharply spinose, each 12.5–22.5 μm long, with 3 pairs of long prevulvar setae, each 50–100 μm long. Submarginal setae in one row, similar to rest of ventral body setae. Interantennal setae totaling 6. Antennae reduced, total length 120–230 μm long, each 4–6 segmented. Clypeolabral shield 295–340 μm wide; labium

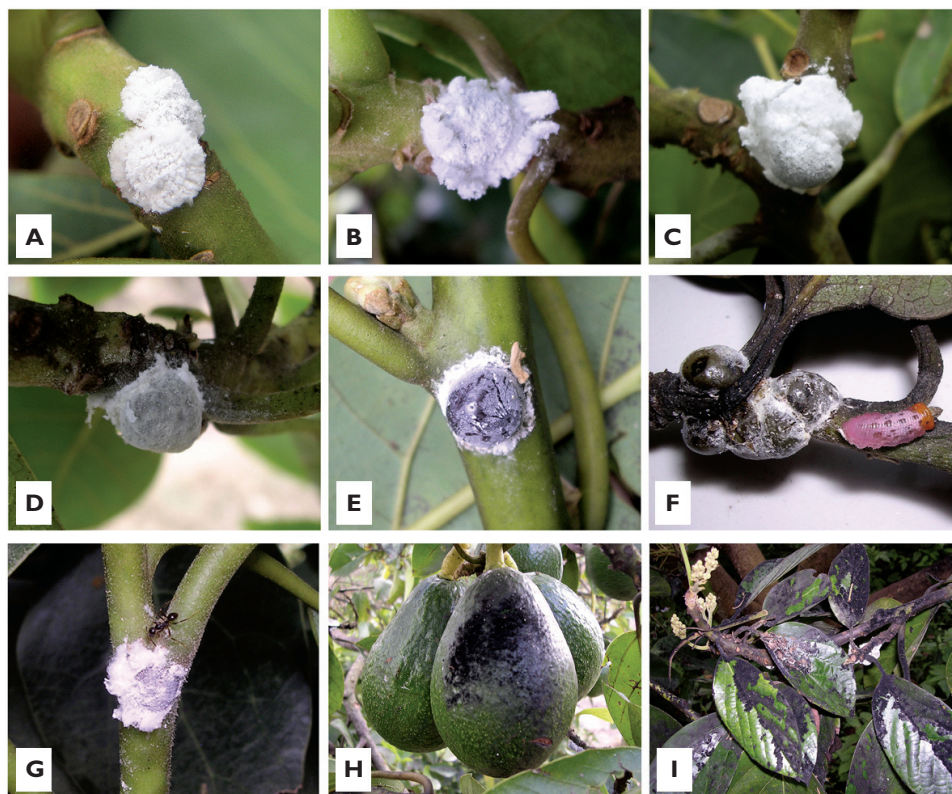


Figure 1. *Bombacoccus aguacatae* Kondo, sp. n. **A** Young adult female **B, C** Older adult female with cottony wax **D** Older adult female with powdery wax **E** Old adult female beginning to lose its wax **F** Left. Old adult females. Right. Larva of a predatory syrphid fly **G** Adult female being visited by *Pheidole* sp. ant **H** Sooty mould on an avocado fruit **I** Sooty mould on leaves of avocado plant. Photo 1.A by A.A. Ramos-Portilla; Photos 1.B–I by T. Kondo.

with 4 pairs of setae. Legs reduced: total length 160–275 μm long; prothoracic legs generally shortest. Tarsal digitules each pointed; claw digitules knobbed; claw without a denticle. Spiracles large, anterior peritreme each 150–240 μm wide, posterior peritreme each 175–275 μm wide. Spiracular pores with 5 loculi, each 6.0–7.0 μm wide; spiracular pore band about same width as peritreme but widening medially, each pore band reaching margins. Tubular ducts absent. Perivulvar pores with 5 loculi, each pore 7.0–8.0 μm wide, abundant, present ventrad to anal plates. Ventral microducts each with duct rim 4.0 μm wide, fairly abundant, scattered throughout venter.

Biology. The insects were found on the tree branches and twigs of avocados of two varieties. Tiny parasitic wasps have been found to emerge from the body of old females and a species of syrphid fly (Diptera: Syrphidae) larvae have been found feeding on the coccid nymphs (Fig. 1F). Insects were observed being tended by *Pheidole* ants (Fig. 1G). Sooty moulds regularly grow on their excreted honeydew covering the branches, leaves and fruit (Figs 1H and I).

do, ex *Persea americana*, var. Booth 8, adult ♀, 1(1) (UNCB). **Paratypes:** same data as holotype, 16(16: 9 adult females + 2 second-instars + 21 first-instar nymphs) (USNM); same data as Holotype, but on *P. americana*, var. Hass, 27 slides (8 adult females + 16 third-instar nymphs + 5 second-instar nymphs + 2 first-instar nymphs).

Notes. *Bombacoccus aguacatae* sp. n. is the only known soft scale insect (family Coccidae) in Colombia with a dorsum covered in a white cottony or powdery wax. Most soft scales of the *Toumeyella*-group are covered by a thin layer of wax; however, a few species in North America are also covered either by a cottony wax, e.g., *Pseudophilippia quaintancii* Cockerell which occurs in the eastern USA and is covered by a profusion of fluffy, snow white wax (Hamon and Williams 1984); *Neolecanium cornuparvum* (Thro), also occurring in the eastern USA, which is usually covered in a white bloom or mealy wax (Hamon and Williams 1984); and one other species from Mexico, *Neotoumeyella leucaenae* (Cockerell) which has been reported to be somewhat covered with small patches of dull white waxy secretion (Cockerell 1903). *Bombacoccus aguacatae* can be easily separated from *P. quaintancii* by the following features (morphological features of *P. quaintancii* in parentheses): (i) preopercular pores present (absent); (ii) dorsal microducts not invaginated (invaginated); and (iii) stigmatic setae present (absent). *Bombacoccus aguacatae* resembles also *N. cornuparvum* and *N. leucaenae*, however, *B. aguacatae* can be easily separated from these two species by the presence of ventral tubular ducts in the perivulvar region of *N. cornuparvum* and *N. leucaenae*, whereas *Bombacoccus aguacatae* completely lacks ventral tubular ducts.

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Two new endemic species of *Chrysopodes* (*Neosuarius*) (Neuroptera, Chrysopidae) from the Galápagos Islands

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Abstract

Two new species that were previously undistinguished from the Galápagos endemic *Chrysopodes* (*Neosuarius*) *nigripilosus* (Banks), are described. These descriptions double, from two to four, the number of endemic green lacewing species known from the archipelago. The four species include: *Chrysoperla galapagoensis* (Banks), *Chrysopodes* (*N.*) *nigricubitus* **sp. n.**; *C. (N.) nigripilosus*; and *C. (N.) pecki* **sp. n.** Three of these species – *C. (N.) nigripilosus*, *C. (N.) nigricubitus* and *Chrysoperla galapagoensis* – each occur on more than one island, whereas *C. (N.) pecki* is known only from the summits of two craters on Isabela Island. A suite of very distinctive features differentiates the three Galápagos *Chrysopodes* (*N.*) species from their congeners on mainland South America. Subtle, but consistent characteristics separate the three Galápagos species from each other. The small degree of morphological divergence among the Galápagos lacewings is in marked contrast to the spectacular radiation of Hawaiian lacewings; the processes of diversification and speciation may differ significantly between the two island archipelagos.

Keywords

Galápagos Islands, endemic lacewings, geographic variation, new species

Introduction

The diversity of insect species reported from the Galápagos Islands is relatively low (e.g., Linsley and Usinger 1966; Parkin et al. 1972; Peck 2001); this generalization appears true for the green lacewings (Chrysopidae). In the most recent synopsis of the Galápagos fauna, Peck (2001) listed only four species: (a) two endemics [*Chrysoperla galapagoensis* (Banks, 1924) and *Chrysopodes (Neosuarius) nigripilosus* (Banks, 1924)] and (b) two others with broad distributions in Central and South America [*Chrysoperla externa* (Hagen, 1861) and *Ceraeochrysa cincta* (Schneider, 1851)]. Both endemic species are known from several islands in the archipelago, and despite numerous scientific expeditions, no new endemic chrysopid species have been described since Neuroptera were first recorded from the Galápagos (Banks 1924).

For several reasons, we considered the possibility that additional species of chrysopids might occur on the islands. First, Banks' (1924) relatively brief description of *C. (N.) nigripilosus* was based on a small series of specimens from one island, and it was written before the systematic value of male or female genitalia were generally appreciated. Second, since Banks' original treatment of the Galápagos lacewings in 1924, a small but substantial number of specimens has accumulated in museums, but no further systematics work has ensued. Third, one of the endemic species [*C. (N.) nigripilosus*] is well differentiated from its closest relatives on the western South American mainland (Tauber, in press). This species' high level of differentiation and its broad inter-island distribution would be consistent with a relatively long evolutionary history on the islands. Given the relatively rapid rates of speciation among Hawaiian lacewings (Zimmerman 1957, Tauber et al. 2007), we hypothesized that cryptic species may be sequestered within the single recognized Galápagos *Chrysopodes* species. And, we thought it especially timely to examine this hypothesis during the celebration of Darwin's bicentennial.

To begin our study, we examined all of the *Chrysopodes* specimens originating from the Galápagos archipelago that we could obtain from museums and compared them with the types of *C. (N.) nigripilosus*. We found that these specimens share many external traits (general body color, size, head and wing features) and that they also have a common suite of genital characters that distinguish them from the other (mainland) species of *Chrysopodes (Neosuarius)* (Tauber, in press). Furthermore, our study revealed that the specimens express subtle variation that, for the most part, appears consistent with intraspecific (geographic) variation in *C. (N.) nigripilosus*; however, in two cases, the variation is strongly indicative of new species.

Here, we (1) re-describe *C. (N.) nigripilosus* from the type locality (Baltra) and (2) characterize the variation in the available specimens of this species from four other islands (Santa Cruz, Isabela, Fernandía, Santa Fe). Finally, (3) we describe two new *Chrysopodes (Neosuarius)* species that our study differentiated from *C. (N.) nigripilosus* – one from Santa Cruz and Pinta Islands, and another from two Volcánes on Isabela Island.

Materials and methods

The *Chrysopodes* specimens from the Galápagos Islands that we studied came from the following collections: American Museum of Natural History, New York (AMNH), Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), Bernice P. Bishop Museum, Honolulu (BPBM), California Academy of Sciences, San Francisco (CAS), National Museum of Natural History, Smithsonian Institution, Washington, D.C., formerly United States National Museum (USNM), the Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSNB) and the National Museum of Scotland, Edinburgh (NMS).

It is noteworthy that most of the pinned specimens that were available are relatively discolored. The discoloration is accentuated because the integument of *Chrysopodes* (*Neosuarius*) species tends to have a heavy coating of waxy material (probably an adaptation to arid conditions); often the coating becomes brownish over time. In contrast, the markings on the specimens that were stored in alcohol (those from the IRSNB) are well preserved and readily visible, in part because the waxy material was dissolved. Thus, our reports of head and body color relied heavily on the specimens preserved in alcohol; our observations from pinned specimens should be considered as estimates.

The procedures in this study followed those used previously (Tauber 2003, 2007; Tauber et al. 2008). In addition to the drawings and images published herein, others are available on the Morphobank website: <http://morphobank.geongrid.org/permalink/?P344>.

Chrysopodes (*Neosuarius*) of the Galápagos Islands

The Galápagos *Chrysopodes* (*Neosuarius*) are generally of a similar, relatively medium size; wing length ranges from ~10.2–13.7 mm. They are also alike in coloration, i.e. tan to light brown bodies with darker brown mottled markings, cream-colored to light brownish heads with dark brown facial markings, hyaline wings with a relatively narrow costal area and white and dark brown venation in a typical *C. (Neosuarius)* pattern (Tauber, in press).

In the above, and several other internal and external traits, the Galápagos *Chrysopodes* (*Neosuarius*) are most similar to the *flavescens* group of *C. (Neosuarius)* species on the mainland (Tauber, in press). However, our study here shows that the Galápagos specimens share a suite of unique genital characters that distinguish them from the mainland species. For example, they are the only *C. (Neosuarius)* in which the males have a pair of large, eversible pouches (probably pheromonal) that extend posterolaterally from the membrane at the tip of the terminal abdominal sternite, and a pair of elongate, setose, ducts that originate within the gonosaccus (immediately below the mediuncus) (Figs 9c, 10c, 11c). The interior of the ducts appears grainy; the ducts may be glandular.

Like other species in the *flavescens* group, the Galápagos females have a distinctive, tubular spermatheca; the spermathecal duct is short and lightly sclerotized (Fig. 13). The bursa is leathery and moderately large (it covers the spermatheca), and the bursal glands are bulbous and bear elongate accessory ducts (Fig. 13). The spermathecae of the three endemic *Chrysopodes* (*N.*) species are unique in that they have a very small mesal swelling and are only slightly bent; they lack the bean-shaped enlargements, coils and sharp bends that characterize the spermathecae of the mainland species.

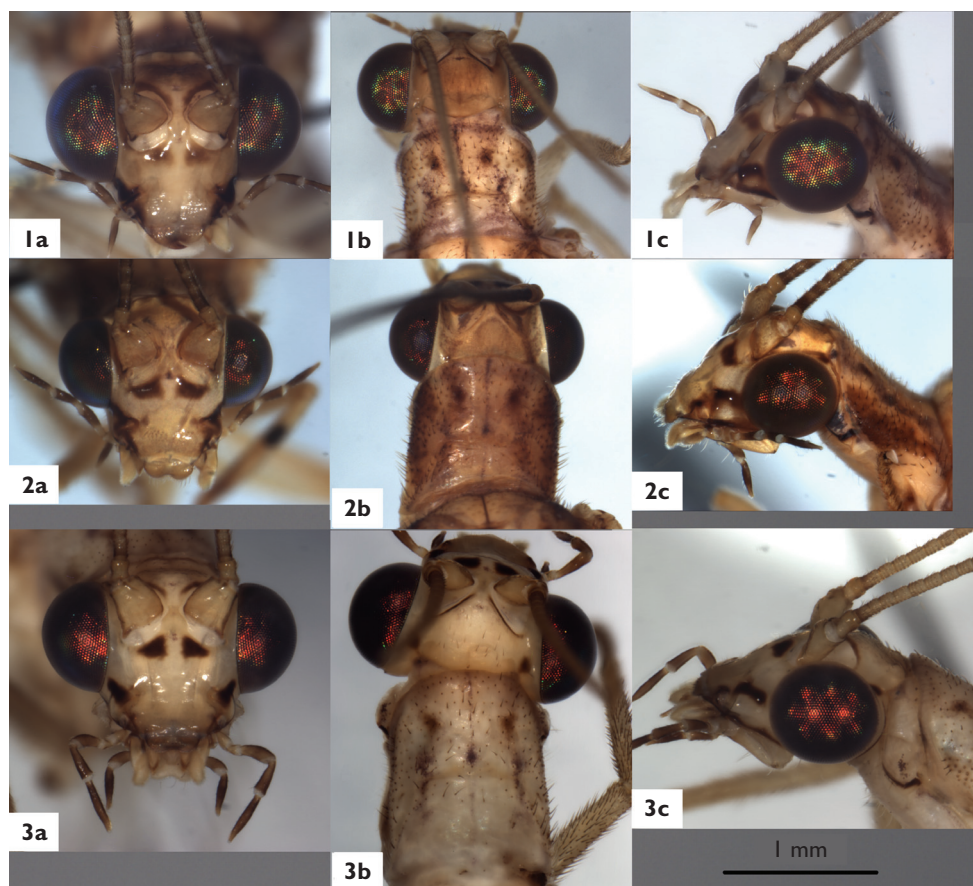
These numerous synapomorphies provide strong evidence that the extant *Chrysopodes* (*Neosuarius*) on the various Galápagos islands have a common evolutionary history of differentiation from an ancestral species that immigrated to the Galápagos from the South American mainland.

***Chrysopodes* (*Neosuarius*) *nigripilosus* (Banks, 1924)**

Diagnosis. *Chrysopodes* (*Neosuarius*) *nigripilosus* specimens from the type locality (Baltra, = South Seymour; all pinned) are distinguished by their overall tan to light tan body color; the pleuron, venter and legs are largely light tan to cream-colored. The vertex is light brown and the facial markings range from light to dark brown (Fig. 1). The forewing membrane is without markings or suffusion; below the stigma there usually are three to four (occasionally two) crossveins between the Subcosta and Radius, (scx); and the second cubital crossvein (cux2) is not bent or crassate, nor does it have an enlarged swelling (Fig. 4a). The venter of the male abdomen is largely cream-colored to light tan throughout; in contrast, the female S5 and S6 are entirely brown, S7 is either brown entirely or basally, and the terminus is light to dark brown (Fig. 6a, b).

In the males: (a) the horizontal apodeme along the ventral margin of T9+ectoproct is arched and its posterior tip is bifurcated (see Note in brackets below); (b) the gonarcus is arcuate, with the gonarcual arms extending downward, not outward (Fig. 9b, c); (c) the eversible pouches at the tip of S8+9 are large and well separated mesally by a distinctly flat membrane (Fig. 8). In the female, the spermathecal duct is short and it lacks tight coils; the bursal glands are large and globose and their accessory ducts may be branched (Figs 13, 14). The subgenitale bears a pair of invaginated pouches that are near the base of the bursal glands; in *C. (N.) nigripilosus*, these pouches typically are flat and folded (Fig. 15a).

[Note: In Chrysopidae the apex of the abdomen is opened by two major apodemes articulating with each other at their bases. One apodeme runs along the ventral portion of tergite 9+ecoproct; it is termed the dorsal apodeme (d.a.). The other apodeme runs along the dorsum of sternite 8+9 and is termed the ventral apodeme (v.a.). The dorsal apodeme can be complex, with a dorsal branch (d.b.) along or below the anterior side of the callus cerci, a ventral branch (v.b.) that projects ventrally towards the gonarcus, and a caudal branch (c.b.) that extends distally below the callus cerci and can project beyond the ectoproct.]



Figures 1–3. Head and prothorax. **1** *Chrysopodes (Neosuarius) nigripilosus* **2** *C. (N.) nigricubitus* **3** *C. (N.) pecki*. (a) frontal view (b) dorsal view (c) lateral view. The scale applies to all images.

Description of specimens from type locality. *Head.* (Table 1, Fig. 1a, b, c): Vertex raised, flat, pentagonal shape, with small, upward fold posteriorly; surface of vertex with small, brown setae. Frons smooth, shiny throughout. Clypeus convex basally; surface smooth, mostly flat, very slightly raised in middle. Labrum flat, surface smooth; distal margin straight. Gena smooth, rounded. *Coloration:* Frons light tan to light brown with pair of brown, subtriangular to roundish marks below toruli; clypeus with lateral margins dark brown. Vertex brown. Toruli light brown, with surrounding sclerotized areas brown to dark brown; dorsal torulus with two dark brown, vertical streaks, larger one extending from below center of scape, smaller one extending from below mesal margin of scape. Genae dark brown, central area with large to small, longitudinal, pale stripe. Scaes light brown to tan, unmarked; pedicel brown basally, lighter distally; flagellum light brown. Maxillary palp: segments 3–5 brown; basal two segments tan. Labial palp with terminal segment brown, basal segments tan. Venter tan to cream-colored; lateral margins of submentum dark brown.

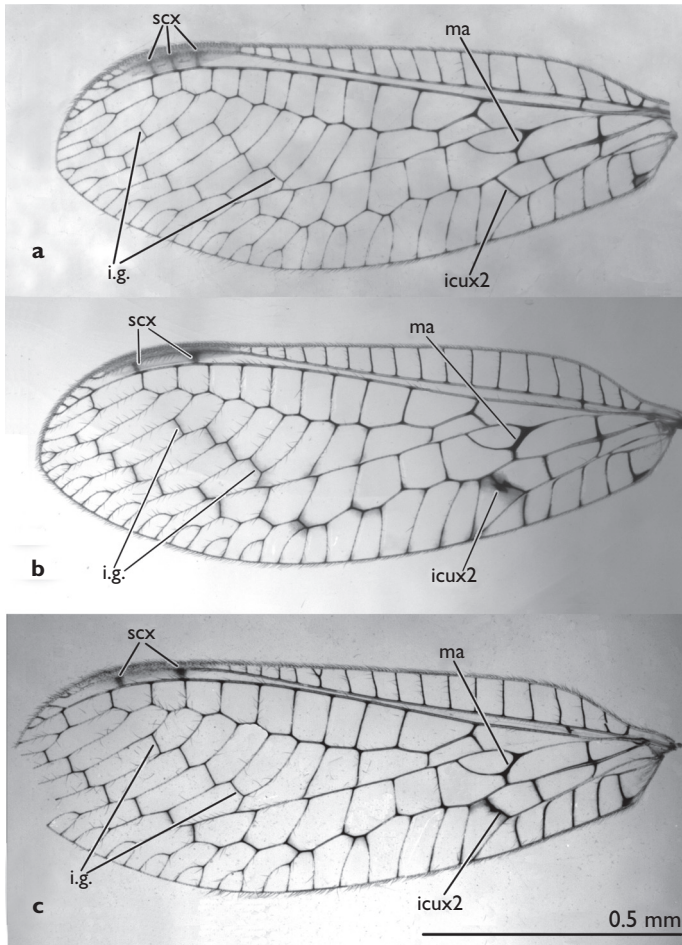


Figure 4. Forewing. **1** *Chrysopodes (Neosuarius) nigripilosus* **2** *C. (N.) nigricubitus* **3** *C. (N.) pecki*. **icux2**, second intracubital crossvein; **i.g.**, inner gradate veins; **ma**, median arcus; **scx**, subcostal crossveins (between subcosta and radius). The scale applies to all images.

Thorax. (Table 1, Fig. 1b). Pronotum tan to light brown, with scattered, brown, mottled markings sublaterally; several long, thin, pale setae laterally, short, robust, dark brown to black setae dorsally. Mesonotum, metanotum light brown mesally, brown laterally; setae on mesonotum short, robust, dark brown; setae on metanotum sparse, thin, pale. Pleural areas tan to cream-colored, sometimes with brown markings. Legs cream-colored without markings, setae light brown. Tarsal claws amber, long, narrow, with broad cleft, small base; area between claws black.

Wings. (Table 3, Figs 4a, 5a). Forewing about three times longer than tall, with apex broad, rounded; anterior margin relatively straight; posterior margin curved. Costal area narrow, greatest height ~0.17–0.18 times height of wing, tallest at costal cell (#5–6). Subcosta, radius (R) slightly sinuate; most costal veinlets, radial crossveins straight; one subcostal crossvein basally, three to four below stigma. Ten to twelve radial crossveins

Table 1. Range of variation in head and thoracic features among geographic populations of two *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

<i>Chrysopodes</i> (<i>N.</i>) <i>nigripilosus</i> (Banks)									
Balra	Santa Cruz	Isabela	Isabel	Isabel	Isabel	Isabel	Santa Fe	Fernandina	
Type locality	Academy Bay	Puerto Villamil	Punta Tortuga	Volcán Wolf	Volcán Alcedo	Volcán Alcedo	5 m, Lagoon	Cabo Hammond	
(N=5)	(N=4)	(N=2)	(N=1)	(N=3, 2 alcohol)	(N=1)	(N=1, alcohol)	(N=1, alcohol)	(N=4, alcohol)	
Head, W, mm	1.54–1.66	1.59–1.69	1.56	1.44–1.64	1.66	1.69	1.57–1.77		
Ratio, head W : eye W	1.95–2.17:1	1.95–2.03:1	1.90:1	1.99–2.23:1	1.79:1	2.23:1	1.62–2.06:1		
Dist.between tentoria, mm	0.36–0.50	0.45–0.51	0.45	0.43–0.53	0.51	0.50	0.44–0.48 (N=3)		
Frons, L, mm	0.44–0.50	0.43–0.52	0.42–0.44	0.44–0.47	0.48	0.47	0.39–0.46 (N=3)		
Clypeus, L, mm	0.22–0.30	0.24–0.29	0.24–0.28	0.18–0.26	0.27	0.30	0.23–0.26 (N=3)		
Antenna, L, mm	10.2 (N=1)	9.2–9.5 (N=3)	9.3–10.3	–	9.4 (N=1)	–	8.4–11.0 (N=2)		
Pronotum, L, mm	0.69–0.73 (N=3)	0.68–0.92	0.71–0.90	0.71	0.63–0.84	0.87	0.66–0.83		
Pronotum, W, mm	1.05–1.14 (N=3)	0.99–1.17	0.98–1.14	1.04	0.92–1.13	1.06	1.01–1.13 (N=3)		
Ratio, pronotum, W:L	1.61–1.70:1 (N=3)	1.65–1.78:1	1.57–1.72:1	0.68:1	0.67–0.75:1	0.8:1	0.73–0.79:1 (N=3)		

<i>Chrysopodes</i> (<i>N.</i>) <i>nigriculitus</i> s.p. n.			
Santa Cruz	Santa Cruz	Pinta	
Table Mtn. (N=4)	Hornemann Farm (N=3)	420 m (N=2)	
Head W, mm	1.59–1.69	1.46–1.59	1.39–1.45
Ratio, head W : eye W	2.17–2.48:1	2.26–2.51:1	2.68:1
Dist.between tentoria, mm	0.47–0.54	0.46–0.52	0.44–0.49
Dist. between antennae, mm	0.09–0.12	0.10–0.11	0.12
Frons L, mm	0.44–0.59	0.44–0.51	0.42–0.44
Clypeus L, mm	0.29–0.33	0.27–0.30	0.27–0.32
Antenna L, mm	8.2–9.6 (N=3)	9.2–9.3 (N=2)	10.1 (N=1)
Pronotum L, mm	1.02–1.35	0.95–1.14	0.88
Pronotum W, mm	1.16–1.56	1.06–1.17	1.00
Ratio, pronotum W : L	0.85–0.93:1	0.90–1.01:1	0.88:1

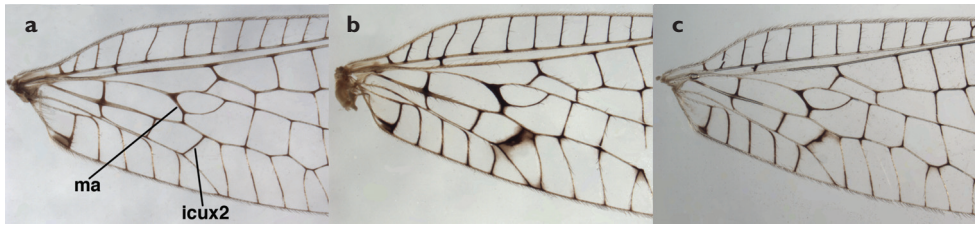


Figure 5. Base of forewing. **a** *Chrysopodes* (*Neosuarius*) *nigripilosus* **b** *C. (N.) nigricubitus* **c** *C. (N.) pecki*. **icux2**, second intracubital crossvein; **ma**, median arcus.

[between R and radial sector (Rs)]; height of tallest radial cell about 0.2 times height of wing. Radial sector slightly thickened at intersection with first radial crossvein (rx1). First intramedian cell ovate, length about 3/4 length of third medial cell; median arcus (ma) thickened. Usually two rows of gradate veins; inner row with three to five gradates in irregular pattern; outer row with six to seven, ~regularly stepped gradates (six specimens with three rows – the middle row with one to two gradates). Four b cells, four b' cells; cubitus (Cu) thickened at furcation; three intracubital cells, distal one open, icu1, icu2 each shorter than icu 3; icu1 longer than icu2; second intracubital crossvein (icux2) relatively straight, not thickened, without swellings. First anal vein (1A) forked.

Hindwing narrow, length over three times greater than height, with apex acute. Ten to eleven radial crossveins; three to five inner gradates; six to seven outer gradate veins; three b cells; no t cell; four b' cells; two intracubital cells, distal one open.

Forewing hyaline, with stigma slightly opaque; costal veinlets within stigma brown, surrounded with suffusion of light brown. Alar membrane almost completely without suffusion of colored pigment. Longitudinal veins cream-colored, marked with dark brown to black at intersections with crossveins. Most costal veinlets, almost all crossveins cream-colored in center, dark brown at tips. Gradates dark brown to black; terminal veinlets dark brown basally, brown at tips, with cream-colored sections mesally. Rs black at intersection with Rx1; ma black; Cu black at furcation; marginal cell below 3A almost completely dark brown to black. Hindwing hyaline; membrane without suffusion of colored pigment; stigma opaque, brownish. Longitudinal veins cream-colored, marked with dark brown at intersections with crossveins; gradates, icu crossvein dark brown; costal veinlets, most crossveins dark brown at tips, cream-colored in center.

Abdomen (male & female) (Table 5, Fig. 6a, b). Tergite 1 light brown to brown; T2, 3, 6, 7, brown; T4, 5 brown distally; pleural regions cream-colored, mottled with brown; sternites 1–4 cream-colored with cream-colored setae; setae brown on S5–9; Female: S5, S6 brown, S7 brown or brown basally; terminus light to dark brown; Male: S5 to S8+9 cream-colored to tan. Tergites 6, 7: roughly quadrate, with relatively straight ventral margins, straight basal margins, rounded distal margins; length: 1.4–1.5 (T6), 1.1–1.2 (T7) times greater than height (lateral view); with long, robust setae. Pleural region, P7 with dense, medium-length setae. Sternite 6: quadrate, dorsal margin relatively straight; length ~0.8 times height, with long, robust setae. Spiracles oval, not enlarged, ~0.02–0.04 mm diameter; atria not enlarged.



Figure 6. Abdomen, ventral view. **a** *Chrysopodes (Neosuarius) nigripilosus* male **b** *Chrysopodes (Neosuarius) nigripilosus* female **c** *C. (N.) nigricubitus* female **d** *C. (N.) pecki* female. The scale applies to all images.

Male. (Table 5, Figs 7, 8, 9a, b, c). Eighth tergite (T8) truncate anteriorly, posteriorly (lateral view). Left and right T9+ectoproct fused dorsally; terminal edge rounded dorsally; vertical margin straight, rounded ventrally; vertical field of long, dense, robust setae distally. Apodeme of T9+ectoproct heavily sclerotized, arched, with three terminal branches: dorsal branch extending upward, internally beneath callus cerci, connecting mesally at top of tergite; short ventral branch extending into membrane below apodeme; caudal branch heavy, extending distally well beyond tip of T9+ectoproct, curved mesally, with rounded, forked tip (Fig. 9a). Callus cerci taller than wide (0.17–0.19 mm tall, 0.13 mm wide), with 31–32 trichobothria. S8+9 length 1.6–1.7 times proximal height; shape in lateral view: triangular to slightly truncate distally, with well sclerotized, sub-basal apodeme extending transversely across entire sternite; terminal membrane modified into pair of eversible, elongate pouches, separated by unmodified, flat, mesal membrane. Subanal plate lightly sclerotized, with large patch of long, delicate setae. Gonarcus arcuate, loosely attached to T9+ectoproct via delicate membrane beneath subanal plate; bridge well-sclerotized, broad, flat transversely, with gonarcual arms extending downward from distal margins of bridge; span of gonarcus near arch 0.31–0.32 mm, span between gonarcual arms distally 0.37–0.46 mm. Gonarcual arms oblong, ~0.32–0.36 mm long. Mediuncus lightly sclerotized, broad basally, more heavily sclerotized, cone-shaped, distally, slightly rounded dorsally; base broadly attached and extending from top of gonarcus, with pair of elongate, internal rods extending along dorsal margin of mediuncus from base to well past middle of mediuncus. Sclerotized surface of mediuncus rough, with very fine striations above, minute microsetae laterally. Tip of mediuncus bent downward, elongate, tapering to rounded, beak-like apex, with thin, mesal flange above beak. Membrane immediately below beak (base of gonosaccus) bearing pair of long, thin, setose glands with grainy

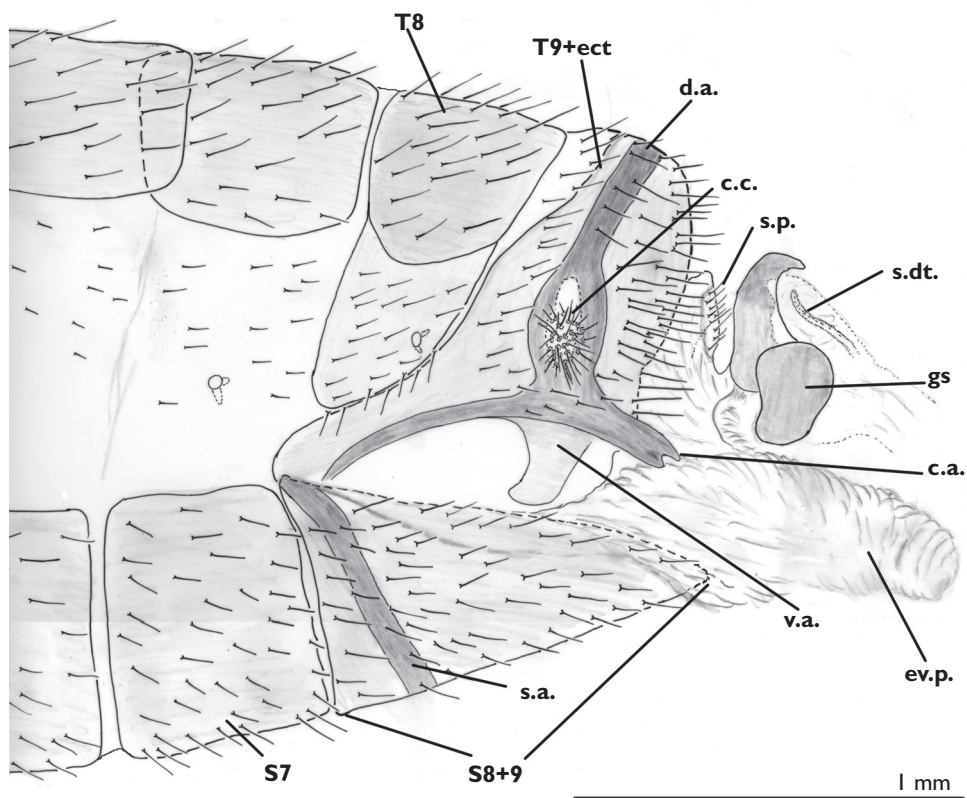


Figure 7. Male abdomen, lateral view. *Chrysopodes (Neosuarius) nigripilosus*. **c.a.** tip of caudal apodeme on T9+ectoproct **c.c.** callus cerci **d.a.** dorsal apodeme on T9+ectoproct **ev.p.** eversible membranous pouch **gs** gonarcus (lateral apodeme) **s.a.** sub-basal apodeme on S8+9 **s.dt.** setose duct **s.p.** setose subrectal plate **S7** seventh sternite **S8+9** fused eighth and ninth sternites **T8** eighth tergite **T9+ect** fused ninth tergite and ectoproct **v.a.** ventrally projecting arm of apodeme on T9+ectoproct.

interior (glands sometimes ribbon-like – probably teneral condition); base of glands sometimes with short, stout setae, sometimes stemming from crescent-shaped sclerotized protuberances; length of glands approximately two times width of gonarcal bridge; terminus of glands apparently merging with gonosaccus membrane well below origin of ducts; gonosaccus membrane distal to gonarcus folded, with rough-textured surface. Hypandrium internum with pair of broad, almost transparent arms, very flat, wing-like comes. Gonopsis absent.

Female (Table 5, Figs 12, 13, 14, 15). Tergite 8: height of fully sclerotized portion approximately equal to length; height of sclerite (including less sclerotized ventral extension) ~two times length, unsclerotized portion with numerous medium-length setae. Ninth tergite + ectoproct (lateral view) very slightly tilted – ventral margin extending slightly beneath T8; proximal margin relatively straight throughout or slightly

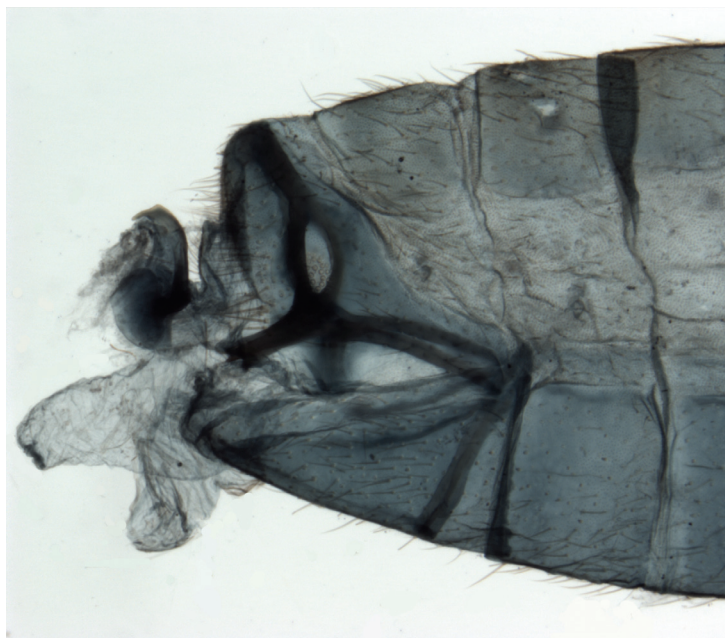


Figure 8. Male abdomen, lateral view. *Chrysopodes* (*Neosuarius*) *nigripilosus*. Note pair of eversible pouches at terminus of S8+9.

convex; distal margin curving beneath ventral margin of gonapophyses laterales (mature specimens). Callus cerci taller than broad (0.16–0.17 mm tall, 0.10–0.14 mm wide), with ~31–36 trichobothria. Gonapophyses laterales 0.4–0.5 times height of T9+ectoproct; ~2.6–4.7 times taller than wide; with robust setae dorsally, shorter, thinner setae ventrally; rounded dorsally, ventrally; orientated posteroventrally (~60–70° angle from midline). Sternite 7: with long, robust setae; length ~1.6 times height of proximal margin (lateral view), with distal 1/4 sloping abruptly to terminus; terminus almost as tall as midpoint of segment. Subgenitale narrow, rounded, with broad, bilobed, distal process; base consisting of light, folded membrane, attached to S7 via delicate, invaginated membrane; lateral margin of base with pair of small, flat pouches, near but separate from base of bursal glands; pouches ~1/6 length of spermatheca. Pair of large, bulbous bursal glands with narrow, elongate ducts opening on dorsolateral margin of bursa (ducts possibly with small setae or scales), with broad, elongate, sometimes branched, accessory ducts distally. Bursa narrow (< 1/2 width of segment), but completely covering spermatheca; membrane heavier basally than distally, dorsum with longitudinal folds, opening ventrally to bursal duct. Bursal duct broadly fluted, transversely folded, immediately below bursa. [The origin of the fluted area below the bursa is not completely clear. We consider it to be an enlarged part of the bursal duct and label it as such on the figures. However, we recognize that it could be part of the bursa copulatrix, in which case the bursal duct would be greatly reduced.] Spermatheca elongate, tubular, with distal end slightly bulbous, one bend, after midsection (to

the right), open to bursa via elongate dorsal slit throughout; 0.12 mm diameter at mouth (distal end), 0.18 mm diameter in midsection (widest area), 0.5–0.6 mm long; invagination oblong, extending ~1/2 length of spermatheca (length 0.23–0.25 mm); velum not identified. Spermathecal duct short, not well sclerotized at tip, ~0.65 mm long (not including pale, brushy tip), extending from slit on dorsal margin of spermatheca, curving, entering subgenitale, making U-shaped curve along dorsal surface of subgenitale cavity, then looping in front of spermatheca; distal ¼ brushy. Colleterial gland elongate, narrow, extending slightly into A6, with smooth, untextured surface, base with bulbous, folded reservoir near terminus of duct; no accessory glands found. Transverse sclerification curved, eliptoid, plate-like, located mesally within gonopophyses laterales, with two rows of setae (setae longer mesally than laterally).

Intraspecific variation. See measurements (Tables 1, 3).

Baltra. The lectotype (AMNH) is teneral. It has a mediuncus that is characteristic of mature specimens, but the gonarcular arms are barely formed, the glandular ducts are visible only in a small region at the base of the gonarcular arms, and the eversible pouches are small and withdrawn. The dissected paralectotype (MCZ) is mature, with structures as described above.

Santa Cruz (Academy Bay). The large series of specimens from this locality are relatively uniform, and in all the features that we measured, they overlap with those from the type locality. Although they tend to have somewhat longer wings (Table 3), their head size and proportions, as well as the features of the wings, are well within the range of the Baltra specimens (Tables 1, 3).

The dorsal surface of specimens from Academy Bay is relatively dark (light brown to brown); the lateral and ventral surfaces of the thorax are light brown to tan; dorsally the abdomen is cream-colored to light brown, with areas marked with brown; ventrally the abdomen is cream-colored to light tan (entirely in the males; with S5, S6 and S7 brown in the females). The facial markings range from medium depth to dark. The membrane of the wings is without markings or suffusion; the degree to which the Rs, ma and Cu are thickened is small; and there are three to four crossveins below the stigma. In the four dissected males, (a) the gonarcular arms are oriented downward; (b) the eversible pouches are large and well separated. [Note: One of the ~65 specimens has a small amount of suffusion around the gradates and some crossveins, but none of the other characteristics of *C. (N.) nigricubitus*; four of 65 specimens (from the 1968 Edinbrough University Expedition) have two crossveins below the stigma; of these, two have three crossveins on the opposite wing.]

Isabela. The *C. (N.) nigripilosus* specimens from Isabela overlap with the Baltra specimens in the features we examined. Among these specimens (both pinned and in alcohol), there were no distinguishing features with regard to head size, head features, or wing size or wing features (See measurements, Tables 1, 3).

The overall body color is tan with mottled, light to medium brown dorsal markings; the ventral abdominal markings of the males and females match those of the Baltra population. The facial markings range from light to medium brown. The membrane of the wings is without markings or suffusion; the degree to which the Rs, ma

and Cu are thickened is small; and there are three to four crossveins below the stigma. On the two dissected male specimens from this island: (a) the gonarcular arms extend downward from the gonarcular bridge, parallel with the mediuncus, and (b) the eversible pouches are short and highly folded; although they are fully separate, the area between them is membranous and loose.

Fernandina. In general, the specimens from this island (2 pinned and 7 in alcohol) overlap with the Baltra specimens. The degree to which the Rs, ma and Cu are thickened is small; the membrane of the forewing is clear and without marks; there are three crossveins below the stigma (Table 3).

Santa Fe, Santiago. The single female specimens from Santa Fe and Santiago Islands have features that are typical of the Baltra population (Tables 1, 3).

Specimens examined (in addition to the type material; all are pinned unless noted otherwise): **Baltra** (= South Seymour). South Seymour, IV/23/1923, Williams Galápagos Exped., Dept. of Tropical Research, N. Y. Zoological Society, William Beebe, Director (1M, Lectotype, AMNH); So. Seymour Isl., IV/20/1923, Am. Mus. Exped. (1M, 2F, 1 abdomen missing, Paralectotypes, MCZ); 30 m, S. Peck, I/24/1989, arid zone, grass+Bursera Forest, UV light, 89–4 (2M, USNM); 10 m, I/23/1989, S. Peck, arid zone, Bursera Forest, UV light, 89–5 (1F, USNM), beating or on ground, 89–12 (1M, USNM). **Santa Cruz** (= Indefatigable). CDRS, Arid zone, II/5–9/1989, dung tp., B. J. Sinclair (1F, USNM); Academy Bay, II/17/1964, P. D. Ashlock, (1M, 1F, BPBM); 0–100 m IX/1970, J. & M. Sedlacek (2F, BPBM); Academy Bay, Darwin Research Station, I/25–II/27/1964, D. Q. Cavagnaro & R. O. Schuster (3M, 11F, CAS), III/21/1964, D. Q. Cavagnaro (1M, CAS), I/30/–III–20/1964, R. O. Schuster (30M, 13F, CAS), I/21–II/1/1964, E. G. Linsley (2M, 1F CAS); CDRS, X/12–27/1968, Edin. Univ. Exped 1969.71 (4F, 2?, NSM, det. A. R. Waterston, 1970). **Isabela** (= Albemarle). nr, Punta Tortuga N, of Tagus Cove, I/28–30/1967, edge of mangrove swamp, among *Bursera graveolens*, I. L. Wiggins (1M, CAS); Puerto Villamil, MVL, III/2/1989, B. Laudry (1M, 1F, USNM); V. Alcedo, arid zone, 200m, Palo Santo woodland uv light, IV/3/1996, S. Peck, 96–78 (1M, 1F, USNM); V. Wolf, summit arid, 1700m, sweeping shrubs, V/21/1996, S. Peck, 96–201 (1F, USNM); Beagle Crater, 3 m. (beach), III/25/1988, 4 m. (beach), III/23/1988, L. Baert, K. Desender & J.-P. Maelfait (6M, 2F, IRSNB, Sample #B.88/0478; alcohol); Volcán Wolf, 4 m. (beach), III/20/1988, L. Baert, K. Desender & J.-P. Maelfait (2M, 5F, IRSNB, Sample #B.88/0446; alcohol); Volcán Wolf, 4 m. (beach), III/23/1988, L. Baert, K. Desender & J.-P. Maelfait (11M, 8F, IRSNB, Sample #B.88/0470; alcohol). **Fernandina** (= Narborough). W side, 1,100', II/5/1964, D. Q. Cavagnaro (2F, CAS); Beginning of encañada, V/4/1991, L. Baert, K. Desender & J.-P. Maelfait (1F, IRSNB, Sample #B.91/0765; alcohol); Cabo Hammond, 5 m, V/12/1991, L. Baert, K. Desender & J.-P. Maelfait (4M, 2F, IRSNB, Sample #B.91/0802; alcohol). **Santa Fe** (= Barrington). Lagoon, 400 m, IV/24/1991, L. Baert, K. Desender & J.-P. Maelfait (1F, IRSNB, Sample #B.91/0722; alcohol). **Santiago** (= San Salvador, James). Settlement, IX/22/1968, Edin. Univ. Exped. 1969.70 (1F, NMS, det. A. R. Waterston 1970).

[Note: Additional specimens from Santa Cruz Island are in the NMS.]

***Chrysopodes (Neosuarius) nigricubitus* sp. n.**

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Diagnosis. *Chrysopodes (Neosuarius) nigricubitus*, the second species of endemic *Chrysopodes (Neosuarius)* to be recognized from the Galápagos Archipelago, currently is known from two islands: Santa Cruz [Table Mountain (440 m) and Horneman Farm (220 m)] and Pinta (west side of island, 420 m). The adults of this species share many features with *C. (N.) nigripilosus* and *C. (N.) pecki*: they have small, robust, brownish bodies, brown head and facial markings, relatively narrow wings with a narrow costal area, and cream-colored wing venation marked with black (Figs 1, 2, 4). However, a suite of distinguishing features (external and internal) in both males and females indicates that these specimens represent a distinct species.

The most prominent distinguishing feature of the species is the suffusion of black or dark brown pigment (coloration) around many of the crossveins on the forewings (Figs 4b, 5b). This suffusion is absent from the other two *Chrysopodes* species on the Galápagos Islands. In *C. (N.) nigricubitus*, the second cubital crossvein bears a distinct, dark brown to black swelling that is absent from *C. (N.) nigripilosus* and small on *C. (N.) pecki*. Also, there are consistent differences between the species in the length : width ratios of the pronotum and abdominal tergite 6; for both structures, the *C. (N.) nigricubitus* ratios are intermediate between those of *C. (N.) nigripilosus* and *C. (N.) pecki* (Tables 2, 5). Among the specimens that we studied, there was no overlap between the species in the values of any of these traits. In addition, the abdominal sternites of female *C. (N.) nigricubitus* are cream-colored to light tan, without dark brown areas like those on the S5-S7 of *C. (N.) nigripilosus* and *C. (N.) pecki* females (Fig. 6).

Although the *C. (N.) nigricubitus* genitalia resemble those of *C. (N.) nigripilosus* and *C. (N.) pecki*, there are distinguishing features in the *C. (N.) nigricubitus* males. First, unlike *C. (N.) nigripilosus* and *C. (N.) pecki*, in which the lateral arms of gonarcus are directed downward next to the mediuncus, in *C. (N.) nigricubitus* the gonarcus arms are spread widely (Fig. 10c vs Figs 9c & 11c). Only the tips of the gonarcus arms bend downward, and the gonarcus structure is relatively flat in lateral view. Second, in *C. (N.) nigricubitus*, the horizontal apodeme along the ventral margin of T9+ectoproct is relatively straight (lateral view), not arched as in *C. (N.) nigripilosus*. The tip of the caudal branch of the apodeme is pointed and without a flange; whereas in *C. (N.) nigripilosus* it is forked, with both tips rounded, and with the upper fork having a flange-like membrane attached (Fig. 10a).

In the female genitalia, we detected small, but consistent differences between *C. (N.) nigricubitus* and the other two Galápagos species. First, the sclerotized portion of the *C. (N.) nigricubitus* spermathecal duct tends to be slightly shorter than that of *C. (N.) nigripilosus* (0.65 vs. 0.40 mm) (Table 5). Second, the tip of the distal knob of subgenitale is slightly more elongate than that on the two other species, and, third, the pouches near the base of the bursal glands are flat and folded as in *C. (N.) nigripilosus* but not *C. (N.) pecki* (Compare Fig. 15b with 15a, 15c).

Table 2. Range of variation in head and thoracic features among three *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

	<i>C. (N.) nigripilosus</i> (Banks)	<i>C. (N.) nigricubitus</i> sp. n.	<i>Chrysopodes (N.) pecki</i> sp. n.
	8 localities, 5 islands [†]	3 localities, 2 islands [‡]	2 localities, 1 island [§]
	N=21	N=7	N=3
Head W, mm	1.44–1.72 (N=21)	1.39–1.69 (N=9)	1.57–1.68, 1.43
Ratio, head W : eye W	1.79–2.23:1 (N=21)	2.17–2.68:1 (N=9)	2.35–2.55, 2.58
Dist.between tentoria, mm	0.43–0.53 (N=20)	0.44–0.54 (N=9)	0.52–0.53, 0.44
Frons L, mm	0.42–0.48 (N=20)	0.42–0.59 (N=9)	0.53–0.56, 0.51
Clypeus L, mm	0.18–0.30 (N=20)	0.27–0.33 (N=9)	0.23–0.29, 0.24
Antenna L, mm	9.2–10.3 (N=10)	8.2–10.1 (N=6)	–
Pronotum L, mm	0.63–0.92 (N=19)	0.88–1.35 (N=9)	1.25–1.30, –
Pronotum W, mm	0.92–1.21 (N=18)	1.00–1.56 (N=9)	1.14–1.20, –
Ratio, pronotum W : L	0.61–0.8:1 (N=18)	0.85–1.01:1 (N=9)	1.09–1.10:1, –

[†] Baltra (no specifics), Santa Cruz (Academy Bay), Isabela (Puerto Villamil, Punta Tortuga, Volcán Wolf, Volcán Alcedo), Santa Fe (lagoon), Fernandina (Cabo Hammond)

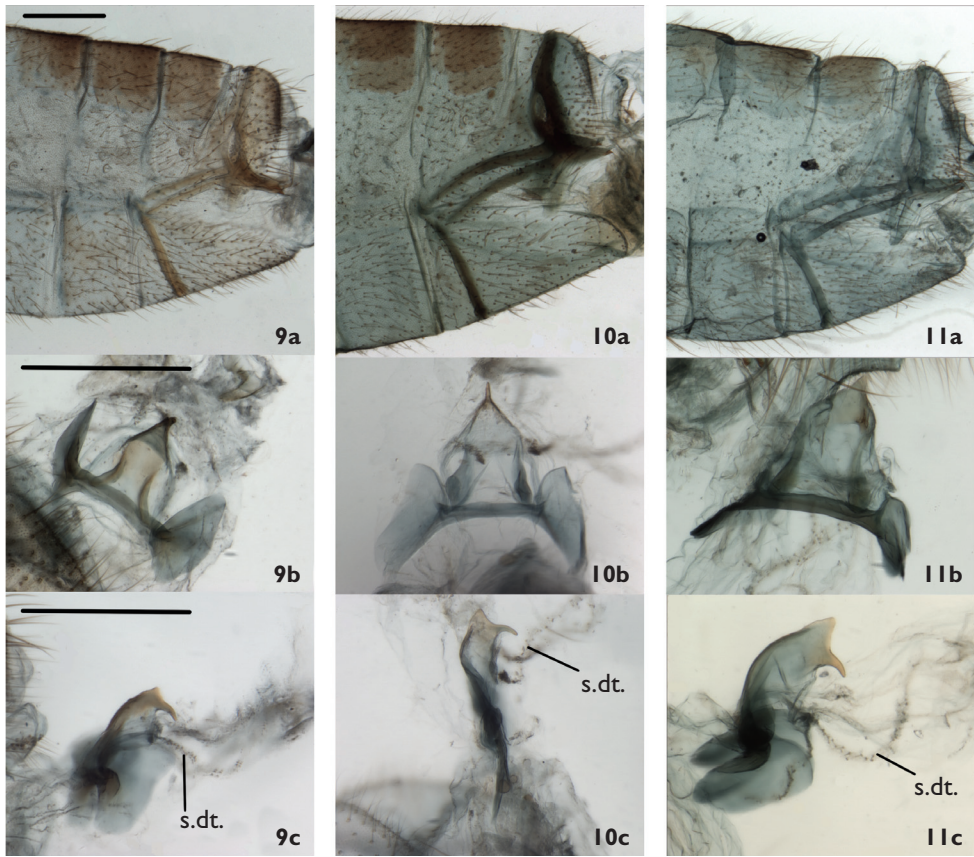
[‡] Santa Cruz (Table Mtn., Hornemann Farm), Pinta (420 m)

[§] Isabela (Volcán Wolf, Volcán Alcedo; N=2F, 1M)

Description. All features are as described for *C. (N.) nigripilosus* except as follows. *Head* (Table 2, Fig. 2): Vertex: surface with small, amber setae. Labrum: distal margin with slight mesal cleft. *Coloration.* Head cream-colored frontally, tan to light brown dorsally, with brown streak lateral to eyes; frons with pair of oblong, brown marks below most of lower margin of torulus; clypeus with lateral margins dark brown; toruli cream-colored to light tan, with brown border surrounding sclerotized margins; dorsal torulus with dark brown, vertical streak. Genae dark brown ventrally, white stripe above, dark brown dorsally. Scapes tan, unmarked; pedicel tan to light brown; flagellum light brown. Maxillary palp: basal two segments cream-colored. Venter: lateral margins of submentum cream-colored to tan.

Thorax (Table 2, Fig. 2b). Pronotum approximately same width as length; with mottled light brown markings. Mesonotum: with setae short, delicate, amber. Pleural areas: cream-colored, without markings. Legs: setae amber.

Wings (Table 4, Figs 4b, 5b). Costal area: greatest height ~0.16–18 times height of wing; tallest at costal cell (#4–6). Subcosta: two subcostal crossveins below stigma. Nine to eleven radial crossveins (between R and Rs); ma considerably more thickened than the Rs at rx1; two rows of gradates; inner row with three to four gradates, outer row with five to six, both rows in regular pattern. Cubitus thickened near furcation; icux2 curved, with dark brown, bubble-like expansion mesally.



Figures 9–11. Male terminal structures. **9** *Chrysopodes (Neosuarius) nigripilosus* **10** *C. (N.) nigricubitus* **11** *C. (N.) pecki* **a** terminal segments of abdomen, lateral view (scale = 0.5 mm, all images in row) **b** gonarcus, dorsal view (scale = 0.1 mm, all images in row) **c** gonarcus, lateral view (scale = 0.1 mm, all images in row). **s.dt.**, setose duct. Note: The gonarcual arms of *C. (N.) nigripilosus* (Fig 9b) are unnaturally splayed here by the coverslip; the tips typically are below the edge of the gonarcual bridge

Hindwing: length approximately three times height. Nine to eleven radial crossveins; three to four inner gradates; five to six outer gradate veins; three b cells; t cell usually present.

Forewing: alar surface surrounding many crossveins with suffusion of brown to dark brown. Stigma very slightly opaque; costal veinlets within stigma brown to black. Base of Rs, rx1 dark brown to black; icux2 dark brown to black, with dark brown, bubble-like swelling mesally. Hindwing: stigma very slightly opaque; veinlets within stigma, dark brown, with dark brown pigment in surrounding area; gradates, icux2 cream-colored to light brown.

Abdomen (male & female) (Table 5, Figs 6, 10). Sternites cream-colored with cream-colored setae, without brown areas. Tergites 6, 7: length: 2.1–2.2 (T6), 1.2–1.9 (T7) times greater than height (lateral view). Spiracles ~0.04–0.05 mm diameter.

Table 3. Range of variation in wing characteristics among geographic populations of two *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

Chrysopodes (Neosuarius) nigripilosus (Banks)							
	Baltra	Santa Cruz	Isabela	Isabela	Santa Fe	Fernandina	Santiago
	Type locality	Academy Bay	misc†	Beagle Crater	5 m. Lagoon	Cabo Hammond	Settlement
	(N=4)	(N=3)	(N=3)	(N=2, alcohol)	(N=1, alcohol)	(N=3, alcohol)	(N=2, image)
Forewing L, mm	10.6–11.4	11.7–12.2	10.6–12.9	10.2–11.6	11.3	11.6–12.2	–
Ratio, forewing L:W	2.95–3.13:1	2.94–3.03:1	2.82–3.03:1	2.96–2.97	2.83	2.93–3.01	–
Sc crossveins (below stigma), n	3–4	2–4	3–4	3–4	3	2–4	3
Tallest costal cell, cell #	5–6	5–7	5	5–7	5	5–6	
Ratio, tallest costal cell H : wing W	0.17–0.19:1	0.16–0.18:1	0.17–0.18:1	0.16–0.18:1	0.18	0.16–0.17	
Radial cells, n	10–12	11	11–12	11	11	11–12	11
Ratio, tallest radial cell L: wing W	0.19–0.22:1	0.19–0.21:1	0.19–0.20:1	0.19–0.21:1	0.20:1	0.20:1	
Ratio, im1 W: m3 W	0.67–0.77:1	0.71–0.85:1	0.42–0.73:1	0.72–0.74:1	0.77:1	0.69–0.75	
Inner gradates, n	3–5	4–5	4–5	4–5	6	4–5	5
Outer gradates, n	7	6–7	7–8	7	7	6–7	7
Gradate cell #2, H, mm	1.05–1.72	1.15–1.63	1.01–1.28	0.91–1.13	1.04	1.21–1.50	
Ratio, gradate cell #2, H : W	2.43–3.16:1	2.78–3.86:1	2.69–2.91:1	2.31–2.65	2.46:1	2.79–3.46:1	
Gradate cell #3, H, mm	0.88–1.61	1.55–1.63	1.11–1.43	1.16–1.31	1.37	0.82–1.67	
Ratio, gradate cell #3, H : W	2.07–4.37:1	4.09–4.26:1	3.13–3.83:1	3.33–3.39:1	3.52:1	2.06–4.26:1	
Hindwing L, mm	9.7–10.0 (N=3)	10.3–11.0	9.7–11.5	9.1–10.5	10.0	10.4–10.9	
Ratio, hindwing L : W	3.23–3.50:1 (N=3)	3.09–3.20:1	3.00–3.23:1	3.09–3.15:1	3.07:1	3.03–3.45:1	
Radial cells, n	10–11	11	11–12	11	11	11–12	11–12
Inner gradates, n	3–5	1–4	1–2	3–4	3	3	4

Outer gradates, n	6-7	6-7	6-7	6-7	6-7	6	6-7	7
Vein width – crassate veins								
ma W, mm	0.045–0.050 (N=2)	0.042–0.056	0.038–0.056	0.044–0.048	0.064		0.048–0.064	
Rs at rx1, W, mm	0.051–0.057 (N=2)	0.058–0.076	0.048–0.053	0.054–0.055	0.066		0.054–0.062	
Cu at Cuf, W, mm	0.093–0.094 (N=2)	0.071–0.106	0.081–0.099	0.077–0.102	0.110		0.09–0.12	
icu2 W, mm	0.027–0.029 (N=2)	0.024–0.032	0.022–0.027	0.023–0.026	0.024		0.026–0.032	
<i>Chrysopodes (Neosuaris) nigricubitus</i> , n. sp.								
	Santa Cruz	Santa Cruz	Pinta					
	Table Mtn.	Hornemann Farm	420 m					
	(N=3)	(N=3)	(N=3)					
Forewing L, mm	11.8–12.0	11.8–12.8	11.9–12.6					
Ratio, forewing, L : W	2.92–3.05:1	3.00–3.12:1	2.92–3.00:1					
Subcostal crossveins (below stigma), n	2	2	2					
Tallest costal cell, cell #	4-6	5	5-6					
Ratio, tallest costal cell H : wing W	0.16–0.17	0.17–0.18:1	0.17–0.18:1					
Radial cells, n	9–10	9–10	10–11					
Ratio, tallest radial cell H : wing W	0.21–0.22:1	0.21–0.22:1	0.19–0.21:1					
Ratio, im1 W : m3 W	0.68–0.77:1	0.63–0.77	0.72–0.78:1					
Inner gradates, n	3	3-4	4					
Outer gradates, n	5-6	5-6	6					
Gradate cell #2, H, mm	1.23–1.53	1.50–1.93	1.34–1.54					
Ratio, gradate cell #2, H : W	2.99–3.29:1	2.93–3.94:1	2.87–3.23:1					
Gradate cell #3, H, mm	1.29–1.61	1.54–2.13	1.48–1.65					
Ratio, gradate cell #3, H : W	2.71–3.75:1	3.43–4.68:1	3.56–3.76:1					
Hindwing L, mm	10.6–10.9	10.6–11.5	10.7–10.8					
Ratio, hindwing L : W	3.08–3.19:1	3.07–3.13:1	3.11–3.13:1					

Radial cells, n	9–10	10–11	10–11
Inner gradates, n	3	3–4	4
Outer gradates, n	5	5–6	6
Vein width – crassate veins			
ma W, mm	0.089–0.095	0.065–0.114	0.067–0.114
Rs at rx1, W, mm	0.047–0.053	0.051–0.066	0.051–0.054
Cu at Cuf, W, mm	0.076–0.088	0.074–0.187	0.094–0.108
icu2 W, mm	0.091–0.128	0.155–0.165	0.175–0.229

† Punta Tortuga, Puerto Villamil

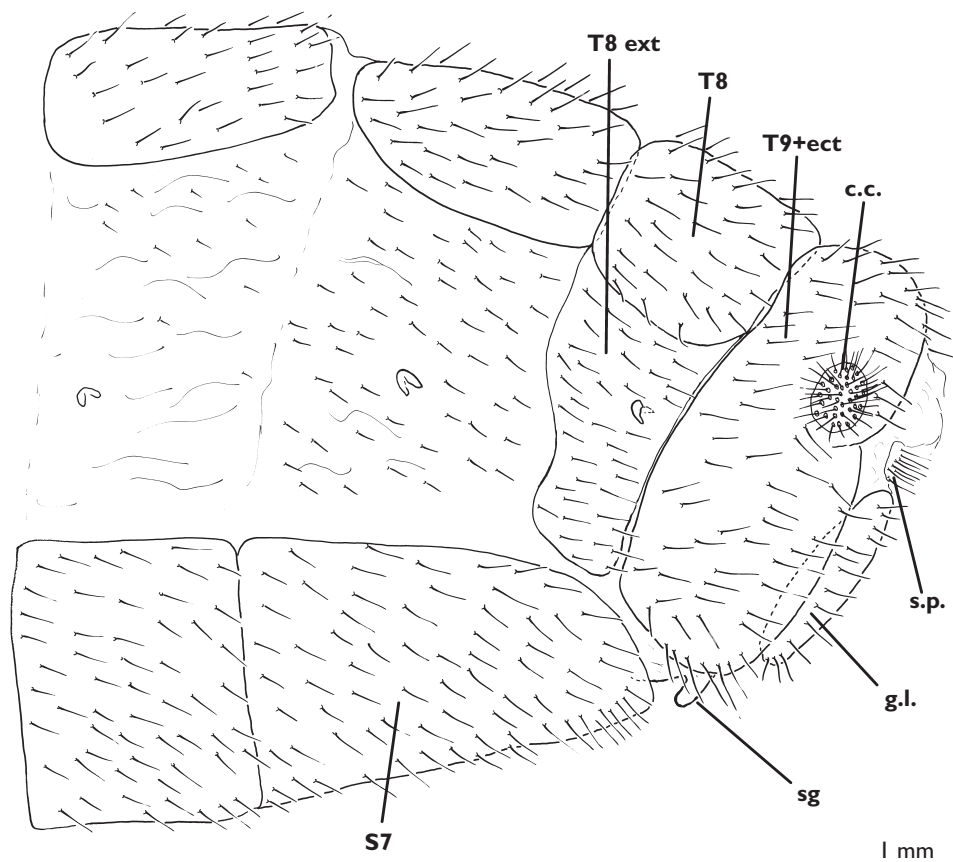


Figure 12. Female terminus, exterior, lateral view. *Chrysopodes (Neosuarius) nigripilosus*. **c.c.** callus cerci **g.l.** gonapophysis lateralis **sg** subgenitale **s.p.** setose subrectal plate **S7** seventh sternite **T8** eighth tergite **T8 ext**, ventral extension of eighth tergite **T9+ect** fused ninth tergite and ectoproct.

Male. (Table 5, Fig. 10): Apodeme of T9+ectoproct straight to very slightly arched; ventral branch lightly sclerotized; caudal branch acute unforked tip (Fig. 10a). Callus cerci taller than wide (0.15–0.23 mm tall, 0.13–0.18 mm wide), with 34–37 trichobothria. S8+9 length 1.5–1.8 times proximal height; shape in lateral view: triangular, tapering to relatively acute apex. Gonarcus: gonarcual arms extending outward from distal margins of bridge; span of gonarcus near arch 0.27–0.35 mm, span between gonarcual apodemes distally 0.64–0.68 mm. Gonarcual apodemes long, narrow, ~0.32–0.37 mm long. Mediuncus: sclerotized surface smooth, with some microsetae laterally; membrane immediately below beak (base of gonosaccus) with large patch of microsetae or gonocristae surrounding base of setose glands.

Female [Table 5, Fig. 15b; see *C. (N.) nigripilosus*, Figs 12, 13, 14]. Tergite 8: height of fully sclerotized portion less than length of sclerite; height of sclerite (including less sclerotized ventral extension) ~1.4–1.6 times length. Ninth tergite + ectoproct

(lateral view): distal margin with dorsal and ventral bulges. Callus cerci taller than broad (0.15–0.19 mm tall, 0.14–0.15 mm wide), with ~28–32 trichobothria. Gonapophyses laterales ~0.4 times height of T9+ectoproct; ~2.9–3.3 times taller than wide. Sternite 7: length ~1.6–1.7 times height of proximal margin (lateral view). Subgenitale narrow, rounded, with broad, tongue-like process distally; base consisting of transversely folded, uninvaginated membrane; lateral margin with pair of small, flat pouches, near but separate from base of bursal glands; pouches ~1/3 length of spermatheca. Bursal glands: accessory ducts not observed to be branched distally. Spermatheca: 0.10 mm diameter at mouth (distal end), 0.18 mm diameter in midsection (widest area), 0.5–0.6 mm long; invagination oblong, extending ~1/2 length of spermatheca (length 0.23–0.25 mm). Spermathecal duct: ~0.4 mm long (not including pale, brushy tip).

Type material. The holotype (a male) is in the California Academy of Sciences Collection, San Francisco, CA. It is from a series of specimens collected in 1964 by David Q. Cavagnaro during an Academy expedition to the Galápagos. The type locality is Ecuador, Galápagos Archipelago, Isla Santa Cruz, Table Mountain, 440 meters. The labels on the holotype read: (1) Galápagos Arch. / Isla SantaCruz / Table Mtn. 440 M. / IV-16-1964; (2) D. Q. Cavagnaro / Collector; (3) HOLOTYPE / *Chrysopodes* (*Neosuarius*) *nigricubitus* Tauber & Tauber, des. 2010 [red]. Good condition; glued to point. Altogether, there are 27 paratypes, including thirteen (3M, 8F, 2 teneral, sex undetermined) with identical collection data and yellow paratype labels. Five other paratypes (3M, 2F) have the following data: (1) Galápagos Arch. / Isla SantaCruz / HornemanFarm / 220M V-7-1964; (2) D. Q. Cavagnaro / Collector; (3) PARATYPE / *Chrysopodes* (*Neosuarius*) *nigricubitus* Tauber & Tauber, des. 2010 [yellow]. Nine paratypes (4M, 5F) are in the Institut royal des Sciences naturelles de Belgique, Bruxelles; these specimens are in alcohol, and their printed labels read: (1) Ecuador, Galápagos, Pinta, western side of island, 420 m, 30/II/2000, L. Baert, K. Desender & J.-P. Maelfait, B.00/0100; (2) PARATYPE / *Chrysopodes* (*Neosuarius*) *nigricubitus* Tauber & Tauber, des. 2010.

Etymology. The name, *nigricubitus*, calls attention to one of the species' most prominent distinguishing features – the dark brown to black, heavily sclerotized, second intracubital crossvein [*nigri*- (Latin, prefix), *cubitus* (Latin, noun, masculine)].

Specimens examined. Type material only.

Intraspecific variation. The variation among the specimens we studied is small. See Tables 1, 3 & 5, for the ranges in head size and wing features. One male in the series from Pinta has particularly weakly pigmented wings and genitalia intermediate between *C. (N.) nigripilosus* and *C. (N.) nigricubitus*.

***Chrysopodes* (*Neosuarius*) *pecki* sp. n.**

urn:lsid:zoobank.org:act:F2F8DB99-A134-433C-9FCB-317A86C40D77

Diagnosis. *Chrysopodes* (*Neosuarius*) *pecki*, the third endemic species of *Chrysopodes* (*Neosuarius*) from the Galápagos, is known from two localities on Isabela Island – Volcán Wolf and Volcán Alcedo, where it is sympatric with *C. (N.) nigripilosus*. Although

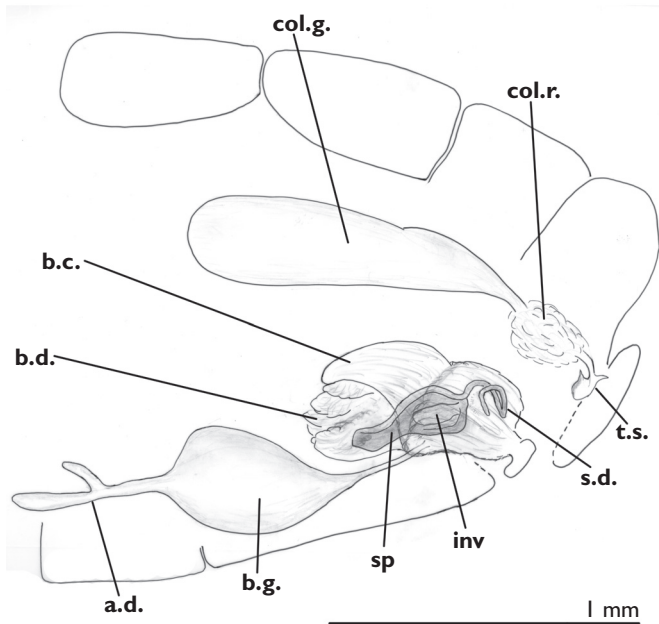


Figure 13. Female terminus, internal, lateral view. *Chrysopodes* (*Neosuarius*) *nigripilosus*. **a.d.** accessory duct on bursal gland **b.c.** bursal copulatrix **b.d.** bursal duct (presumed) **b.g.** bursal gland **col.g.** colleterial gland **col. r.** colleterial reservoir **inv** invagination **sp** spermatheca **s.d.** spermathecal duct **t.s.** transverse sclerification.

the number of specimens that are available is small ($N=3$) and they share many external and internal features with *C. (N.) nigripilosus* and *C. (N.) nigricubitus*, their distinctive size and other features lead us to assign them to a new species.

The most prominent external features of *C. (N.) pecki* that are absent from the other two Galápagos species include: (a) a pair of brown spots on the dorsum of the head, posterolateral to the vertex (Fig. 3b) and (b) distinctive markings on the venter of the female abdomen (Fig. 6d). On the *C. (N.) pecki* females, S5 is dark brown, S6 has light brown pigmentation basally, and the distal portion of S6 and all of S7 are cream-colored. In comparison, *C. (N.) nigripilosus* females have dark brown pigmentation throughout S5, S6, and the base of S7, and *C. (N.) nigricubitus* females are without dark brown marks on the sternites. *C. (N.) pecki* is the only one of the three Galápagos species that has wings exceeding 13 mm in length. Like those of *C. (N.) nigripilosus*, the *C. (N.) pecki* wings do not show dark suffusion around the crossveins, but like *C. (N.) nigricubitus*, the second cubital crossvein is very dark and the center of the vein bears a dark brown swelling. In all three *C. (N.) pecki* specimens, the swelling tends to be smaller than that of *C. (N.) nigricubitus* (Table 4, Fig. 5c).

C. (N.) pecki adults may also be characterized by an elongated pronotum. Both female specimens (preserved in alcohol) have a pronotum that is longer than that on *C. (N.) nigripilosus* (Table 2), and the *C. (N.) pecki* pronotal length : width ratio is

Table 4. Range of variation in wing characteristics among three *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

	<i>C. (N.) nigripilosus</i> (Banks)	<i>C. (N.) nigricubitus</i> sp. n.	<i>Chrysopodes (N.) pecki</i> sp. n.
	8 localities, 5 islands [†]	3 localities, 2 islands [‡]	2 localities, 1 island [§]
	N=18	N=9	N=2
Forewing L, mm	10.2–12.9 (N=16)	11.8–12.8	13.0–13.7
Ratio, forewing, L : W	2.82–3.13:1 (N=16)	2.92–3.12:1	2.89:1 (N=1)
Subcostal crossveins (below stigma), n	2–4	2	2
Tallest costal cell, cell #	5–7	4–6	4–5
Ratio, tallest costal cell H: wing W	0.16–0.19 (N=16)	0.16–0.18:1	0.17:1 (N=1)
Radial cells, n	11–12	9–11	10
Ratio, tallest radial cell H : wing W	0.19–0.22 (N=16)	0.19–0.22:1	0.21 (N=1)
Ratio, im1 W : m3 W	0.42–0.85:1 (N=16)	0.63–0.78:1	0.70–0.81:1
Inner gradates, n	3–6	3–4	4 (N=1)
Outer gradates, n	6–8	5–6	6 (N=1)
Gradate cell #2, H, mm	0.91–1.72 (N=16)	1.23–1.93	1.54 (N=1)
Ratio, gradate cell #2, H : W	2.31–3.86:1 (N=16)	2.87–3.94:1	2.93:1 (N=1)
Gradate cell #3, H, mm	0.82–1.67:1 (N=16)	1.29–2.13	1.69 (N=1)
Ratio, gradate cell #3, H : W	3.13–4.26:1	2.71–4.69:1	3.45:1 (N=1)
Hindwing L, mm	9.1–11.5 (N=165)	10.6–11.5	11.8 (N=1)
Ratio, hindwing L : W	3.00–3.45:1	3.07–3.19:1	3.02 (N=1)
Radial cells, n	11–12	9–11	10
Inner gradates, n	1–4	3–4	4
Outer gradates, n	6–7	5–6	6
Vein width – crassate veins			
ma W, mm	0.038–0.064 (N=14)	0.067–0.114	0.051–0.84
Rs at rx1, W, mm	0.048–0.076 (N=14)	0.047–0.066	0.051–0.054
Cu at Cuf, W, mm	0.077–0.120 (N=14)	0.074–0.094	0.054–0.088
icu2 W, mm	0.022–0.032 (N=14)	0.091–0.229	0.054–0.111

[†] Baltra, Santa Cruz (Academy Bay), Isabela (Puerto Villamil, Punta Tortuga, Volcán Wolf, Volcán Alcedo), Santa Fe (lagoon), Fernandina (Cabo Hammond), Santiago Settlement
[‡] Santa Cruz (Table Mtn., Hornemann Farm), Pinta (420 m)
[§] Isabela (Volcán Wolf, Volcán Alcedo)

greater than that of either *C. (N.) nigripilosus* or *C. (N.) nigricubitus*. The pronotum of the single male specimen (pinned) is distorted and compressed below the mesothorax; its length cannot be measured readily. However, we estimated the length from a lateral view, and it appears to be about as long as those on the female specimens

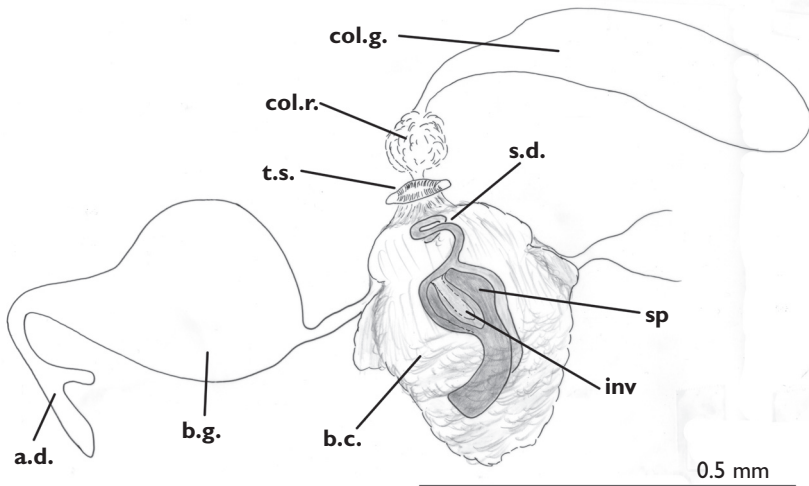


Figure 14. Female, internal reproductive structures, dorsal view. *Chrysopodes (Neosuarius) nigripilosus*. **a.d.** accessory duct on bursal gland **b.c.** bursa copulatrix **b.g.** bursal gland **col.g.** colleterial gland **col.r.** colleterial reservoir **inv** invagination **sp** spermatheca **s.d.** spermathecal duct **t.s.** transverse sclerification.

C. (N.) pecki males have abdominal sclerites and genitalia that generally resemble those of *C. (N.) nigripilosus* and *C. (N.) nigricubitus* (Fig. 11). However, there are some distinguishing features. First, the size of the gonarcus (length of arms, bridge width) is larger than that of either *C. (N.) nigripilosus* or *nigricubitus* (Table 5). And, the lateral arms of the gonarcus are directed inward next to the mediuncus as in *C. (N.) nigripilosus* (Fig. 11b, c). Second, as in *C. (N.) nigricubitus*, the dorsal apodeme along the ventral margin of T9+ectoproct is relatively straight, and the caudal branch has a well sclerotized, unforked, pointed tip (Fig. 11a). However, in *C. (N.) pecki* the tip has a small, beak-like flange with a membrane attached (not visible on Fig. 11a). Third, unlike either of the other species, the ventral branch of the dorsal apodeme is elongate, well sclerotized, and angled anteriorly; distally it turns and invaginates within S8+9 (Fig. 11a). And, fourth, although the dorsal apodeme itself is thin (lateral view), the base of the dorsal branch (that extends under the callus cerci) is heavy and densely sclerotized.

In addition to the ventral marks on the abdomen, we detected some other characteristics that distinguish the female terminalia of the *C. (N.) pecki* specimen we examined. First, the sixth and seventh tergites were slightly longer in actual length, and in their length to height ratio, than those on any of the *C. (N.) nigripilosus* or *C. (N.) nigricubitus* specimens (Table 5). Second, as in the two other species, the membrane that is basolateral to the subgenitale bears a pair of invaginated pouches that are near, but separate from, the base of the bursal glands. In *C. (N.) pecki*, these pouches are clear and bulbous, not flat and folded as in the other two species (Fig. 15c). In all other traits, the female that we measured tended to be large, but the measurements overlapped with those of large *C. (N.) nigricubitus* specimens.

Table 5. Range of variation in abdominal features among three *Chrysopodes* (*Neosuarius*) species from the Galápagos Islands.

	<i>C. (N.) nigripilosus</i> (Banks)	<i>C. (N.) nigricubitus</i> n. sp.	<i>Chrysopodes (N.)</i> <i>pecki</i> n. sp.
	8 localities, 5 islands ¹ (N=3M, 3F)	3 localities, 2 islands ² (N=3M, 3F)	2 localities, 1 island ³ (N=1M, 1F)
MALE & FEMALE			
Abdomen, T6, Ratio, L : H	1.4–1.5:1	2.1–2.2:1	2.3, 3.0:1
Abdomen, T7, Ratio, L : H	1.1–1.2:1	1.2–1.9:1	1.8, 2:1
Abdomen, S6, Ratio, L:H	0.8:1	0.8–0.9:1	1.0, 0.9:1
MALE			
Abdomen, S8+9, Ratio, L : H	1.6–1.7:1	1.5–1.8:1	1.8:1
Callus cerci H, mm	0.17–0.19	0.15–0.23	0.23
Callus cerci W, mm	0.13	0.13–0.18	0.16
Trichobothria, n	31–32	36–37	30
Gonarcial apodemes, basal span, mm	0.31–0.32	0.27–0.34	0.39
Gonarcial apodemes, distal span, mm	0.37–0.46	0.77–0.79	0.57
Gonarcial apodemes, L, mm	0.32–0.36	0.32–0.37	0.39
FEMALE			
Abdomen, S7, Ratio, L : H	1.6:1	1.6–1.7:1	1.6:1
Callus cerci H, mm	0.16–0.17	0.15–0.19	0.19
Callus cerci W, mm	0.10–0.14	0.14–0.15	0.17
Trichobothria, n	31–36	28–32	35
Spermatheca L, mm	0.5–0.6	0.5–0.6	0.6
Spermatheca diameter (at mouth), mm	0.12	0.10	0.13
Spermatheca diameter (widest), mm	0.18	0.16	0.19
Spermathecal duct (sclerotized portion) L, mm	~0.65	~0.40	~0.70

¹ Baltra, Santa Cruz (Academy Bay), Isabela (Puerto Villamil, Punta Tortuga, Volcán Wolf, Volcán Alcedo), Santa Fe (lagoon), Fernandina (Cabo Hammond)

² Santa Cruz (Table Mtn., Hornemann Farm), Pinta (420 m)

³ Isabela (Volcán Wolf, Volcán Alcedo)

Description. All features as in *C. (N.) nigripilosus* except as noted below. *Head* (Table 2; Fig. 3). Vertex: surface with small, amber setae. Labrum: distal margin with slight mesal cleft. *Coloration.* Head cream-colored frontally, lateral to eyes, tan dorsally; frons with pair of triangular to bowl-shaped, dark brown marks below torulus; clypeus with lateral margins dark tan, dark brown streak extending dorsolaterally from distal margin of tentorial pits almost to eye; toruli cream-colored, with light tan border surrounding sclerotized margins; dorsal torulus with or without grape-brown, vertical streak. Genae cream-colored with dark brown on ventral margin, dark brown dorsally.

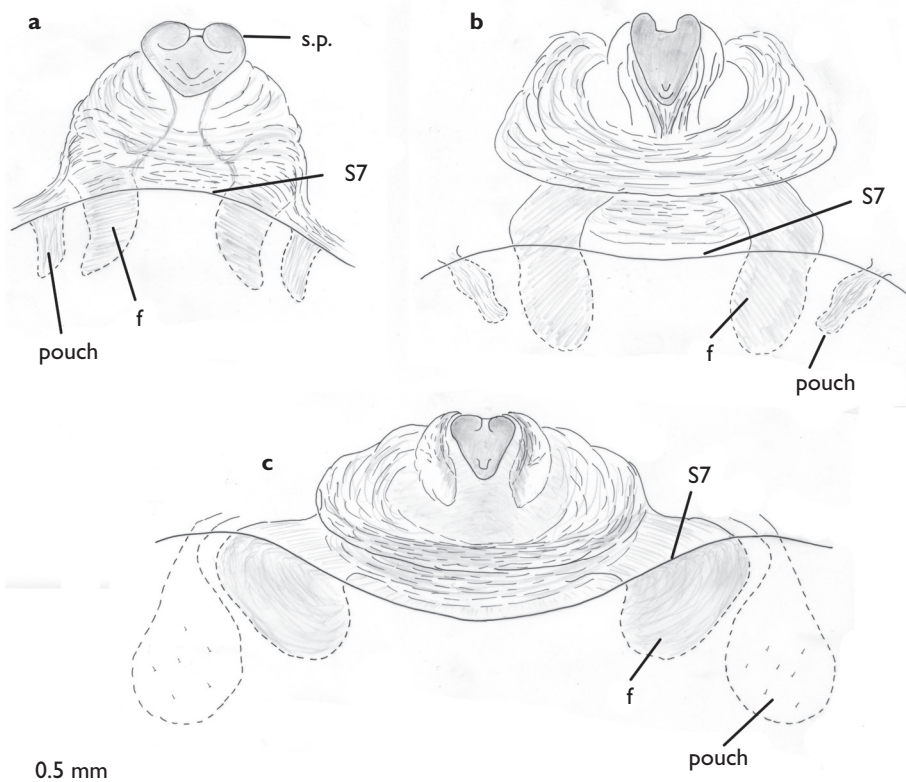


Figure 15. Subgenital, ventral view. **a** *Chrysopodes (Neosuarius) nigripilosus* **b** *C. (N.) nigricubitus* **c** *C. (N.) pecki*. **f** membranous fold; **pouch** invaginated pouch **s.p.** sclerotized process at terminal end of subgenital **S7** terminal margin of seventh sternite. The scale applies to all three images.

Scapes tan, unmarked; pedicel tan to light brown; flagellum tan. Venter: basilateral margins of submentum dark brown.

Thorax (Table 2; Fig. 3b). Pronotum (females) wider than long; large basal section without setae; cream-colored, with sublateral, mesal, mottled light brown markings. Meso-, metanota cream to light tan, without spots; setae on mesonotum, amber. Pleural areas cream-colored, without markings. Legs: setae amber.

Wings (Table 4; Figs 4, 5). Forewing about three times longer than tall. Costal area: greatest height ~0.17 times height of wing; tallest at costal cell (#4–5). Subcosta: two crossveins below stigma. Ten radial crossveins (between R and Rs); two rows of gradates; inner row with four gradates, outer row with six, both rows in regular, parallel pattern. Cubitus: icu2 curved, thickened, with small, bubble-like expansion mesally.

Hindwing narrow, length approximately three times height. Ten radial crossveins; four inner gradates; six outer gradate veins; three b cells; t cell present.

Forewing hyaline, very slight suffusion of brown to dark brown coloration around Rs at intersection with rcx1, first outer gradate, Cu near icu2. Subcostal crossveins

within stigma brown, surrounded with dark brown suffusion. Costal veinlets, gradates dark brown to black; ma1 black; icux2, small bubble-like swelling dark brown to black; marginal cell below 3A partially dark brown. Hindwing: stigma slightly opaque, veinlets within stigma brown, with brown pigment in surrounding membrane; icux2 cream-colored to light brown.

Abdomen (male & female) (Table 5; Figs 6, 11). Cream-colored, dorsally with faint, broken, brown mesal stripe, mottled brown spotting sublaterally; pleural regions cream-colored, without marks; sternites cream-colored, except S5, 6 (male) dark brown, S5 (female) dark brown; setae (female) cream-colored basally, brown distally; setae (male) long, cream-colored throughout. Tergites 6, 7: length: 2.3–3.0 (T6), 1.8–2.1 (T7) times greater than height (lateral view). Sternite 6: length ~0.9–1.0 times height. Spiracles ~0.05–0.06 mm diameter; atria noticeably larger than spiracular openings.

Male (Table 5, Fig. 11). Apodeme of T9+ectoproct thin (dorsal apodeme): dorsal branch very heavily sclerotized basally, becoming abruptly thinner, extending upward, around and below callus cerci, fused mesally at top of tergite; ventral branch extending anteroventrally well into membrane below tergite, narrow, well-sclerotized, curving inward and invaginating distally; caudal branch with acute, unforked tip; tip with dorsal flange of heavy membrane. Callus cerci taller than wide (0.22 mm tall, 0.16 mm wide), with 30 trichobothria. S8+9 length 1.8 times proximal height; shape in lateral view: gradually tapering to truncate apex. Gonarcus: span near arch 0.39 mm, span between gonarcular arms distally 0.57 mm. Gonarcular arms long, narrow, ~0.39 mm length. Mediuncus: sclerotized surface slightly textured, with sparse microsetae; membrane immediately below beak (base of gonosaccus) smooth, tight, bearing setose glands; base of glands with small protuberances; gonosaccus delicate.

Female [Table 5, Fig. 15c; see *C. (N.) nigripilosus*, Figs 12, 13, 14]. Tergite 8: height of sclerite (including less sclerotized ventral extension) ~1.8 times length of sclerite. Ninth tergite + ectoproct (lateral view): distal margin with dorsal and ventral bulges. Callus cerci taller than broad (0.19 mm tall, 0.17 mm wide), with 35 trichobothria. Gonapophyses laterales ~0.5 times height of T9+ectoproct; 3.3 times taller than wide; orientated posteroventrally (~40° angle from midline). Subgenitale: base consisting of transversely folded, uninvaginated membrane, attached to terminus of S7; lateral margins of base with pair of sparsely setose, bulbous pouches, near, but separate from base of bursal glands; pouches slightly shorter than spermatheca. Bursal glands: with broad, elongate accessory ducts distally. Spermatheca: 0.13 mm diameter at mouth (distal end), 0.19 mm diameter in midsection (widest area), 0.6 mm long; invagination extending ~0.3 times length of spermatheca (length 0.17 mm). Spermathecal duct ~0.7 mm long (not including pale, brushy tip), after leaving subgenitale, bending right, becoming pale; distal ~1/10 brushy.

Type material. The holotype (a male, pinned) is in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., (USNM). The type locality is Ecuador, Galápagos Archipelago, Isla Isabela, Volcán Wolf, 4 km NE Puerto Bravo. The labels on the holotype read: (1) ECU: Galap: Isabela / V. Wolf, 4 km NE. P. Bravo / humid for, 17.V.96 / uv light / S. Peck, 96–192; (2) HOLOTYPE / *Chrysopodes* (*Neo-*

suarius) pecki Tauber & Tauber, des. 2010 [red]. There are two paratypes (females, in alcohol) in the Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSNB). Their labels read: (1) Ecuador, Galápagos Arch., Isla Isabela, Volcán Alcedo, SE crater rim at “Geyser”, 1000 m, 3/IV/1996, L. Baert, K. Desender & J.-P. Maelfait, B96/0074; (2) PARATYPE / *Chrysopodes (Neosuarius) pecki* Tauber & Tauber, des. 2010 [yellow].

Etymology. The species is named in honor of Stewart B. Peck, Carlton University (Canada), in recognition of his contributions and devotion to the study of Galápagos insects.

Specimens examined. Type material only.

Intraspecific variation. Sample size very small, but see Tables 2, 4, and 5.

Undetermined specimen

There is a single specimen from Floreana (a male) that we were unable to place within any of the three species. Externally, it is very similar to *C. (N.) nigripilosus*, but the genitalia, in part, resemble those of *C. (N.) nigricubitus* and in part, they are unique. Specifically, the head coloration and markings are very similar to those of *C. (N.) nigripilosus* from Baltra; the dorsum is largely light brown and the pleural and ventral regions appear to be cream-colored as in the Baltra and Isabela populations. The membrane of the forewing has no markings or suffusion of pigment; the size and pattern of venation and thickened veins do not differ from those of *C. (N.) nigripilosus*; there are three crossveins below the stigma.

The genitalia resemble those of *C. nigricubitus* in that the gonaracus is relatively flat; the gonarcular arms extend laterally from the gonarcular bridge; and only the tips of the gonarcular arms bend downward toward the mediuncus. However, unlike any other specimens we have examined, the eversible pouches at the tip of S8+9 are relatively short, tapered distally, juxtaposed and partially fused mesally, and the membrane between the pouches is loose and large. Further study, especially analysis of the reproductive pheromones, might demonstrate that this is yet another undescribed, cryptic species.

Specimen examined: Floreana (= Charles, Santa Maria). Black Beach, II/17/1964, R. L. Usinger (1M, CAS).

Discussion

The Galápagos lacewings. The two new cryptic species previously nested within *C. (N.) nigripilosus* indicate that the Galápagos lacewing fauna may not be impoverished to the degree originally estimated. The number of named, endemic Galápagos *Chrysopodes* lacewings has increased from one to three species, and the possibility of another exists. Although clearly distinct, the Galápagos lineage of *Chrysopodes* shows marked af-

finities with the *Chrysopodes* (*Neosuarius*) fauna of the western Andean region – particularly the *C. (N.) flavescens* group to which it has been assigned (C. A. Tauber, in press).

Overall, including *Chrysoperla* [*Chrysoperla galapagoensis* (Banks, 1924)], four endemic chrysopid species are now documented from the Galápagos Islands. In addition, an endemic brown lacewing (Hemerobiidae) has been reported (*Megalomus darwini* Banks 1924) (Peck 2001). It is noteworthy: like many endemic Galápagos species of insects, at least four of the five endemic lacewings occur on more than one island. Thus, the pattern of a relatively depauperate, endemic arthropod fauna with broad inter-island distributions, noted by Linsley and Usinger (1966), Parkin et al. (1972), and Peck (2001), remains true for the Galápagos lacewings, but the number of recognized species has increased.

Each of the lacewing families is also represented by non-endemic, broadly ranging species on the Galápagos archipelago – Chrysopidae: *Chrysoperla externa* (Hagen, 1861) and *Ceraeochrysa cincta* (Schneider, 1851) and Hemerobiidae: *Symphorobius barberi* (Banks, 1903). All three of these species occur throughout Central and South America; one is also wide-ranging in the Pacific region. All are found on many of the Galápagos islands. [Note: *C. cincta* was erroneously reported to be endemic to the Galápagos Islands (Baert et al. 1992, Peck 2001); however, its distribution extends throughout Central and South America (Adams and Penny 1985).]

Comparison with the endemic lineages of Hawaiian lacewings. Statements regarding the low diversity of the Galápagos biota are particularly intriguing when the lacewings of the Galápagos are compared with those of another isolated Volcánic archipelago in the Pacific – the Hawaiian Islands. Hawai'i's extant endemic green lacewing fauna (Chrysopidae) consists of a single radiation of approximately 20 species in the monophyletic genus, *Anomalochrysa*. Among the endemic *Anomalochrysa*, 14 species are found only on a single island and only four species occur on three or more islands (Zimmerman 1957).

Hawai'i's endemic brown lacewing fauna (Hemerobiidae) consists of a similarly sized group of *Micromus* species that is presumed to be a single, monophyletic lineage. Among these species, sixteen are restricted to a single island and eight occur on more than one island (Zimmerman 1957, Monserrat 1993).

Unlike the Galápagos endemics, the endemic Hawaiian chrysopid and hemerobiid species are well differentiated; they are generally distinguishable by large external differences in morphology, as well as distinct genital differences among males (there are no reports on the female genitalia). Also unlike the Galápagos endemics, the geographic origins and phylogenetic relationships of *Anomalochrysa* and the Hawaiian lineage of *Micromus* remain unknown.

In summary: On the Hawaiian Islands, each of the two families of lacewings is represented by a single, diverse endemic lineage of unknown origins; each of the lineages currently contains ~20 well differentiated species, the majority of which are confined to a single island. In comparison, the Galápagos has three endemic “lineages” of lacewings, each stemming from the separate introduction of a genus known to inhabit the South American mainland. Two of “lineages” currently consist of only one described

species. The *Chrysopodes* (*Neosuarius*) lineage, consisting of three (perhaps four) species, also is small. In all three lineages, the degree of morphological differentiation is slight; differences between species are subtle, quite unlike the large interspecific variation within the endemic Hawaiian lineages.

There are numerous possible causes for the marked contrasts in the extent of radiation and the degree of diversification between the Hawaiian and Galápagos endemic lacewing lineages. Differences in the age, size, isolation, and ecological diversity of the island archipelagos may be factors; differences in the amount of time since the initial introductions, the especially harsh Galápagos environment and the biological characteristics of the original immigrant species are others to be considered.

Species relationships. The pattern of intraspecific and interspecific variation among the Galápagos lacewing specimens that we had on hand is noteworthy. In most cases, the differences among the species were consistent, and specimens could be easily and confidently identified to species. However, in one case, e.g., a male specimen in the series of *C. (N.) nigripilosus* from Pinta has particularly weakly pigmented wings and genitalia that resemble those of *C. (N.) nigripilosus*. As in some species of Darwin's finches on the Galápagos (Grant and Grant 2008), there may be a low incidence of hybridization between the *Chrysopodes* species.

Given the above, it is important to point out that in examining our *C. (N.) nigripilosus* and *C. (N.) nigricubitus* specimens carefully, we did not find morphological differences that would warrant splitting the group further. Nevertheless, a pattern of diversification and speciation without significant morphological changes has been well documented within several chrysopid taxa – e.g., *Chrysoperla*, *Chrysopa* (Tauber and Tauber 1997, Tauber et al. 1995, Henry et al. 2001). Thus, it is possible that additional cryptic species remain within any of the nominal *Chrysopodes* species on the Galápagos. The unique morphological characteristics of the male abdomen and genitalia (i.e., the large eversible pouches at the terminus of the abdomen and the setose ducts within the gonarcus) are consistent with reproduction involving chemical signals – long-range or contact pheromones. It has been demonstrated that changes in the chemistry of such signals in insects can result in reproductive isolation, without noticeable changes in morphology (long-range pheromones, e.g., Roelofs and Rooney 2003; contact pheromones: e.g., Grula et al. 1980). We hope that future studies will examine the variation in pheromone chemistry and molecular characteristics among the Galápagos lacewings.

Conservation. During the bicentennial celebrations of Darwin's life and his contributions, many well-founded pleas have been made for the continued protection and study of the Galápagos Islands and their unique flora and fauna (e.g., J. E. McCosker & R. H. Rosenblatt, Darwin and the Galápagos Symposium, AAAS, Pacific Region, Aug. 14–15, 2009, California Academy of Sciences, San Francisco). Our findings here, and the questions that they raise, add an additional, small but significant reason for supporting these international and national conservation efforts.

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Revision of *Arcastes* Baly, 1865 from the Oriental Region (Coleoptera, Chrysomelidae, Galerucinae)

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Abstract

The species of the genus *Arcastes* Baly, 1865 from Oriental Region are revised. The type species is *A. biplagiata* Baly, 1865 by original designation. The genus *Arcastes* was erected by Baly based on a peculiar shape of the antennae. Subsequently, eight other species have been described in this genus. Up to now this genus was not revised, in particular the male and female genitalia have not yet been studied. Studies of the type material revealed, that *A. biplagiata* possess a very peculiar shape of median lobe and endophallic structures. Next to the genotype, only two valid species remain in this genus: *Arcastes suturalis* Jacoby, 1884 (with *A. ismaili* Mohamedsaid, 2000 as new synonym), and *Arcastes dimidiata* Laboissière, 1929. *Arcastes sumatrensis* Jacoby, 1884 is a new junior synonym of *Neolepta biplagiata* Jacoby, 1884. All other species need to be transferred to other genera that will be subject of the ongoing revision of the Oriental Galerucinae. Distribution of the three species of *Arcastes* is restricted to Singapore, Malaysia, and Indonesia, southward to Java. In this paper we provide redescrptions of the genus and the valid species, including illustrations of external and genitalic characters, photographs of the primary type specimens, distribution maps and a key.

Keywords

Galerucinae, *Arcastes*, Oriental region, revision, taxonomy, redescription, new synonym

* 33rd contribution to the taxonomy, phylogeny and biogeography of the Galerucinae

Introduction

The genus *Arcastes* was established by Baly in 1865 when he described *Arcastes biplagiata* Baly, 1865, which he originally designated as the genotype. Wilcox (1973) placed it in the section “Monoleptites” due to the strongly elongated basi-metatarsus. Since the introduction of the genus, eight species have been described: *A. sanguinea* Jacoby, 1892 from Perak (Malaysia), *A. sumatrensis* Jacoby, 1884 from Sumatra, *A. suturalis* Jacoby, 1884 from Sumatra, *A. dimidiata* Laboissière, 1929 from Siberut Island (Indonesia), *A. astridae* Laboissière, 1932 from Sumatra, *A. nigripennis* Laboissière, 1932 from Borneo, *A. tectonae* Laboissière, 1932 from Java, and *A. ismaili* Mohamedsaid, 2000 from Sabah (Malaysia).

Baly (1865) and subsequent authors assigned species to *Arcastes* based on merely external morphological characters, in particular the enlarged third to seventh antennomeres. After checking the genitalic patterns of the species named above and many other oriental “Monoleptites”, it became clear that the median lobe has a peculiar outer shape and asymmetric endophallic structures. Both characters are very useful to delimit this genus from others, while enlarged medial antennomeres also occur in some species of *Monolepta* and *Neolepta*.

Only three species remain in *Arcastes* based mainly on characters of the genitalic structures of the type species. *Arcastes sumatrensis* Jacoby, 1884 is a new junior synonym of *Neolepta biplagiata* Jacoby, 1884. All other species need to be transferred to other genera that will be subject on the ongoing revision of Oriental Galerucinae. An illustration of external and genitalic characters are presented here for these taxa, photographs of the primary type specimens, distribution maps and a key are also included.

Materials and methods

A standard set of figures is given for each species. These include illustrations of the coloration (dorsal view), including the right antenna, where black coloration is indicated by black, yellow coloration by white, red coloration by light grey, and brown by dark grey shading.

The antennomeres of males and females, dorsal, ventral and lateral view of the median lobe including the endophallic structures, spermathecae of three females (if available) and bursa-sclerites (if available) usually of one female are figured. For the redescription of the genus, illustrations of the pro-, meso- and metathorax, female and male abdomen, right legs in ventral view and of the right hind wing in dorsal view are given.

Measurements were made for external characters. Absolute measurements are: total length from the clypeus to apex of the elytron, length of the elytron, maximal width of both elytra (usually in the middle or posterior third of the elytra), and width of the pronotum. Relative measurements are: length to width of the pronotum, maximal width of both elytra to length of the elytron, length of the second to third antennomer-

es, and length of the third to fourth antennomeres. A number of specimens measured is given in the description under “total length”. Further materials examined are listed, and all label data are exactly re-written.

The subsequent redescrptions are based on labelled specimens from the following collections (Table 1). Acronyms used and responsible curators in brackets: The Natural History Museum, London (BMNH; S. Shute); Institute Royal des Sciences Naturelle de Belgique, Brussels (IRSN; P. Limbourg); Museum of Comparative Zoology, Harvard University (MCZH); Museum für Naturkunde der Humboldt Universität, Berlin (MNHU; J. Frisch, J. Willers); Swedish Museum of Natural History Stockholm (NHRS; Bert Viklund); Nationaal Natuurhistorisch Museum, Leiden (NNML; F. van Assen); Center for Insect Systematics, UKM, Malaysia (UKM; R. Yusop), Collection of Jan Bezděk, Bruno (CJB).

For location data, geographical coordinates were given in degree and minute. These coordinates were mostly taken from Google Earth. The distribution maps have been produced by ArcGis.

Redescription *Arcastes Baly, 1865*

Type species. *Arcastes biplagiata* Baly, 1865 by original designation.

Total length. 4.45–7.35 mm (mean: 5.67)

Head. Brownish-red to red. Very finely punctuated, with significant transverse impression between posterior third of eyes. Eyes large, strongly convex (Fig. 1). Labial palpi slender and maxillary palpi enlarged, occasionally dark brown to black (Fig. 2a). Labrum pale to dark brown and occasionally blackish in middle. Mandible pale yellow to dark brown and blackish towards apex. Antennae elongated, extended to apical third of elytra (Fig. 1); third to terminal antennomere densely covered by bristle-like setae. First to eighth or ninth antennomeres black, two to three terminal antennomeres contrasting pale yellow to yellowish-brown, only in *A. dimidiata* two basal antennomeres also yellowish. First antennomere club-shaped, second shortest, third antenno-

Table 1. Numbers of material examined and collections investigated.

Collections	<i>A. biplagiata</i> Baly, 1865	<i>A. suturalis</i> Jacoby, 1884	<i>A. dimidiata</i> Laboissière, 1929
BMNH	37	40	5
IRSN	3	3	–
UKM	–	39	–
NNML	24	27	–
MCZH	–	1	–
MNHU	3	3	–
NHRS	1	–	–
CJB	12	5	–
Total	80	118	5

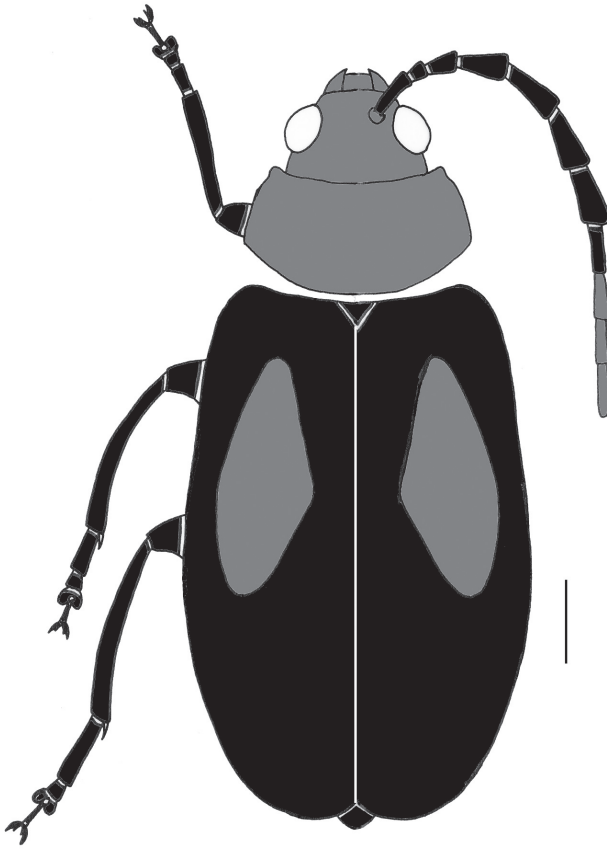


Figure 1. *Arcastes biplagiata* Baly, 1865. Dorsal colour pattern. scale bar: 1 mm (same for all following Figures)

mere about two times longer than second; ratio length of second to third antennomere 0.50–0.57 (mean: 0.54); third to seventh antennomere broad, significantly enlarged, ratio length of third to fourth antennomeres 0.60–0.70 (mean: 0.65), eighth to eleventh antennomeres much slenderer (Figs 8, 14, 20).

Thorax. Pronotum transverse, very broad, broadest in middle, anterior angle significantly protruding, posterior angle slightly marked, pronotum with deeply impressed line along lateral margins (Fig. 1). Brownish-red to red as head, shiny, smooth, and finely punctuated, without transverse depression. Pronotal width 1.55–2.25 mm (mean: 1.90), ratio length to width 0.48–0.57 (mean: 0.53). Scutellum large, triangular, impunctate, brownish, red or black. Procoxal cavities partly open (Fig. 2b). Meso- and metathorax reddish-brown to black. Metasternum broad (Fig. 2c). Elytra elongated, either black throughout, or black with longitudinal yellowish-red spot on disc of each elytron, or black with yellowish to reddish suture that in some species reaches

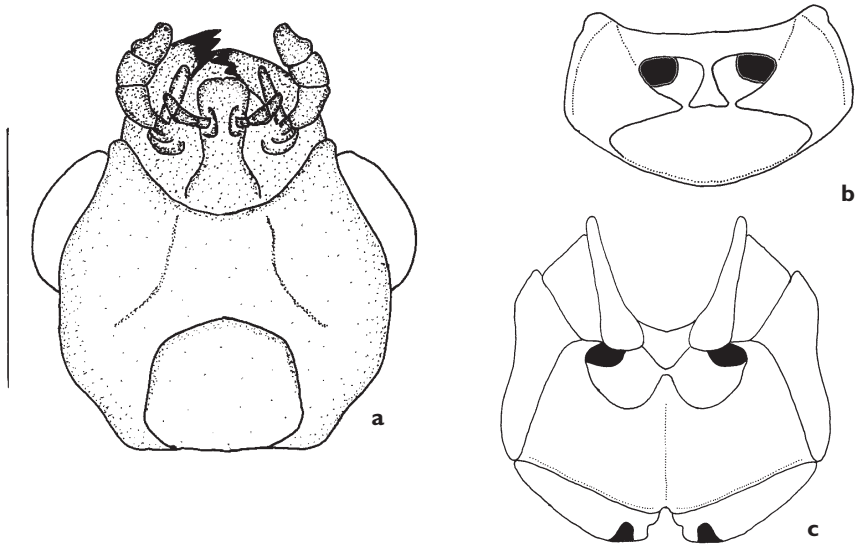


Figure 2. *Arcastes biplagiata* Baly, 1865. **a** Head **b** prothorax **c** meso- and metathorax, ventral view.

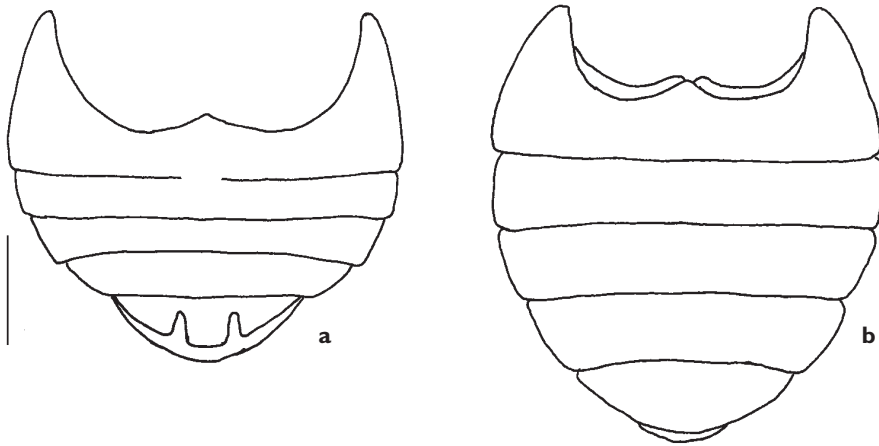


Figure 3. *Arcastes biplagiata* Baly, 1865. Abdomen, ventral **a** male **b** female.

up to one third of each elytron, or basal third completely red and apical two thirds black. Elytra shiny, punctuation fine, irregular, slightly coarser and denser than that of pronotum. Elytral length 3.80–5.90 mm (mean: 4.73), maximum width of both elytra together 1.50–4.00 mm (mean: 2.79), ratio of maximum width of both elytra together to length of elytra 0.61–0.72 (mean: 0.66). Alae fully developed (Fig. 4). Legs long and slender, basi-metatarsus elongated (Fig. 5), coxa and trochanter reddish like underside, femur, tibia and tarsus black throughout, tibia with dense and fine setae.

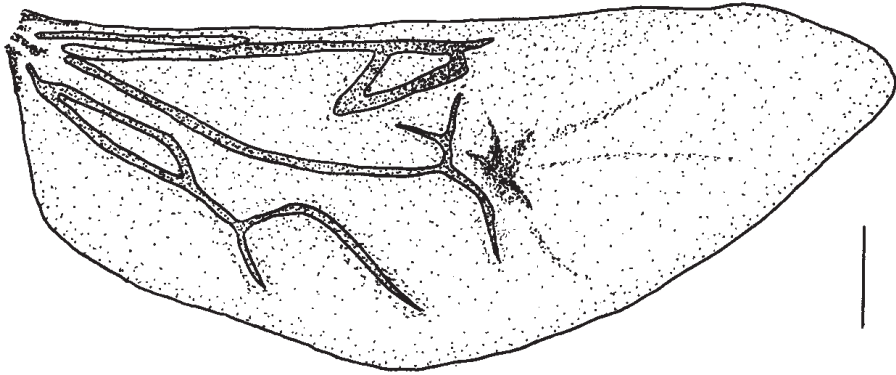


Figure 4. *Arcastes biplagiata* Baly, 1865. Hindwing, right, dorsal view.

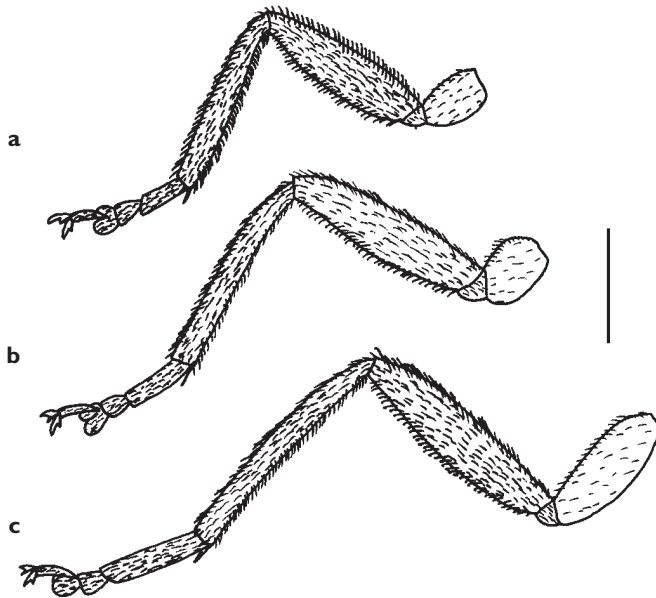


Figure 5. *Arcastes biplagiata* Baly, 1865. Legs: **a** prothoracic **b** mesothoracic **c** metathoracic.

Abdomen. Pale yellow to reddish-brown, occasionally darker in middle, and seventh sternite usually dark brown to black. Last visible sternite in females rounded at apex, and in males with two deep, parallel-sided incisions (Fig. 3).

Male genitalia. The outer shape of median lobe is symmetrical, strongly sclerotized, apex tapered, slightly rounded and not incised. Orifice wide, more or less circular to slightly rectangular. Endophallic structures asymmetrically arranged, ventral spiculae hammer-like, median spiculae narrower, slender, lateral spiculae enlarged and slender, with claw-like small spine medially and tube-like, curved spines. Tectum not

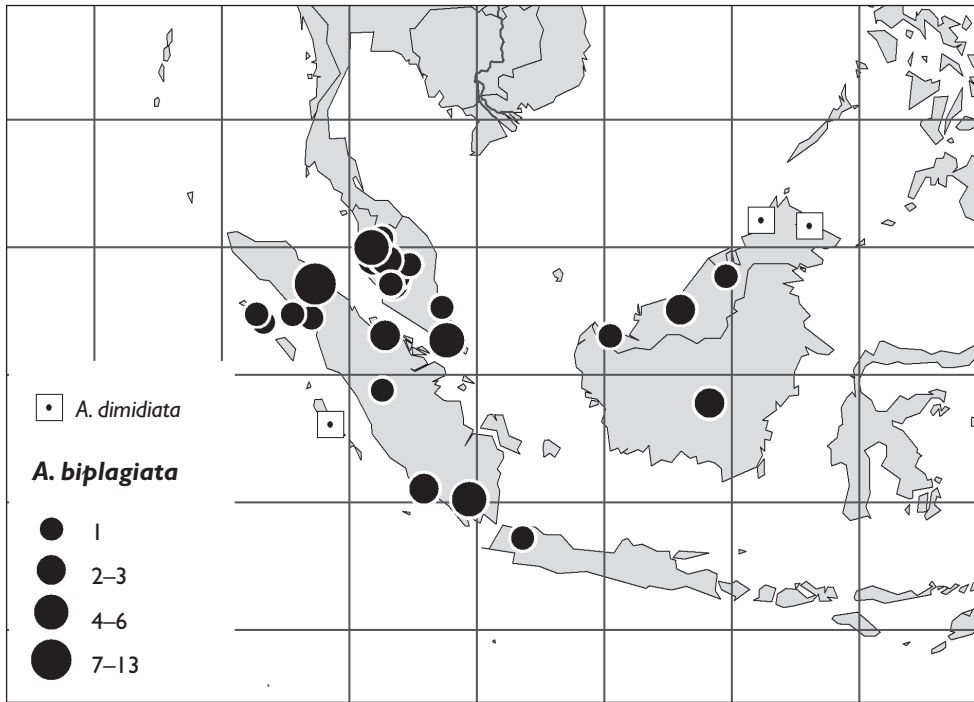


Figure 6. Distribution of *Arcastes biplagiata* Baly, 1865 and *A. dimidiata* Laboissière, 1929

incised at apex, almost reaching apex of the median lobe, constricted at middle part and enlarged at base (Figs 9, 15, 21).

Female genitalia. Spermatheca with oval to slender and elongated nodulus. Middle part long and slightly curved, cornu long and curved (Figs 10, 16, 22). Without stronger sclerotized bursa sclerites.

Distribution. The species are restricted to South-East Asia and up to now only recorded from Singapore, Malaysia (Peninsular) and Indonesia (Borneo, Sumatra), southwards to Java (Figs 6, 17).

Diagnosis. Beetles of the genus *Arcastes* are medium sized Galerucinae with strongly elongated basi-metatarsus, without pronotal impressions, reddish head and pronotum and usually contrasting black antennae, legs and elytra, the latter often with yellowish to red spots, suture or base. The significantly enlarged third to eighth antennomeres are very characteristic. *Arcastes* is the most similar to *Neolepta* Jacoby, 1884, with the type species, *Neolepta biplagiata* Jacoby, 1884, looking very similar to *Arcastes biplagiata* at the first glance. Antennae of these beetles are similar with slightly to strongly enlarged antennomeres in the middle, while terminal antennomeres in *Neolepta* are also black, the basal two antennomeres are reddish, and much slenderer than in *Arcastes*. The dorsal coloration is also similar, but *N. biplagiata* possesses a pale yellowish transverse band or nearly circular spot in the middle of each elytron. The genitalic patterns of both sexes possess very strong differences. Asymmetric endophallic spiculae of certain shape



Figure 7. *Arcastes biplagiata* Baly, 1865. Photographs of the lectotype of *A. biplagiata* Baly, 1865 **a** with labels **b** detail.

(Figs 9, 15, 21) as in *Arcastes* are a unique pattern in oriental galerucines with elongated basi-metatarsus, while the median lobe in *Neolepta*, as in *Monolepta*, and *Candezea*, is narrower and has symmetrically arranged endophallic spiculae which are much smaller (cf. Wagner 2001, Wagner and Kurtscheid 2005). The shape of spermatheca of *Arcastes* resembles that of *Monolepta*, but in *Arcastes* it lacks sclerotized bursa-sclerites, while in *Monolepta* there are two distinct types of this structure. Also *Neolepta* and *Candezea* have strongly sclerotized bursa-sclerites.

The pronotum of *Arcastes* (ratio length to width 0.48–0.57), is on average broader than in *Monolepta* and *Neolepta* (0.52–0.65), and within the range of *Candezea* (0.42–0.59). Procoxal cavities are similarly structured (partly open) in all these genera. The third antennomere of *Arcastes* is roughly twice as long as the second (ratio length of second to third antennomere: 0.50–0.57), which is similar to *Candezea* (0.49–0.63) but different from *Neolepta* and *Monolepta* which both have the second and third antennomere of about equal length (0.82–1.10). While *Candezea* have strongly elongated, slender antennomeres, *Arcastes* species can be clearly differentiated by the enlarged median ones.

Redescriptions of species

Arcastes biplagiata Baly, 1865

Arcastes biplagiata Baly, 1865: 147

Total length. 4.45–7.35 mm (mean: 5.96 mm, n=12)

Head. Reddish-brown to red. Antennae entirely black and only the terminal three antennomeres usually contrasting pale yellow to reddish (Figs 1, 7). Ratio of length of second to third antennomeres 0.50–0.57 (mean: 0.53); third to seventh antennomeres enlarged, ratio of length of third to fourth antennomeres 0.60–0.67 (mean: 0.63), eighth to eleventh antennomeres very slender (Fig. 8).

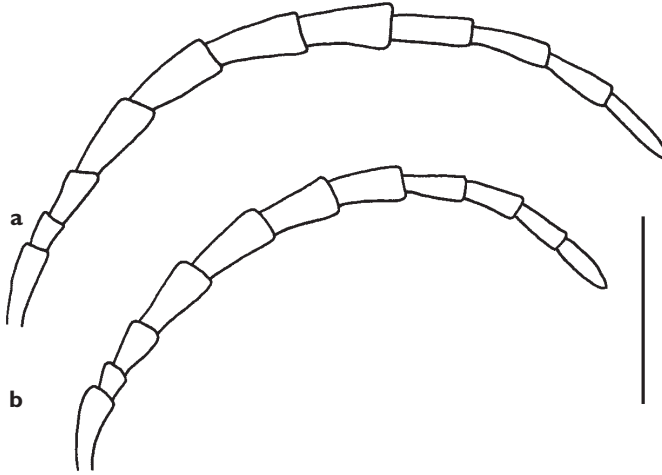


Figure 8. *Arcastes biplagiata* Baly, 1865. Antennae: **a** male **b** female.

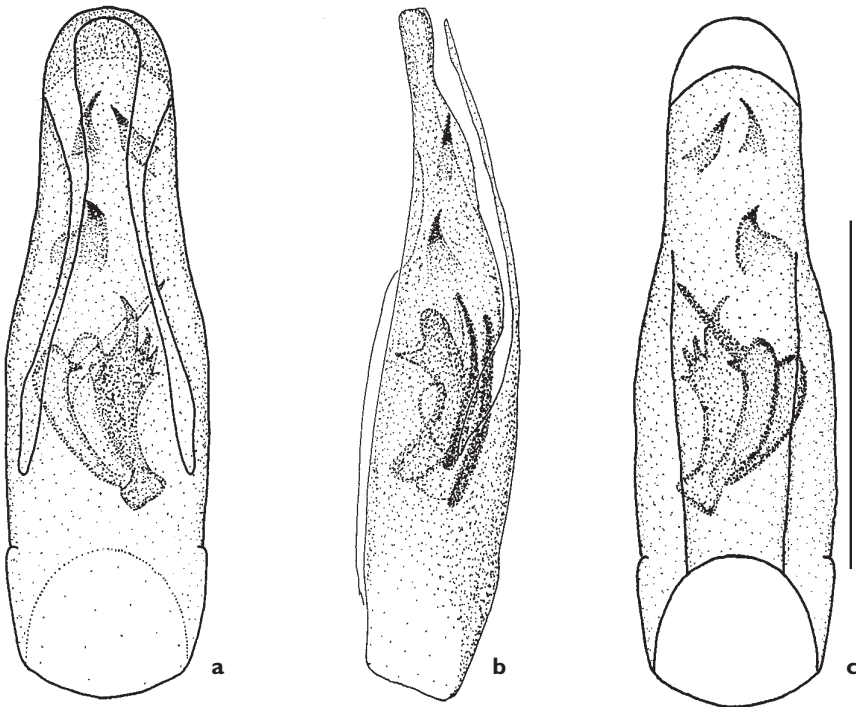


Figure 9. *Arcastes biplagiata* Baly, 1865. Median lobe: **a** dorsal **b** lateral **c** ventral.

Thorax. Pronotal width 1.65–2.25 mm (mean: 1.94 mm), ratio length to width 0.48–0.57 (mean: 0.53). Elytra elongated, black with two longitudinal reddish to yellowish-red oval spots in basal half (Figs 1, 7), in few specimens enlarged up to apical

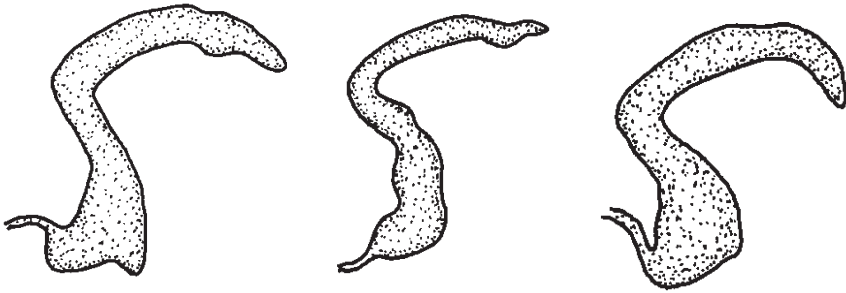


Figure 10. *Arcastes biplagiata* Baly, 1865. Three different spermathecae.

third of elytron. Elytral length 3.80–5.90 mm (mean: 4.93 mm), maximal width of both elytra together 2.50–3.60 mm (mean: 3.15 mm), ratio of maximal width of both elytra together to length of elytra 0.61–0.67 (mean: 0.64).

Abdomen. Pale yellow to brown, occasionally darker on middle, last sternite usually dark brown to black.

Male genitalia. Outer shape of median lobe symmetrical, strongly sclerotized, apex tapered and insignificantly rounded, not incised. Endophallic structure asymmetrical, ventral spiculae large, hammer-like, median spiculae long, slender, lateral spiculae enlarged, with claw-like small spine medially, only one present. Three big spurs located at upper part of endophallic spiculae, most distal one near apex. Tectum not incised at apex, almost reaching apex of median lobe, constricted at middle part and enlarged at base (Fig. 9).

Female genitalia. Spermatheca with slender to oval nodulus. Middle part long and slightly curved, cornu long and curved (Fig. 10).

Distribution. Malaysia, Singapore and Indonesia (Borneo Island and Sumatra), southwards to Java (Fig. 6).

Diagnosis. *Arcastes biplagiata* is the most similar in body outline and general coloration to *A. suturalis*, but the latter has either completely black elytra or a yellowish to yellowish-red spot beyond the scutellum that can be stretched along the entire suture or can be enlarged to a broad reddish sutural band (Figs 11, 12, 13), while *A. biplagiata* has only elongated spots on the disc of each elytron (Figs 1, 7). Endophallic armature of *A. biplagiata* is also different from the other two species of this genus (Fig. 9).

Type material. Lectotype: ♂, "Singapore, Baly Coll." (BMNH) (Fig. 7). Type Locality: Singapore, 1°21'N/103°49'E. – Paralectotype: 1 male, same data as lectotype (BMNH). Baly gave no data on the number of specimens in his description. There are at least two specimens available in BMNH, and we herein designate a lectotype to fix the name on a single specimen.

Further material examined. *Indonesia.* 3 ex., Sumatra, Manna, M. Knappert, Coll Vath, 4°27'S/102°59'E (NNML); 1 ex., Dr. B. Hagen, Tandjong Morawa, Serdang, N.O. Sumatra, 1°21'N/103°49'E (NNML); 1 ex., Java, Dolok Bara, Coll.

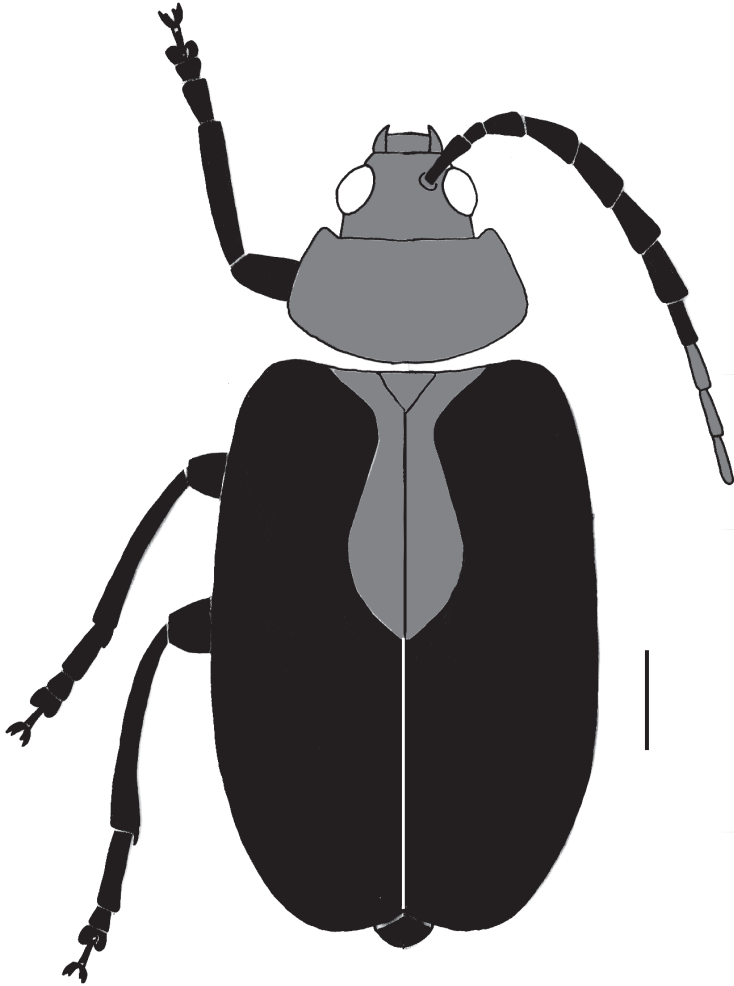


Figure 11. *Arcastes suturalis* Jacoby, 1884. Dorsal colour pattern

Vath, 6°23'S/106°48'E (NNML); 13 ex., N. E. Sumatra, Deli, Kuala Simpang, VIII.1953, A. Sollart, Lowland forests, Museum Leiden, 3°33'N/98°40'E (NNML); 2 ex., Bandar Baroe, Sumatra, J. J. D. V., 0°45'N/98°49'E (NNML); 1 ex., Dolok, Baros, Sumatra, 2°14'N/98°31'E (NNML); 1 ex., Sinabang, Sima, lur Sum, II.1913, Edw. Jacobson, 2°4'N/96°22'E (NNML); 1 ex., Puru Babi, Sima, sum 4.1913, Edw. Jacobson, 2°4'N/96°39'E (NNML); 2 ex., Sumatra, Lampung BBS Np, Way Canguk, Primary Forest, 30.X.2001 (H7), leg. K. Smets, 4°52'S/104°43'E (IRSN); 1 ex., Dohrn, Sumatra, Soekaranda, 71489, 0°37'S/94°29'E (MNHU); 1 ex., Nord Sumatra, Singkil, 17.IX.1972, D. Erber leg., 2°22'N/97°46'E (MNHU); 1 ex., Sumatra, 0°35'S/101°20'E (NHRS); 3 ex., S Sumatra, Lampung prov., Bukit Barisan Selatan, N.P. ±600 m, 5km SW, 7.–17.II.2000, Liwa, J. Bezděk leg., 5°4'S/104°4'E



Figure 12. *Arcastes suturalis* Jacoby, 1884. Photographs of the lectotype of *A. suturalis* Jacoby, 1884: **a** with labels **b** detail.



Figure 13. *Arcastes suturalis* Jacoby, 1884. Photographs of one paratype of *A. ismaili* Mohamedsaid, 2000: **a** with labels **b** detail.

(CJB); 2 ex., E Sumatra, Riau prov., Bukit Tiga Puluh N.P. 18.–25.I.2000, J. Bezděk leg., 0°50'S/102°26'E (CJB). —*Malaysia*. 4 ex., Perak F. M. S., Larut Hills, 3700–4600 ft, 24th Feb. 1932, H. M. Pendlebury, 5°N/100°53'E (BMNH); 2 ex., Pahang, F. M. S., Cameron Highlands, 4500–5000 ft, 18/06/1935, H. M. Pendlebury, 4°30'N/101°28'E (BMNH); 2 ex., Bukit Kutu Selangor, April 1915, 3000–3400, 3°33'N/101°43'E (BMNH); 1 ex., Perak, Maxwell Hill, 04/1–15 August, 1908, 5°N/100°53'E (BMNH); 1 ex., Malay Penin. Perak, F. M. S., 2000 ft, Aug. 30 1922, 4°48'N/101°9'E (BMNH); 1 ex., Penang, 1500–2428, May 1917, 5°22'N/101°17'E (BMNH); 6 ex., Gunong Kledang, Perak, 2646, Nov. 1916, Ex. FMS Museum, B. M. 1955–354, 4°35'N/101°1'E (BMNH); 1 ex., Semangko Pass, Selangor, Pahang, 2700, March 1912, 3°33'N/101°37'E (BMNH); 2 ex., Borneo, 1°6'S/114°8'E (BMNH); 1 ex., Malay Penin, Pahang, FMS, Gunong Benom, 6300ft, 3rd August 1925, I. H. N Evans, 3°50'N/101°55'E (BMNH); 1 ex., Sarawak, 4th division, Gn.

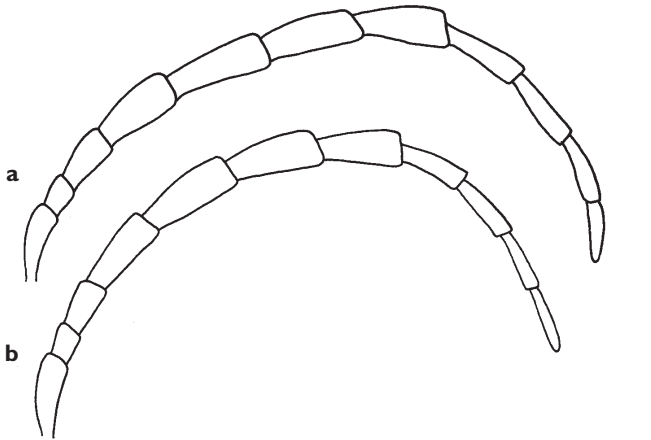


Figure 14. *Arcastes suturalis* Jacoby, 1884. Antennae: **a** male **b** female.

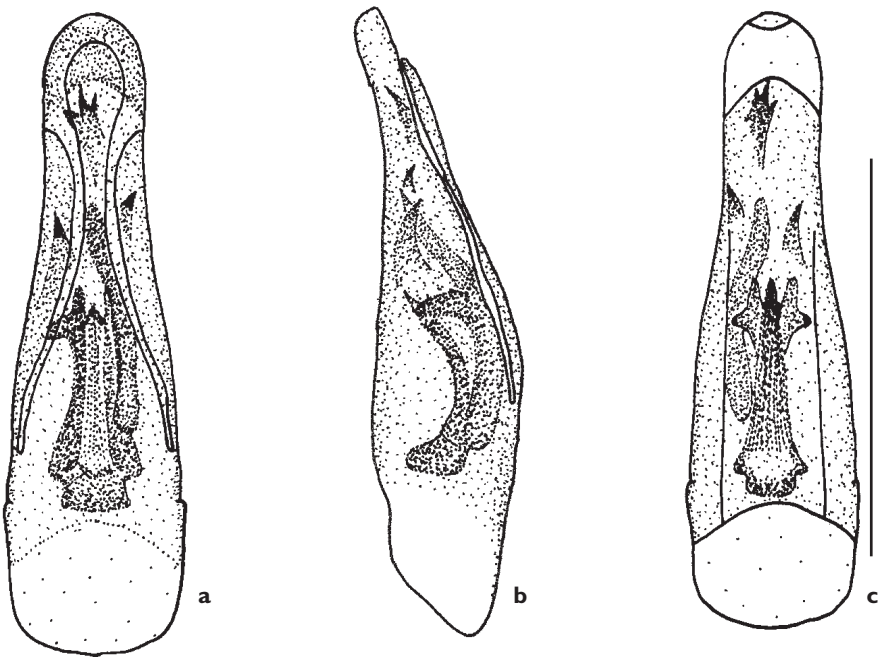


Figure 15. *Arcastes suturalis* Jacoby, 1884. Median lobe: **a** dorsal **b** lateral **c** ventral.

Mulu NP, Below Camp 4, lower montane forest, P. M. Hammond & J. E. Marshall, V.–VIII.1978, B.M. 1978–49, 3°52'N/114°46'E (BMNH); 3 ex., Quop, W. Sarawak, III.–IV 1914, G. E. Bryant, 1°33'N/101°24'E (BMNH); 1 ex., Sarawak, J. E. A. Lewis, 1910–116, 2°33'N/113°E (BMNH); 1 ex., Pahang, Taman Negara, 1.–13.III.1984, L. Jessop, B. M. 1984–230, 4°19'N/102°23'E (BMNH); 1 ex., Pa-

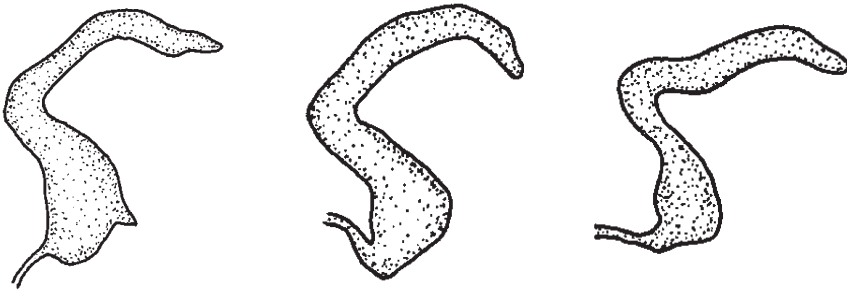


Figure 16. *Arcastes suturalis* Jacoby, 1884. Three different spermathecae.

hang, Gunong Jasar, 4000–5000 ft, 6.X.–14.XI.1980, 4°29'N/101°16'E (BMNH); 1 ex., Johor, Endau Rompin, 1.–4.VI.2007, 2°38'N/103°39'E (BMNH); 1 ex., Matang, 3 1/2 mile, Sarawak, 8.V.1909, 1°32'N/110°15'E (BMNH); 2 ex., Sarawak, 2°33'N/113° (BMNH); 1ex., Mal., Baly Coll. (ST), 4°12'N/101°58'E (BMNH); 1ex., Malacca, Perak, Jachan V., 2°12'N/102°15'E (MNHU); 1 ex., Malaysia, prov. Pahang, Tasik Chini (Lake), primaval forests surrounding lake, 2.–5.III.2007, V. Hula, L. Purchart, Růžická F., 3°23'N/102°55'E (CJB); 2 ex., Malaysia, Perak, 1200 m, 25 km near Ipoh, Banjaran Titiwangsa, Mts. Korbu, 6.–12.V.2007, M. Říha, leg., 4°56'N/101°38'E (CJB); 2 ex., Malaysia, Pahang distr., 30 km NE Raub, Lata Lem-bik, 200–400 m, 22.IV.–15.V.2002, E. Jendek & O. Šauša leg., 3°56'N/101°38'E (CJB); 2 ex., Malaysia, Taman Negara NP, Kuala Tahan, primaval forests, 5.–9. III.2007, V. Hula, L. Purchart, Růžická F., 4°19'N/102°20'E (CJB). – *Singapore*. 2 ex., 7.VIII.1922, F. N. Coll, 1°21'N/103°49'E (BMNH); 1 ex., Sime Forest, Mal. Trap, station 25131, 20.V.2005, leg. P. Grootaert, 1°21'N/103°49'E (IRSN).

***Arcastes suturalis* Jacoby, 1884**

Arcastes suturalis Jacoby, 1884: 217.

= *A. ismaili* Mohamedsaid, 2000: 282; syn. n.

Total length. 4.70–6.35 mm (mean: 5.30, n=12)

Head. Reddish-brown to red. Details of mouthparts and impressions on vertex like the description of the genus. Antennae entirely black and only the terminal three antennomeres usually contrasting pale yellow to reddish (Figs 11, 12). Shape of antennomeres like the description of the genus. Ratio length of second to third antennomere 0.50–0.57 (mean: 0.54), ratio length of third to fourth antennomere 0.67–0.70 (mean: 0.68), apical three antennomeres significantly slenderer (Fig 14).

Thorax. Shape and coloration of pronotum and scutellum like in the description of the genus (Figs 11, 12, 13). Pronotal width 1.55–2.10 mm (mean: 1.80 mm), ratio

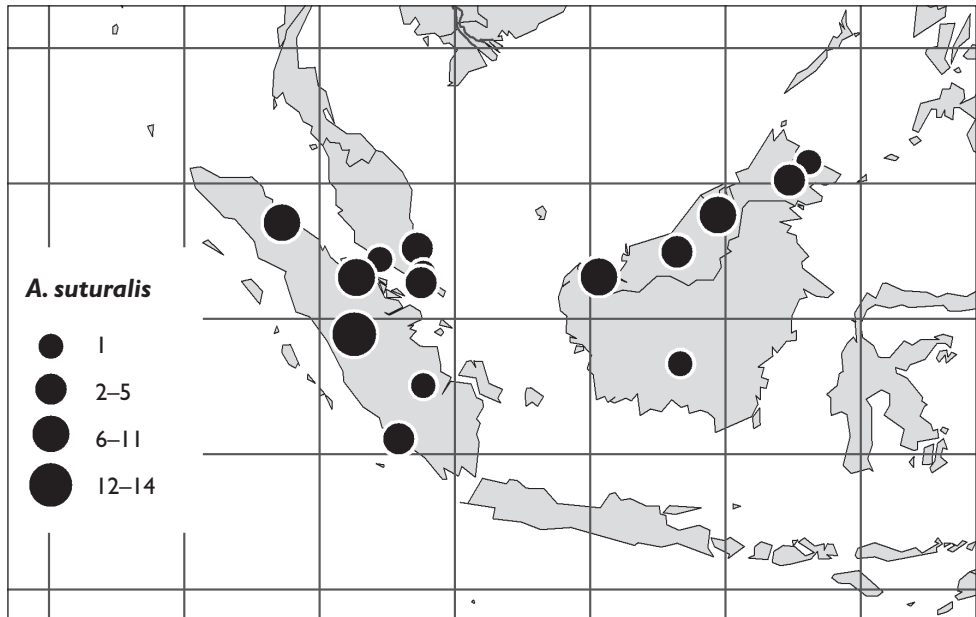


Figure 17. Distribution of *A. suturalis* Jacoby, 1884.

length to width 0.50–0.55 (mean: 0.53). Scutellum in about one third of material studied black, others brown, red or yellowish-red. Elytra elongated, black throughout in 35 % of the material examined, about 10 % with yellowish scutellar elytral spot, 50 % with entirely yellowish-red suture, and remaining material with enlarged yellowish-red elytral disc like in the specimens of *A. ismaili* (Fig. 13). Elytral length 3.80–5.05 mm (mean: 4.40 mm), maximal width of both elytra together 1.50–3.30 mm (mean: 2.40 mm), ratio of maximal width of both elytra together to length of elytra 0.63–0.69 (mean: 0.66). Underside and legs like in the description of the genus.

Abdomen. Pale yellow to brown on the sides of sternites, dark brown to black in the middle, terminal sternite usually completely black.

Male genitalia. The outer shape as in the description of the genus. Endophallus with three spur located at the upper part, the biggest one next to the lateral spiculae. Tectum not incised at apex, slender, almost reaching towards the apex of the median lobe (Fig. 15).

Female genitalia. Spermatheca with slender to oval nodulus. Middle part moderately long and slightly curved, cornu long and curved (Fig. 16).

Distribution. Recorded from Malaysia, Singapore and Indonesia (Fig. 17).

Diagnosis. *Arcastes suturalis* can be distinguished from the other two species of *Arcastes* by the elytral coloration, which is either completely black, or posses a yellowish to reddish sutural coloration that can be occasionally enlarged to pale a yellowish elytral disc. No specimen examined had longitudinal elytral stripes as it is typical for *A. biplagiata* (Figs 1, 7). Finally a check of genitalia can confirm the identification (Figs 9, 15).

Type material. *Arcastes suturalis*: Lectotype: ♂, “*Arcastes suturalis* Jac./ Dr. B. Hagen, Tandjong Morawa Serdang, (N.O. Sumatra).” (Fig. 12) (NNML). Type locality: 1°21'N/103°49'E. – Paralectotypes: 11 ex., same data as lectotype (NNML), and at least one additional type specimen is deposited in MCZH. We herein designate a lectotype to fix the name on single specimen. – Invalid types: 2 ex. from Sumatra, Lianggagas, and Soekaranda, Januar 1894, Dohrn (MNHU) are labelled as co-type, but are not from the type series.

Arcastes ismaili: Holotype: ♂, “Malaysia, Sabah, Danum, Ekspedisi Gunung Danum, 6–12.vi.1989, Ismail” (Fig. 13) (UKM). Holotype by original designation. Type locality: 5°8'N/117°24'E. – Paratypes: 7 ♂, 9 ♀, same data as holotype; 1 ♀, Sabah, Lembah Danum, 21.VIII.1989, Salleh, Ismail & Nor; 2 ♂, 1 ♀, 16.–19.V.1991, Zaidi, Ismail & Ruslan; 1 ♂, 1 ♀, 27.–31.VIII.1991, Salleh, Zaidi, Mail & Lan; 1 ♂, 3 ♀, 17.–20.IV.1992, Ismail, Yusuf & Razali; 4 ♂, 2 ♀, 22.–25.VIII.1992, Ismail, Yusuf & Sham; 1 ♂, 5.–8.XII.1992, Ismail, Yusuf & Razali. Due to the original publication, the holotype is deposited in the Center for Insect Systematics, Universiti Kebangsaan Malaysia, Bangi (UKM), and two pairs of paratypes (2 ♂, 2 ♀) in the Insect Collection, Forest Research Centre, Sandakan, Sabah.

Further material examined. *Indonesia*. 1 ex., Borneo, Kalimantan Tengah, Busang/Rekut. Confl. FIT, Primary Forest, Brendell/Mendel, August 2001, 1°40'S/113°22'E (BMNH); 1 ex., Bari, Jan. 190?, Jacoby Coll. 1909–28a, 0°31'S/104°30'E (BMNH); 1 ex., Soekaranda, Januar 1894, Dohrn, 0°37'S/94°29'E (NNML); 2 ex., Sumatra, Manna 1902, M Knap Pert., 4°27'S/102°59'E (NNML); 1 ex., Dohrn, Sumatra. Lianggagas, 0°37'S/94°29'E (NNML); 3 ex., Medan, Sumatra, J. J. D. V, 3°30'N/98°37'E (NNML); 9 ex., N. E. Sumatra, Deli, Kuala Simpang, VIII 1953, A. Sollart, Lowland forests, Museum Leiden, 3°33'N/98°40'E (NNML); 1 ex., Dohrn, Sumatra, Lianggagas, co-type, 0°37'S/94°29'E (MNHU); 1 ex., Soekaranda, Januar 1894, Dohrn, co-type, 0°37'S/94°29'E (MNHU); 1 ex., Tamiang, Sumatra, 2°29'S/103°54'E (MNHU). – *Malaysia*. 10 ex., Sarawak, 4th Division, Gn. Mulu NP, nr Base Camp, 50–100 m, P. M. Hammond & J. E. Marshall, V.–VIII.1978, B. M. 1978–49, 3°52'N/114°46'E (BMNH); 11 ex., Quop, W. Sarawak, II.–IV.1914, G. E. Bryant, G. Bryant 1919–147, 1° 33'N/101°24'E (BMNH); 6 ex., Mt. Matang, W. Sarawak, Dec. 1913, G. F. Bryant, G. Bryant coll. 1919–147, 1.55N/110.35E (BMNH); 3 ex., Sarawak, C. J. Brooks, B. M. 1928–193, 2°30'N/113°15'E (BMNH); 1 ex., Sarawak, 1907–1909, C. J. Brooks, B. M. 1936–681 (BMNH); 2 ex., Mt. Matang, 3 1/2 mile, 8.V.1909, Sarawak, J. E. A Lewis, 1910–116, 1.55N/110.35E (BMNH); 1 ex., N. Borneo, Samawang, Nr. Sandakan, July 1927, 5°50'N/118°6'E (BMNH); 1 ex., Johor, Kota Tinggi, 27.XI.2007, M. Y. Ruslan, 1°43'N/103°54'E (UKM); 4 ex., Johor, Endau Rompin, 1.–4.VI.2007, B. H. Izfa, 2°38'N/103°39'E (UKM); 1 ex., Malaysia, prov. Pahang, Tasik Chini (Lake), primaval forests surrounding lake, 2.–5.III.2007, V. Hula, L. Purchart, Růžička F., 3°23'N/102°55'E (CJB); 1 ex., Malaysia, Pahang prov., Taman Negara, N.P., Kuala Tahan, 14.III.2007, Igt. Jiří Foit, 4°19'N/102°20'E (CJB); 1 ex., Pahang, Hutan Simpan Kuala Lompat, 24–26.V.1990, Zaidi, Ismail & Ruslan,

3°41'N/102°13'E (CJB); 2 ex., Malaysia, Taman Negara NP, Kuala Tahan, primaval forests, 5–9.III.2007, V. Hula, L. Purchart, Růžička F., 4°19'N/102°20'E (CJB). – *Singapore*. 3 ex., Nee Soon, 14.X.2005, Swamp Forest, Malaise trap 1, station 25388, leg. P. Grootaert, 1°21'N/103°49'E (IRSN).

***Arcastes dimidiata* Laboissière, 1929**

Arcastes dimidiata Laboissière, 1929: 92.

Total length. 4.70–6.80 mm (mean: 5.85, n=5)

Head. Reddish-brown to red. Details of mouthparts and impressions on vertex like the description of the genus. Basal two and terminal two to three antennomeres yellowish-red, some specimens also with black antennal base (Figs 18, 19). Shape of antennomeres like description of the genus, but median antennomeres less enlarged. Ratio length of second to third antennomere 0.50–0.57 (mean: 0.53), ratio length of third to fourth antennomere 0.60–0.70 (mean: 0.66; Fig. 20).

Thorax. Shape and coloration of pronotum and scutellum like in the description of the genus (Figs 18, 19). Pronotal width 1.70–2.20 mm (mean: 1.99 mm), ratio length to width 0.53–0.55 (mean: 0.54). Basal third of elytra entirely reddish-brown to red, apical two third black (Figs 18, 19). Elytral length 4.00–5.90 mm (mean: 5.04 mm), maximal width of both elytra together 2.90–4.00 mm (mean: 3.46 mm), ratio of maximal width of both elytra together to length of elytra 0.66–0.70 (mean: 0.68). Underside and legs like in the description of the genus, some specimens also with reddish femur.

Abdomen. Pale yellow to brown, occasionally darker on middle, and last sternite usually dark brown to black.

Male genitalia. The outer shape as in the description of the genus. Endophallus with three spurs located at the upper part, the biggest one next to the lateral spiculae. Tectum not incised at apex, slender, almost reaching towards the apex of the median lobe (Fig. 21).

Female genitalia. Spermatheca with oval to elongated nodulus. Middle part more less long and slightly curved, cornu long and curved (Fig. 22).

Distribution. Recorded from Sabah (Borneo) and western Sumatra (Fig. 6).

Diagnosis. *Arcastes dimidiata* can be easily differentiated from *A. biplagiata* and *A. suturalis* by the elytral coloration. The basal elytral third is reddish and strongly contrasting with the black two terminal thirds, while it possess neither a pale suture nor elytral spots (Figs 1, 11, 18).

Type material. Holotype, 1 ♂, “Siberut Island, West Sumatra, Sept. 1924, G. B. K and N. S, *Arcastes dimidiata* Laboissière, 1929” (Fig. 19) (BMNH). Holotype by monotypy. Type locality: 1°55'S/99°17'E.

Further material examined. *Malaysia*. 1 ex., N. Borneo, Samawang, Nr. Sandakan, 14th July. 1927, Ex. F. M. S. Museum. B. M. 1955–354, 5°50'N/118°6'E

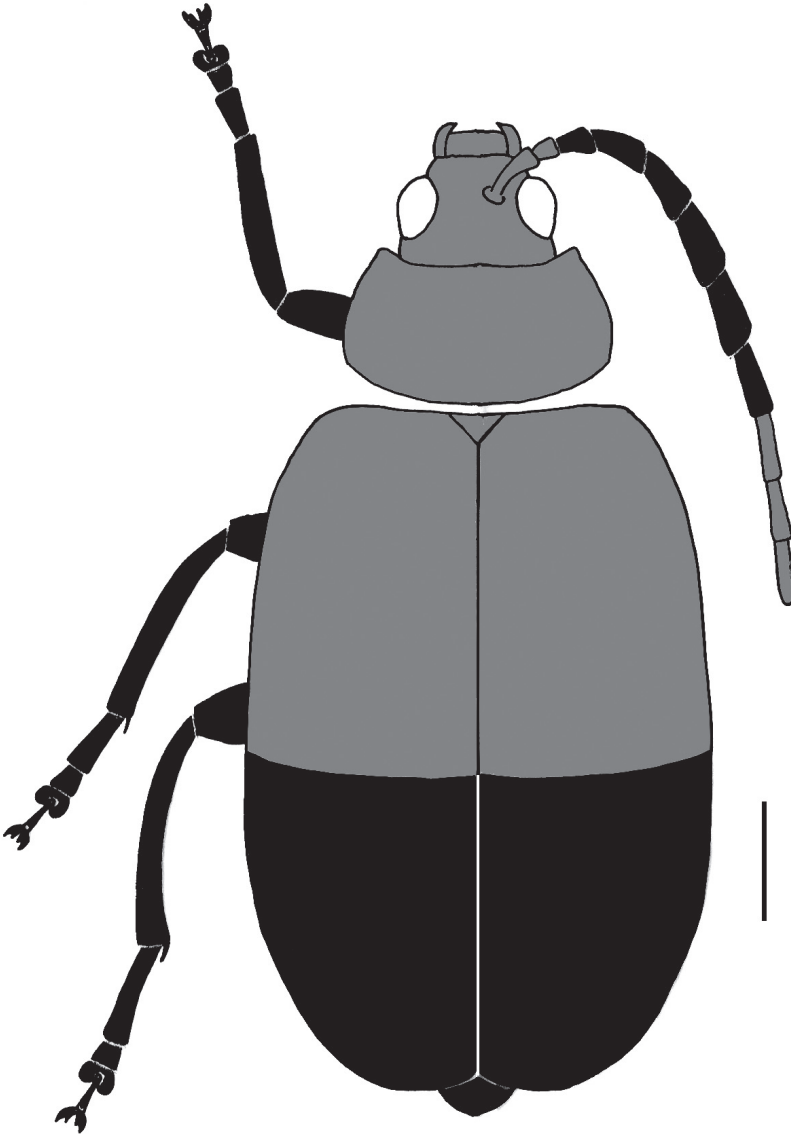


Figure 18. *Arcastes dimidiata* Laboissière, 1929. Dorsal colour pattern.

(BMNH); 2 ex., N. Borneo, Mt. Kinabalu, Pinosuk Plateau, 14.–17.III.1964, 5,225 ft, Royal Soc. Exped., col. S. Kueh, B. M. 1964–250, 6°4'N/116°33'E (BMNH); 1 ex., Borneo. Kinabalu, Jacoby Coll. 1909–28a, 6°4'N/116°33'E (BMNH).



Figure 19. *Arcastes dimidiata* Laboissière, 1929. Photographs of the holotype *A. dimidiata* Laboissière, 1929: **a** with labels **b** detail.

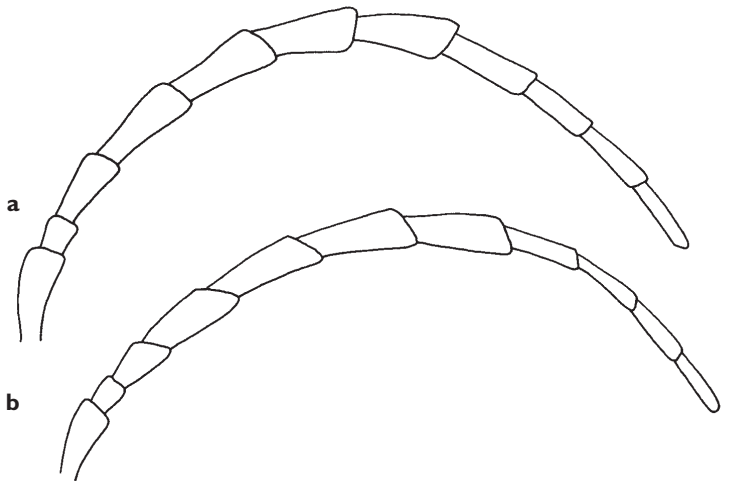


Figure 20. *Arcastes dimidiata* Laboissière, 1929. Antennae: **a** male **b** female.

Identification key of *Arcastes*

1. Elytra usually with yellowish to red spots or suture, rarely entirely black; first to seventh antennomere black, outer antennomeres usually contrasting pale yellow to reddish..... **2**
- Basal third of elytra reddish-brown to red, apical two third black, basal two and terminal two to three antennomeres yellowish-red..... ***A. dimidiata***
2. Each elytron with median, usually longitudinal reddish to yellowish-red oval spots in the basal half, in few specimens enlarged up to the apical third of elytron ***A. biplagiata***
- Elytra black throughout or with yellowish scutellar elytral spot, yellowish-red suture, or rarely with enlarged yellowish-red elytral disc..... ***A. suturalis***

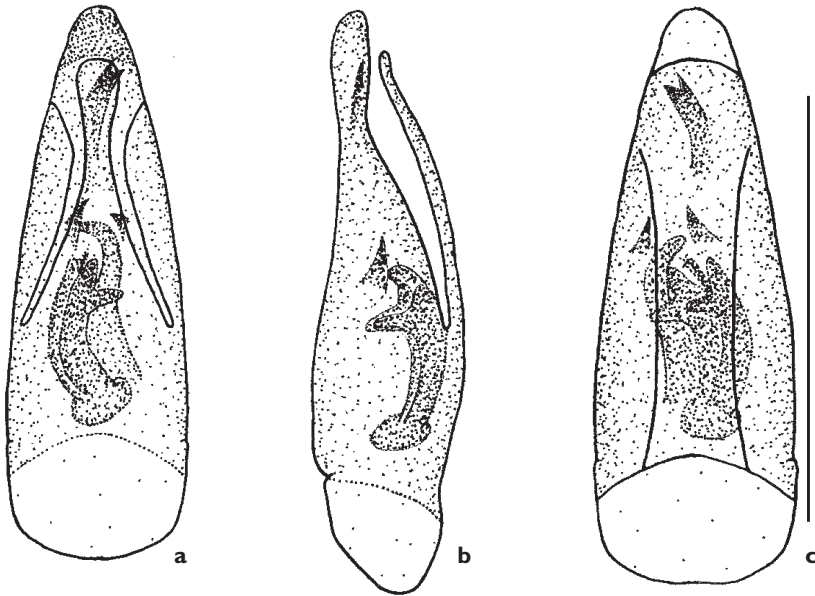


Figure 21. *Arcastes dimidiata* Laboissière, 1929. Median lobe: **a** dorsal **b** lateral **c** ventral.



Figure 22. *Arcastes dimidiata* Laboissière, 1929. Two different spermathecae.

Acknowledgements

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Taxonomic notes on *Borgmeiermyia* Townsend (Diptera, Tachinidae) with the first host record for the genus

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Abstract

Borgmeiermyia Townsend, 1935 is a small Neotropical genus of Tachinidae (Diptera) with four described species. Brief descriptions are given to the previously unknown females of *B. brasiliana* Townsend, 1935 and *B. paraguayana* Sehnael, 1998, and the male of *B. peruana* Arnaud, 1963. An identification key to the four known species is given, as well as comments on characters with intraspecific variation. Change of depository of the holotype of *B. brasiliana* from one institution to another is discussed and its current location is given. Also, the first host is recorded for the genus with the occurrence of *B. paraguayana* parasitizing *Phylloptera* aff. *ovalifolia* Burmeister, 1839 (Orthoptera: Tettigoniidae: Phaneropterinae).

Keywords

multifissicorn antenna, taxonomy, *Phylloptera*, host record, Neotropical region

Introduction

Borgmeiermyia Townsend, 1935 is a South American tachinid genus with four known species. The males of *Borgmeiermyia* species are typically characterized by remarkable multifissicorn antennae, also present in a few other Neotropical genera (e.g. *Talarocera* Williston, *Cryptocladocera* Bezzi, *Ucayalimyia* Townsend).

The genus was described by Townsend (1935) to include a single new species *B. brasiliiana* Townsend from Rio de Janeiro, based on one male specimen collected by Father Borgmeier (see comments below). Arnaud (1963) studied a further 15 specimens of this genus, redescribed the male of *B. brasiliiana* and described two new species: *B. rozeni* Arnaud from Nova Teutônia, Brazil (both sexes described), and *B. peruana* Arnaud from Tingo Maria, Peru (a single female described). Sehnal (1998) described the new species *B. paraguayana* Sehnal from San Bernardino, Paraguay (based on two males).

The multifissicorn first flagellomere of the males is an extremely conspicuous feature, and this has contributed to the uncertainty about the systematic placement of this genus. Townsend (1935) placed the genus in the tribe Frontinini; Arnaud (1963) suggested the placement was not correct but did not propose any reassignment; whereas, in the Neotropical catalogue, Guimarães (1971) treated the genus within the Siphonini. We have not assigned any systematic discussion about the tribal placement of the genus.

Arnaud (1963) stated that the hosts of this genus of parasitoid flies were unknown, but suggested they could be Lepidoptera. However, we record the first host of a *Borgmeiermyia* species as a tettigoniid grasshopper (*Phylloptera* aff. *ovalifolia* Burmeister (Orthoptera, Tettigoniidae, Phaneropterinae)) parasitized by specimens of *B. paraguayana*.

In the present study, the available material enables us to describe for the first time the females of *B. brasiliiana* and *B. paraguayana*, and the male of *B. peruana*. Also, an identification key to the species is given. Some examined characters showed intraspecific variation and we present a brief discussion on their reliability and usefulness for diagnosing and separating the species.

Material and methods

The material examined is deposited in the Instituto Alexander von Humboldt, Bogotá, Colombia (IAVH), Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA), Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ), Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZSP), and The Natural History Museum, London, United Kingdom (BMNH).

The morphological terminology used follows Mcalpine (1981) and Wood (1987). There is an important note to be made here about the terms usually applied for the scutellar setae of *Borgmeiermyia* species. Arnaud (1963) recognized “four lateral scutellar bristles” and one “apical” pair, and within the lateral pairs he distinguished about one “subapical lateral” and one “apical lateral” pairs. Sehnal (1998) recognized “basal”, “lateral”, “subapical” and “apical” scutellar setae. His “subapical” is equivalent to the “subapical lateral” of Arnaud (1963), and his “apical” is the “apical lateral” of Arnaud. Sehnal (1998) did not recognise the apical setae. The apical setae is indeed present, but sometimes it is undeveloped or it may be weakly developed so that one can overlook it easily. Herein, we recognized the following scutellar setae: one pair of basal, three

pairs of lateral, one pair of apical and one pair of discal (there is no disagreement about the recognition and terminology of this latter). The three lateral scutellar pairs are termed here: anterior, median and posterior lateral scutellar setae. The median lateral is equivalent to the “subapical lateral” of Arnaud (1963), and the posterior lateral is his “apical lateral”.

Systematics

Borgmeiermyia Townsend, 1935

Borgmeiermyia Townsend 1935: 292 (genus description, description of type species, key to multifissicorn genera), type species: *Borgmeiermyia brasiliiana* Townsend, by original designation.

Borgmeiermyia: Townsend 1936: 168 (key to Frontinini genera); Townsend 1940: 315 (generic diagnosis); Arnaud 1963: 2 (genus revision, description of *B. rozeni* and *B. peruana*, identification key); Guimarães 1971: 166 (cat., Siphonini); O'Hara 1989: 16 (comments); Sehna 1998: 349 (description of *B. paraguayana*).

Diagnosis. Small flies, from 4 to 5.5 mm. Colour blackish, with golden and silvery pruinosity. Head: fronto-orbital plate, parafacialia and gena usually golden pruinose; eye with extremely fine, short, sparse hairs (considered bare); male flagellomere multifissicorn, split into about 20 pubescent rami on inner and outer sides of a median rib; female flagellomere elongate and non-ramate; one or two pairs of proclinate fronto-orbital setae and one pair of reclinate fronto-orbital setae; facial ridge with erect supravibrissal setae, increasing in length and thickness from above to below, not reaching arisal base. Thorax: mesonotum black in ground colour with golden pruinosity; pleural areas brown to dark-brown with golden pruinosity above and silvery to golden pruinose below; scutellum with one pair of basal, three pairs of lateral, one pair of apical and one pair of discal setae; apical scutellar setae much shorter than posterior lateral setae; wing with R1 dorsally setulose, R₄₊₅ dorsally setulose from base to half-way or beyond r-m crossvein. Abdomen: black with narrow silvery to golden pruinose bands on tergites 3, 4 and 5; tergites 1+2, 3 and 4 with lateral marginal setae; tergites 2, 3, 4 and 5 with 2 or 3 hairlike marginal setae.

Discussion. The systematic position of this genus is uncertain. It was placed within the siphonines by Guimarães (1971) and shares the following features with members of this tribe: wing with R₄₊₅ dorsally setulose and posterior lateral scutellar setae convergent. Some few siphonine taxa present a modification on male first flagellomere under three diverse conditions: bilobed, trilobed or pectinate (=multifissicorn) (O'Hara 1989). The pectinate condition is also very rare among the siphonines, shared by *Borgmeiermyia* and some species of *Peribaea* Robineau-Desvoidy. *Borgmeiermyia* can also be distinguished from other siphonines by the presence of three pairs of lateral scutellar setae.

Key to species of *Borgmeiermyia*

1. Median lateral scutellar setae long, at least 2/3 length of posterior lateral scutellar setae **2**
- Median lateral scutellar setae short, about one-half length of posterior lateral scutellar setae (sometimes slightly longer than one-half) **3**
2. Male cercus and surstylus broad and cercus strongly curved dorsally at mid length in lateral view and with apex rounded (Figure 2) (Colombia, Peru, Brazil) ***peruana***
- Male cercus and surstylus less broad (not as above) and cercus slightly curved dorsally in lateral view and with apex truncated (Brazil, Paraguay) ***paraguayana***
3. Vein R_{4+5} setulose dorsally between half and the whole distance to r-m crossvein, but not beyond r-m; male with outer rami of flagellomere brown and the inner rami yellow; wing costal margin with a brown continuous macula from apex of Sc to apex of R_{2+3} (Figure 5) (Brazil) ***brasiliانا***
- Vein R_{4+5} setulose dorsally far beyond r-m crossvein; male with inner and outer rami of flagellomere brown; wing costal margin with a brown macula from apex of Sc to apex of R_{2+3} but this macula partially interrupted after apex of R_1 (Figure 7) (Brazil) ***rozeni***

Remarks on the key and variable characters

This identification key was prepared based on the characters mentioned by Arnaud (1963), Sehnal (1998) and our examinations. Sehnal (1998) compared the length of the median lateral scutellar seta with scutellum length: longer than scutellum in *B. paraguayana* and shorter than scutellum in *B. brasiliانا* and *B. rozeni*. However, this relative length is variable for *B. brasiliانا* given that an examined female has the median lateral seta shorter than scutellum, whereas the male holotype (MNRJ) has the seta slightly longer than scutellum. On the other hand, the relative length of the median and posterior lateral scutellar setae, as used by Arnaud (1963), proved to be a more reliable character to distinguish and recognize the species of *Borgmeiermyia*.

The dorsal setulosity of vein R_{4+5} has been used to recognize and distinguish between *B. peruana* and *B. paraguayana* (Sehnal 1998), and other species (Arnaud 1963). Arnaud (1963) described this character for *B. peruana* as “ R_5 above bristled to R_6 , with one bristle beyond and removed from R_6 ”; whereas Sehnal (1998) described *B. paraguayana* as having “ R_{4+5} dorsally bristled over little more than half distance to r-m”. This character proved to be intraspecifically variable and not reliable for diagnostic purposes, at least for these two resembling species. We found specimens of *B. peruana* that fitted the original description, although other specimens had R_{4+5} setulose either over three-fourths of the distance to r-m crossvein or the whole distance to r-m. With *B. paraguayana*, we also observed some variation but to a lesser degree: specimens whose setulosity fits the original description, and others with the setulae almost reach-

ing r-m. Variation was also observed in the holotype of *B. brasiliiana* examined here (setulose to r-m crossvein) and a male examined by Arnaud (1963) (“ R_5 above bristled only one-half of distance to R_6 ”). Although intraspecific variation has been found in *B. brasiliiana*, this character is diagnostic and useful for separating *B. brasiliiana* and *B. rozeni*, as the latter is the only species with the setulosity extending far beyond the r-m crossvein.

***Borgmeiermyia brasiliiana* Townsend, 1935**

Fig. 5

Borgmeiermyia brasiliiana Townsend 1935: 293, Figs 1–2 (male description), holotype male (Museu Nacional, Rio de Janeiro; formerly at “Instituto de Biologia Vegetal, Rio de Janeiro”; see comments on type depository below), type locality: Brazil, Rio de Janeiro, Jardim Botânico [22°58'03"S, 43°13'28"W].

Borgmeiermyia brasiliiana; Townsend 1940: 315 (redescription, type data); Arnaud 1963: 5, Figs 5, 8, 12–14 (male redescription, key); Guimarães 1971: 166 (cat.); Sehnaal 1998: 353 (comments).

Type material examined: Holotype male (MNRJ) labelled as follows “HOLOTYPUS” (red label); “*Borgmeiermyia* / *brasiliiana* TT / Holotype ♂ / Det CHTT”; “Rio de Janeiro / Jard. Botânico / 7–934 / H. Souza Lopes [sic]”; “EMBRAPA” (pink label), in excellent condition. See comments on type collector below.

Other material examined: BRAZIL, *State of Rio de Janeiro*, Itatiaia, 1 female, no date, J.F. Zikán leg. (MZSP).

Description of female. Body length: 5.4 mm (n=1), wing length: 4.1 mm (n=1). Differs from the male redescription provided by Arnaud (1963) by the following: Frons at vertex level about 0.35 of head width; frons at most four times width of parafrons (at narrowest point, beside ocellar triangle); parafacialia narrowing slightly below (not strongly as male); antenna not multifissicorn and yellow, but brown at extreme base and apical fourth of arista and posterior portion of flagellomere; flagellomere elongate, reaching level of vibrissa; gena about one-sixth of eye height. Length of median lateral scutellar seta about 1/2 or slightly longer than 1/2 of the posterior lateral scutellar seta (the male holotype between 1/2 and 3/5). Both female specimen and the male holotype have R_{4+5} setulose dorsally on the whole distance to the r-m crossvein, although the male of Santa Catarina (examined by Arnaud, 1963) was characterized as setulose at only half the distance to r-m.

Comments: Male described by Townsend (1935), with head illustration (Figs 1–2); and later redescribed and richly illustrated by Arnaud (1963). His redescription, based on one male from Santa Catarina, was compared with the male holotype (MNRJ) and confirmed. Also, the female described herein was compared with the holotype. This species can be distinguished from *B. paraguayana* and *B. peruana* by the median lateral scutellar seta short, about one-half length of posterior lateral scutellar setae (sometimes slightly longer than one-half but not about or over 2/3) and from *B.*

rozeni by the vein R_{4+5} setulose dorsally between half and the whole distance to r-m crossvein, not beyond r-m, and by the color of male flagellomere.

Type depository and type collector: The holotype male was originally deposited in the “Instituto de Biologia Vegetal” (Rio de Janeiro) (Townsend 1935: 293), but this institution was closed in 1938 by a federal order and the “Centro Nacional de Estudos e Pesquisas Agronômicas” was then created. This latter was the primordial agency which became what is now EMBRAPA. Consequently, the holotype of *B. brasiliiana* passed from one institution to another until the middle of the 20th century when it was donated by EMBRAPA to the Museu Nacional (MNRJ) wherein it is now securely deposited. The holotype collector in the label is not correct. The type was collected by Father Borgmeier as mentioned by Townsend (1935: 293) in the original description and by Arnaud (1963: 10) who exchanged correspondence with Father Borgmeier about some interesting facts on *B. brasiliiana* as illustrated here “Father Borgmeier informed me (*in litt.*) that the holotype specimen of *B. brasiliiana* was collected on the inside of a window in his former office in the Jardim Botânico.” (Arnaud, 1963: 10).

Distribution: BRAZIL (Rio de Janeiro, Santa Catarina)

Borgmeiermyia paraguayana Sehnal, 1998

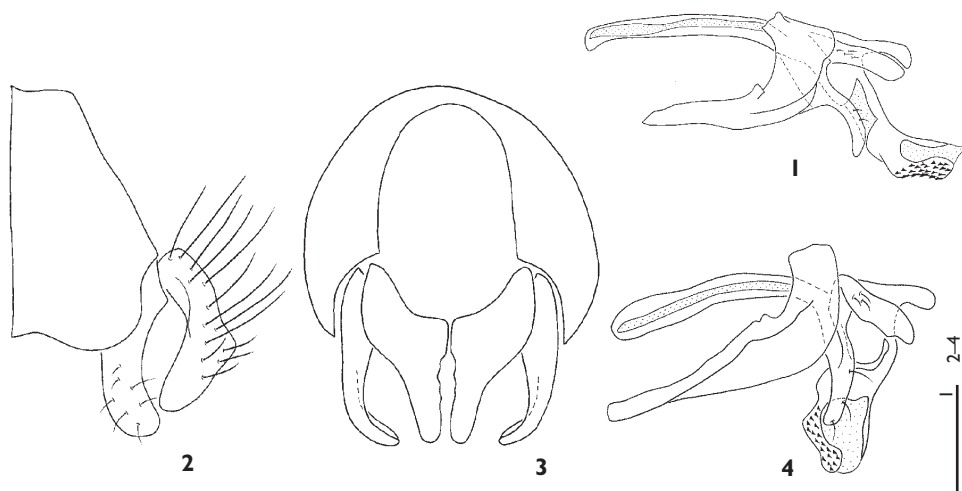
Figs 1, 6, 10

Borgmeiermyia paraguayana Sehnal 1998: 350, Figs 1–5 (male description), holotype male (Naturhistorisches Museum Wien), type locality: Paraguay, San Bernardino [ca. 25°16'S, 57°19'W].

Material examined: BRAZIL, *State of São Paulo*, São Paulo, Ipiranga, 6 males and 1 female, xi.1998, C. [Carlos] Campaner leg. (MZSP) (one male dissected).

Description of female. Body length: 5.3 mm (n=1), wing length: 3.8 mm (n=1). Differs from the male description (Sehnal 1998) by its parafacial with silvery yellowish pruinosity below; the antenna yellow and not multifissicorn; the narrow band on the basal portion of tergites 3, 4 and 5 silvery yellowish pruinose. Length of median lateral scutellar seta between 2/3 and 3/4 length of posterior lateral scutellar seta.

Comments: The male was described by Sehnal (1998) with illustrations of habitus and right wing of the holotype, and the terminalia and sternite 5 of a paratype. The male aedeagus is illustrated in more detail here (Figure 1) based on a dissected male from southeastern Brazil. This species differs from *B. brasiliiana* and *B. rozeni* by the median pair of lateral scutellar setae long, clearly longer than one-half length of posterior lateral scutellar setae and from *B. peruana* by the cerci curved not so strongly. The cerci of *B. paraguayana* differ from that of *B. brasiliiana* by the apical portion of this structure broader (subtruncate) in the lateral view and by the median-posterior region not curved. As mentioned above, we found intraspecific variation in the dorsal setulosity of R_{4+5} (see comments on the Key to identification).



Figures 1–4. *Borgmeiermyia paraguayana*: **1** male aedeagus, lateral view (São Paulo); *B. peruana* **2** male terminalia, lateral view (Amazonas, Manaus) **3** male terminalia, dorsal view **4** male aedeagus, lateral view. (Scale bars = 0.25 mm).

Puparium. (Figure 10). Length: 4.9 mm (n=4), width: 2.1 mm. Medium-sized, moderately elongate, reddish-brown. Anal spiracular plates shiny black, close to each other, not prominent and clearly above midline of puparium. Each anal spiracular plate with four sinuate respiratory slits somewhat convergent with the median scar.

Host record: The specimens from São Paulo were reared by Carlos Campaner (Museu de Zoologia, São Paulo) from one adult tettigoniid. The host was identified as *Phylloptera* sp., probably *Phylloptera ovalifolia* Burmeister, 1839 (Orthoptera, Tettigoniidae, Phaneropterinae). This is the first host record known for *Borgmeiermyia*.

Distribution: BRAZIL (Sao Paulo) rec. n., PARAGUAY (San Bernardino)

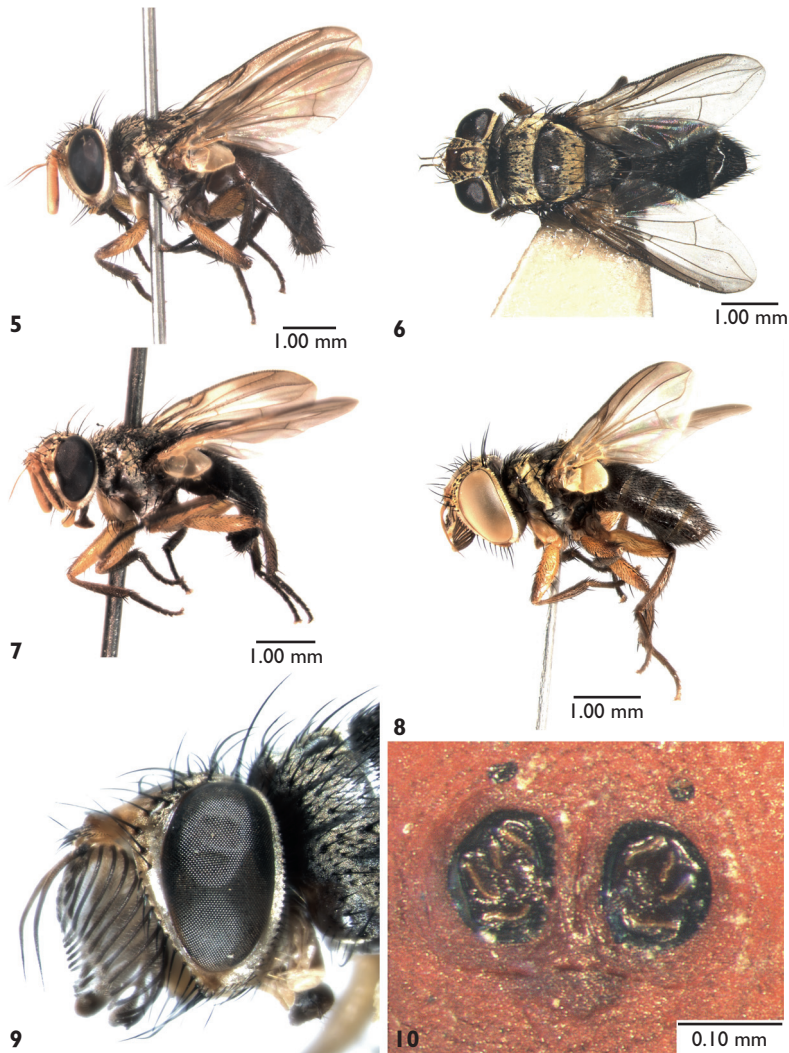
Borgmeiermyia peruana Arnaud, 1963

Figs 2–4, 8

Borgmeiermyia peruana Arnaud 1963: 10, fig. 11 (female description, key), holotype female (California Academy of Sciences), type locality: Peru, Tingo Maria, Monson Valley [ca. 09°17'S, 75°59'W].

Borgmeiermyia peruana; Guimarães 1971: 166 (cat.), Sehnaal 1998: 354 (comments).

Material examined: COLOMBIA, Dept. Putumayo: P.N.N. La Paya, Cabaña Viviano, 0°7'S 74°56'W, 320m, 1 male, 26.IX–1.X.2001, R. Cobete leg. (IAVH) (terminalia dissected); “Putumayo”, 1 female, X.1934, Apolinar Maria leg. (MZSP); BRAZIL, State of Amazonas, Manaus, J.A. Rafael leg., 04.XI.1978, 2 males (MZSP), VII.1979, 1 male (MZSP) (terminalia dissected); Manaus, C. Univers. [Cidade Universitária], malaise,



Figures 5–10. **5** *Borgmeiermyia brasiliiana*, female, lateral habitus (Rio de Janeiro, Itatiaia) **6** *B. paraguayana*, female, dorsal habitus (São Paulo) **7** *B. rozeni*, female, lateral habitus (Santa Catarina, Nova Teutônia) **8** *B. peruana*, male, lateral habitus (Amazonas, Manaus) **9** *B. rozeni*, male paratype, head, lateral view (Santa Catarina, Nova Teutônia) **10** *B. paraguayana*, anal spiracles of puparium, posterior view.

J.A. Rafael leg., 1 male, 07.VI.1982 (INPA), 1 male, 24.VI.1982 (INPA); Manaus, F. Esteio, R. 1401, km 17, 1 male, 17–31.I.1996, malaise, L.E.F.R. Silva leg. (INPA).

Description of male. Body length: 4.25 mm (n=2), wing length: 3.0 mm (n=2). Differs from the female by the following: head with frons width at vertex 0.29 of head width; antenna with first flagellomere multifissicorn; antenna with scape, pedicel and inner rami of flagellomere yellow, and the extreme base of arista and the outer rami of flagellomere brown, arista brownish; gena about one-sixth of eye height; proboscis black-setulose on prementum and golden-setulose on labella. Length of median lateral

scutellar seta varying in length from slightly longer than $2/3$ (specimens from Amazonas) to about $4/5$ (specimen from Colombia) length of posterior lateral scutellar seta.

Terminalia (Figs 2–4): Very similar to those of *B. brasiliensis* when compared with the illustration of terminalia given by Arnaud (1963), differing by the cerci and surstylus broader and the first strongly curved dorsally at midlength in lateral view. Surstylus in posterior view with basal halves broader.

Comments: Female described by Arnaud (1963), with the wing illustrated (fig. 11). The males herein described were compared with the female description given by Arnaud (1963). The illustrated terminalia was dissected from a male from Manaus (Amazonia, Brazil), and the photographed male is also from Manaus. The specimens examined here showed variation in the length of median lateral scutellar seta. The female holotype from Peru has the pair of median lateral scutellar setae “more than four-fifths of length of apical [posterior] lateral scutellar bristles” (Arnaud 1963), as well as the Colombian male and female here examined, but this length differs from that found in males from Amazonas, which have the median lateral scutellar seta slightly longer than $2/3$ length of posterior lateral one.

Distribution: COLOMBIA (Putumayo) rec. n., PERU (Huánuco), BRAZIL (Amazonas) rec. n.

***Borgmeiermyia rozeni* Arnaud, 1963**

Figs 7, 9

Borgmeiermyia rozeni Arnaud 1963: 12, Figs 1–4, 6–7, 9–10, 15–17 (male and female description, key), holotype male (American Museum of Natural History), type locality: Brazil, Santa Catarina, Nova Teutônia [ca. 27°09'S, 52°18'W].

Borgmeiermyia rozeni; Guimarães 1971: 166 (cat.); Sehnael 1998: 353 (comments).

Type material examined: one paratype male, BRAZIL, *State of Santa Catarina*, Nova Teutônia, 06.iii.1962, F. Plaumann leg. (MZSP); one paratype male, same locality and collector, 02.v.1959 (BMNH).

Additional material examined: same data as paratypes, but V.1967, 3 males and 2 females (MZSP), III.1971, 2 males (MZSP), IV.1971, 4 males (MZSP), 28.IV.1938, 1 female (BMNH), 01.III.1938, 1 female (BMNH); *State of Amazonas*, Manaus, 04.XI.1978, 5 males, J.A. Rafael leg. (MZSP) (one male with the terminalia dissected).

Comments: Both male and female described and richly illustrated by Arnaud (1963). Here we present the lateral habitus of a female from Nova Teutônia (Figure 7) and, for detailed observation, the head of the male paratype in profile (Figure 9). The geographical distribution of *B. rozeni* has been extended northwards with the recognition of 5 male specimens from Manaus (Amazonas). The identification of these specimens was confirmed by comparing the terminalia of a dissected male with the figures of the male terminalia of *B. rozeni* in Arnaud (1963).

Distribution: BRAZIL (Amazonas rec. n., Santa Catarina).

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