RESEARCH ARTICLE



Two new species of the gorgonian inhabiting barnacle, Conopea (Crustacea, Cirripedia, Thoracica), from the Gulf of Guinea

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Academic editor: Niel Bruce | Received 27 July 2012 | Accepted 29 January 2013 | Published 18 February 2013 urn:kid:zoobank.org:pub:0E640728-1644-4AFB-9B0F-35021638E381

Citation: Carrison-Stone D, Syoc RV, Williams G, Simison WB (2013) Two new species of the gorgonian inhabiting barnacle, *Conopea* (Crustacea, Cirripedia, Thoracica), from the Gulf of Guinea. ZooKeys 270: 1–20. doi: 10.3897/ zooKeys.270.3736

Abstract

Two new species of *Conopea* (Say 1822) are described from the Gulf of Guinea: *Conopea saotomensis* **sp. n.** and *Conopea fidelis* **sp. n.** These two new species were collected from the historically isolated volcanic islands of São Tomé and Príncipe. The relationship between *Conopea saotomensis* **sp. n.**, *Conopea fidelis* **sp. n.** and two other Atlantic barnacle species, *Conopea calceola* (Ellis 1758) and *Conopea galeata* (Linnaeus 1771), is examined. The methods employed are the construction of a molecular phylogeny using mitochondrial COI and nuclear H3 gene sequence data along with morphological comparisons of calcareous and cuticular body parts. It is found that *Conopea saotomensis* **sp. n.**, *Conopea fidelis* **sp. n.** and *Conopea calceola* are most closely related to each other but the relationship among them is unresolved. Gorgonian hosts are identified. Preliminary observations show species level host specificity for *C. fidelis* **sp. n.**

Keywords

Barnacle, Cirripedia, *Conopea calceola, Conopea fidelis* sp. n., *Conopea galeata, Conopea saotomensis* sp. n., COI, endemic, gorgonian, Gulf of Guinea, H3, host specificity, octocoral, phylogeny

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Introduction

The Gulf of Guinea island chain consists of Bioko, São Tomé, Príncipe, and Annobón. This study focuses on São Tomé and Príncipe, which are approximately 140 km apart and 274 km west of northern Gabon. They are the products of large shield volcanoes originating 3,000 m below the ocean's surface along the Cameroon line. São Tomé and Príncipe are old islands, 13 and 30 myo, respectively, and have never been connected to the African mainland.

Genus Conopea

Say (1822) designated a new genus *Conopea* to accommodate a new species, *C. elon-gata*, he described from eastern Florida. He included a previously known barnacle *Balanus galeatus* (=*Lepas galeata* Linnaeus 1771) in *Conopea. Conopea elongata* is later listed, by Darwin (1854), as a junior synonym of *C. galeata*. Say describes *Conopea* as 'Shell sessile, fixed, composed of two cones joined by their bases, the lines of junction carinate each side: inferior cone entire, attached by its anterior side and tip to marine bodies; with an aperture at the summit, closed by a quadrivalved operculum.'

Conopea is a widespread genus that is found in temperate and tropical oceans around the world. Currently, there are 21 described species of *Conopea*. In general, *Conopea* is not a well documented group. There is very little data on host associations, species ranges are not well defined, published descriptions are often incomplete and occasionally contain questionable information. Darwin (1854) thought *Conopea* to be closely related to the genera *Megabalanus* and *Acasta* whereas Hoek (1913) thought *Conopea* to be closely related to *Balanus*. All species of *Conopea* live in an obligate commensal symbiotic relationship with either a gorgonian or an antipatharian. The barnacle lives almost completely covered by host tissue, the basis of its shell clasps the axis of the host, with only the opercular opening exposed.

Atlantic species of Conopea

There are three known species of *Conopea* found in the Atlantic Ocean and Caribbean Sea: *C. calceola, C. galeata,* and *C. merrilli. Conopea calceola* was originally described from the Strait of Gibraltar, by Ellis (1758). *Conopea calceola* has subsequently been recorded from the Mediterranean to South Africa, the Persian Gulf to western Australia, the Indian Ocean, and Japan (see Newman and Ross 1976 for literature summary). *Conopea merrilli* was described from South Carolina (Zullo 1966) and has since been recorded from the west coast of Florida and Puerto Rico (see Newman and Ross 1976). *Conopea galeata* was described by Linnaeus in 1771 but no type locality was given and the type specimen is lost (Pilsbry 1916). Darwin (1854) gave a description of *C. galeata* (as *Balanus galeatus*) and listed its known localities as South Carolina,

Florida, West Indies, and Central America. Pilsbry (1916) also gave a description of *C. galeata* (as *Balanus galeatus*) and listed the distribution as South Carolina to the West Indies and Central America, and southern California. The current distribution range of *Conopea galeata* is North Carolina through the West Indies, the Gulf of Mexico to Venezuela, southern California to Panama, and the Galápagos Islands (see Newman and Ross 1976).

Morphologically *C. merrilli* and *C. galeata* are clearly different and easily distinguishable from *C. calceola*, *C. saotomensis* sp. n., and *C. fidelis* sp. n.. *Conopea calceola* is morphologically similar to the Gulf of Guinea species and is therefore compared in detail to aid in future identifications. *Conopea galeata* was chosen over *C. merrilli* as an outgroup for molecular analysis because of its larger distribution range and greater availability of specimens.

Materials and methods

Approximately 40 individuals of *Conopea saotomensis* sp. n. and 20 individuals of *Conopea fidelis* sp. n. were collected from São Tomé and Príncipe by Carrison-Stone, Van Syoc, and Williams in 2006 and 2009. Barnacles were collected from three different localities on São Tomé: Diogo Vaz (0°18.89'N, 6°29.39"E), Ponta Baleia (0°2.13'N, 6°33.51'E), and Ilheu Santana (0°16'N, 6°45.48'E) and two different localities on Príncipe: Ilheu BomBom (1°42'8.8"N, 7°24'14"E) and Pedra de Galé (1°43'30.1"N, 7°22'51.5"E). Collections were done via SCUBA at depths of 9–33m. Seven individuals of *Conopea calceola* were collected from 3 separate sites at Porto Covo, Portugal, by Van Syoc in 2008. Samples of the associated gorgonian were also collected. All specimens were preserved in 95% EtOH.

Conopea galeata from St. Catherine Is., Georgia (USA) were borrowed from the California Academy of Sciences Invertebrate Zoology Department (CASIZ). *Conopea galeata* from South Padre Is., Texas and Mexico Beach, Florida were collected by Mary Wicksten. *Conopea galeata* from Port Aransas, Texas were collected by Carol Cox.

Barnacle cirri, mouthparts and opercular plates from São Tomé, Príncipe, and Portugal specimens were dissected for morphological comparisons. These physical traits, along with shell shape, in particular basis shape and presence/absence of longitudinal tubes in shell wall plates, are traditionally used for identification. The cirri and mouthparts were mounted on microslides and photographed at 100x with a Leitz microscope imaging system. Images of the opercular plates were taken with a scanning electron microscope (SEM, LEO/Zeiss 1450VP).

Identification of host gorgonians was based on external and sclerite morphology. Branching patterns, polyp shape, color and sclerite types were examined. Sclerites were isolated by dissolving small amounts of gorgonian tissue in sodium hypochlorite solution, followed by rinsing with water and then 75% ethanol. Images of the sclerites were taken with SEM and Leitz optical microscope imaging systems. All gorgonians harboring barnacles were identified using Grasshoff (1988, 1992). However some bar-

Barnacle taxon	Gorgonian host	CASIZ Catalog	GenBank accession's	Collection Locality
Conopea calceola	Eunicella verrucosa	175916	HQ290142, HQ290155	Porto Covo, Portugal
Conopea calceola	Eunicella verrucosa	175917	HQ290143, HQ290156	Porto Covo, Portugal
Conopea calceola	Eunicella verrucosa	180065	HQ290135, KC349910	Porto Covo, Portugal
Conopea galeata	unknown	106216	HQ290146, HQ290147	St.Catherine Is., Georgia
Conopea galeata	unknown	184331	JQ966287, JQ966283	South Padre Is., Texas
Conopea galeata	Leptogorgia setacea	183496	JQ966288, JQ966284	Port Aransas, Texas
Conopea galeata *	unknown	184416A 184416B	JQ966289, JQ966285 JQ966290, JQ966286	Mexico Beach, Florida
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia viminalis	173189	HQ290134, HQ290149	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Eunicella kochi	173190	HQ290136, KC349911	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia ruberrima	174321	KC349913, KC349922	Ilheu Santana, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia dakarensis	174804	KC349904, KC349916	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia varians	174805	KC349906, KC349917	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia gaini	174806	HQ290152, KC349918	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia ruberrima	175525	KC349907, KC349919	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia dichotoma	175526	KC349908, KC349920	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	unknown	178662	KC349909, KC349925	Diogo Vaz, São Tomé
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia dakarensis	178655	HQ290137, HQ290159	Bom Bom Is., Príncipe
<i>Conopea</i> <i>saotomensis</i> sp. n.	unknown	178656	HQ290160, KC349924	Bom Bom Is., Príncipe
<i>Conopea</i> <i>saotomensis</i> sp. n.	Leptogorgia sp.	180025	JQ966291	Pedra de Galé, Príncipe
Conopea saotomensis sp. n.	Leptogorgia dichotoma	185253		Diogo Vaz, São Tomé
<i>Conopea fidelis</i> sp. n.*	Muriceopsis tuberculata	174803A 174803B	HQ290140, HQ290151 KC349905, KC349915	Diogo Vaz, São Tomé

Table I. Data associated with the specimens used in this study.

Barnacle taxon	Gorgonian host	CASIZ Catalog	GenBank accession's	Collection Locality
<i>Conopea fidelis</i> sp. n.	Muriceopsis tuberculata	174320	KC349912, KC349921	Ponta Baleia, São Tomé
<i>Conopea fidelis</i> sp. n.	Muriceopsis tuberculata	174322A 174322B	HQ290140, HQ290150 KC349914, KC349923	Ponta Baleia, São Tomé
<i>Conopea fidelis</i> sp. n.*	Muriceopsis tuberculata	178651A 178651B	HQ290138, HQ290139 HQ290157, HQ290158	Pedra de Galé, Príncipe
<i>Conopea fidelis</i> sp. n.	Muriceopsis tuberculata	185252		Ponta Baleia, São Tomé

* Two barnacles were used from this lot.

nacle specimens lacked host tissue and were found attached to only the gorgonian axis. Therefore, identification of those hosts was impossible.

Genomic DNA was extracted from adductor muscle tissue using the Qiagen DNeasy Blood and Tissue kit (Valencia, CA). The cytochrome c oxidase subunit I (COI) primers COI-N: TGAGAAATTATTCCGAAGGCTGG (Van Syoc 1994, 1995) and LCO 1490: GGTCAACAAATCATAAAGATATTGG (Folmer et al. 1994) were used to amplify approximately 700 base pairs of the mitochondrial genome (mtDNA). Additionally, the Histone 3 primers H3F: ATGGCTCGTACCAAGCA-GAC VGC and H3R: ATATCCTTRGGCATRATRGTGAC (Colgan et al. 1998) were used to amplify approximately 350 base pairs of the nuclear protein coding gene (nDNA). The COI thermal profile was an initial step of 94°C for 3 min, then 35 cycles of: 94°C for 30sec, 47°C for 30sec, and 72°C for 1 min. H3 thermal profile was 3 initial steps of 94°C for 3 min, 50°C for 2 min, 72°C for 2 min, then 35 cycles of: 94°C for 30 sec, and 72°C for 40 sec. The resulting sequence data were edited in Sequencher 4.7 (Gene Codes) and BioEdit 7.0.9 (Hall 1997). Alignments were initially performed with ClustalW 1.8 and then edited by hand.

Molecular phylogeny was determined by Bayesian and likelihood analyses. *Semibalanus balanoides* (GenBank accession AF242660.1), another archaeobalanid, was used as an outgroup. Bayesian analyses were run in Mr. Bayes (Huelsenbeck and Ronquist 2001) for 50 million generations with a sample frequency of 1000 using the CAS CCG PhyloCluster (a 280-core Apple Xserve High Performance Computing Cluster with 8–12 GB RAM/node (232 GB total)). The concatenated dataset was partitioned into 1st, 2nd, and 3rd codon positions so that models of substitution could be estimated for each site with Mr.Modeltest 2.3 (Nylander 2004). Burn-in and convergence values were determined using Tracer v1.5 (Drummond and Rambaut 2007). Likelihood analyses were run in PAUP* 4.0b10 (Swofford 2003). Heuristic searches were performed along with bootstrap analyses; 10,000 bootstrap replicates with 10 random sequence additions to each bootstrap. The best-fit DNA substitution models were determined with Mr.Modeltest. All analyses were performed on the gene datasets separately as well as concatenated. Uncorrected nucleotide pairwise-distance matrices among and within groups were determined in MEGA 5.05 (Tamura et al. 2007).

Results

Molecular analyses

Two major clades resulted from molecular analysis. One clade contains *C. calceola*, *C. saotomensis* sp. n. and *C. fidelis* sp. n, and the other contains *C. galeata*. Unfortunately, the gene data used was not sufficient to completely resolve the relationship among the three eastern Atlantic species. We do know that they are each other's closest relatives but we do not know which two of the three are most closely related. Bayesian (Fig. 1) and likelihood phylogenies, based on concatenated COI and H3 datasets, between *C.*



Figure I. Bayesian phylogeny based on concatenated H3 nDNA and COI mtDNA sequences. Posterior probabilities of 0.95 or greater are shown. The relationship among the Gulf of Guinea species and *C. calceola* is unresolved.

saotomensis sp. n., *C. fidelis* sp. n., and *C. calceola* are unresolved. Bayesian phylogeny generated solely on COI data shows the two Gulf of Guinea species as being more closely related to each other than to *C. calceola*. However the likelihood phylogeny generated with solely COI data again showed an unresolved relationship among *C. saotomensis* sp. n., *C. fidelis* sp. n., and *C. calceola*. Separate Bayesian and likelihood analyses of H3 sequence data showed similar unresolved topologies among the three eastern Atlantic species.

Pairwise uncorrected p-distances (Table 2) of COI and H3 also could not resolve the relationship. Distances for COI indicate that *C. saotomensis* sp. n. and *Conopea fidelis* sp. n. are more closely related to each other (8.2%) than to *C. calceola* (8.8% and 10.4%, respectively) whereas H3 distances indicate that *C. saotomensis* sp. n. and *Conopea fidelis* sp. n. are more closely related to *C. calceola* (1.4% and 1.3%, respectively) than to each other (2.2%). Pairwise uncorrected p-distances within groups is as follows: *C. saotomensis* sp. n. = 0.8%/0.0%, *C. fidelis* sp. n. = 0.7%/0.2%, *C. calceola* = 0.7%/0.0%, *C. galeata* = 0.3%/0.1% (COI/H3 respectively).

Barnacle taxon	C. saotomensis sp. n.	C. fidelis sp. n.	C. calceola	C. galeata
C. saotomensis sp. n.		0.022	0.014	0.110
<i>C. fidelis</i> sp. n.	0.082		0.013	0.106
C. calceola	0.088	0.104		0.102
C. galeata	0.148	0.165	0.166	

Table 2. Uncorrected pairwise distances among groups, COI (lower half of matrix) and H3 (upper half of matrix).

Systematics

Subclass Cirripedia Burmeister, 1834 Superorder Thoracica Darwin, 1854 Order Sessilia Lamarck, 1818 Suborder Balanomorpha Pilsbry, 1916 Superfamily Balanoidea Leach, 1817 Family Archaeobalanidae Newman & Ross, 1976 Genus *Conopea* Say, 1822

Conopea saotomensis sp. n. urn:lsid:zoobank.org:act:1164CCD8-C9F3-46E2-BBB9-1F6411123DA7 http://species-id.net/wiki/Conopea_saotomensis Figures 2–5, Table 3

Type material. Holotype: CASIZ185253, separated from CASIZ175526, 95% EtOH. Diogo Vaz, São Tomé, Gulf of Guinea, 0°18.89'N, 6°29.39'E, collected by hand/SCUBA, 12–27 m, attached to *Leptogorgia* c.f. *dichotoma*, G. Williams, 29 May 2006. Original label: "S-3", California Academy of Sciences, San Francisco.

Paratypes: CASIZ173189 (4 specimens) and CASIZ174804, Diogo Vaz, São Tomé, Gulf of Guinea (0°18.89'N, 6°29.39'E), collected by hand/SCUBA, 9–26 m, R. Van Syoc, 29 May 2006; CASIZ 173190 (3 specimens), 174805 (4 specimens), 174806 (2 specimens), and 175526 (7 specimens), Diogo Vaz, São Tomé, Gulf of Guinea (0°18.89'N, 6°29.39'E), collected by hand/SCUBA, 12–27 m, G. Williams, 29 May 2006; CASIZ178655 (2 specimens) and CASIZ178656 (2 specimens), Il-heu BomBom, Príncipe, Gulf of Guinea (1°42'8.8"N, 7°24'14"E), collected by hand/SCUBA, 11 m, R. Van Syoc, 24 Jan 2009.

Description. Exterior of shell with minute bumps, most prominent on parieties. Color variable, white with varying shades of purple concentrated on parietes and basis often at carina side of shell. Radii usually white but can be colored, basis lighter shade of purple to light purplish-red (Fig. 2A–B). Opercular opening round to diamond shaped, small in comparison to shell. Mantle tissue purple near opercular opening. Basis boat shaped (Fig. 2A–B) highly variable depth and length. Basis length of the paratypes 9–21mm. Basis elongated in rostro-carina axis, often deeply indented and/ or warped from growing around axis of gorgonian. Carina convex. Rostrum often elongate. Basis and parieties with longitudinal tubes, alae and radii solid. Tubes of basis hollow near wall plate suture where outgrowths from wall plates articulate, otherwise secondarily filled. Wall plates with small, hollow tubes close to external plate surface. Sutural margins denticulated. Shell strong, not disarticulating in sodium hypochlorite solution.

Scutum (Fig. 3A–D) with fairly straight tergal and occludent margins, occludent margin may be concave. Basal margin curved. Apex acute. Articular ridge about ²/₃ length of tergal margin. Articular furrow present. Adductor ridge absent. Depressor muscle pit deep, medium to large in diameter. Adductor muscle pit shallow. Interior surface of articular ridge and above adductor muscle pit rough with small flat ridges, remainder of interior surface smooth. Interior and exterior of tergum white with varying degrees of purple coloration, most often dark purple, concentrated at apex.

Tergum (Fig. 3E–H) with concave scutal and convex carinal margins, basal margin slightly convex or straight. Apex acute. Basiscutal angle shallow upper corner recessed. Spur smooth, broad, corners rounded approximately ½ to ¼ width of tergum. Spur margin bearing 3–5 small teeth. Length of spur teeth variable. Spur furrow open. Articular ridge low ¼ to ½ length of scutal margin. Articular furrow shallow. Depressor muscle crests faint. Interior surface rough with multiple low longitudinal ridges. Coloration matches that of scutum.

Labrum (Fig. 4A) with deep medial notch, 0–3 teeth on both or one side of notch.

Mandibular palp (Fig. 4B) elongate; superior margin convex, partially covered with long setae; apex with long setae; inferior margin with many shorter setae (Fig. 3).

Mandible (Fig. 4C) with 4–5 teeth excluding inferior angle, decreasing in size, tooth 1 largest, well separated from tooth 2, 2 separated from 3 by smaller distance, teeth 3–5 smallest and closest together, teeth 2–5 may be bidentate. Inferior margin densely setose near angle, superior margin and cutting margin below teeth sparsely setose.



Figure 2. *Conopea saotomensis* sp. n., **A** whole shell (CASIZ174804) **B** whole shell attached to gorgonian axis (CASIZ174806). Scale bar = 2 mm.



Figure 3. *Conopea saotomensis* sp. n. Opercular plates. **A** scutum exterior (CASIZ175526) **B** scutum interior (CASIZ178655) **C** scutum interior (CASIZ175526) **D** scutum interior (CASIZ174804) **E** tergum exterior (CASIZ175526) **F** tergum interior (CASIZ178655) **G** tergum interior (CASIZ175526) **H** tergum interior (CASIZ174804). Scale bar = 200μm.

Table 3. Cirral formula for C. saotomensis sp. n. (CASIZ 175526; 174805; 178655)

Cirrus	Ι	II	III	IV	V	VI
Anterior ramus	15-18	13–16	11–13	17–25	27	21-27
Posterior ramus	10-17	11–13	9–12	21–25	22–28	24–29

Maxilla I (Fig. 4D–E) with 7–10 large thick spines, either evenly distributed or concentrated on $\frac{2}{3}$ of the cutting margin near superior margin, remaining cutting margin covered in short fine setae. Many fine short setae along inferior margin near cutting margin and a few fine setae along superior margin near cutting margin.

Maxilla II (Fig. 4F) small, oblong, bi-lobed, covered in long fine setae.

Cirrus I (Fig. 5A) with tapered rami, unequal in length, anterior ramus usually ¹/₃ longer, posterior ramus more distinct segmentation, setae fine, simple, moderately dense.



Figure 4. *Conopea saotomensis* sp. n. Mouth parts. **A** labrum (CASIZ174805) **B** mandibular palp (CA-SIZ174805) **C** mandible (CASIZ174805) **D** maxilla I (CASIZ173190) **E** maxilla I (CASIZ175526) **F** maxilla II (CASIZ178655). Scale bar = 200μm.

Cirrus II (Fig. 5B) rami thick, not tapered, unequal in length but less so than CI, anterior ramus longer, setae simple and dense, segmentation distinct, annulated.

Cirrus III (Fig. 5C) rami thick, slightly tapered, disparate in length, anterior ramus longer, setae simple, dense, thicker than CI or CII, segmentation distinct, annulated.

Cirrus IV (Fig. 5D) rami long, tapered, similar length, segments 1–20, end segment varies, with small spines at base of inferior setae, setae simple, superior setae short, sparse, inferior setae long, dense (Fig. 5E).

Cirrus V (Fig. 5F) rami long, tapered, similar length, setae simple, superior setae short, sparse, inferior setae long, dense

Cirrus VI (Fig. 5G) rami long, tapered, similar length, setae simple, superior setae short, sparse, inferior setae long, dense.

All cirral setae simple.

Penis long, covered in sparse fine setae, large basidorsal point (Fig. 5H), tuft of setae distally (Fig. 5I).

Etymology. *Conopea saotomensis* sp. n. is named after the island from which it was first collected, São Tomé.

Distribution. *Conopea saotomensis* sp. n. is known from São Tomé and Príncipe at depths ranging from 5–34 m living on species of *Leptogorgia* and *Eunicella*.

Remarks. Conopea saotomensis sp. n. differs from Conopea calceola by the following: distance between scutal depressor muscle pit and articular furrow is wider in *C.* saotomensis sp. n. than in *C. calceola*; angle between tergal spur and basal margin is smaller in *C. saotomensis* sp. n. than in *C. calceola*; in *C. saotomensis* sp. n. large spines on cutting edge of maxilla span ²/₃ or entire length, span entire length in *C. calceola*.



Figure 5. *Conopea saotomensis* sp. n. Cirri and penis. **A** CI (CASIZ174805) **B** CII (CASIZ174805) **C** CIII (CASIZ174805) **D** CIV (CASIZ174805) **E** CIV spines (CASIZ175526) **F** CV (CASIZ174805) **G** CVI (CASIZ174805) **H** penis basidorsal point (CASIZ175526) **I** penis tip (CASIZ175526). Scale bar = 200 μm.

Conopea fidelis sp. n.

urn:lsid:zoobank.org:act:252522DE-A3D4-4FBA-8EF4-5D4014FED8CD http://species-id.net/wiki/Conopea_fidelis Figures 6–9, Table 4

Type material. Holotype: CASIZ185252, separated from CASIZ174322, 95% EtOH. Ponta Baleia, São Tomé, Gulf of Guinea, 0°2.13'N, 6°33.51'E, collected by hand/SCUBA, 24 m, attached to *Muriceopsis tuberculata*, R. Van Syoc, 30 May 2006. Original label: "RVS – 539, S-6, 30 May 2006, Sao Tome" [handwritten label], California Academy of Sciences, San Francisco.

Paratypes: CASIZ174803 (2 specimens), Diogo Vaz, São Tomé, Gulf of Guinea (0°18.89'N, 6°29.39'E), collected by hand/SCUBA, 9–26 m, R. Van Syoc, 29 May 2006; CASIZ174322 (14 specimens), Ponta Baleia, São Tomé, Gulf of Guinea (0°2.13'N, 6°33.51'E), collected by hand/SCUBA, 24 m, R.Van Syoc, 30 May 2006;



Figure 6. *Conopea fidelis* sp. n. **A** whole shell (CASIZ174322A) **B** whole shell attached to gorgonian axis (CASIZ174322B). Scale bar = 2 mm.



Figure 7. *Conopea fidelis* sp. n. Opercular plates. **A** scutum exterior (CASIZ174803) **B** scutum interior (CASIZ174322) **C** scutum interior (CASIZ178651) **D** scutum interior (CASIZ174803) **E** tergum exterior (CASIZ174803) **F** tergum interior (CASIZ174322) **G** tergum interior (CASIZ174803). Scale bar = 200μm.

CASIZ178651 (2 specimens), Pedra da Gale, Príncipe, Gulf of Guinea (1°43'30.1"N, 7°22'51.5"E), collected by hand/SCUBA, 30 m, R.Van Syoc, 20 Jan 2009.

Description. Exterior of shell covered in very small bumps; color variable, white with pink or light purple on parietes and basis, radii usually white or lighter in color, rostrum often white (Fig. 6A–B). Opercular opening round to diamond shaped, small compared to shell size. Mantle tissue purple near opercular opening. Basis boat shaped (Fig. 6A–B), highly variable depth and length. Basis length of paratypes 14–32 mm. Basis elongated in rostro-carina axis, often deeply indented and/or warped from growing around axis of gorgonian. Carina convex. Rostrum often elongate. Basis with radiating longitudinal tubes, secondarily filled, hollow near wall plate suture. Wall plates with small longitudinal tubes near external surface of shell. Alae and radii lacking tubes. Sutural margins denticulated. Shell wall compartments strongly fused, not disarticulating in sodium hypochlorite solution.

Scutum (Fig. 7A–D) with straight to mildly convex tergal margin, occludent margin usually straight, occasionally with curve above basioccludent angle. Basal margin



Figure 8. *Conopea fidelis* sp. n. Mouth parts. **A**: labrum (CASIZ174322) **B** mandibular palp (CASIZ174803) **C** mandible (CASIZ174322) **D** maxilla I (CASIZ174322) **E** maxilla II (CASIZ174322). Scale bar = 200μm.

Table 4. Cirral formula for Conopea fidelis sp. n. (CASIZ 178651; 174803A; 174322F)

Cirrus	Ι	II	III	IV	V	VI
Anterior ramus	14-17	11-12	11-12	19–21	23–24	23–25
Posterior ramus	9-11	9–10	10-11	21-22	24–26	23–26

variable, sinuous. Apex subacute. Articular ridge prominent, extending ²/₃– ³/₄ length of scutum. Articular furrow present. Adductor ridge absent. Adductor muscle pit shallow, fairly large. Depressor muscle pit large, deep, broad, may converge with basil margin. Majority of interior surface of scutum smooth, articular ridge and apex with low, flat ridges. Interior and exterior white with varying shades of purple coloration concentrated at apex.

Tergum (Fig. 7E–G) scutal and carinal margins curved. Basal margin straight or slightly curved. Apex acute. Basicutal angle shallow, upper corner recessed. Spur broad, bears no teeth, about ½ to ¼ width of tergum, spur furrow open. Articular ridge ¼ to ½ length of tergum. Articular furrow shallow. Depressor muscle crests faint. Interior rough with multiple small ridges. Coloration matches that of scutum.

Labrum (Fig. 8A) with deep notch, 0-3 teeth on both or one side of notch.

Mandibular palp (Fig. 8B) slightly convex oval shape, superior margin with curved ridge and sparse fine long setae, inferior margin with dense shorter setae.

Mandible (Fig. 8C) with 4–6 teeth excluding inferior angle, decreasing in size, tooth 1 largest, well separated from tooth 2, 2 separated from 3 by smaller distance, teeth 3-6 smallest and closest together, teeth 1 and 2 may be bidentate, 4 and 5 may be bifurcated. Inferior margin densely setose near angle, superior margin and cutting margin below teeth sparsely setose.



Figure 9. *Conopea fidelis* sp. n. Cirri and penis. **A** CI (CASIZ178651) **B** CII (CASIZ178651) **C** CIII (CASIZ178651) **D** CIV (CASIZ178651) **E** CIV spines (CASIZ178651) **F** CV (CASIZ178651) **G** VI (CASIZ178651) **H** penis basidorsal point (CASIZ174803) **I** penis tip (CASIZ174322). Scale bar = 200μm.

Maxilla I (Fig. 8D) with 10–12 large thick spines, many smaller, thinner spines along cutting margin, short setae below margin, dense setae on anterior margin, posterior margin sparsely setose, may have shallow notch.

Maxilla II (Fig. 8E) small, oval shaped, bi-lobed, covered in long, fine setae.

Cirrus I (Fig. 9A) rami densely setose, tapered and unequal in length, anterior rami about ¹/₃ longer, posterior rami with more annulated segmentation.

Cirrus II (Fig. 9B) rami slightly unequal in length, width thick, segmentation distinct, annulated, thick dense setae.

Cirrus III (Fig. 9C) rami unequal in length but less so than CI, anterior ramus longer, width thick, dense thick setae, segmentation distinct, annulated.

Cirrus IV (Fig. 9D) rami long, tapered, anterior side with long dense setae and small spines at base of setae (Fig. 9E) extending from first to twentieth segment (end segment variable), posterior side with short sparse setae at segment divisions.

Cirrus V (Fig. 9F) rami long with long dense setae on anterior side and short sparse setae at segment divisions on posterior side, about equal in length.

Cirrus VI (Fig. 9G) rami long with long dense setae on anterior side, short sparse setae only at segment divisions of posterior side, similar length.

All cirral setae simple.

Penis long with large basidorsal point (Fig. 9H), covered in short very sparse setae, tuft of setae distally (Fig. 9I).

Etymology. *Conopea fidelis* sp. n. is named so because it is found to be faithful to one host species of gorgonian, *Muriceopsis tuberculata*. From the Latin fidelis: faithful or true.

Distribution. *Conopea fidelis* sp. n. is known from São Tomé and Príncipe at depths ranging from 5–34 m and is found living on the gorgonian *Muriceopsis tuberculata*.

Remarks. Morphological differences between *Conopea fidelis* sp. n. and *Conopea calceola* are as follows: *C. fidelis* sp. n. does not have tergal spur teeth, *C. calceola* does; scutal depressor muscle pit may converge with basal margin in *C. fidelis* sp. n., it does not in *C. calceola*; *C. fidelis* sp. n. maximum basis length is longer than that of *C. calceola*.

Morphological differences between *Conopea saotomensis* sp. n. and *Conopea fidelis* sp. n. are as follows: *C. saotomensis* sp. n. shell color ranges from light purple to light purplish-red, *C. fidelis* sp. n. shell color ranges from light purple to pink; *C. fidelis* sp. n. basis length maximum is longer than that of *C. saotomensis* sp. n.; length of scutal articular furrow in *C. saotomensis* sp. n. is shorter than *C. fidelis* sp. n.; scutal depressor pit may converge with basal margin in *C. fidelis* sp. n. but not in *C. saotomensis* sp. n.; angle between tergal spur and basal margin is smaller in *C. saotomensis* sp. n. than *C. fidelis* sp. n.; tergal spur teeth present in *C. saotomensis* sp. n., absent in *C. fidelis* sp. n.; *C. saotomensis* sp. n. length of tergal articular ridge is equal or longer to that of *C. fidelis* sp. n.; cutting edge spines of maxilla I span entire margin or just ³/₄ in *C. saotomensis* sp. n. gr. n.; *C. saotomensis* sp. n. does not.

Discussion

COI has been shown to be useful for delimiting species within the Crustacea (Lefébure et al. 2006) and, in particular, within the Cirripedia (Van Syoc 1995, Wares 2001, Rawson et al. 2003). Costa et al. (2007) found within genus COI divergence levels of crustaceans to range from 4.92% to 31.39%. Van Syoc (1994) found COI divergence levels averaging 1.2% among distantly separated sub-populations of *Pollicipes elegans* (Lesson 1831) (Crustacea: Cirripedia: Scalpelliformes). Van Syoc (1995) and Van Syoc et al. (2010) also found a range of 15%–28% among species of *P. elegans, P. polymerus* (Sowerby 1833), and *P.pollicipes* (Gmelin 1790). Regarding barnacles, histone genes have been shown to be highly conserved and can be used for deep metazoan phylogenetic analysis of arthropods (Colgan et al. 1998) and thoracic barnacles (Pérez-Losada et al. 2004). Expected divergence levels of H3 among closely related cirriped species is not

known but Van Syoc et al. (2010) found low levels, 0–1.3%, of sequence divergence between species of *Pollicipes*. The overall difference in divergence between genes, higher for mitochondrial COI and lower for nuclear H3, is expected as nuclear genes typically evolve slower than mitochondrial genes for arthropods (Avise et al. 1994, Burton and Lee 1994). COI and H3 divergence levels found for *C. saotomensis* and *C. fidelis* are both satisfactory for determining a species within Cirripedia.

The barnacles collected from the Gulf of Guinea for this study were originally identified as *C*. cf. *calceola*. The initial identifications were tentative because *C. calceola* is not well studied, has a reportedly large distribution, the original species description (Ellis 1758) contains sparse morphological data, and Darwin's description of *C. calceola* (used as our reference for morphology) relied on locality for identification. Ellis (1758) designated the type locality of *C. calceola* as the Strait of Gibraltar, which connects the eastern Atlantic Ocean to the Mediterranean Sea. Darwin (1854) recorded the presence of *C. calceola* off the west coast of Africa. For his identification he noted that the original description of *C. calceola*, by Ellis, does not adequately distinguish any morphological characters for positive identification so he relied on locality, the eastern Atlantic. The *C. calceola* specimens from Portugal used in our phylogenetic and morphological analyses match the morphology of the specimens from the coast of Africa that Darwin described as *C. calceola*.

Attempts to obtain specimens of *C. calceola* from other locations/institutions were unsuccessful. Darwin's (1854) description of *C. calceola* was used as the guideline for the species along with the literature of Hoek (1913), (Hiro 1937), and Ren and Liu (1978). Unfortunately, none of these papers state the number of tergal spur teeth and the images are too poor to count them accurately. Therefore, a comparison of number of tergal spur teeth could not be made. But there is a difference between the 7 Portuguese *C. calceola* specimens of this paper and *C. saotomensis* sp. n. *Conopea calceola* was found to have 6–9 tergal spur teeth and *C. saotomensis* sp. n. 3–5.

Gorgonian host preference

Barnacles are found permanently attached to many different types of living and nonliving substrata. Locating a living substratum, especially one that is mobile or spatially rare, can be challenging for a small marine larva. For example; a gorgonian, a turtle, or a whale is harder to locate than a rock bed. When barnacle larvae locate and settle onto a gorgonian they may be recognizing the substratum, the presence of conspecifics, or both. It has been shown that barnacle larvae can determine where to settle by recognizing pheromone cues from their cohorts (Crisp and Meadows 1962, Knight-Jones 1995, Dreanno et al. 2006, 2007) or chemical cues from their host (Pasternak et al. 2004, Nogata and Matsumura 2005). It has also been shown that gorgonians produce barnacle settlement inducers as well as inhibitors (Standing et al. 1983) and prostaglandins that promote hatching (Clare et al. 1985). The inhibitors are water soluble

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and so found in the water near the gorgonian whereas the inducers are found absorbed in the gorgonian tissue.

Although the details of the settling barnacle larvae and gorgonian interaction are not completely known, it appears, from our observations (specifically that *Conopea fidelis* sp. n. was found only on *Muriceopsis tuberculata*) that barnacle larvae may be capable of distinguishing between gorgonian species. Of course, more collections, identifications, and laboratory work testing settlement preference would be needed to answer this question.

Endemism

The possibility that *Conopea saotomensis* sp. n. and *Conopea fidelis* sp. n. are endemic to the Gulf of Guinea Islands is likely for the following reasons: the islands' distance (approx. 274 km), age (approx. 13 and 30 myo), and historic isolation from mainland Africa; they are not known from any previous locality; many endemic species, terrestrial and marine, are found on the Gulf of Guinea islands (Jones 1994, Measey et al. 2007). However, further sampling from the west coast of Africa is essential to determine if they are indeed endemic.

Acknowledgments

The authors would like to thank Robert Drewes (California Academy of Sciences) for initiating and organizing biodiversity research on the Gulf of Guinea Islands; Sarah Cohen (San Francisco State University/RTC) for academic support; Ned Seligman of the Step-Up Foundation for help with collecting permits and making local contacts on the islands; Africa's Eden for lodging in São Tomé and Príncipe and dive operations in Príncipe; Mary Wicksten for specimens of *Conopea galeata*; Christina Piotrowski and Anna Sellas for their help in the Center for Comparative Genomics lab at the California Academy of Sciences; an anonymous referee and D. Jones for their participation as Zookeys reviewers, and editor Niel Bruce (Queensland museum). Molecular lab work was funded by a CCG student start-up grant.

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RESEARCH ARTICLE



A new Vaejovis C.L. Koch, 1836, the second known vorhiesi group species from the Santa Catalina Mountains of Arizona (Scorpiones, Vaejovidae)

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Academic editor: W. Lourenço | Received 13 December 2012 | Accepted 23 January 2013 | Published 18 February 2013

urn:lsid:zoobank.org:pub:FE68D993-194C-4A8C-BF38-DE8ECB6FCC7F

Citation: Ayrey RF, Webber MM (2013) A new *Vaejovis* C.L. Koch, 1836, the second known *vorhiesi* group species from the Santa Catalina Mountains of Arizona (Scorpiones, Vaejovidae). ZooKeys 270: 21–35. doi: 10.3897/zookeys.270.4500

Abstract

A new species of the *vorhiesi* group of *Vaejovis* C.L. Koch, 1836, *Vaejovis brysoni* **sp. n.**, is described from the Santa Catalina Mountains in southern Arizona. *Vaejovis deboerae* Ayrey also inhabits this mountain range, making this the first documented case of two *vorhiesi* group species distributed on the same mountain. When compared to all other *vorhiesi* group species, *Vaejovis brysoni* **sp. n.** is distinct based on several combinations of morphological characters and morphometric ratios.

Keywords

Madrean sky islands, speciation, taxonomy, Vaejovis vorhiesi group

Introduction

For over 50 years, only four species of montane scorpions in the specious genus Vaejovis were known from the topographically complex states of Arizona, New Mexico and Sonora. That number has more than doubled over the past six years, with a total of 13 species now known (see Graham et al. 2012), all belonging to the Vaejovis vorhiesi group (Soleglad and Fet 2008). All 13 species have allopatric distributions in Arizona (Sissom et al. 2012), and no records of co-occurrence have been documented. Interestingly, however, several species are distributed across overlapping ecological communities. For example, Vaejovis jonesi Stahnke (1940) inhabits rocky juniper woodlands on the Colorado Plateau, and Vaejovis lapidicola Stahnke (1940) is distributed across pine-oak woodlands along the southern edge of the Colorado Plateau. These ecological communities overlap across the rim of the Mogollon Plateau, yet to date V. jonesi and V. lapidicola have not been found syntopically. Vaejovis deboerae Ayrey (2009) was recently described from the high pine-oak forests of the Santa Catalina Mountains in southern Arizona. The type series was collected at an elevation of 2142 m. Other records suggest that V. deboerae may range as high as 2800 m and as low as 1520 m (Sissom et al. 2012). This vertical distribution encompasses a gradient of ecological communities, ranging from cold pine forest on the high peaks of the Santa Catalina to drier juniper desert scrub in the lower canyons. Recent collecting in the Santa Catalina along the transition zone between desert grassland and pine-oak forest revealed a distinct second species of V. vorhiesi group scorpion. Here we describe this new species, which represents the first record of two *vorhiesi* group species inhabiting the same mountain range.

Materials and methods

The systematics adhered to in this paper follow the classification established in Fet and Soleglad (2005) and as modified by Soleglad and Fet (2006), Graham and Soleglad (2007), Fet and Soleglad (2007), Soleglad et al. (2007), and Soleglad and Fet (2008). Measurements are as described in Stahnke (1970), trichobothrial patterns are as in Vachon (1974), and pedipalp finger dentition follows Soleglad and Sissom (2001).

Acronyms of depositories — RFA, Richard F. Ayrey; MES, Michael E. Soleglad; USNM, United States National Museum, Smithsonian.

Material – In addition to the type material listed below for the new species, the following additional specimens were examined:

Vaejovis brysoni sp. n. USA: Arizona: Pima Co.: above Molino Basin on Catalina Highway near Seven Cataracts Vista, Santa Catalina Mountains. 32.35796°N 110.72538°W, 1626 m. 16 March 2012. R.W. Bryson Jr. 1 ♂, 7 ♀ (RFA). Same locality. 5 April 2012. R.W. Bryson Jr. & D. Hartman 8 \bigcirc (RFA). Same locality. 18 August 2012. R. F. Ayrey & M. DeBoer-Ayrey. 8 \bigcirc (RFA).

- Vaejovis cashi Graham, 2007. USA: Arizona: Cochise Co.: Cave Creek Canyon, Chiricahua Mountains. 2 August 2008. R. F. Ayrey & M. M. DeBoer-Ayrey 4 ∂, 4 ♀ (RFA). Same locality. 23 August 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 3 ∂, 4 ♀ (RFA).
- Vaejovis crumpi Ayrey et Soleglad, 2011. USA: Arizona: Yavapai Co.: by Lynx Lake, Prescott. 14 August 2008. R. F. Ayrey & M. M. DeBoer-Ayrey 3 ♂, 5 ♀ topotypes (RFA). Same locality. 14 September 2009. R. F. Ayrey & M. M. DeBoer-Ayrey 4 ♂, 4 ♀ (RFA). Same locality. 8 August 2010. R. F. Ayrey & M. M. DeBoer-Ayrey 3 ♂, 5 ♀ (RFA).
- Vaejovis deboerae Ayrey, 2009. USA: Arizona: Pima Co.: Rose Canyon Campground, Santa Catalina Mountains. 28 August 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 3 ♂, 5 ♀ (RFA). Same locality. 29 August 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 4 ♂, 4 ♀ (RFA).
- Vaejovis electrum Hughes, 2011. USA: Arizona: Graham Co.: Upper Arcadia Campground, Mount Graham. 17 July 2009. R. F. Ayrey & M. M. DeBoer-Ayrey 2 ♂, 6 ♀ (RFA). USA: Arizona: Graham Co.: 9415 feet asl, Mt Graham Hwy., Mt. Graham. 18 July 2009. R. F. Ayrey & M. M. DeBoer-Ayrey 1 ♂, 4 ♀ (RFA).
- *Vaejovis feti* Graham, 2007. USA: New Mexico: Meadow Creek, Black Mountains. 6 July 1978. M. H. Muma 4 ♂, 3 ♀ (MES).
- Vaejovis halli Ayrey, 2012. USA: Arizona: Gila Co.: Mount Ord. 11 September 2010.
 R. F. Ayrey & M. M. DeBoer-Ayrey 2 ♂, 6 ♀, paratypes (RFA). Same locality. 2 May 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 3 ♂, 5 ♀, paratypes (RFA).
- Vaejovis jonesi Stahnke, 1940. USA: Arizona: Coconino County: near Wupatki National Monument. 1 April 2011. R. F. Ayrey. 1 ♀ topotype (RFA).
- Vaejovis lapidicola Stahnke, 1940. USA: Arizona: Coconino County: Red Sandstone Quarry, Flagstaff. 1 June 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 1 ♂, 7 ♀ topotypes (RFA).
- Vaejovis paysonensis Soleglad, 1973. USA: Arizona: Coconino County: Control Road, 25 miles East of Payson. 5 July 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 1 ∂, 7 ♀ topotypes (RFA). Same locality. 6 July 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 2 ∂, 6 ♀ topotypes (RFA).
- *Vaejovis tenuipalpus* Sissom et al., 2012. USA: Arizona: Mojave Co.: Getz Peak, Hualapai Mountains. 9 August 2009. R. F. Ayrey & M. M. DeBoer-Ayrey 1 ♂, 7 ♀ paratopotypes (RFA).
- Vaejovis vorhiesi Stahnke, 1940. USA: Arizona: Cochise Co.: Miller Canyon, Huachuca Mountains. 24 May 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 1 ∂, 7
 ♀ topotypes (RFA). Garden Canyon, Huachuca Mountains. 26 August 2011.
 R. F. Ayrey & M. M. DeBoer-Ayrey 4 ∂, 6 ♀ (RFA). Lutz Canyon, Huachuca Mountains. 27 March 2011. R. F. Ayrey & M. M. DeBoer-Ayrey 2 ∂, 2 ♀ (RFA).

Taxonomy

Order Scorpiones C. L. Koch, 1850 Suborder Neoscorpiones Thorell et Lindström, 1885 Infraorder Orthosterni Pocock, 1911 Parvorder Iurida Soleglad et Fet, 2003 Superfamily Chactoidea Pocock, 1893 Family Vaejovidae Thorell, 1876 Subfamily Vaejovinae Thorell, 1876

Vaejovis brysoni sp. n.

urn:lsid:zoobank.org:act:80FC6074-1CD9-4DED-B155-2F7FE348495C http://species-id.net/wiki/Vaejovis_brysoni Figs 1–10, 12; Table 1

Type material. Female holotype. USA: Arizona: Pima Co.: above Molino Basin on Catalina Highway near Seven Cataracts Vista, Santa Catalina Mountains. 32.35796°N, 110.72538°W, 1626 m. 16 March 2012. R.W. Bryson Jr. (RFA specimen number 632, deposited in USNM). Paratypes. Same locality as holotype. 16 March 2012. R.W. Bryson Jr. 1 \Diamond (RFA specimen number 633) 2 \heartsuit (RFA specimen numbers 634 and 635). 17 August 2012. R. F. Ayrey. 1 \heartsuit (RFA specimen number 643).

Etymology. The specific epithet is a patronym honoring our colleague Dr. Robert W. Bryson, Jr., the collector of the holotype.

Diagnosis. Relatively small-bodied scorpion from the Seven Cataracts Overlook area of the Santa Catalina Mountains, southern Arizona (total body length of the female holotype is 27.50 mm). Color is light to medium brown, light brown to yellow on the legs, with underlying dark mottling on carapace and mesosoma. Metasoma is light brown with darker carinae.

Significant characters that distinguish *V. brysoni* sp. n. from other known species in the *vorhiesi* group are described below.

Vaejovis jonesi, V. lapidicola, V. paysonensis, V. crumpi, and V. bigelowi all possess 7 inner denticles (*ID*) on the chela movable finger, not 6 as in V. brysoni sp. n.. The new species can be distinguished from V. halli by having significantly larger metasomal segment L/W ratios on I, II, and V (Table 1). Vaejovis brysoni can be distinguished from V. bandido by having larger metasomal segment I L/W ratios in addition to larger fixed finger L/chela L ratios. Vaejovis brysoni sp. n. can be distinguished from V. deboerae by having a smaller and less-developed subaculear tubercle. Vaejovis brysoni sp. n. also have shorter total body lengths and shorter carapace lengths. In addition, V. deboerae have larger telson vesicle L/W ratios. However, V. brysoni sp. n. have larger metasomal segment I L/W ratios and larger fixed finger L/chela L ratios. Vaejovis brysoni sp. n. also have fewer pectinal teeth than V. deboerae. Vaejovis brysoni sp. n. can be distinguished from V. vorhiesi have larger chela L/W ratios. Vaejovis brysoni sp. n. also have firme from V. vorhiesi have larger chela L/W ratios. Vaejovis brysoni sp. n. also have form V. vorhiesi have larger chela L/W ratios. Vaejovis brysoni sp. n. also have Table 1. Morphometrics (mm) of female V. brysoni sp.n. versus other Vaejovis sorbiesi group species. Data on pectinal teeth with * from (Hughes 2011) and ** from (Sissom et al. 2012). Bold numbers are those which have no overlap with V. brysoni sp. n.

			N.	<i>brysoni</i> Ratio	Comparisons				
Vaejovis spp.	brysoni (8)	bandido (5)	halli (3)	deboerae (3)	vorhiesi (3)	cashi (3)	feti (3)	electrum (3)	tenuipalpus (3)
Total length	22.88-27.50	24.65-27.75	21.87-23.43	29.64-33.14	24.62-26.55	20.90-22.10	22.00-23.46	24.48-25.38	28.38-31.24
Carapace length	2.88-3.75	3.12-3.38	2.90 - 3.18	3.79 - 4.38	3.21-3.39	2.86-3.11	3.01 - 3.19	3.48-3.60	3.52-3.71
Ca L/MetV L	0.88 - 1.03	0.97-0.98	0.98-0.99	0.89-0.97	0.98 - 1.06	0.96 - 1.14	0.96 - 1.05	1.02 - 1.13	0.93-0.98
Segment I length/ width	0.93 - 1.00	0.73-0.78	0.70-0.77	0.72-0.79	0.68-0.73	0.61–0.66	0.69–0.73	0.65–0.68	0.90-0.94
Segment II length/ width	0.90 - 1.03	0.88-0.94	0.79-0.87	0.98-1.03	0.85-0.92	0.74-0.80	0.69–0.73	0.68–0.89	1.09-1.18
Segment III length/width	1.00-1.09	0.96-1.04	0.94-1.00	1.02-1.14	0.96–0.98	0.89-0.92	0.93-1.13	0.93–0.98	1.29–1.36
Segment IV length/width	1.34–1.61	1.35–1.44	1.27–1.50	1.48–1.60	1.39–1.62	1.28-1.39	1.35–1.60	1.33–1.46	1.74-1.83
Segment V length/ width	2.15-2.82	2.02–2.16	1.79–2.11	2.10-2.32	2.08–2.22	2.05–2.15	2.07–2.24	1.81–1.91	2.49–2.52
Telson Vesicle- Length/width	1.60-2.06	1.59–1.69	1.68–1.85	2.22-2.43	1.63–1.72	1.56–1.71	1.62-1.87	1.45–1.62	1.60-1.77
Femurlength/width	2.87-3.22	2.86-3.07	2.83-3.33	2.74-2.90	2.87-3.22	2.74-3.02	2.89–3.41	2.78-3.19	3.81-3.83
Patellalength/width	2.47-3.29	2.83-3.21	2.89-3.63	2.91–3.16	3.12-3.19	2.86-3.03	2.53-2.66	2.86-2.94	3.72-3.85
Chela length/width	3.71-4.55	4.09 - 4.48	4.33-4.79	4.17-4.53	4.57-5.30	3.84-4.52	3.59-3.91	3.74-4.19	5.05-5.43
Ff L/Ca L	0.68 - 0.83	0.65 - 0.69	0.67-0.77	0.71 - 0.77	0.72-0.81	0.68-0.73	0.69 - 0.80	0.68 - 0.69	0.83 - 0.87
FfL/ChL	0.51 - 0.56	0.48-0.49	0.46 - 0.53	0.48-0.52	0.47-0.54	0.47 - 0.49	0.48-0.50	0.47 - 0.51	0.50-0.51
Pectinal	11-12	11-12	11–13	12–13	12-13	10-12	10	11-12	11-12
Teeth	11.5(16)	11.1(10)	11.94(16)	12.17(6)	12.87(339)*	10.98(337)*	10.00(6)	11.75(96)*	$11.15(26)^{**}$



Figure 1. Vaejovis brysoni sp. n., paratype female in natural habitat.

fewer pectinal teeth than V. vorhiesi. Vaejovis brysoni sp. n. can be distinguished from V. cashi by having longer total body lengths, and larger metasomal segment L/W ratios on segments I, II, and III. In addition, V. brysoni sp. n. exhibit larger fixed finger L/ chela L ratios. Vaejovis brysoni sp. n. can be distinguished from V. feti by having larger metasomal segment I and II L/W ratios. Additionally, V. brysoni sp. n. also have larger fixed finger L/chela L ratios than V. feti. Vaejovis brysoni sp. n. can also be distinguished from V. feti by having a higher number of pectinal teeth. Vaejovis brysoni sp. n. can be distinguished from V. feti and V. feti by having a higher number of pectinal teeth. Vaejovis brysoni sp. n. can be distinguished from V. feti and V. In addition, V. brysoni sp. n. also have larger fixed finger L/chela L ratios than V. feti by having larger metasomal segment L/W ratios on segments I, II, III, and V. In addition, V. brysoni sp. n. also have larger fixed finger L/chela L ratios than V. electrum. Finally, Vaejovis brysoni sp. n. can be distinguished from V. tenuipalpus by having smaller metasomal segment L/W ratios on segments II, III, and V. addition smaller metasomal segment L/W ratios on segments I, III, and V. In addition, V. brysoni sp. n. can be distinguished from V. tenuipalpus by having smaller metasomal segment L/W ratios on segments II, III, and V. addition metasomal segment L/W ratios on segments II, III, and V. addition metasomal segment L/W ratios on segments II, III, and V. addition metasomal segment L/W ratios on segments II, III, and V. addition metasomal segment L/W ratios on segments II, III, and V. addition metasomal segment L/W ratios on segments II, III, and IV. Vaejovis tenuipalpus also have larger femur, patella, and chela L/W ratios.

Description of the holotype. Color of the holotype is light to medium brown, light brown to yellow on the legs, with underlying dark mottling on carapace and mesosoma. Metasoma is light brown with darker carinae. Metasomal segments are slightly wider than the vesicle. Small spinoid subaculear tubercle is present (Fig. 1). The pedipalp fixed finger has 5 to 6 ID denticles and movable finger has 6 ID denticles. Carapace: Anterior margin of the carapace is slightly emarginated, the posterior margin is straight. The carapace is moderately granular, with three lateral eyes present on each side. The median furrow is moderate and traverses the entire length of the carapace. The ratio of the location of the median eyes on the carapace (anterior edge/



Figure 2. Vaejovis brysoni sp. n., paratype female dorsal and ventral views.

carapace length 0.73/3.75) = 0.19; carapace length/width at median eyes 3.75/2.35 = 1.60. The carapace is longer than metasomal segment V. Mesosoma: Tergites are moderately granular with vestigial median carina on tergites I–VI. Tergite VII with weak median carina on anterior third and strong dorsal lateral and lateral supramedian granular carinae. Sternites I–V are finely granular and without carinae. Sternite V with weak granular ventral lateral carinae on middle 1/3. Presternites are smooth. Spiracles are ovoid with median side rotated 35 degrees from posterior sternite margin. Sternites with variable number of microsetae. Pectines: Pectinal tooth count is11/12. All pectinal teeth have exterodistal angling with a large sensorial area. Middle lamellae are 6/6. Fulcra are present. Each fulcra with 1–3 central setae. Metasoma: The carapace of the holotype female is longer than the fifth metasomal segment. Ratio of segment I length/width 0.93; of segment II length/width 1.03; of segment III length/width 1.18; of segment IV length/width 1.50; of segment V length/width 2.32. Segments I–IV:



Figure 3. Vaejovis brysoni sp. n., paratype female with first instar juveniles.



Figure 4. Vaejovis brysoni sp. n., paratype male right hemispermatophore.

dorsolateral carinae are strong and granular to slightly dentate, with the distal denticle of I–IV enlarged and spinoid. Lateral supramedian carinae I–IV are strong and crenulate, with enlarged spinoid distal denticle. Lateral inframedian carinae are moderately granular on posterior 4/5 of segment I, 4/5 of II, 1/2 of III, and nearly obsolete on segment IV. Ventrolateral carinae on segment I, II, and III are moderate and granular; on IV moderate, granular and slightly serrate. Ventral submedian carinae are weak on segment I, weak to moderate on II, moderate, granular to slightly serrate on III and



Figures 5–10. *Vaejovis brysoni* sp. n., paratype female carapace **5**; telson **6**; pectines **7**; paratype male pectines and sternites **8**; paratype female metasoma dorsal **9**; and ventral **10**.

IV. The dorsal and lateral intercarinal spaces are very finely granular. Segment I-IV: ventral submedian setae count is 3/3. Segment V: dorsolateral carinae are moderate and slightly serrate on anterior 1/3. Lateromedian carinae are weak to moderate and granular on basal 3/5, and obsolete on distal 2/5. Ventrolateral and ventromedian carinae are strong and crenate to serrate. Intercarinal spaces are finely granular. Ventrolateral setae count 4/4. Telson: Smooth with four pairs of large setae on the ventral surface, three large setae are along both lateral edges of the vesicle with numerous smaller setae. A small spinoid subaculear tubercle is present. Chelicerae: The dorsal edge of movable cheliceral finger with two subdistal (sd) denticles. Ventral edge is smooth, with well developed serrula on distal half. Pedipalps: Trichobothrial pattern type C (Vachon 1974) (Fig. 12). Trichobothria ib and it near base of fixed finger. Pedipalp ratios: chela length/width 4.00; femur length/width 2.69; patella length/width 2.59; fixed finger length/carapace length 0.68. Chela: Carinae are moderate. Fixed and movable finger median denticles (MD) are aligned and divided into 6 subrows by 5 outer denticles (OD) and usually 6 ID denticles. Femur: Dorsal internal and external are moderate and granular; ventral internal granular to crenulate; ventral external are slightly serrate; dorsal and ventral surfaces are covered with fine granules; external surface is smooth. Patella: Internal surface are covered with very strong dentate to serrate granules on the DPSc carina. Dorsal external and internal are moderate and granular. Ventral internal carinae are strong and granular. External surface is rounded with scattered granulation; dorsal and ventral surfaces are covered with minute granules. Legs: Ventral surface of tarsomere II with single median row of spinules terminating distally with one spinule pair.

Variability. Variability of fixed finger ID denticle count was found. For *V. brysoni* sp. n., fixed finger ID denticle counts ranged from 5 (n=3) to 6 (n=5). Variation also existed for female *V. brysoni* sp. n. in the number of pectinal teeth 11/11 (n=2), 11/12 (n=3), 12/11 (n=1), 12/12 (n=2) with a mean of 11.5 for females, and 13/14 for the paratype male (n=1). In addition, there was variation in the number of middle lamellae 5/5 (n=1), 6/6 (n=5), 7/6 (n=1), 7/7 (n=1) and for the paratype male 8/9 (n=1). The right hemispermatophore was extracted from the paratype male. The right hemispermatophore is 3.10 mm in total length, and its lamina is 1.20 mm in length and 0.39 mm in width. The hemispermatophore is lightly sclerotized near the dorsal trough, and possesses a subtle distal crest on the inner distal aspect of the lamina. The lamellar hook is strong and widely bifurcated, and emanates from the dorsal trough. A medium, defined truncal flexure is visible on the external aspect of the trunk/lamina juncture. The male paratype also possesses an area of reduced pigmentation (white patch) on the posterior ¹/₄ of the third sternal plate. (Graham and Bryson 2010).

Mensuration (mm). Female holotype: total length 27.5; carapace length 3.75; mesosoma length 8.13; metasoma length 15.63. Metasoma: segment I length/ width/depth 1.81/1.94/1.38; segment II length/width/depth 2.00/1.94/1.25; segment III length/width/depth 2.06/1.75/1.31; segment IV length/width/depth 2.63/1.75/1.25; segment V length/width/depth 3.63/1.56/1.25. Telson: length 3.50; vesicle length/width/depth 2.25/1.25/1.06; aculeus length 1.25. Pedipalps:



Figure 11. Vaejovis brysoni sp. n. habitat.

total length 10.44; femur length/width 2.69/1.00; patella length/width 2.75/1.06; chela length 5.00; palm length/width/depth 2.44/1.25/1.13; movable finger length 2.69; fixed finger length 2.56. Male paratype: total length 21.1; carapace length 2.75; mesosoma length 5.25; metasoma length 13.1; Metasoma: segment I length/width/depth 1.44/1.81/1.25; segment II length/width/depth 1.56/1.88/1.13; segment III length/width/depth 1.75/1.63/1.19; segment IV length/width/depth 2.38/1.63/1.19; segment V length/width/depth 3.25/2.26/1.13. Telson: length 2.69; vesicle length/width/depth 1.81/1.00/1.00; aculeus length 0.88. Pedipalps: total length 9.5; femur length/width 2.44/0.81; patella length/width 2.63/0.88; chela length 4.44; palm length/width/depth 1.88/1.06/1.06; movable finger length 2.69; fixed finger length 2.56.

Distribution and natural history. *Vaejovis brysoni* sp. n. is known only from the type locality above Molino Basin on the Catalina Highway near the Seven Cataracts Vista, Santa Catalina Mountains, Arizona, USA. The type localities of the 12 described species in the *vorhiesi* group from Arizona and western New Mexico are shown in Figure 13. *Vaejovis brysoni* sp. n. is widely allopatric with *V. halli, V. vorhiesi, V. cashi, V. feti,* and *V. electrum* (Fig. 13). *Vaejovis brysoni* sp. n. and *V. deboerae* both occur within



Figure 12. Vaejovis brysoni sp. n. trichobothrial pattern.

the Santa Catalina Mountains, and their ranges may overlap, perhaps along the midelevation pine-oak woodlands between 1800–1900 m.

The type specimens were found at night using a UV flashlight alongside the Catalina Highway. This area lies within open oak woodland and the transition zone from drier desert grassland to pine-oak woodland (Whittaker and Niering 1965).



Figure 13. Map of Arizona and extreme western New Mexico showing the type localities of 13 of the 14 species in the *Vaejovis vorhiesi* group discussed in this paper, including the new species *Vaejovis brysoni* sp. n. The *V. bandido* type locality is south of Arizona in Sonora, Mexico. Localities are divided into those species exhibiting seven inner denticles (*ID*) on the chelal movable finger (white rectangles with black numbering) and those with primarily six *ID* denticles (black rectangles with white numbering). Seven *IDs*: **1** *V. jonesi* **2** *V. lapidicola* **3** *V. paysonensis* **4** *V. crumpi* and **5** *V. bigelowi*. Six *IDs*: **6** *V. vorhiesi* **7** *V. cashi* **8** *V. feti* **9** *V. deboerae* **10** *V. electrum* **11** *V. tenuipalpus* **12** *V. halli* and **13** *V. brysoni* sp. n.

Several *Pseudouroctonus apacheanus* (Gertsch & Soleglad, 1972) and *Centruroides sculpturatus* Ewing, 1928 were also observed. In August of 2012, three captive female *V. brysoni* were observed with first instar juveniles (Fig. 3). The mean juvenile count was 23.67. The 1st instar orientation on the mother's back was non-random, as is seen with many other species of *Vaejovis* (Hjelle 1974). They were facing anteriorly with the prosoma down and the metasoma raised over the prosoma of the juvenile immediately posterior to them.

Acknowledgments

We would like to thank Dr. Robert W. Bryson Jr. for originally discovering the scorpions, Dr. Matthew R. Graham for valuable comments on earlier versions of this manuscript and two anonymous reviewers.

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RESEARCH ARTICLE



Corroborating molecular species discovery: Four new pine-feeding species of *Chionaspis* (Hemiptera, Diaspididae)

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urn:lsid:zoobank.org:author:7C99F545-4A8B-446C-B7A9-3B56E321B39D

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Academic editor: *R. Blackman* | Received 20 November 2012 | Accepted 19 December 2012 | Published 18 February 2013

urn:lsid:zoobank.org:pub:C0347556-25CF-4D57-A273-85B66D9913C0

Citation: Vea IM, Gwiazdowski RA, Normark BB (2012) Corroborating molecular species discovery: Four new pine-feeding species of *Chionaspis* (Hemiptera, Diaspididae). ZooKeys 270: 37–58. doi: 10.3897/zookeys.270.2910

Abstract

The genus *Chionaspis* (Hemiptera, Diaspididae) includes two North American species of armored scale insects feeding on Pinaceae: *Chionaspis heterophyllae* Cooley, and *C. pinifoliae* (Fitch). Despite the economic impact of conifer-feeding *Chionaspis* on horticulture, the species diversity in this group has only recently been systematically investigated using samples from across the group's geographic and host range. This paper provides morphological recognition characters for four new species that were recently hypothesized to exist on the basis of molecular evidence. The new species, here described, are *Chionaspis brachycephalon* Vea **sp. n.**, *Chionaspis caudata* Vea **sp. n.**, *Chionaspis sonorae* Vea **sp. n.** and *Chionaspis torreyanae* Vea **sp. n.** One of the new species, *C. caudata* Vea, has a gland spine at the apex of the pygidium, between the median lobes, unlike any other species of *Chionaspis*. An identification key to the species of *Chionaspis* feeding on pine in North America is provided.

Keywords

Armored scale insects, Diaspidini, Diaspidinae, cryptic species, endemic, North America, Pinus

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Introduction

The armored scales insects (Hemiptera, Diaspididae) are a group of over 2500 described species of plant parasites (Ben-Dov et al. 2012). Adult females are characterized by a reduced morphology and a sessile habit on plant surfaces (Miller and Davidson 2005). Because armored scale insects are often cryptic in the field and are not susceptible to mass-collecting techniques, they are often overlooked in faunal surveys, and so new species tend to be discovered as agricultural pests (Evans et al. 2009, Wolff and Claps 2010, Dones and Evans 2011). Conventionally, new species of armored scales are discovered based on unique combinations of morphological characters.

However, some shortcomings of conventional morphological species descriptions are their reliance on specimens sampled from a limited number of locations, or hosts, as is often the case when identifying agricultural pests. Such limited sampling may fail to observe a range of intraspecific morphological variation across hosts and geography. More importantly, conventional species descriptions of armored scales are not often corroborated with genetic measures of species boundaries (but see Evans et al. (2009) and Rugman-Jones et al. (2009)). This reliance on morphology alone may obscure the nature of species diversity in armored scales. Some putative species, identified only by molecular markers, may be cryptic species (Bickford et al. 2007) - which show no interspecific morphological variation (Andersen et al. 2010, Gwiazdowski et al. 2011). Because conventional, morphological criteria for species differences may fail to distinguish new species, Gwiazdowski et al. (2011) undertook a molecular study of species diversity of *Chionaspis* collected across North America from 54 species of *Pinus*. Here we report a parallel morphological study of species diversity in this same sample.

Current taxonomy of the genus *Chionaspis* Signoret recognizes two pine-feeding species, *C. heterophyllae* Cooley and *C. pinifoliae* (Fitch). These species are native to North America (Watson 2005), and are considered pests on *Pinus* in forests and ornamental settings (Miller 1996, Miller and Davidson 2005). *Chionaspis pinifoliae* has been recognized as a pest for over 150 years and has been a subject of at least 189 publications. *Chionaspis heterophyllae* has been a subject of at least 55 publications (Veilleux et al. 2011), and together, the two species have been the focus of three PhD dissertations (Nielsen 1970, Shour 1986, Gwiazdowski 2011).

Aspidiotus pinifoliae was first described by Fitch as a pest of pines, "which fixes itself upon the leaves, exhausting them of their juices and then causing them to perish and fall, and the end of the limbs to die when thus defoliated" (Fitch 1956:488). Fitch described the species based on specimens on pine needles that were sent to him from Robert W. Kennicott who collected them in the "yard of S. Francis, Esq. in the city of Springfield" in Illinois. Fitch describes the arrangement of the scale insects on the pine needle as well as their general shape and color, but the pine species was not identified and the scale insects were never prepared and mounted on a slide. Nevertheless, the series of specimens on needles used for the description were found at the New York State Agricultural Society (New York State Museum). This should allow the designation of a lectotype for *C. pinifoliae* (not treated here). The species was subsequently placed

in five different genera (*Mytilaspis pinifoliae*, LeBaron 1872: 83; *Chionaspis pinifoliae*, Comstock 1881: 318; *Leucaspis pinifoliae*, García Mercet 1912: 215; *Chionaspis (Phenacaspis) pinifoliae*, Balachowsky 1930d: 266; *Polyaspis pinifolii*, Lindinger 1935: 140; *Phenacaspis pinifoliae*, Ferris 1937: SI-93.)

Chionaspis pinifoliae heterophyllae was first described by Cooley in 1897 (1897:281-282) from specimens collected in Florida (Cooley 1899). Cooley's original description distinguished this subspecies (which he called a variety) from *Chionaspis pinifoliae* by its smaller body size and more rounded and less conspicuous median lobes (Cooley 1897, Andresen 1957). The differences in these characters were later illustrated, on plate 7, of Cooley's monograph of *Chionaspis* (Cooley 1899). Subsequently, *C. pinifoliae heterophyllae* has undergone two taxonomic changes; the first in rank to full species by the name *Phenacaspis heterophyllae*, (MacGillivray 1921:347), and the second by reassignment to *Chionaspis* as *Chionaspis heterophyllae*, (Borchsenius 1966: 122).

Since 1921 (MacGillivray 1921) taxonomists have only recognized two pine-feeding *Chionaspis* (previously *Phenacaspis*) in North America, but the recent reanalysis of species diversity within this group by Gwiazdowski et al. (2011) indicated the presence of at least 10 closely related species feeding on pine. The methods of Gwiazdowski et al. (2011) used multi-locus genealogical concordance to delimit species. This method is expected to be conservative because it should only detect species boundaries that are old and impermeable enough for monophyly to have evolved at a majority of loci (Neigel and Avise 1986, Hudson and Coyne 2002).

Most of the specimens collected by Gwiazdowski et al. (2011) are morphologically indistinguishable from *C. pinifoliae* or *C. heterophyllae*. The few specimens that could be distinguished from both *C. pinifoliae* and *C. heterophyllae* could be placed in five morphological groups, and these groups would be recognized as species by conventional morphological criteria (Miller and Davidson 2005, Watson 2005). Only one of these four morphological groups was recognized as a species by Gwiazdowski et al. (2011), whereas the other four morphological groups were subsumed within more inclusive undescribed species. All morphological groups are tightly correlated with geography, host affiliation or both (see Gwiazdowski et al. (2011) and species descriptions below).

These results highlight the possibility that even species that are well known, as in the case of pest species, may be more diverse than previously thought (i.e. contain cryptic species). It is not immediately clear how best to assign taxonomic status to cryptic species (but see Cook et al. (2010)), and so here we provide morphological descriptions for four new species of *Chionaspis* which are distinguished in the analyses of Gwiazdowski et al. (2011) as belonging to clearly diverged lineages, and possessing a unique combination of morphological characters distinct from both *C. pinifoliae* and *C. heterophyllae*.

Materials and methods

Field collection and slide mounting of all specimens were accomplished using the protocols described by Gwiazdowski et al. (2011). While some species of *Chionaspis* can show a tissue-specific morphology -- where broodmates developing on different plant tissues (e.g. leaves or bark) have very different morphology (Takagi 1985, Liu et al. 1989) -- specimens from Gwiazdowski et al. (2011) were all collected from the same host tissue: pine needles. Illustrations were made by hand using a camera lucida on a Zeiss 47 46 20-9900 microscope and an Olympus CHBS, and digitally edited with Photoshop CS4 14.0.0. They follow the convention used in scale insect illustration, with each figure displaying the dorsal body surface on the left side and the ventral body surface on the right side. Enlargements of significant features are located around the body. The morphological terminology and measurements in the descriptions below follows the conventions of Miller and Davidson (2005). In brief, abbreviations in the text refer to different pygidial lobes (trullae of Takagi): L1 for the median lobes, L2 for the second pair of lobes, L3 for the third pair of lobes and L4 for the fourth pair of lobes. Formulas are provided for the number of gland spines and microducts present between the pygidial lobes. For example, 1-1-1 indicates 1 gland spine in the first space (between L1 and L2); one in the 2nd space (between L2 and L3); and one in the 3rd space (between L3 and the position where L4 would be). Occasionally, the number of microducts subtending gland spines differs from the number of gland spines, and the microduct formula (microducts subtending gland spines in the 1st-2nd-3rd spaces) is indicated in parentheses. Length measurements are given as ranges with the median value in parentheses. The distance between the median lobes is measured from the medial margins, at the midpoint between base and apex. The species described here correspond to the morphological groups indicated by the letters B, C, D, and E in Figures 2 through 4 from Gwiazdowski et al. (2011). Here, each species name is followed by the corresponding morphogroup letter from Gwiazdowski et al. (2011).

Slide mounted type specimens have been deposited at the National Insect Collection, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (CNIN), the United States National Entomological Collection (Coccoidea collection) at the U.S. National Museum of Natural History (USNM), USA and the University of Massachusetts Insect Collection, Amherst, MA, USA (UMAM). Genomic DNA from all types, as well as lots supplying the type material (additional specimens in-situ on host tissue) from the study of Gwiazdowski et al. (2011), has been deposited at the American Museum of Natural History's Ambrose Monell Cryo Collection (AMCC). The DNA sequences used by Gwiazdowski et al. (2011) comprise three loci: the D2-D3 portion of the large ribosomal subunit rDNA (28S), elongation factor 1-alpha (EF-1a), and a mitochondrial fragment spanning parts of cytochrome C oxidase subunits I and II (COI-COII). Sequences for these three loci, for all type specimens, have been deposited in GenBank (Benson et al. 2012). The repository, associated accession numbers, and locality information for all type material and material with published DNA sequences is provided in the species description and Appendix 1 and 2. The USNM and CNIN do not assign accession numbers to type specimens; types are incorporated within the general Coccoidea collections, and these are arranged alphabetically by family, genus, species. Holotype specimens are prominently marked in red, additionally CNIN paratypes are marked in green.

Taxonomy

Chionaspis brachycephalon Vea, sp. n.

urn:lsid:zoobank.org:act:45770622-189F-47C8-A6B3-369B5BDDF3EB http://species-id.net/wiki/Chionaspis_brachycephalon Figure1

Morphogroup D in Gwiazdowski et al. (2011)

Type material. Type locality: Mexico, Durango state, Navios, 23°53.95'N, 105°2.83'W, on needle of *Pinus cooperi* Blanco, 24 September 2007, R. Gwiazdowski and A. Garcia Arévalo coll.

Type specimen: Holotype adult female, slide-mount in balsam. Original label: "D1765A, Mexico, Durango, Resturante "Los Pinos", Navios, 1.ix.2007, 23°53' 56.9"N, 105°02'49.6"W, R. Gwiazdowski, A. Garcia Arévalo, *Pinus cooperi*", deposited at CNIN.

Paratype: Adult female, slide-mount in balsam. D1765B, same collection data as holotype, deposited at USNM.

Other material examined: Adult female, slide-mount in balsam. Original label "D1718A, Mexico: Mexico, Hwy 95 South of Tres Marias, 1.ix.2007, 19°01'37.5"N, 99°12'35.2"W, R. Gwiazdowski, D. Gernandt, *Pinus pseudostrobus* Lindl.", deposited at UMAM. Adult females on separate slides, D1718C, D and F, same collection data as D1718A, deposited at CNIN.

Diagnosis. *Chionaspis brachycephalon* Vea differs from other *Chionaspis* by the following combination of characters (Table 1): small head, gland spine formula variable from 1-1-1 to 2-2-2 (median: 2-2-2), microduct formula also variable from 2-2-2 to 3-3-4 (median: 3-2-2); numerous marginal gland spines on abdominal segments 3 to 5, absent from abdominal segment 1 and 2; variable number of notches present on all pygidial lobes.

Description. Field characters: All pine-feeding *Chionaspis* discussed here, including *C. heterophyllae* and *C. pinifoliae*, are indistinguishable by eye in the field. The adult female for all species possesses a white oystershell-shaped and slightly convex cover, with the amount of posterior expansion varying according to the diameter of host needles. Body elongate, color varying from yellow when immature to reddish brownish in specimens containing eggs, with lateral protrusion on the anterior abdominal segments. Found on needles.

Slide-mounted adult female (Figure 1), broadest at metathorax, with thoracic segments lobed laterally, prothorax becoming narrower towards the anterior, ending with a pointed head, giving the appearance of a reduced, shrunken head; length of holotype 1.33 mm, range (n= 6) 0.85 - 1.33 mm; maximum width of holotype: 0.63 mm; range (n=6) 0.45 - 0.66 mm.

Pygidium: Lobes. Posterior margin with 3 pairs of definite lobes (L1, L2 and L3), fourth pair (L4) appearing as series of low, sclerotized points; paraphyses absent. L1 separated by space 0.31 - 0.6 (0.4) times width of lobes, with a heavily sclerotized

Features	C. pinifoliae (Fitch)	C. heterophyllae Cooley	C. brachycephalon Vea, sp. n.	<i>C. caudata</i> Vea, sp. n.	<i>C. sonorae</i> Vea, sp. n.	<i>C. torreyanae</i> Vea, sp. n.
Margins of prothorax	slightly convergent towards anterior	slightly convergent towards anterior	sharply convergent towards anterior	slightly convergent towards anterior	slightly convergent towards anterior	slightly convergent towards anterior
Gland spine formula	1-1-1	1-1-1	2-2-2	2-2-1	1-1-1	2-2-2
Microduct formula	1-1-1	1-1-1	3-2-2	2-2-1	1-1-1	2-2-2
Shape of the median lobes (L1)	basally slightly diverging, then parallel sided	diverging throughout	diverging throughout	parallel sided	medial margin parallel sided to mid margin then diverging	basally slightly diverging, then parallel sided
Gland spine between L1	0	0	0	1	0	0
Gland spines on segment 5	1	1	1 – 2 (2)	0	1	1
Gland spines on segment 4	1 – 3	1 – 3	2–5 (4)	1 – 2 (1)	1 – 4 (2)	1 – 2 (2)
Gland spines on segment 3	2-7	2-5	2 - 6 (4)	1 – 7 (4)	4 – 7 (5)	2 - 4 (3)
Submedial macroducts on segment 6	2 – 6 (3)	2-4(3)	4 – 7 (5)	3 - 4 (3)	4 – 5 (5)	3 - 6 (4)
L1 margin	Entire or medial notches	Lateral and medial notches	Medial notches	Entire (rarely notched)	Notches on diverging part of medial margin	Entire (rarely one notch)
L2 margin	Entire	Entire or with a few small notches	Sometimes notched	Medial lobule slightly notched, lateral lobule entire	Entire	Entire
L3	Entire	Inner lobule entire or with a few small notches, outer lobule strongly notched	Inner lobule with minute notches, outer lobule notched and obsolete	Medial lobule entire, lateral lobule recessed, and notched	Entire or with slight notches	Entire

Table 1. Diagnostic morphological characters for six species of pine-feeding Chionaspis.

yoke, lateral and medial margins of L1 diverging from base to apex, medial margin convex with notches towards apex, lateral margin entire; L2 bilobed, smaller than L1, medial lobule larger than lateral, sometimes with notches, lateral lobule minutely notched; L3 bilobed, lateral lobule shorter than medial lobule, with minute notches, in some specimens appearing membranous or obsolete. **Gland spines.** Gland spine formula varying from 1-1-1 to 2-2-2 (2-2-2) (microduct formula varying from 2-2-2 to 3-3-4 (3-2-2)), gland spines projecting beyond L1; with 1 - 2 (2) gland spines on



Figure 1. Chionaspis brachycephalon Vea sp. n., adult female.

abdominal segment 5; without gland spines between L1. **Ducts.** Large macroducts in submedian area of segments 5 and 6 (with 5 – 10 (8) on segment 5 and 4 – 7 (5) on segment 6); in submarginal areas of segment 5 (with 8 – 10 (9)); marginal area of segments 5 to 7 (with 1 on segment 7, 2 on segment 6, 2 – 3 (2) on segment 5); absent on segment 8. Largest macroduct on segment 7 (between L1 and L2) 15 – 17.5 (17.5) µm long. Pygidial microducts always on venter in submarginal areas of segment 5 to 7, with 2 – 4 (2) ducts on segment 5, 1 – 3 (2) ducts on segment 6 and 1 ducts on segment 7; pygidial microduct absent from dorsum. **Pores.** Perivulvar pores with 5 loculi, in 5 groups, 1 median with 9-15 (13) pores, 2 anterolateral with 19 – 33 (23) pores, 2 posterolateral with 19 – 33 (25) pores. **Anal opening.** Located 6.8 – 10.2 (8.4) times length of anal opening from base of median lobes, diameter 15 – 20 (17.5) µm.

Setae. Dorsal setae: 2 setose on L1, 1 setose (15 μ m) between lobules of L2 and L3 lobes. Ventral setae: 1 small on median lobe, 1 marginal at base of each gland spine cluster and 1 in submarginal area of each segment, 2 in submedian area of segment 6, half as long as dorsal setae; 2 pairs of setae in a row anterior to the vulva.

Prepygidium: Gland spines. Near each body margin on segments 3 and 4, absent from segment 1 and 2; with 2 - 6 (4) on segment 3 and 2-5 (4) gland spines on segment 4, all protruding from margin..**Ducts**. Macroducts of 2 sizes; large macroducts in submedian and submarginal areas of abdominal segments 3 and 4. Small macroducts in submedian area of any or all of segments 2 to 4, and in marginal areas from meso- or metathorax to segment 3. Prepygidial microducts present on venter and dorsum from segment 1 to 4, sparsely distributed.

Cephalothorax: Microducts present on venter and dorsum with a slight concentration around thoracic spiracles. Perispiracular pores with 3 loculi, anterior spiracles with 3 – 5 (5) pores, posterior spiracles with 1 – 5 (2) pores. Eyes represented by small sclerotized area, located on body margin at level near anterior clypeolabral shield. Antennae each with 1 long seta and 2 minute setae, distance between antennae 42.5 – 90 (57.5) μ m.

Etymology. The epithet *brachycephalon* is a noun, derived from Greek, meaning "short head", from *brachy-* short + *cephalon* head. The epithet refers to the head shape of this species, which appears smaller than that of other pine-feeding *Chionaspis*.

Chionaspis caudata Vea, sp. n.

urn:lsid:zoobank.org:act:CEE3C93A-372F-40B2-A1E1-B778BC1500F4 http://species-id.net/wiki/Chionaspis_caudata Figure 2

Morphogroup C in Gwiazdowski et al. (2011).

Type material. Type locality: Mexico, Oaxaca state, Oaxaca, 16°11.99'N, 96°31.52'W, on needle of *Pinus patulata longipedunculata* (Loock ex Martínez), 28 August 2007, R. Gwiazdowski and M. Dahlberg coll.



Figure 2. Chionaspis caudata Vea sp. n., adult female.

Type specimens: Holotype adult female, slide-mount in balsam. Original label "D1703D Mexico: Oaxaca, Oaxaca, Hwy 175, 28.viii. 2007, 16°11'59"N, 96°31'30.9"W, R. Gwiazdowski, M. Dahlberg, *Pinus patulata longipedunculata*", deposited at CNIN.

Paratypes: adult female, slide-mount in balsam, D1703A, same information as the holotype, deposited at USNM. Adult female, slide mount in balsam, D1703G, same collection data as the holotype, deposited at USNM. Adult females on separate slides, D1703F, H, I, J, K and L, same information as D1703D, deposited UNAM for all but D1703F, deposited at CNIN.

Other material examined: Adult female, slide mount in balsam. Original label "D1702A, Mexico: Oaxaca, Oaxaca, Hwy 175, 28.iii.2007, 16°10'31.3"N, 96°30'24.2"W, R. Gwiazdowski and M. Dahlberg, *Pinus pseudostrobus oaxacana*", deposited at UMAM. Adult female, slide mount in balsam. Original label "D2275C, Mexico, Xalapa, HWY 131, ~2.6 km N of Atzalan, 15.i.2009, *Pinus chiapensis*"; adult female, slide mount in balsam. Orginal label "D2292C, Mexico, Guerrero, ~30 km, North E of Atoyac de Alvarez along road perpendicular to HWY 200, 20.i.2009, *Pinus chiapensis*"; adult female, slide mount in balsam. D2292D, same collection data as D2292C; adult female, slide mount in balsam. Original label "D2296B. Mexico, Chiapas, ~13.5 km North of Chamula, 24.i.2009, *Pinus chiapensis*"; adult female, slide mount in balsam.

Diagnosis. *Chionaspis caudata* Vea differs from other *Chionaspis* with the following combination of characters (Table 1): median lobes (L1) unyoked, parallelsided, with a single gland spine between them, subtended by a microduct; submedian microducts absent on abdominal segment 7; gland spine absent on abdominal segment 5; head square-shaped, body with an extended thorax relative to other pine-feeding *Chionaspis*.

Description. Field characters: All pine-feeding *Chionaspis* reported here, including *C. heterophyllae* and *C. pinifoliae* are indistinguishable by eye in the field. See the description above for *Chionaspis brachycephalon* Vea.

Slide-mounted adult female (Figure 2), spindle-shaped and elongate, slightly lobed to parallel-sided laterally; length of holotype 1.75 mm, range (n=11) 1.38 – 2.03mm; maximum width of holotype: 0.61 mm; range (n=11) 0.48 – 0.7mm.

Pygidium: Lobes. Posterior margin with 3 pairs of lobes (L1, L2 and L3), fourth pair (L4) appears as series of low, sclerotized points; paraphyses absent. L1 separated by a space 0.6 - 1 (0.73) times width of lobes, without a yoke, lobes completely separated, lateral margins parallel-sided, entire, rarely notched; L2 bilobed, smaller than L1, lobules subequal, inner lobule slightly notched, outer lobule entire; L3 bilobed, medial lobule similar to L2, lateral lobule recessed and serrated. **Gland spines**. Gland spine formula varying from 1-1-1 to 3-3-2 (2-2-1) (microduct formula varying from 1-1-1 to 3-3-1 (2-2-1)), with always 1 gland spine between L1, subtended by 1 microduct; gland spine on segment 5 always absent. Gland spine microduct slender

with a relatively developed collar at apex. Ducts. Large macroducts in submedian area of segments 5 and 6 (with 4 - 6 (6) on segment 5 and 3 - 4 (3) on segment 6); in submarginal areas of segment 5 (with 4 - 8 (7) macroducts); marginal area of segments 5 to 7 (with 1 on segment 7, 2 - 3 (2) on segment 6, 2 - 3 (2) on segment 5); absent on segment 8. Largest macroduct on segment 7 (between L1 and L2) 15 -22.5 (20) µm long. Pygidial microducts always on venter in submarginal areas of segment 5 and 6, with 1 - 2 (2) duct on segment 5 and 2-3 (2) ducts on segment 6, always absent from segment 7; pygidial microducts absent from dorsum. Pores. Perivulvar pores with 5 loculi, in 5 groups, 1 median group with 10 - 15 (13) pores, 2 anterolateral groups with 23 - 27 (25) pores, 2 posterolateral groups with 18 - 27(24) pores. Anal opening. Diameter 15 – 22.5 (17.5) μm, located 6.7 – 11.7 (9.9) times length of anal opening from base of median lobes. Setae. Dorsal setae: 2 setose on L1, 1 spinose between lobules of L2 and L3. Ventral setae: 1 small on L1, 1 marginal at base of each gland spine cluster and 1 submarginal area of each segment, 2 on submedian aerea of segment 6, half as long as dorsal setae; 2 pairs of setae in a row anterior to the vulva.

Prepygidium: Gland spines. Near each body margin from segment 1 or 2 to 4, with 0 - 4 on segment 1, 0 - 5 (4) on segment 2, 1 - 7 (4) on segment 3 and 1 - 2 (1) gland spines on segment 4, which are short and protrude from the margin. Gland spines from segment 1 to 3 are the smallest, and never protrude from the margin. **Ducts.** Macroducts of 2 sizes; largest macroducts in submedian areas of abdominal segments 4 and 3. Small macroducts in submedian area of segments 3 and 4, and in submarginal areas of segments 1 to 4. Prepygidial microducts present on venter from segment 1 to segment 3, in marginal or submarginal areas from head to segments 2 to 3. Prepygidial microducts on dorsum on segments 1 to 4, often in conspicuous clusters submedially.

Cephalothorax: Small macroducts present on last thoracic segment, marginally and submarginally. Microducts present on both surfaces, evenly distributed. Perispiracular pores primarily with 3 loculi, anterior spiracles with 6 - 8 (7) pores, posterior spiracles with 2 - 3 (2) pores. Eyes represented by small sclerotized area, located on body margin at level near anterior clypeolabral shield. Antennae each with 1 long seta. Distance between antennae 122.5 – 375 (135) µm.

Etymology. *Chionaspis caudata* Vea possesses an unusual median gland spine between the median lobes. The epithet *caudata* is a Latin adjective meaning tailed (caudate), derived from *cauda*, tail, and referring to this peculiar feature.

Notes. *Chionaspis caudata* Vea differs from the other species by the rather squareshaped head and noticeably longer body, the presence of a single gland spine subtended by one microduct between the median lobes, and the gland spine formula. The presence of the median gland spine is striking as this feature prevents this species from keying to the genus *Chionaspis* (or indeed any related genus) in available keys to genera; however, the phylogenetic analyses of Gwiazdowski et al. (2011) unambiguously place *C. caudata* Vea within *Chionaspis*.

Chionaspis sonorae Vea, sp. n.

urn:lsid:zoobank.org:act:B04204CC-3A4F-4BC2-9BB3-25A3CAC95C44 http://species-id.net/wiki/Chionaspis_sonorae Figure 3

Morphogroup B in Gwiazdowski et al. (2011)

Type material. Type locality. Mexico, Sonora state, Tecora, 28°22.45'N, 108°56.11'W, on needle of *Pinus engelmannii* Carr, 8 October 2007, R. Gwiazdowski, T.R. Van Devender and A. Lilia Reina coll.

Type specimens: Holotype adult female, slide-mount in balsam. Original label "D1781A, Mexico: Sonora, Yecora, 8.x.2007, 28°22'26.8"N, 108°56'06.3"W, R. Gwiazdowski, T. R. Van Devender, L.Van Devender, *Pinus engelmannii* (Carr.)", deposited at CNIN.

Paratypes: Adult females on separate slides, D1781C and F same collection data as D1781A; D1781C deposited at CNIN and D1781 F deposited at UMAM.

Other material examined: Adult female, original label "D1780A, Mexico, Sonora, West of Yecora, 7.x.2007, 28°21'33.5"N, 109°01'48.3"W, R. Gwiazdowski, T. R. Van Devender, L. Van Devender, Pinus engelmannii (Carr.)", deposited at USNM. Adult females on separate slides, D1780B, C, D, E, F and G, same collection data as D1780A, deposited at UMAM.

Diagnosis. *Chionaspis sonorae* Vea is distinguishable from other *Chionaspis* by the combination of the following characters (Table 1): median lobe shape unusual, broad, medial margins parallel or slightly convergent in basal half, abruptly angled near midpoint, with distal half divergent, serrated; yoke horseshoe-shaped; microducts sparse.

Description. Field characters: All pine-feeding *Chionaspis* reported here, including *C. heterophyllae* and *C. pinifoliae* are indistinguishable by eye in the field. See the description above for *Chionaspis brachycephalon* Vea.

Slide-mounted adult female (Figure 3) spindle-shaped and elongate, lobed laterally and broader posteriorly (broadest at metathorax or abdominal segment 1), length of holotype 1.29 mm, range (n=10) 1.29 - 1.83 mm; maximum width of holotype: 0.59 mm; range (n=10) 0.59 - 0.7 mm.

Pygidium: Lobes. Posterior margin with 3 pairs of definite lobes, fourth pair of lobes appearing as series of low, sclerotized points; paraphyses absent. L1 separated by space 0.3 times width of lobes, with a horseshoe-shaped yoke, lateral margins of lobes divergent, medial margin parallel from the base to midpoint, then diverging in apical half (with notches on diverging part); L2 bilobed, entire, shorter than L1, medial lobule larger; L3 slightly notched on lateral side or entire, bilobed but with outer lobule membranous, subequal or slightly smaller than inner lobule. **Gland spines.** Gland spine formula 1-1-1 (microduct formula 1-1-1), with 1 gland spine near each body margin of abdominal segment 5; without gland spines between L1. **Ducts.** Large macroducts in submedian area of segments 5 and 6 (with 4 - 7 (5) on segment 5 and 4 - 5 (5) on segment 6), in submarginal areas of segment 5 (with 5 - 7 (7)), and in marginal area of seg-



Figure 3. Chionaspis sonorae Vea sp. n., adult female.

ments 5 to 7 (with 1 on segment 7, 2 on segment 6, 2 on segment 5); absent on segment 8. Largest macroduct on segment 7 (between L1 and L2) $15 - 20 (17.5) \mu m$ long. Small macroducts sparse on segment 5 (sometimes 2). Pygidial microducts on venter in submarginal areas of segment 5 to 7, with 0 - 2 (2) ducts on segment 5, 1 - 4 (2) ducts on segment 6 and 1 - 2 (2) ducts on segment 7; pygidial microducts absent from dorsum. **Pores.** Perivulvar pores with 5 loculi, in 5 groups, 1 median with 12 - 24 (15) pores, 2 anterolateral with 24 - 35 (28) pores, 2 posterolateral with 27 - 33 (30) pores. **Anal opening.** Located 7.7 - 16.3 (11) times length of anal opening from base of median lobes, diameter $10 - 17.5 (14.5) \mu m \log$. **Setae.** Dorsal setae: 2 setose on L1, 1 setose (~ 11 µm) between lobules of L2 and L3. Ventral setae: 1 small on L1, 1 marginal at base of each gland spine cluster and 1 on submarginal area of segment, 2 in submedian area of segment 6, half as long as dorsal setae; 2 pairs of setae in a row anterior to the vulva.

Prepygidium: Gland spines. Near each body margin from segment 2 to 4, absent from mesothorax, metathorax and segment 1; 4 - 8 (6) on segment 2, 4 - 7 (5) on segment 3 and 1 - 4 (2) on segment 4. Gland spines on segments 3 and 4 protruding from margin and about same size as those on segment 5. Gland spines on segment 2 the smallest and never protruding from the margin. **Ducts.** Macroducts of 2 sizes; larger macroducts in submedian areas of abdominal segments 4 and 3. Small macroducts in submedian area of any or all of segments 3 and 4, in marginal areas from meso- or metathorax to segment 3. Prepygidial microducts almost absent on both surfaces, with a few on segment 2.

Cephalothorax: Microducts sparse on venter and dorsum, with a slight concentration around posterior thoracic spiracles and head. Perispiracular pores with 3 loculi, anterior spiracles with 5 - 6 (6) pores, posterior spiracles with 1 - 3 (2) pores. Eyes represented by small sclerotized area, located on body margin at level near anterior clypeolabral shield. Antennae each with 1 long seta and 2 minute setae, distance between antennae 60 - 117.5 (80) µm.

Etymology. The epithet *sonorae* is a Latin noun, the genitive form of Sonora, meaning "of Sonora".

Chionaspis torreyanae Vea, sp. n.

urn:lsid:zoobank.org:act:1EF8C3A2-CE72-420E-BE4D-9B07AD27BBA5 http://species-id.net/wiki/Chionaspis_torreyanae Figure 4

Morphogroup E in Gwiazdowski et al. (2011)

Type material. Type location: U.S.A., California, Channel Islands, Santa Rosa Island, 33°59.09'N, 120°1.42'W, on needle of *Pinus torreyana insularis* Schoenherr *et al.*, 23 January 2008, C. Greene coll.

Type specimen: Holotype adult female, slide-mount in balsam. Original label "D2238A, USA: California, Santa Rosa Island, 23.i.2008, 33°59'5.4"N, 120°01'25.4"W, Carolyn Greene, *Pinus torreyana insularis*", deposited at UMAM.



Figure 4. Chionaspis torreyanae Vea sp. n., adult female.

Paratypes: Adult females on separate slides, D2238D, E and G, same information as D2238A, deposited at USNM.

Other material examined: Adult female, slide-mount in balsam, original label "D1557A, USA: California, San Diego, 30.viii.2006, 32°56'27.2"N, 117°15'41.0"W, Rodger Gwiazdowski, *Pinus torreyana*", deposited at UMAM. Adult females on separate slides, D1557D, E, F and G, same collection as D1557A, deposited at UMAM.

Adult female, slide-mount in balsam, original label "D1559A, USA: California, San Diego, 30.iii.2006, 32°55'12.9"N, 117°15'09.9"W, R. Gwiazdowski, *Pinus torrey-ana*', deposited at UMAM. Adult female, D1559C, same collection data as D1559A, deposited at UMAM.

Adult female, slide-mount in balsam, original label "D2235A, USA: California, Santa Rosa Island, 23.i.2008, 33°59'04"N, 120°01'34.9"N, Carolyn Greene, *Pinus torreyana insularis* ", deposited at USNM. DNA: AMCC: 205821. Adult female, slide-mount in balsam, original label "D2236A, USA: California, Santa Rosa Island, 23.i.2008, 33°59'4.9"N, 120°01'35"W, Carolyn Greene, *Pinus torreyana insularis*", deposited at UMAM.

Adult female, slide mount in balsam, original label "D2240A, USA: California, Santa Rosa Island, 33°59'2.3"N, 120° 1'11.7"W", Carolyn Greene, *Pinus torreyana insularis*", deposited at UMAM. Adult females on separate slides, D2240C and D, same collection data as D2240A, deposited at UMAM.

Diagnosis. *Chionaspis torreyanae* Vea differs from other *Chionaspis* with the combination of following characters (Table 1): gland spine formula 2-2-2, microduct formula 2-2-2, other abdominal gland spines usually each subtended by 2 microducts, unnotched pygidial lobes.

Description. Field characters: All pine-feeding *Chionaspis* reported here, including *C. heterophyllae* and *C. pinifoliae* are indistinguishable by eye in the field. See the description above for *Chionaspis brachycephalon* Vea.

Slide-mounted adult female (Figure 4): spindle-shaped and elongate, lobed laterally and broader posteriorly (generally broadest at metathorax), length of holotype 1.55 mm, range (n=16) 1.15 mm – 1.65 mm; maximum width of holotype: 0.65 mm; range (n=16) 0.475 - 0.875 mm, maximum width at metathorax, rarely on first abdominal segment.

Pygidium: Lobes. Posterior margin with 3 pairs of definite lobes (L1, L2 and L3), fourth pair (L4) of lobes appear as series of low, sclerotized points; paraphyses absent. L1 separated by space 0.3 - 1 (0.6) times width of lobes, with a thick, protruding, U-shaped yoke uniting L1, lateral margins of lobes parallel, slightly diverging near apex, medial margin parallel-sided. L1 usually entire (1 minute notch may be present); L2 bilobed, smaller than L1, medial lobule always larger, both lobules entire; L3 bilobed, lateral lobule usually obsolete, or, when present, shorter than medial lobule but about equal in width. **Gland spines.** Gland spine formula 2-2-2 (microduct formula 2-2-2), with 1 short gland spine near each body margin on abdominal segment 5; without gland spines between median lobes. **Ducts.** Large macroducts in submedian area of segments 5 and 6 (with 4 - 6 (5) on segment 5 and 3 - 6 (4) on segment 6); in sub-

marginal areas of segment 5 (with 5 - 8 (6)); in marginal area of segments 5 to 7 (with 2 - 3 (2) on segment 5, 2 on segment 6 and 1 on segment 7); absent on segment 8. Largest macroduct on segment 7 (between L1 and L2) 15 - 22.5 (20) µm long. Pygidial microducts always on venter in submarginal areas of segment 5 to 7, with 1 - 2 (1) duct on segment 5, 2 ducts on segment 6 and 1 duct on segment 7; pygidial microducts absent from dorsum. **Pores.** Perivulvar pores with 5 loculi, in 5 groups, 1 median with 8 - 17 (8) pores, 2 anterolateral with 20 - 27 (23) pores, 2 posterolateral with 17 - 26 (20) pores. **Anal opening.** Located 6.1 - 11.2 (9) times length of anal opening from base of median lobes, diameter 12.5 - 17.5 (15) µm. **Setae.** Dorsal setae: 2 setose on L1, 1 setose (~ 11 m) between lobules of L2 and L3. Ventral setae: 1 small on L1, 1 marginal at base of each gland spine cluster and 1 in submarginal area of each segment, 2 in submedian area of segment 6, small and short; 2 pairs of setae in a row anterior to the vulva.

Prepygidium: Gland spines. Near each body margin from segment 1 or 2 to 4, absent from mesothorax and metathorax; with 0 - 3 (0) on segment 1, 1 - 7 (3) on segment 2, 2 - 4 (3) on segment 3 and 1 - 2 (2) gland spine on segment 4 with 2 microducts extending, short and protruding from margin. Gland spines from segment 1 to 3 the smallest and never protruding from margin. **Ducts.** Macroducts of 2 sizes; largest macroducts in submedian and submarginal areas of abdominal segments 4 and 3. Small macroducts in submedian area of either or both of segments 3 and 4, in marginal areas from meso- or metathorax to segment 3. Prepygidial microducts sparsely present on venter and dorsum from segment 1 to 4.

Cephalothorax: Microducts sparsely present on venter and dorsum. Perispiracular pores primarily with 3 loculi, anterior spiracles with 5 - 8 (6) pores, posterior spiracles with 2 - 5 (3) pores. Eyes represented by small sclerotized area, located on body margin at level near anterior clypeolabral shield. Antennae each with 1 long seta and 2 shorter setae, distance between two antennae 65 - 135 (85) µm.

Etymology. The epithet *torreyanae* is a Latin noun, genitive case, meaning "of *tor-reyana*", referring to the pine species *Pinus torreyana*, on which *Chionaspis torreyanae* Vea was collected.

Key to the species of pine feeding Chionaspis in North America:

1	Gland spine present between median lobes; zygosis absent between medial
	lobes (Figure 2) Chionaspis caudata Vea sp. n.
_	Gland spine absent between median lobes; zygosis present between median
	lobes
2	Head reduced, with margins converging rapidly toward anterior end of ceph-
	alothorax; gland spine cluster in 1st, 2nd, and 3rd spaces each with 2 or more
	microducts (Figure 1) Chionaspis brachycephalon Vea sp. n.
_	Head normally developed, rounded; gland spine cluster in 1st, 2nd, and 3rd
	spaces each with 1 or more microducts

3	Gland spine cluster in 1 st , 2 nd and 3 rd spaces each with a single microduct4
_	Gland spine cluster in 1 st , 2 nd and 3 rd spaces each with two microducts (Figure
	4) Chionaspis torreyanae Vea sp. n.
4	Medial margins of median lobes curving abruptly outward near midpoint be-
	tween base and apex: parallel near base and becoming suddenly divergent (and
	slightly notched) in apical half (Figure 3) Chionaspis sonorae Vea sp. n.
_	Medial margins of median lobes not curving abruptly near midpoint: either
	diverging throughout their length, or parallel for most of their length and
	slightly diverging near apex
5	Space between median lobes, at midpoint between base and apex, > 1.5 width
	of median lobe; median lobes usually continually diverging throughout their
	length Chionaspis heterophyllae Cooley
_	Space between median lobes, at midpoint between base and apex, < 1.5 width
	of median lobe; median lobes usually parallel for much of their length

Discussion

Chionaspis caudata Vea and a modified diagnosis of the genus Chionaspis

The gland spine located between the median lobes of *Chionaspis caudata* Vea is unique among the species of *Chionaspis*. Takagi (1985), in his description of the genus, describes the median lobes as "united together in a basal zygosis". If considering this character, conventional taxonomy would not place *C. caudata* Vea in *Chionaspis*, even though this species also possesses a suite of morphological features consistent with the genus, such as the relative position of perivulvar pores, macroducts and gland spines on the pygidium and other abdominal segments. Ferris's (1937) key to North American diaspidids, still the most useful resource for the Mexican fauna, is utterly confounded by *C. caudata* Vea (it comes closest to the genus *Pseudoparlatoria* Cockerell, which has pair of conjoined gland spines between the median lobes). The phylogenetic results from Gwiazdowski et al. (2011) unambiguously place *C. caudata* Vea within the pine-feeding *Chionaspis* species complex, and the genus *Chionaspis*. Mexico is an undersampled region where specimens have only been collected recently, and these recent collections indicate that the genus *Chionaspis* is more variable than previously thought, especially regarding variation concerning key characters involving the pygidial median lobes.

Morphogroup A and other yet-undescribed species

Gwiazdowski et al. (2011) mentioned a fifth novel morphogroup, Morphogroup A, which we have not described here. Although this group of specimens (from *Pinus cembroides* in the state of Queretaro) at first appeared to have a distinctive morphology, we

found it challenging to write a key that could consistently discriminate it from *Chionaspis pinifoliae*, so we have conservatively omitted to describe it here. The molecular evidence of Gwiazdowski et al. (2011) suggests that several additional species of pinefeeding *Chionaspis* remain undescribed.

Acknowledgments

For help with specimen collection we thank A. G. Arévalo, M. Dahlberg, D. Gernandt, C. Greene, R. Greig, J. Rull, T. R. Van Devender and A. L. Reina-G.

For logistical support we thank the Applied Entomology Group of Martin R. Aluja and Juan Rull of the Instituto de Ecología, The Gernandt lab at Universidad Nacional Autónoma de Mexico, the Ecology and Natural resource unit of the Instituto de Ecología from both Durango and Veracruz as well as Dug Miller of the USDA Systematic Entomology Lab in Beltsville, MD. For technical assistance with slide-mounting and cataloguing specimens we thank Erica Fitzpatrick, Alice Trei, and Hedda Monaghan. For comments on a previous version of this manuscript, we thank Dug Miller.

This work was supported by the National Institute for Food and Agriculture (AFRI 2009-02310), the US Department of Agriculture, and the Massachusetts Agricultural Experiment Station, under project number MAS 000941. Funding for cataloguing the specimens and data-sharing was provided by NSF (EF-1115191). Funding for RAG was provided by the National Science Foundation (DEB-0447880 and DEB-0118718) and the University of Massachusetts Natural History Collections.

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Appendix I

Voucher information for all type specimens. (doi: 10.3897/zookeys.270.2910.app1) File format: Microsoft Word document (doc).

Explanation note: Voucher information for all type specimens; each specimen has several kinds of vouchered material. Specimens are conventionally slidemounted in balsam, and each is associated with extracted, whole genomic DNA. Additionally type lots from which the specimens have been drawn are preserved as in-situ frozen tissue associated with host plant tissue, and some specimens have DNA sequence data vouchered in GenBank. The Sample ID number directly corresponds to Sample ID number in Appendix 2.

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Citation: Vea IM, Gwiazdowski RA, Normark BB (2012) Corroborating molecular species discovery: Four new pine-feeding species of *Chionaspis* (Hemiptera, Diaspididae). ZooKeys 270: 37–58. doi: 10.3897/zooKeys.270.2910.app1

Appendix 2

Locality information for all type specimens. (doi: 10.3897/zookeys.270.2910.app2) File format: Microsoft Word document (doc).

Explanation note: Locality information for all type specimens; the Sample ID number directly corresponds to Sample ID number in Appendix 2. The geodetic system used for all GPS points is WGS 1984.

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Citation: Vea IM, Gwiazdowski RA, Normark BB (2012) Corroborating molecular species discovery: Four new pine-feeding species of *Chionaspis* (Hemiptera, Diaspididae). ZooKeys 270: 37–58. doi: 10.3897/zooKeys.270.2910.app2

RESEARCH ARTICLE



New spider flies from the Neotropical Region (Diptera, Acroceridae) with a key to New World genera

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Academic editor: M. Hauser | Received 11 December 2012 | Accepted 21 January 2013 | Published 18 February 2013

urn:lsid:zoobank.org:pub:96106804-F6BC-4B0A-B759-7A9F2A5AA9F1

Citation: Schlinger EI, Gillung JP, Borkent CJ (2013) New spider flies from the Neotropical Region (Diptera, Acroceridae) with a key to New World genera. ZooKeys 270: 59–93. doi: 10.3897/zookeys.270.4476

Abstract

Two new genera and five new species of spider flies (Diptera: Acroceridae) are described from the Neotropical Region. A new genus of Philopotinae (*Neophilopota brevirostris* Schlinger **gen. et sp. n.**) is described from Mexico, while an unusual new species of *Sphaerops* Philippi, 1865 (Acrocerinae: *S. micella* Schlinger **sp. n.**) is described from Chile. A new Panopinae genus near *Lasia* Wiedemann, 1824 (*Coquena stangei* Schlinger **gen. et sp. n.**), is described from Argentina and two new species of *Pialea* Erichson, 1840 (*P. brunea* Schlinger **sp. n.** and *P. corbiculata* Schlinger **sp. n.**) are described from Venezuela. Each genus is diagnosed and figured, and a key to species provided. The Neotropical fauna presently includes 19 genera, containing approximately 100 species. A key to New World genera is also included.

Keywords

Acrocerinae, Panopinae, Philopotinae, parasitoid, small-headed flies

Introduction

Spiders flies (Diptera, Acroceridae), also known as small-headed flies, are a family of infrequently collected lower brachyceran flies. The sister family is thought to be the Nemestrinidae, and these two families are sometimes united as the Nemestrinoidea, or are considered the sister lineages to the remainder of the Muscomorpha (see further discussion in Woodley et al. 2009). The family is widespread geographically, with species found in all biogeographical regions. Species are very diverse in size, shape and coloration, but they typically present a small head, greatly enlarged lower calypter and swollen abdomen (Schlinger 1981, 1987). Some species feed at flowers, and may be specialized pollinators, as suggested by their long proboscises (often equal to their body length), nectar feeding habits and pollen loads (Borkent and Schlinger 2008a, b). All species with known immature habits are parasitoids of spiders (Schlinger 1981, 1987; Cady et al. 1993; Larrivée and Borkent 2009).

Acroceridae comprise approximately 520 species in 53 genera (Pape et al. 2011; Gillung and Winterton 2011; Winterton 2012; Winterton and Gillung 2012). The family is classified into three extant subfamilies (Panopinae, Acrocerinae, and Philopotinae) based on adult morphology and host preference. Panopinae is considered by some authors as the sister group to the remaining Acroceridae (Schlinger 1987, 2009). However, phylogenetic analyses using DNA sequence data disagree with this subfamilial arrangement, and suggest that Acrocerinae are polyphyletic, due to placement of the Philopotinae in between two groups of Acrocerinae, and Panopinae are instead a derived clade (Winterton et al. 2007).

The Neotropical spider fly fauna includes all three subfamilies and is represented by 19 genera and approximately 100 species. Five philopotine genera are recorded for the Neotropics: *Megalybus* Philippi, 1865 (Chile); *Terphis* Erichson, 1840 (Brazil); *Quasi* Gillung and Winterton, 2011 (Mexico); *Philopota* Wiedemann, 1830, (Neotropical) and the new genus *Neophilopota* gen. n. *Neophilopota* is described here from Mexico and appears closely related to *Philopota*.

Panopinae is the most diverse subfamily, represented by ten genera in the New World. Six of these are endemic to South America - Archipialea Schlinger, 1973; Camposella Cole, 1919; Exetasis Walker, 1852; Lasioides Gil Collado, 1928; Coquena gen. n. Schlinger; Pialea Erichson, 1840; and Pteropexus Macquart, 1846. Coquena is described from Argentina and appears closely related to Lasia, based on head and wing characters. Apelleia Bellardi, 1862 is apparently endemic to Central America, Lasia Wiedemann, 1824 and Ocnaea Erichson, 1840 are distributed from Central to South America, and Eulonchus Gerstaecker, 1856 is restricted to North America.

Acrocerinae is represented in the Neotropical Region by six genera, three of them, *Sphaerops* Philippi, 1865; *Villalus* Cole, 1918; and *Holops* Philippi 1865, are endemic to Chile, while *Pterodontia* Gray, 1832; *Ogcodes* Latreille, 1797; and *Acrocera* Meigen, 1803 are largely cosmopolitan (Cole 1919; Schlinger 1981, 2009). *Sphaerops* is a monotypic genus described by Philippi from Chile. The only included species, *S.*

appendiculata Philippi, is remarkable in its biology. While most acrocerid larvae are internal parasitoids of spiders, larvae of *S. appendiculata* are suggested to be external parasitoids (Schlinger 1987). Winterton et al. (2007) placed *Sphaerops* with *Acrocera* in a clade that is sister to the rest of Acroceridae, while the remaining acrocerine genera sampled were recovered in a second polyphyletic 'acrocerine' clade sister to Panopinae.

In this manuscript we describe two new acrocerid genera (a philopotine and a panopine) and five new species. A complete key to all 21 genera occurring in the New World is provided.

Material and methods

Terminology follows Schlinger (1981) as modified by Cumming and Wood (2009), Gillung and Winterton (2011) and Winterton (2012). Type specimens are deposited in the California Academy of Sciences, San Francisco, CA, USA (CAS), and the National Museum of Natural History, Washington DC, USA (USNM). Specimen images were taken at different focal points using a digital camera and subsequently combined into a serial montage image using Helicon Focus software. All new nomenclatural acts and literature are registered in Zoobank (Pyle and Michel 2008).

Forty-three specimens were examined from the two collections listed above. The specimens were compared to previously published descriptions and figures and did not agree with any described species in the case of *Sphaerops* and *Pialea*, or described genera in the case of the two new genera. The exact label information for primary types is provided, with line breaks indicated with '/' and handwriting in italics. Any inferred label information is in square brackets. Wing measurements were taken as the length from the base of the distal median plate to the wing tip. Body length was recorded as the distance from the anterior margin of the scutum to the posterior margin of abdominal segment VI when viewed dorsally. The holotype was always included in the series of measured specimens. Distribution maps were made using Simplemappr (Shorthouse 2010).

Taxonomy

Key to New World genera of Acroceridae

1	Postpronotal lobes greatly enlarged, meeting or nearly meeting along midline to
	form collar for head; body shape strongly arched (Figs 6, 7) Philopotinae: 3
_	Postpronotal lobes not greatly enlarged, separate along midline; body not
	strongly arched (Figs 3, 13)2
2. (1)	Antenna with flagellum stylate (never longer than head length) (Figs 1, 3);
	tibiae without apical spines (except in <i>Pterodontia</i> , see couplet 12)
	Acrocerinae: 7

_	Antenna with flagellum cylindrical, tapered, or flattened (usually longer than head length) (Fig. 11, 20); tibiae with apical spines Panopinae: 13
3. (1)	Wing venation reduced, M with only one or two branches, and only basal cell (1)
	(br) present (Fig. 10)
_	Wing venation relatively complete, all branches of M present as well as discal
(()	and r ₄₊₅ cells (South America) <i>Megalybus</i> Philippi
4. (3)	Eyes bare
_	Eyes covered with short pile (Fig. 8)6
5. (4)	Pairs of tubercles present on tergites II–IV of abdomen; occiput extended pos-
	teriorly to form an acute ridge (South America) (Fig. 25) Terphis Erichson
-	Abdomen without tubercles; occiput rounded, not extended posteriorly (Gil-
	lung and Winterton 2011: Figs 3–5) (Central America)
	Quasi Gillung and Winterton
6. (4)	Frons well developed, almost twice as long as wide and longer than antennae;
	antennae inserted in the middle of frons; lower facial margin the same width
	in the upper and lateral portions; clypeus longer than antennae (Figs 26, 27)
_	Frons not developed, as long as wide and shorter than antennae; antennae
	inserted in the lower part of frons, closer to mouthparts: lower facial margin
	wider in the upper portion than in lateral portions: clypeus shorter than an-
	tennae (Figs 8 9)
7(2)	Cell m. present and well defined (i.e. Fig. 28)
7.(2)	Cell m clearly absent (Fig. 10) or fusion of m with discal cell indicated by
_	Cell Π_3 clearly absent (Fig. 10), δr , fusion of Π_3 with discar cell indicated by
0 (7)	A standard and an annual half of hand annual to fing (E: 2)
8. (/)	Antennae located on upper hair of nead, usually proximal to froms (Fig. 5)9
-	Antennae located on lower half of head, adjacent to mouthparts
9. (8)	Vein R_{4+5} present as a single, unforked vein originating along anterior margin
	at (or near) apex of cell r_{4+5} (Figs 2, 5); antennae not immediately adjacent to
	ocellar tubercle (rarely immediately adjacent)10
_	Vein R_{4+5} originating at apex of basal cell r_{4+5} and then forking into veins R_4
	and R_5 (i.e. Fig. 36); antennae always located on head immediately adjacent
	to ocellar tubercle
10. (9)	Eyes sparsely pilose, setae barely evident; wing veins A_1 and CuA_2 either sepa-
	rate (Fig. 2) or fusing near wing margin (Fig. 5); flagellum with minute termi-
	nal seta; genitalic capsule relatively enlarged and bulbous; body dark (Chile)
	Sphaerops Philippi
_	Eyes densely pilose; A, not joined to CuA,, either incomplete, or open to
	wing margin (Fig. 37); flagellum with relatively large terminal seta; genitalic
	capsule not enlarged or bulbous; body orange (Chile)
11. (9)	Wing with single medial vein; at most two wing cells present (br and bm):
(-)	alula well developed (Schlinger 1981: figs 17–20) (Cosmopolitan)
	Acrocera Meioen

-	Wing with three medial veins originating from discal cell; four wing cells pre- sent; alula reduced (Schlinger 1981: figs 21–22) (Nearctic and Caribbean)
12. (8)	Tibial spines present; mouthparts present (Cosmopolitan); wing with at least
	four closed cells (Fig. 29) Pterodontia Gray
_	Tibial spines absent, mouthparts absent, buccal cavity closed; wing with at
	most two closed wing cells (Winterton 2012: fig. 3C) (Cosmopolitan)
13. (2)	Pulvilli and empodium present (i.e. Cumming and Wood 2009: fig. 49);
	flagellum shape variable14
_	Pulvilli and empodium absent; flagellum extremely large and paddle-like
	(South America, known only from male)Camposella Cole
14. (13)	Mouthparts longer than head
_	Mouthparts shorter than head
15. (14)	Wing costal margin abruptly bent distally so that wing apex is truncated (i.e.,
	Schlinger 1981: fig. 15) (South America) Pteropexus Macquart
_	Wing costal margin uniform and continuous with rounded apex (i.e. Fig.
	15)
16. (15)	Eyes contiguous below the antennae; palp present; alula absent (Nearctic)
	<i>Eulonchus</i> Gerstaecker
_	Eves separated below the antennae (i.e. Fig. 26); palp absent; alula present
	(Neotropical and Nearctic)
17. (16)	Antenna elongate, tapered cylinder, not strongly flattened; ocellar tubercle
	rarely raised (New World)
_	Antenna strongly flattened laterally and paddle-like (i.e. Figs 11, 12); ocellar
	tubercle prominent (South America)
18. (14)	Scapes exhibiting total (Fig. 30) or partial (Fig. 31) fusion (South America).
~ /	<i>Pialea</i> Erichson
_	Scapes separate
19. (18)	Ocellar tubercle strongly raised (twice as high as wide), shaped like a crown
	(Fig. 13) (South America)
_	Ocellar tubercle not strongly raised
20. (19)	Antennae inserted adjacent to ocellar tubercle (Neotropical and Nearctic) 21
_	Antennae inserted between the middle of frons and mouthparts (Central
	America)
21. (20)	Eves bare (Central America)
_	Eves pilose (i.e. Figs 30, 31)
22. (21)	Vein R. absent (South America)
_	Vein R, present (i.e. Fig. 19) (Neotropical and Nearctic)
23. (22)	Eves widely separated above antennae (Cole 1919: fig. 12a); ocellar tubercle
()	raised (Neotropical and Nearctic)
_	Eves narrowly separated above antennae: ocellar tubercle at most slightly
	raised (Chile)
	, .,

New Acroceridae from the Neotropical Region

Subfamily Acrocerinae Zetterstedt, 1837

Sphaerops Philippi, 1865

http://species-id.net/wiki/Sphaerops

Diagnosis. Body shape not arched; coloration non-metallic. Head width slightly less than thorax width; nearly spherical in shape; ocellar tubercle raised and rounded with three ocelli; postocular ridge and occiput rounded; posterior margin of eye rounded; eye sparsely pilose with minute setae (not more than 4× length of single ommatidium); eyes either contiguous above antennal base or with antennal base adjacent to dorsal eye margin, contiguous below antennal base; palpus absent; proboscis length greatly reduced with sparse pile; antennae located near or adjacent to ocellar tubercle; flagellum stylate, apex with terminal seta(e); scapes not fused together; postpronotal lobes not enlarged or contiguous medially; antepronotum narrow; subscutellum enlarged; legs not elongated; tibial spines absent; pulvilli present; wing markings and microtrichia absent. Costal vein ending near wing apex; costal margin straight; humeral crossvein absent; R₁ inflated at pterostigma; radial veins straight, veins R₄ and R₅ present as single fused vein; crossvein 2r-m present between M_1 and R_{4+5} , bisecting cell r_{4+5} , basal portion of cell narrow elongate; two M veins present, not reaching wing margin; discal cell closed; cell m₃ absent; CuA₁ joining M₃; anal lobe well developed; alula well developed. Abdomen greatly rounded, inflated, tergites smooth.

Comments. Sphaerops is an endemic Chilean genus than can be readily differentiated from all other acrocerine genera based on the sparsely pilose eyes, wing vein A_1 fused to CuA_2 and the bulbous genitalia. Sphaerops is also unique in exhibiting the widest range in size variation within acrocerids. The genus shows remarkable similarity to the Chilean endemic genus Villalus, sharing numerous characteristics such as having the antennae placed away from the ocellar tubercle (except in *S. micella*) and vein R_{4+5} present as a single, unforked, vein. Evert I. Schlinger has reared numerous Sphaerops individuals and reported that the mature larvae fed externally on spiders for up to three weeks. This type of development is unique as all other acrocerids with known larval habits are endoparasitoids until emerging to pupate (Schlinger 1987).

Key to species of Sphaerops

Sphaerops micella Schlinger, sp. n.

urn:lsid:zoobank.org:act:32AB0AE4-47D5-42C9-9BCC-2AC1CB4B281A http://species-id.net/wiki/Sphaerops_micella Figs 1, 2, 24

Material examined. Holotype male: Top label: "CHILE, **Region III, Copiapó Prov** / 125 km SE Copiapó; Fundo La / Semilla; malaise on alluvium nr river; / 30.x-9.xi.2003; ME Irwin; FD Parker / 2358 m; 28°15.04'S, 69°44.46'W". Bottom label: red "HOLO-TYPE &/ Sphaerops micella/ Schlinger new species/ Det. E.I. Schlinger 2012" (CAS).

Paratypes. All from Chile and bearing yellow paratype labels. Some with genitalia dissected and placed in glycerin in microvial on pin with specimen. Same data as holotype (4 ♂, CAS); Same except: 2 km E Puente La Semilla: 119 km SE Copiapó; malaise nr wash with water; 11–17.x.2003; ME Irwin; 2082 m; 28°12.90'S, 69°45.66'W (1 ♂, CAS); Quillota Province; Palma de Ocoa; Parque Nacional Campanas; malaise in hillside draw; 215 m; 29.xii.1999; ME Irwin, EI Schlinger; 32.9324°S, 71.0781°W (EI Schlinger #010913; 1 ♂, CAS); same except: 2–10.i.2000 (EI Schlinger #013443-013449; 7 ♂, CAS); Region VI, Limarí Prov. Frey Jorge Nat'l Park, Quebrada Honda I; malaise in small wash; 15–31.x.2003; ME Irwin, FD Parker; 122 m; 30°41.4'S, 71°37.8'W (8 ♂); same except: 1–7.xi.2003 (ME Irwin #174749-174752, #174754-174756; 6 ♂, 1?, CAS); same except: El Mineral, malaise in wash upstream of seep, 23.xi–12.xii.2003; ME Irwin, FD Parker; 224 m; 30°39.44'S, 71°39.90'W (2 ♂, CAS).

Diagnosis. This species is much smaller than *S. appendiculata* (1.9 mm versus 6.3 mm) and has shorter pile on the thorax and abdomen. It is also unique in having the antennae placed immediately adjacent to the ocellar tubercle, the wing veins pale yellow, and wing veins CuA_2 and A_1 remaining separate.

Description. Male with small body length: $1.9 \pm 0.6 \text{ mm} (1.4-2.4 \text{ mm}, n = 10)$ and wing just longer than body: $2.2 \pm 0.5 \text{ mm} (1.7 - 2.5 \text{ mm}, n = 10)$ setae covering body and legs is fine and short (Fig. 1). Female unknown. *Head.* Eye dark brown, occiput black, covered with pale yellow pile; ocellar tubercle black; ocelli white, frons dark brown, antennae light brown and placed on mediodorsal eye margin, face dark brown with pale yellow pile, clypeus light brown, bare and shorter than the antennae, mouthparts yellow and strongly reduced. *Thorax.* Uniformly dark brown with covering pale yellow setae; coxae light brown, femora light brown with apex yellow, tibia light brown with basal third yellow , tarsi light brown, basal and apical tarsomeres longer than middle tarsomeres, lower calypter translucent white and covered with pale yellow setae, halter pale yellow. *Wing.* (Fig. 2) All wing veins pale yellow except costa, subcosta and R₁ pale brown, tergite III with posteriomedial portion yellow, tergites IV-VI medially yellow, sternites brown.

Comments. Based on an examination of the voucher specimens of *Sphaerops* sequenced by Winterton et al. (2007) these were representatives of *S. micella* sp. n. not



Figure 1. Sphaerops micella Schlinger sp. n., male paratype, lateral view. Scale bar = 1.0 mm.



Figure 2. *Sphaerops micella* Schlinger sp. n., wing. Scale bar = 1.0 mm.

S. appendiculata as reported. Therefore the taxon associated with Genbank accession numbers AY140877, AF539875, AY144436, and AY144403 will be changed to *S. micella* sp. n.

Etymology. The species epithet is derived from the Latin: *micella* (diminutive feminine) meaning; little, crumb, or small, in reference to the minute size of this species relative to *S. appendiculata*.

Sphaerops appendiculata Philippi, 1865

http://species-id.net/wiki/Sphaerops_appendiculata Figs 3–5, 24

Material examined. CHILE; Santiago Prov.; 3 km N. El Arrayan; 7.ix.1966; 1150 m; 33°21'S, 70°28'W; EI Schlinger, ME Irwin. [reared from Sequestriidae (Araneae), remains of spider host pinned with specimen], (EIS # 2951, 2952 (host); 1 ♂, CAS); [Chile] Santiago, 15.xi.[19]39, Stuardo (EIS # 2974; 1 ♂, CAS); [Chile] El Canalo, 15.x.1933; Stuardo (EIS # 2978; 1 ♂, CAS).

Diagnosis. Pile covering body and legs is much longer and denser than in *S. micella* **sp. n.** (Fig. 3). Antennae are inserted on the head near but not immediately adjacent to the ocellar tubercle. This species is also much larger (6.3 vs 1.9 mm), has brown rather than yellow wing veins, and the wing veins CuA, and A, join near the wing margin.

Description. Male with medium body size: (Fig. 3) $6.3 \pm 1.2 \text{ mm} (5.8 - 7.0 \text{ mm}, n = 3)$ and wing shorter than the body: $5.9 \pm 1.4 \text{ mm} (5.1 - 6.4 \text{ mm}, n = 3)$. *Head.* (Fig. 4) Eye dark brown, occiput and ocellar tubercle dark brown, covered with pale yellow pile; ocelli light brown, frons dark brown and strongly reduced, antennae light brown, face dark brown with pale yellow pile, clypeus dark brown, bare and as long as scape and pedicel combined, mouthparts yellow and strongly reduced. *Thorax.* Uniformly dark brown with dense covering pale yellow pile; coxae dark brown, femora, tibia and tarsi light brown, basal tarsomere longer than remaining tarsomeres, lower calypter pale yellow with light brown margin and covered with dense pale yellow pile, halter yellow. *Wing.* (Fig. 5) All wing veins brown. *Abdomen.* Tergites dark brown, sternites dark brown with posterior margin yellow.

Subfamily Philopotinae Schiner, 1868

Neophilopota Schlinger, gen. n.

urn:lsid:zoobank.org:act:793E27B2-FC10-4CE5-AAD2-F60E07C81901 http://species-id.net/wiki/Neophilopota Figs 6–10

Type species. *Neophilopota brevirostris* sp. n., by present designation.

Diagnosis. Neophilopota gen. n. is an endemic Mexican genus similar to Quasi, Oligoneura and Philopota. It can be easily distinguished from the Central American genus Quasi as Neophilopota has pilose eyes and well developed mouthparts (forming an elongate proboscis). It shows greater similarity to both the Palearctic Oligoneura



Figure 3. Sphaerops appendiculata Philippi, 1865, male, lateral view. Scale bar = 1.0 mm.

and the Neotropical *Philopota* in having elongate mouthparts and the ocellar tubercle poorly developed. It is easily distinguished from *Philopota* by having the frons as long as wide (though shorter than the antennae), the insertion of the antennae on the lower part of the frons, the lower facial margin wider in the upper portion than in lateral portions, and the clypeus shorter than the antennae. It can be readily differentiated from *Oligoneura* by the absence of the palpi, the presence of pile on the frons, the insertion of antennae on the lower portion of the head, the clypeus being shorter than the antennae and the legs greatly elongated. *Neophilopota* was referred to as 'New Genus A' in the *Manual of Central American Diptera* (Schlinger 2009).

Description. Body shape arched (Fig. 6); coloration non-metallic. Head width slightly smaller than thorax width (Fig. 7); nearly spherical; ocellar tubercle slightly raised, rounded with three ocelli (Fig. 8); postocular ridge and occiput extended posteriorly into acute ridge; posterior margin of eye rounded; eye sparsely pilose; eyes contiguous above antennal base; not contiguous below; palpus absent; proboscis length subequal to or slightly greater than head length; without pile, or setae barely evident; antennae located nearer to mouthparts (Figs 8, 9); flagellum stylate; apex lacking terminal setae; scapes not fused together; postpronotal lobes enlarged, medially contiguous forming a collar; antepronotum narrow; subscutellum enlarged; legs greatly elongated; tibial spines absent; pulvilli present; wing markings and microtrichia absent (Fig. 10); costa ending near wing apex; costal margin straight; humeral crossvein present; radial



Figure 4. Sphaerops appendiculata Philippi, 1865, male, anterior view. Scale bar = 1.0 mm.



Figure 5. Sphaerops appendiculata Philippi, 1865, wing. Scale bar = 1.0 mm.

veins straight, R_1 not inflated distally; veins R_4 and R_5 present as single vein; crossvein 2r-m absent; two M veins present, not reaching wing margin; discal cell open distally; cell m_3 absent; CuA₁ reduced, not reaching wing margin; CuA₂ reduced; anal lobe



Figure 6. Neophilopota brevirostris Schlinger sp. n., male holotype, lateral view. Scale bar = 2.0 mm.

well developed; alula well developed; abdomen conical, tapering towards apex; tergites smooth, rounded.

Included species. Neophilopota brevirostris sp. n.

Etymology. The prefix of the genus epithet (*neo*) is derived from the Latin for "new", referring to this being a new genus. The suffix, *-philopota*, is used in reference to *Neophilopota*'s similarity to *Philopota*.

Neophilopota brevirostris Schlinger, sp. n. urn:lsid:zoobank.org:act:4305FC9E-7691-433D-9737-40F322F8C2CB http://species-id.net/wiki/Neophilopota_brevirostris Figs 6–10, 24

Material examined. Holotype male: Top label "Fortin de las / Flores, Ver., / Mex.". "Doyen and / Foster Collec.". "USNM". Middle label bright green "Acroceridae / E.I.



Figure 7. Neophilopota brevirostris Schlinger sp. n., male holotype, dorsal view. Scale bar = 2.0 mm.

Schlinger / Specimen / 004294". Bottom label: red "HOLOTYPE ♂ / Neophilopota/ brevirostris/ Schlinger" (USNM).

Paratype male: "Rio Metlac, MEX. / Fortin de las Flores / Veracruz / VIII-17-1965 / L.R. Gillogly". "E.I. Schlinger / Collection". red label "Genitalia / Dissection No. 78-6-22k. / by E.I. Schlinger". bright green label "Acroceridae / E.I. Schlinger / Specimen / 004293". Bottom label: yellow "Paratype ♂ / Neophilopota / brevirostris / Schlinger" (CAS). Genitalia dissected and placed in glycerin in glass microvial on pin with specimen.

Description. Male with medium body size (male body: 9.5–12.3 (holotype) mm; n = 2) and wing longer than the body (male wing: 10.8–15.1 (holotype) mm; n = 2). *Head.* (Figs 8, 9) Ocellar tubercle brown; antennae brown (Fig. 6), longer than frons; postocular ridge brown, wider than clypeus; face black; clypeus brown, shorter than antennae and bare. *Thorax.* (Fig. 7) Brown with dark brown markings; legs elongate; coxae brown; femora brown with apex light brown; tibia brown; tarsi brown; lower calypter brown with dark brown margin. *Wing.* (Fig. 10) Infuscate, without markings; wing veins brown. *Abdomen.* Tergite I entirely brown; tergites II-VI brown with lateral margin yellow; sternites yellow.

Comments. The proboscis in the holotype is broken (Fig. 6), but in the paratype it is longer than the head height and shorter than the body length.

Etymology. The species epithet is derived from the Latin: *brevis* (short) and *rostris* (beak), in reference to the short length of proboscis in comparison to species of *Philopota*.



Figure 8. Neophilopota brevirostris Schlinger sp. n., head, lateral view. Scale bar = 1.0 mm.



Figure 9. Neophilopota brevirostris Schlinger sp. n., head, frontal view. Scale bar = 1.0 mm.


Figure 10. Neophilopota brevirostris Schlinger sp. n., wing, dorsal view. Scale bar = 1.0 mm.

Subfamily Panopinae Schiner, 1868

Coquena Schlinger, gen. n.

urn:lsid:zoobank.org:act:B51436F7-465D-498C-B56A-2074E2986AF8 http://species-id.net/wiki/Coquena Figs 11–15

Type species. Coquena stangei Schlinger sp. n.

Diagnosis. *Coquena* is a South American genus readily distinguished from other panopine genera by the minute mouthparts, the ocellar tubercle extremely raised and the iridescent body color. It is closely related to the Neotropical genera *Lasioides* and *Pteropexus*, the Nearctic genus *Eulonchus*, and the New World genus *Lasia*, as it shares the same wing venation. However it does not have the elongate proboscis present in these genera. *Coquena* and *Lasioides* are closely related, monotypic, genera. The mouthparts in *Coquena stangei* are strongly reduced, whereas they are elongate in *Lasioides peruanus* Gil Collado, 1928. *Coquena* shares some attributes with *Lasia* such as the presence of an alula and having the eyes separate below the antennae. It also shares several characteristics with *Eulonchus*, principally the extremely raised ocellar tubercle and presence of maxillary palpi.

Description. Body shape not arched (Figs 11, 13); coloration metallic iridescent. Head width slightly narrower than thorax width (Figs 12, 14); hemispherical; ocellar tubercle shape greatly raised and irregularly shaped, 1/4 to 1/2 as high as head; two ocelli, anterior ocellus absent; postocular ridge and occiput rounded; posterior margin of eye rounded; eye densely pilose; eyes not contiguous above antennal base; palpus present; proboscis greatly reduced, without pile, or setae barely evident; antennae located on middle of frons; flagellum elongate, paddle-shaped, much larger in male, apex lacking terminal setae; scapes not fused together; postpronotal lobes not enlarged or contiguous medially; antepronotum narrow; subscutellum barely visible beneath scutellum; legs not elongate; tibial spines present apically; pulvilli present; wing markings and microtrichia absent (Fig. 15); costa circumscribing entire wing margin, costal margin straight; humeral crossvein present; radial veins straight; R₁ not inflated distally; veins R₄ and R₅ present; crossvein 2r-m present between M₁ and R₄₊₅; bisecting cell r₄₊₅; cell formed by 2r-m present, narrow and elongate; M₁, M₂ and M₃



Figure 11. Coquena stangei Schlinger sp. n., male holotype, lateral view. Scale bar = 1.0 mm.

present (M_3 fused with CuA_1), reaching wing margin; discal cell closed completely; cell m_3 present; CuA_1 joining M_3 , and running to margin; CuA_2 fused to A_1 before wing margin and then running to margin; anal lobe well developed; alula well developed; abdomen greatly rounded, inflated, tergites smooth.

Etymology. The genus epithet is derived from the *Coquena* legend of north-western Argentina. *Coquena* was the son of Mother Earth and was portrayed as a short man dressed in a hat and bright colored poncho. The iridescent coloration, hat-like ocellar tubercle and type locality in northwest Argentina of the type species led to the choice of this name for the genus.

Coquena stangei Schlinger, sp. n. urn:lsid:zoobank.org:act:51AC7C00-FAF5-4581-87B1-7D893266698F http://species-id.net/wiki/Coquena_stangei Figs 11–15, 24

Material examined. Holotype male: Top label: "El Solidad, Argentina/ 11 km. W Las Cejas/ Tucuman Prov./ IV-30 to V-13-1967/ L. Stange (malaise)" [26.895318°S,



Figure 12. Coquena stangei Schlinger sp. n., male holotype, anterior view. Scale bar = 1.0 mm.

64.835332°W]. Second label: "Genitalia *IX-10-69*/ Dissection No. 9/ by E.I. Schlinger". Third label: bright green "ACROCERIDAE/ E.I. Schlinger/ Specimen #/ 013435". Bottom label: red "HOLOTYPE *I Coquena stangei*/ Schlinger new species/ Det. E.I. Schlinger 2012" (CAS). Genitalia dissected and placed in glycerin in glass microvial on pin with specimen.

Paratypes. Four females, same data as holotype except: genitalia not dissected; EIS specimen numbers are: 013436, 013437, 013438, 013441; and with yellow paratype labels.

Description. Male holotype with medium body size (Fig. 11): 7.80 mm and wing shorter than body: 7.0 mm. Female with medium body size (Fig. 13): 6.7 ± 1.21 mm (6.0 - 7.5 mm, n= 4) and wing longer than the body: 7.8 ± 1.2 mm (7.0 - 8.5 mm, n= 4). *Head.* Eyes dark brown and densely covered with pale yellow pile (Figs 12, 14), occiput and ocellar tubercle dark brown and covered with yellow pile, ocelli light brown, frons dark brown with region adjacent to antennae yellow, scape and pedicel light brown with apex yellow, pedicel with light brown pile, flagellum light brown, male flagellum length ~2× height of the eye and petal-shaped, female flagellum length ½ the height of the eye and tapering to apex. Face dark brown with yellow pile, cl-ypeus brown, bare and slightly longer than scape and pedicel combined, mouthparts pale yellow and strongly reduced. *Thorax.* Iridescent green and densely covered with long yellow pile. Coxae light brown, femora light brown with apical third yellow, tibia and tarsi light brown. Lower calypter transparent covered with dense yellow pile, halter yellow. *Wing.* Transparent (clear or pale brown), veins brown (Fig. 13). *Abdo*-



Figure 13. Coquena stangei Schlinger sp. n., female paratype, lateral view. Scale bar = 1.0 mm.

men. Tergites iridescent brown densely covered with yellow pile; sternites brown and densely covered with yellow pile.

Etymology. This species is named in honor of Dr. Lionel A. Stange, Florida State Collection of Arthropods, who collected the type series.

Pialea Erichson, 1840

http://species-id.net/wiki/Pialea

Diagnosis. Body shape not arched; coloration non-metallic. Head width much narrower than thorax width; hemispherical; ocellar tubercle shape raised, rounded, two ocelli present, anterior ocellus absent; postocular ridge and occiput rounded; posterior margin of



Figure 14. Coquena stangei Schlinger sp. n., female paratype, anterior view. Scale bar = 1.0 mm.



Figure 15. Coquena stangei Schlinger sp. n., wing. Scale bar = 1.0 mm.

eye rounded; eyes densely pilose; not contiguous above antennal base, rarely contiguous below; palpus absent; proboscis length greatly reduced, with sparse pile; antennae located on middle of frons, either nearer to ocellar tubercle or to mouthparts; flagellum elongate, slightly tapered or paddle-shaped; apex with terminal setae present or absent; scapes fused;

postpronotal lobes not enlarged or contiguous medially; antepronotum narrow; subscutellum barely visible beneath scutellum; legs not elongated; tibial spines present apically; pulvilli present; wing markings and microtrichia absent; costal vein ending near wing apex; costal margin straight; humeral crossvein absent; radial veins straight; R_1 not inflated distally; R_{4+5} originating at apex of basal cell r_{4+5} and then forking into veins R_4 and R_5 (Fig. 36); crossvein 2r-m present between M_1 and R_{4+5} , bisecting cell r_{4+5} ; cell formed by 2r-m narrow, elongate; R_4 without spur vein; M_1 , M_2 and M_3 present (M_3 fused with CuA₁), rarely one M vein or two M veins present, all typically reaching wing margin; discal cell closed; cell m_3 present, CuA₁ joining M_3 and running towards margin; CuA₂ fused to A₁ before wing margin and running towards margin; anal lobe well developed; alula weakly developed; abdomen greatly rounded, inflated; tergites smooth, rounded.

Comments. *Pialea* is a relatively rare South American genus that comprises four species described from Brazil and another one described from Ecuador. The genus was described by Erichson (1840) for his new species *P. lomata* from Brazil. Later, Westwood (1876) named a second species, *P. lutescens*, also from Brazil. Two more species from the Oriental Region were later described in this genus, *P. jardinei* and *P. auripila* (Brunetti 1912), but they were subsequently transferred to *Astomella* Latreille, 1809 and *Astomelloides* Schlinger, 1959, respectively (Schlinger 1956, 1959). Schlinger (1956) revised the genus and described three more species, *P. antiqua*, *P. capitella* and *P. ecuadoriensis. Pialea* is presumably closely related to *Stenopialea* Speiser, 1920 (a South African endemic genus) and *Archipialea* Schlinger, 1973 (Chile) based on antennal and wing characters (Schlinger 1973; Barraclough 1985). *Pialea* are characterized by the fusion of the scapes and the dichoptic eyes (except in *P. capitella*). Species in this genus also show strong sexual dimorphism in the length, insertion and shape of the antennae, the length of the abdomen and the color and maculation of the body.

Key to species of Pialea

1	M, present
_	M, absent
2. (1)	Tibia and first tarsomere of hind leg greatly swollen (Figs 20, 22), twice as
	wide as the second tarsomere; additional r-m crossvein (2r-m) present (Fig.
	23) (W. Venezuela)
_	Tibia and first tarsomere of hind leg not swollen (Figs 16, 35), almost as wide as
	the second tarsomere; additional r-m crossvein (2r-m) absent (Figs 19, 28)3
3. (2)	Ocellar tubercle raised; thorax yellow with two longitudinal black stripes
	(Brazil)
_	Ocellar tubercle not raised; thorax brown, without stripes (Figs 31-34) (Bra-
	zil)
4. (1)	R _{1,3} complete, reaching wing margin (Fig. 36) (Brazil)
	<i>P. lomata</i> Erichson, 1840
_	R _{1,3} incomplete, not reaching wing margin (Fig. 19)
5. (4)	Eyes holoptic below antennae (Brazil)

Pialea brunea Schlinger, sp. n.

urn:lsid:zoobank.org:act:992C5682-3628-4BAC-9E2A-1DD703AD80F7 http://species-id.net/wiki/Pialea_brunea Figs 16–19, 24

Material examined. Holotype female: Top label: "*Venezuela | Páramo | La Negra | Lichy col. |* [vertically on left side] *viii.48*". Bottom label: red "HOLOTYPE Q/ *Pialea brunea*/ Schlinger new species/ Det. E.I. Schlinger 2012" (CAS).

Diagnosis. Antennae inserted in the middle of the head (female, Fig. 17); post pedicel longer than head height (Fig. 18); body entirely brown, without yellow markings; R_{2+3} not reaching wing margin (Fig. 19); M_2 present; first tarsomere of hind leg much longer than the remaining tarsomeres combined.



Figure 16. Pialea brunea Schlinger sp. n., female holotype, lateral view. Scale bar = 1.0 mm.



Figure 17. Pialea brunea Schlinger sp. n., female holotype, anterior view. Scale bar = 1.0 mm.

Description. Female holotype with medium body size (Fig. 16, female body: 9.2 mm) and wing shorter than body (female wing: 8.2 mm). *Head.* Eyes black and densely covered with long (equal to length of scape) brown pile (Fig. 17), occiput and ocellar tubercle dark brown and covered with brown pile, ocelli brown, frons brown, scape and pedicel brown, pedicel with several long setae, flagellum brown and tapering to apex which bears setae (Fig. 18). Face dark brown with brown pile; clypeus dark brown, half the length of the scape and covered with fine setae; mouthparts light brown and strongly reduced. *Thorax.* Uniformly light brown and densely covered with



Figure 18. Pialea brunea Schlinger sp. n., female, head, lateral view. Scale bar = 1.0 mm.



Figure 19. Pialea brunea Schlinger sp. n., wing. Scale bar = 1.0 mm.

long brown pile. Legs brown and densely covered with long brown pile. Lower calypter brown and densely covered with yellow pile; halter light brown. *Wing.* Transparent with light brown wing veins (Fig. 19). R_{2+3} incomplete, not reaching wing margin, M_1 absent, M_2 present. *Abdomen.* Both tergites and sternites uniformly dark brown.

Comments. *Pialea brunea* is closely related to *P. capitella* Schlinger, 1956 and *P. ecuadorensis* Schlinger, 1956, sharing with these species the absence of wing vein M_1 . It differs from *P. capitella* in the eyes being separate below the antennae, and from *P. ecuadorensis* in the overall brown coloration and presence of M_2 .

Etymology. The specific epithet is derived from the Latin, *bruneus* – brown; referring to the distinctive entirely brown coloration of the body, which lacks yellow markings.

Pialea corbiculata Schlinger, sp. n.

urn:lsid:zoobank.org:act:9188FD90-4D9A-430B-A014-BE5D13D604CE http://species-id.net/wiki/Pialea_corbiculata Figs 20–24

Material examined. Holotype male: Top label: "VENEZUELA / Mérida, 3500 m. / Páramo Mucubaji / nr. Laguna Negra". Second label: "29.iv-3.v.81 / Malaise trap / L. Masner / 8115". Third label: bright green "ACROCERIDAE/ E.I. Schlinger/ Specimen #/ 004215". Bottom label: red "HOLOTYPE ⁽³⁾/ Pialea corbiculata/ Schlinger new species/ Det. E.I. Schlinger 2012" (CAS).

Diagnosis. Antennae inserted in the middle of the head (male); post pedicel as long as the head height; head, thorax and scutellum black; legs and abdomen black with yellow markings; hind leg with tibia and first tarsomere swollen (Figs 20, 22), twice as wide as the second tarsomere; additional r-m crossvein (2r-m) present.

Description. Male holotype with medium body size (Fig. 20, male body length: 7.3 mm) and wing longer than body (male wing: 8.6 mm). *Head*. Eyes black and densely covered with dark brown, long (equal to scape length) pile (Fig. 21), occiput and ocellar tubercle dark brown and densely covered with long dark



Figure 20. Pialea corbiculata Schlinger sp. n., male holotype, lateral view. Scale bar = 1.0 mm.



Figure 21. Pialea corbiculata Schlinger sp. n., male holotype, anterior view. Scale bar = 1.0 mm.

brown pile, ocelli light brown, frons dark brown, scape and pedicel dark brown, pedicel with yellow setae, flagellum light brown, lacking apical setae. Male flagellum petal like, length ~2× length of scape and pedicel combined. Face dark brown with brown pile, clypeus dark brown, with light brown pile and shorter than scape, mouthparts dark brown and strongly reduced. *Thorax*. Dark brown and densely covered with long brown pile (Fig. 22). Coxae dark brown, femora yellow with apex of ventral surface brown, tibia yellow with apex brown, tarsi brown, hind leg longer than fore- and mid-leg and with tibia and first tarsomere swollen (twice as wide as mid-leg). Lower calypter brown and densely covered long brown pile, halter brown. *Wing.* Transparent light brown with brown wing veins; M_1 and M_2 present. *Abdomen.* Densely covered with light brown pile (Fig. 22). Tergite I and VI brown, tergites II-V yellow with anterior margin and medial line brown; sternites I and VI brown sternite II–V yellow.

Comments. *Pialea corbiculata* sp. n. is closely related to *P. lutescens* Westwood, 1876 and *P. antiqua* Schlinger, 1956, based on the presence of wing vein M₁. It dif-



Figure 22. Pialea corbiculata Schlinger sp. n., male holotype, dorsal view. Scale bar = 1.0 mm.



Figure 23. Pialea corbiculata Schlinger sp. n., wing. Scale bar = 1.0 mm.



Figure 24. Distribution of *Sphaerops micella* Schlinger sp. n. (black squares), *Sphaerops appendiculata* Philippi, 1865. (red squares), *Neophilopota brevirostris* Schlinger sp. n. (green triangle), *Coquena stangei* Schlinger sp. n. (orange star), *Pialea brunea* Schlinger sp. n. (blue circle) and *Pialea corbiculata* Schlinger sp. n. (green circle).



Figure 25. Terphis nodosa Erichson, 1840, female, lateral view. Scale bar = 1.0 mm.



Figure 26. *Philopota conica* Wiedemann, 1830, female, head, anterior view. Scale bar = 1.0 mm. **clyp** clypeus **fc** face **flg** flagellum **frn** frons **lfm** lower facial margin **oc tr** ocellar triangle **ped** pedicel **pocl r** postocular ridge **scp** scape.



Figure 27. *Philopota conica* Wiedemann, 1830, female, head, lateral view. Scale bar = 1.0 mm. **clyp** clypeus **fc** face **fgl** flagellum **frn** frons **lab** labium **lbr** labrum **lfm** lower facial margin **ped** pedicel **premnt** prementum **pocl r** postocular ridge **scp** scape **vrt** vertex.



Figure 28. Pialea antiqua Schlinger, 1956, female, wing. Scale bar = 1.0 mm.



Figure 29. Pterodontia davisi Paramonov, 1957, female, wing. Scale bar = 1.0 mm.



Figure 30. Pialea lomata Erichson, 1840, head, dorsal view. Scale bar = 0.5 mm



Figure 31. *Pialea antiqua* Schlinger, 1956, head, dorsal view. Scale bar = 0.5 mm.



Figure 32. *Pialea antiqua* Schlinger, 1956, male, lateral view. Scale bar = 1.0 mm.



Figure 33. Pialea antiqua Schlinger, 1956, female, lateral view. Scale bar = 1.0 mm.



Figure 34. Pialea antiqua Schlinger, 1956, male, head, lateral view. Scale bar = 1.0 mm.



Figure 35. *Pialea lomata* Erichson, 1840, male, lateral view. Scale bar = 1.0 mm.



Figure 36. Pialea lomata Erichson, 1840, wing. Scale bar = 1.0 mm.



Figure 37. Villalus chilensis Cole, 1918, wing. Scale bar = 1.0 mm.

fers from those two species by the swollen tibia and first tarsomere of the hind leg and the presence of an additional r-m crossvein (2r-m), which are unique features within *Pialea*.

Etymology. The species epithet, *corbiculata*, is in reference to the swollen hind tibia and tarsi which resemble the pollen collecting corbicula of many bees.

Acknowledgements

Thank you to Shaun L. Winterton for his encouragement and support during the writing of this manuscript as well as his comments on a previous version of this manuscript. We also thank Drs. Norman E. Woodley, Owen Lonsdale and Martin Hauser for their comments and suggestions on a previous version of the manuscript. Thank you to Norman Penny (CAS), and Norman E. Woodley (USNM) for the loan of

specimens. Dr. F. Christian Thompson provided assistance with nomenclatural accounts and bibliographic records. This research was supported by the National Science Foundation (DEB award number 0614213) and the Australian Biological Resource Study (ABRS-209-48). Statements and viewpoints expressed herein do not necessarily reflect the opinion of NSF or ABRS. **Disclosure**: this paper was compiled from notes and specimen determination labels authored by Evert I. Schlinger with the final manuscript prepared by Jessica P. Gillung and Christopher J. Borkent.

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