The Coleopterists Bulletin, 72(2): 219–229. 2018.

BATRISCYDMAENUS PARKER AND OWENS, NEW GENUS, AND CONVERGENT EVOLUTION OF A "REDUCTIVE" ECOMORPH IN SOCIALLY SYMBIOTIC PSELAPHINAE (COLEOPTERA: STAPHYLINIDAE)

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ABSTRACT

We describe a **new genus and new species** of pselaphine rove beetle, *Batriscydmaenus tishechkini* Parker and Owens, from lowland Panamanian rainforest. The new taxon marks a radical departure from the basic pselaphine anatomical groundplan, with a globose body shape and a dramatic reduction of foveae, sulci and striae—features that are considered plesiomorphic in Pselaphinae. This overt simplification of the integument is typical of myrmecophile and termitophile taxa within Pselaphinae. A probable symbiotic lifestyle of members of *Batriscydmaenus* is further implied by their compact antennae and the presence of suberect, spatulate setae covering the dorsum. The convergent evolution of this trend towards character loss in inquilinous pselaphines implies a "reductive" ecomorph, specialized for living inside social insect societies in part by abandoning many cuticular features of free-living pselaphines. *Batriscydmaenus* represents possibly the most extreme manifestation of this ecomorph known to date. Reductive anatomy poses a challenge to taxonomic assignment, but we confirm molecularly that the genus belongs to the tribe Batrisini, using gene fragments amplified from a paratype.

Key Words: taxonomy, myrmecophily, symbiosis, convergence, new species

DOI.org/10.1649/0010-065X-72.2.219
Zoobank.org/urn:lsid:zoobank.org:pub:B45930A3-84BD-4561-874C-361720B70C83

Intense selection pressures within social insect colonies have biased evolutionary occurrences of social parasitism to a select few groups of Coleoptera that are preadapted for colony living (Parker 2016a). Such groups often specialize on colonies in characteristic ways, manifested in the convergent evolution of symbiotic "ecomorphs" that occupy certain niches inside nests. Within the rove beetle subfamily Aleocharinae, convergent evolution of the ant-mimicking "myrmecoid" ecomorph is seen in numerous lineages associated with army ants (Seevers 1965; Kistner and Jacobson 1990; Jacobson and Kistner 1991, 1992; Kistner 1993; Maruyama and Parker 2017). The termite-mimicking "physogastric" ecomorph evolved in multiple termitophile genera (Seevers 1957; Kistner 1979). And the defensive, tear drop-shaped "limuloid" ecomorph is exhibited by numerous taxa associated with both ants or termites (Seevers 1957, 1965; Parker 2016a; Yamamoto *et al.* 2016). In the subfamily Pselaphinae, a further symbiotic ecomorph evolved in a diversity of taxa that display gland-associated trichomes—structures that are typically paired at the dorsal base of the abdomen and mediate chemical communication with hosts (Parker and Grimaldi 2014; Parker 2016a). Convergent evolution of these symbiotic phenotypes is evidence of their adaptive utility in the context of social parasitism. However, convergence presumably also stems from constraints on possible modes of ecological specialization inside colonies. Aleocharines and pselaphines may be capable of evolving only a relatively finite number of solutions to gain footholds in symbiotic niches (Parker 2016a).

Herein, we identify an additional ecomorph of socially parasitic Pselaphinae. During a survey of material collected as part of the IBISCA rainforest biodiversity program in Panama (Didham and Fagan 2003), we discovered a series of a new pselaphine genus and species that is putatively myrmecophilous. The new taxon has a remarkable anatomy that appears to have arisen largely through character loss. When interpreted alongside similar phenotypes of other known inquilinous species, the new taxon exemplifies a "reductive" ecomorph that has evolved convergently numerous times in Pselaphinae. This ecomorph is characterized by a globose body shape, increased glabrosity, and an absence of stereotypical cuticular features in Pselaphinae, including loss of numerous sulci, carinae, and foveae that typically decorate the ectoderm of free-living species in a pattern that is broadly conserved and plesiomorphic within the subfamily (Chandler 2001). This reductive simplification of external anatomy is seen in a diversity of pselaphine lineages associated with both ants and termites (Chandler 2001; Parker 2016a), but the new Panamanian genus appears to mark possibly the most extreme manifestation of this ecomorph so far known, with the largest number of losses of cuticular structures and hence the most overtly "reduced" anatomy.

In this study, we describe the new taxon and place it phylogenetically using molecular data within the tribe Batrisini. Compared to other pselaphine tribes, taxa with the reductive ecomorph appear to have evolved convergently with greatest frequency in Batrisini, including in a new genus from China that is strikingly similar to the new one described in a sister publication in this same issue of The Coleopterists Bulletin (Yin 2018). We discuss the possible adaptive function of the reductive ecomorph for social parasitism and suggest that developmental evolution of this ecomorph may be relatively trivial, via degeneration of processes underlying the various integumental modifications. Simplicity of mechanism may have contributed to the frequency with which the reductive ecomorph has convergently evolved in Pselaphinae.

Materials and Methods

Morphological Description. Specimens were removed from mounts and relaxed for a few hours in an SDS-based buffer with Proteinase K, and then remounted for photography using a Visionary Digital photomicrographic apparatus with Infinity optics and a Canon 60D camera, installed at the American Museum of Natural History, New York. Montage images were constructed from stacks using Helicon Focus. One male paratype was fully digested in DNA extraction buffer (see below), washed, and disarticulated in ethanol before mounting in Gary's Magic Mountant (GMM; a mixture of Canada Balsam and methyl salicylate) for imaging with a Zeiss compound microscope and a Leica SP5 confocal microscope.

In the label data, the symbol "//" is used to separate different data labels attached to the specimens. The terminology used to describe the foveal system follows Park (1942) and Chandler (2001), with "mesosternal" and "metasternal" substituted by "mesoventral" and "metaventral", following Herman (2013).

DNA Extraction, Sequencing, and Phylogenetic Analysis. DNA was extracted according to a protocol described by Parker and Maruyama (2013). Briefly, a whole specimen was immersed without damage in a sodium dodecyl sulphate/Proteinase K extraction buffer (Gilbert *et al.* 2007) for two days, followed by phenol/chloroform extraction of DNA. The specimen was removed and disarticulated for compound and confocal microscopy. Fragments of mitochondrial *16s rRNA* and Cytochrome Oxidase I (COI) and nuclear *28s rRNA* genes were amplified and sequenced using primer sets and methods described by Parker and Grimaldi (2014). Sequence data from the newly described taxon were integrated with a subset of previously published pselaphine sequences spanning a range of tribes and supertribes (Parker and Grimaldi 2014). In addition, new sequences were obtained from a sampling of species belonging to Batrisitae (tribes Batrisini and Amauropini)—the supertribe to which we speculated the new taxon belongs. Sequences are deposited in the National Center for Biotechnology Information (NCBI) database. The 29 taxa, along with NCBI accession numbers and locality data, are provided in Supplemental Table S1 (DOI.org/10.1649/0010-065X-72.2.219s1).

Sequences were aligned with MUSCLE (Edgar 2004) and concatenated with SequenceMatrix (Vaidya *et al.* 2011), giving a final alignment of 2,295 characters. Partitionfinder2 (Lanfear *et al.* 2012) was used to find the optimal partitioning scheme and substitution model under the Bayesian Information Criterion, which produced the following scheme of four partitions: *16s rRNA* (GTR+G); *28s rRNA* (GTR+I+G); COI codon positions 1 and 2 (GTR+I+G); and COI position 3: (GTR+G). In MrBayes 3.2.1 (Ronquist *et al.* 2012), two runs of eight chains searched for two million generations, until the standard deviation of split frequencies dropped below 0.005. The first 25% of trees was discarded as burn-in. The final Bayesian consensus tree was rooted using two species belonging to Faronitae—the earliest diverging pselaphine supertribe (Newton and Thayer 1995; Parker 2016b).

Results

Batriscydmaenus Parker and Owens, new genus

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Type Species. *Batriscydmaenus tishechkini* Parker and Owens, new species, here designated.

Diagnosis. *Batriscydmaenus*, and its single species *B. tishechkini*, can be distinguished from all other Batrisini (and indeed all other Pselaphinae) by the unique character state of anteriorly open pro- and mesocoxal cavities that leave the coxal bases exposed. The following combination of characters also separates *Batriscydmaenus* from other Pselaphinae: antenna lacking distinct club, antennal scape apically notched, entire dorsal surface devoid of sulci and completely afoveate; ventral surface with only gular fovea, possible prepectal or lateral mesoventral foveae, median mesoventral fovea, and metaventral preapical fovea; visible abdominal segments lacking paratergites or any trace of marginal carinae, with tergites smoothly fused dorsoventrally with respective sternites; non-conical procoxa strongly projecting ventrally.

Description. Body length ~1.6 mm (Fig. 1A, B); head, pronotum, and elytral/abdominal body regions all distinctly globular, strongly convex and smoothly rounded (Fig. 1A, B). **Head:** Moderately transverse (Figs. 1A, 2B), ~1.2X wider than long. Widest immediately posterior to eyes (Fig. 2B); smoothly tapering from eyes to neck and lacking abrupt occipital constriction. Vertex smoothly convex, devoid of foveae and sulci, frontal rostrum absent; antenna received subcontiguously by large antennal cavity (Fig. 2A), antennae separated medially by narrow frontal declivity. Eye crescent-shaped, facing somewhat anteriorly (Fig. 2A), positioned on frontolateral surface of head immediately behind antennal cavity (Fig. 2A). Ocular-mandibular carina present (Fig. 2A, arrow). Gular region convexly inflated ventrally, lacking gular sulcus or gular carina; gular fovea present. Antenna (Fig. 2A) 11-segmented, lacking distinct club. Antennal scape with apex dorsally and ventrally notched (Fig. 2B). Maxillary palpus 5-segmented with lateral margin of enlarged palpomere 4 concave from midpoint of palpomere length to apex (Fig. 2B, arrow). Anterior margin of labrum with 4 short, thick setae positioned medially (Fig. 2C, arrow). **Thorax:** Pronotum approximately as wide as head (Fig. 2A), obovate, widest anterior to middle, 1.2X longer than wide, with apical margin 1.2X wider than basal margin. Pronotal lateral margin smoothly rounded and disc smoothly convex, lacking foveae or sulci (Fig. 1A). Prosternum (Fig. 3A) lacking

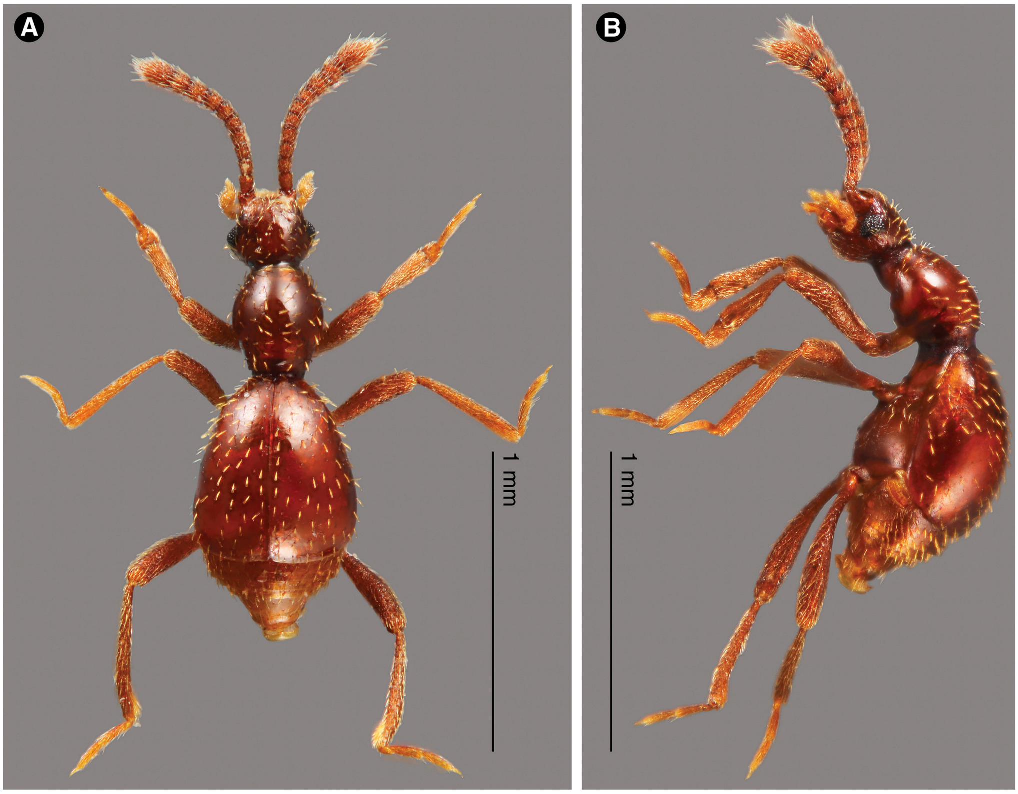

Fig. 1. *Batriscydmaenus tishechkini*, holotype male. A) Dorsal habitus, B) Lateral habitus.

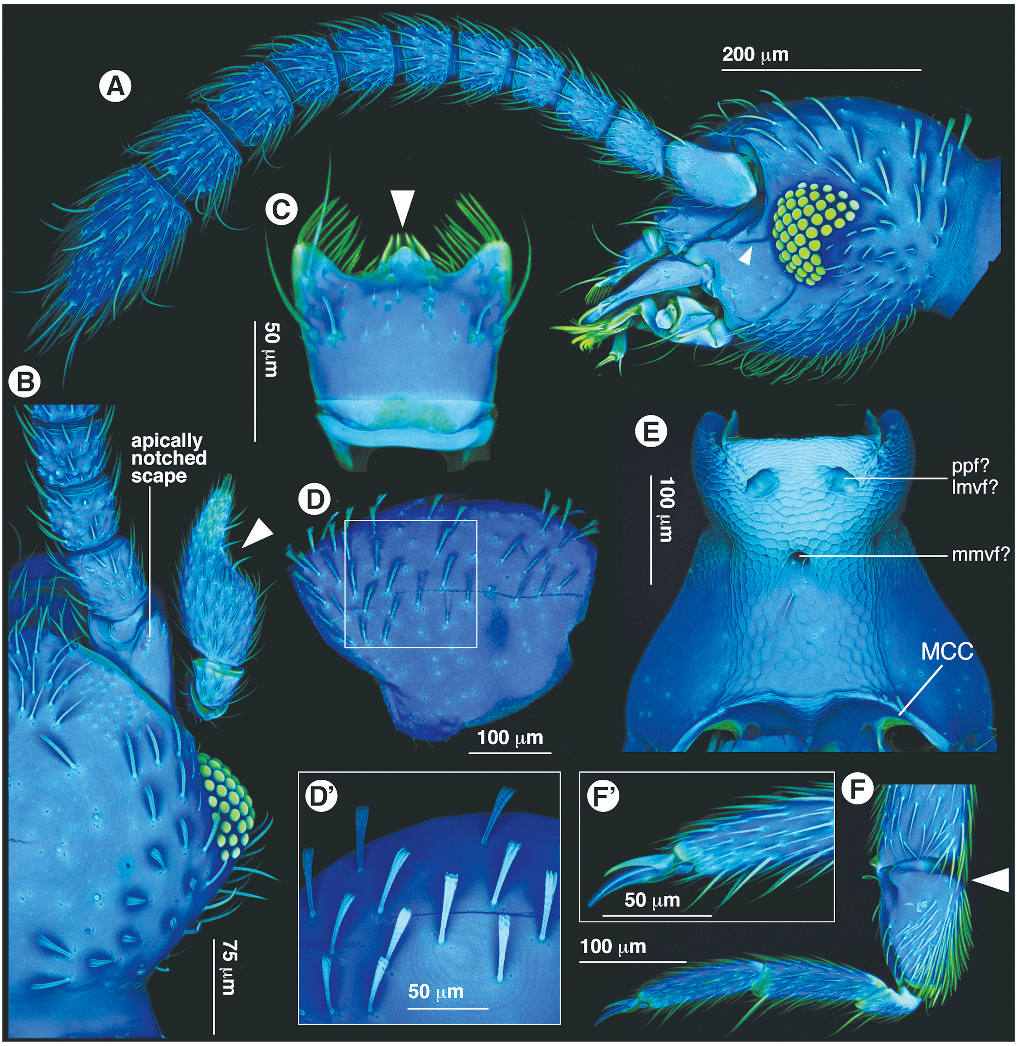

Fig. 2. *Batriscydmaenus tishechkini*, confocal images of male paratype. A) Head, lateral view, arrow indicates ocular-mandibular carina, B) Head, dorsal view, with apically notched scape and laterally notched palpomere 4 (arrow) indicated, C) Labrum with four setae (arrow) on epipharynx, D) Prothorax, lateral view, boxed region enlarged in D' to show spatulate setae; E) Mesoventrite with foveae labeled according to their possible homology to the pselaphine foveation pattern of Chandler (2001): ppf = prepectal fovea; lmvf = lateral mesoventral fovea; mmvf = median mesoventral fovea; MCC = anterior edge of mesocoxal cavity, F) Protarsus (apical tarsomere enlarged in F' to show tarsal claws) and apical protibial region showing transverse sulcus (arrow).

foveae and with a single, large procoxal cavity (Fig. 3A, PCC) with rounded margin; intercoxal process recessed inside PCC, exposing contiguous procoxal bases. Mesoventrite (Fig. 2E) lacking carinate mesoventral plate, and with single mesocoxal cavity (Fig. 2E, MCC) lacking external intercoxal process, such that contiguous mesocoxal base is exposed and visible. Mesothoracic foveae of unclear homology to stereotypical pselaphine foveae in this body region (Chandler 2001): putative prepectal or lateral mesoventral foveae and median mesoventral fovea present (Fig. 3E, ppf?, lmvf?, and mmvf?); all other mesoventral foveae absent. Metaventrite medially inflected to form preapical fovea. **Abdomen:** Short; length with telescoping segments fully contracted ~0.2–0.3X as long as elytron and abruptly tapering to abdominal apex (Fig. 1A, B). All segments lacking paratergites or marginal longitudinal carinae, creating seamless dorsoventral fusion of tergite and sternite. Tergites IV–VIII visible. Tergite IV

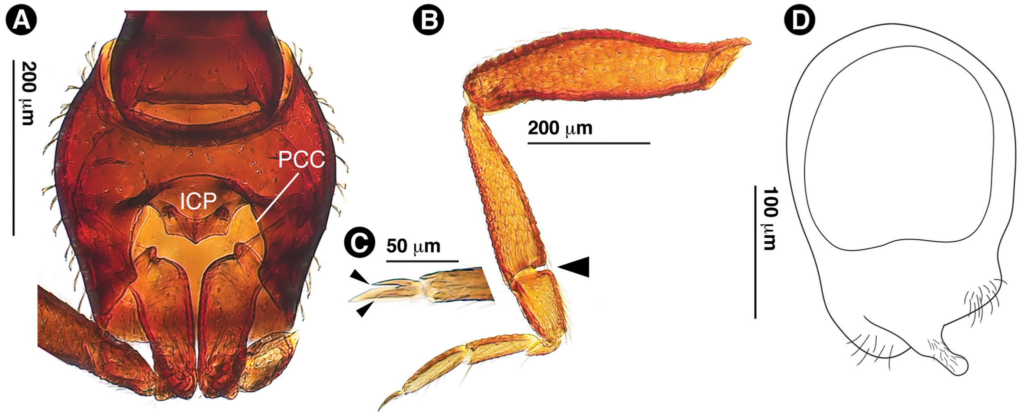

Fig. 3. *Batriscydmaenus tishechkini*, male. A) Prosternum showing single, large procoxal cavity (PCC), with circular margin indicated; the intercoxal process (ICP) is recessed inside the procoxal cavity, B) Foreleg with tibial sulcus (arrow); C) Protarsus with projections of bifid anterior tarsal claw (arrows), D) Aedeagus.

longest, approximately equal in length to following tergites combined. Sternites III–VIII visible: short sternite III visible between metacoxae, with median longitudinal carina along length. Sternites IV–VII subequal in length along midline, sternite IV broadening laterally. All tergites and sternites lacking foveae or sulci. Genital aperture formed from contiguous apical margins of tergite VIII and sternite VIII, with penial plate not externally apparent. **Elytra and flight wings:** Elytra at base as wide as basal margin of pronotum, broadening apically to ~1.8X maximum pronotal width (Fig. 1A). Elytron widest in basal third before narrowing slightly to apex. Elytron 1.5X wider than long, with smoothly rounded, convex apical margin (Fig. 11); lacking fovea, sulci, or striae. Short humeral carina present. Flight wings present. **Legs:** Procoxae contiguous and strongly projecting ventrally (Fig. 12). Mesocoxae contiguous. Metacoxae moderately projecting apically, subcontiguous, separated by narrow intercoxal process of abdominal sternite III. Trochanter short, with minimal separation between coxal apex and femoral base. Femur simple, unmodified. Male protibia with abrupt transverse sulcus at 2/3 length (arrows in Figs. 2F, 3B). Tarsus 3-segmented with short tarsomere 1; tarsomeres 2 and 3 subequal in length (Fig. 2F). Tarsal claws unequal in size (Fig. 2F’), anterior tarsal claws well-developed, posterior claws small. Anterior claw of male protarsus bifid, split longitudinally into major and minor claw (Fig. 3C). Aedeagus asymmetrical and highly reduced: single piece composed of flat, disc-like median lobe without parameres (Fig. 3D).

Etymology. The generic name is a combination of *Batrisus* Aubé and *Scydmaenus* Latreille, type genera of Batrisini and Scydmaeninae, respectively. The name is chosen on account of the new taxon’s membership of Batrisini and its smooth, globular, and overtly simplified morphology that is reminiscent of some scydmaenines.

Relationships. *Batriscydmaenus* is modified in so many aspects that it is not possible to suggest a close relationship with any other batrisine genus at this time. Numerous aspects of its external and genitalic morphology have been subject to extreme loss or reduction, and the genus also exhibits character states that are not seen elsewhere in Pselaphinae (see genus diagnosis). We note that *Batriscydmaenus* bears a remarkable resemblance to *Loeblibatrus* Yin described in this same issue. However, *Batriscydmaenus* can be distinguished by the margin of palpomere 4 with an apical concavity, the more compact antennae, and the rudimentary, disc-like form of the aedeagus. *Batriscydmaenus* also has anteriorly open pro- and mesocoxal cavities, whereas *Loeblibatrus* has more distinct intercoxal processes. *Loeblibatrus* also possesses at least one fovea that *Batriscydmaenus* lacks (the lateral mesocoxal fovea) (Yin 2018).

Batriscydmaenus tishechkini Parker and Owens, new species

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Type Material. Holotype ♂: **PANAMA:** Colón Pr. San Lorenzo Forest 9°17′N 79°58′W. Forest litter, Winkler extraction IBISCA site B1. W 12558 // 10.x.2003. A.Dejean, G.Orivel, B.Cobrara, H.-P. Aberlenc & M.Leponce. Paratypes (5): ♂ **PANAMA:** Colón Prov. San Lorenzo Forest, STRI crane site. 9°17′N 79°58′W FIT-C3-17. 21-24 May 2004 A.K.Tishechkin. AT — 522; ♂ **PANAMA:** Colón Prov. San Lorenzo Forest. 9°17′N 79°58′W. F.I.T., 1.3m 14d FL-C281.3a. 17.x.2003 R.Didham, L.Fagan. IBISCA; ♀ **PANAMA:** Colón Prov. San

Lorenzo Forest, STRI crane site. 9°17′N 79°58′W FIT-I3-15. 15-17 May 2004 A.K. Tishechkin. IBISCA’04; ♀ **PANAMA:** Colón Prov. San Lorenzo Forest, STRI crane site. 9°17′N 79° 8′W FIT-B3-14. 20-21 May 2004 A.K. Tishechkin. IBISCA’04; ♂ **PANAMA:** Colón Prov. San Lorenzo Forest. 9°17′N 79°58′W. F.I.T., 1.3m 10d FL-C1A1.3b. 23. x.2003 R.Didham, L.Fagan. IBISCA. The male holotype, two male paratypes, and one female paratype are deposited in Field Museum of Natural History (FMNH), Chicago, IL, USA. A male and female paratype are held at the Louisiana State Arthropod Museum (LSAM), Baton Rouge, LA, USA.

Diagnosis. As for the genus, additionally with vestiture of regularly spaced, spatulate setae on dorsal surface, and aedeagus with narrow distal process and patches of erect setae on distal surface.

Description. Holotype male body length 1.57 mm (Fig. 1A, B). Upper body surface shiny and glabrous except for sparse but regularly spaced large, suberect, spatulate setae (Figs. 1A, B, 2A, B, D, D’). Body and antenna light reddish brown, appendages and maxillary palpi orange-yellow (Fig. 1A, B). **Head:** Moderately transverse (Figs 1A; 2B). Integument smooth, shiny; dorsal surface with evenly spaced, spatulate setae; ventral surface with dense vestiture of simple, closely spaced setae. Vertex gently convex, smooth, lacking foveae, sulci, or carinae. Eye small, semi-circular, composed of approximately 45 facets (Fig. 2A). Postocular margins longer than eye length, gently rounded, narrowing from eyes towards base. Antennomeres 1–3 longer than wide; 3–10 subrectangular, about as long as wide; 11 largest (Fig. 2A). **Thorax:** Pronotum slightly wider than long, widest point at about 1/3 length; lateral margin rounded; disc smoothly shiny with evenly spaced, spatulate setae (Figs. 1A, 2D). Mesoventrite with fine lattice microsculpture medially (Fig. 2E). Metaventrite smoothly shiny, vestiture of simple, closely spaced setae becoming denser in area between meso- and metacoxae. **Abdomen:** Wider than long, narrowed posteriorly (Fig. 1A, B). Aedeagus with dorsal diaphragm large, centrally positioned within disc; parameres absent; distal process narrow; distal surface with patches of short, erect setae (Fig. 3D). **Elytra:** Subtrapezoidal (Fig. 1A), base much narrower than apex; foveae and striae absent; surface smoothly shiny, covered with evenly spaced, spatulate setae (Fig. 1A, B). **Legs:** Simple, elongate, unmodified except protibia with transverse sulcus in apical third.

Female. Externally similar to male. Eye slightly smaller, approximately 25 facets. Lacking transverse sulcus on protibia.

Etymology. The specific name honors our colleague and friend Alexey Tishechkin, histerid expert and myrmecophile enthusiast, who collected several specimens of the type series.

Biological Information. All specimens were collected by either flight intercept traps or a Winkler extractor, so the biology of the species is unknown. However, we think it highly likely that *B. tishechkini* is a myrmecophile or possibly a termitophile based on a suite of morphological features. The extensive loss of foveae, sulci, and striae to produce a smooth cuticle is a trait common to many inquilinous Pselaphinae (Chandler 2001). The spatulate setae closely match the form of known pselaphine myrmecophiles such as the trogastrine *Jubogaster* Parker and Maruyama (Parker and Maruyama 2013) and some myrmecophilous aleocharines such as *Phyllodinarda* Wasmann. The robust, nearly moniliform antennae, composed of compact antennomeres, are also a feature of numerous pselaphine myrmecophiles and termitophiles (Chandler 2001). Moreover, *B. tishechkini* is strikingly similar in appearance to *Loeblibatrus yunnanus* Yin, a myrmecophile of *Ectomomyrmex* Mayr in China (Yin 2018). In the absence of molecular data from *Loeblibatrus*, we presently hypothesize that this close similarity is the outcome of convergent evolution in response to selection inside social insect colonies, rather than from shared ancestry.

Comments. No further specimens of this genus were recovered despite searching in the following museum collections that have extensive holdings of Neotropical pselaphine material: FMNH, American Museum of Natural History, New York, Snow Entomological Museum Collection, Kansas, Natural History Museum, London, UK, and the personal collection of Donald Chandler (University of New Hampshire).

Phylogenetic Position of *Batriscydmaenus*. Our initial impression of *Batriscydmaenus* was of a new and highly unusual genus, almost scydmaenine-like in form, but with shortened elytra and three-segmented tarsi that suggested a placement in Pselaphinae. The new taxon appeared to be highly atypical for a pselaphine, however, with several remarkable character states that are otherwise invariant within the subfamily. The overtly simplified morphology, with profound losses of foveae, sulci, and other characters used routinely for tribal placement, meant that unambiguous external characters to link the new genus to a higher taxonomic group were not forthcoming. One character—the apically notched antennal scape—suggested possible membership in the supertribe Batrisitae, but the approximation of this character state elsewhere in Pselaphinae (Kurbatov 2007) prevented unequivocal placement. Batrisites possess a modified metaventrite margin that is curved at the midline to form a preapical fovea (Chandler 2001), and we noticed that *Batriscydmaenus* has this feature. Furthermore, upon dissection we discovered the genus possesses four setae on the labrum—a proposed autapomorphy of Batrisitae (Kurbatov 2007). Still, the radical departure from the typical pselaphine (and batrisine) habitus was perplexing.

To circumvent the challenge posed by the morphology of the new genus to a definitive tribal placement, we assessed the phylogenetic position of *Batriscydmaenus* molecularly. We recovered fragments of nuclear *28s rRNA* and mitochondrial *16s rRNA* and COI from one of the paratypes. Bayesian analysis revealed that *Batriscydmaenus* emerges within a maximally supported Batrisitae clade (Fig. 4). These results establish with confidence that the new taxon is indeed a morphologically derived member of Batrisitae. Our tree includes nine members of Batrisini as well as *Arianops* Brendel, a Nearctic member of the troglobitic batrisite tribe Amauropini. The position of *Arianops* within a clade otherwise composed of Batrisini genera indicates that Amauropini should be synonymized with Batrisini, as suggested previously (Parker 2016b). We refrain from doing so until a greater range of amauropine genera can be sampled, but nevertheless conclude that *Batriscydmaenus* belongs within Batrisini rather than Amauropini. Notably, batrisines have undergone explosive genus-level diversification in the African and, in particular, the East Asian tropics, but up to now only six genera have been recorded from the Neotropics: *Arthmius* LeConte, *Batoctenus* Sharp, *Iteticus* Raffray, *Oxarthrius* Reitter, *Syrbatus* Reitter, and *Syrmocerus* Raffray (Park 1942). *Batriscydmaenus* thus represents the seventh Neotropical batrisine genus. In our tree, *Batriscydmaenus* is resolved as sister to the Neotropical genus *Oxarthrius*, but limited gene and taxon sampling precludes a more exact placement within Batrisini with any confidence.

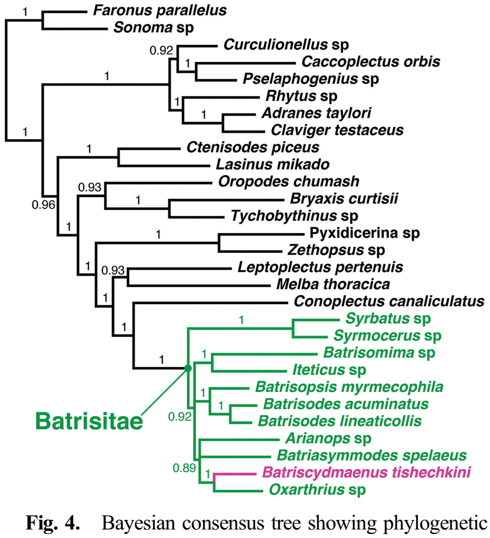

Fig. 4. Bayesian consensus tree showing phylogenetic position of *Batriscydmaenus* within Batrisitae. Numbers above branches are posterior probabilities.

Discussion

In Pselaphinae, morphological evolution is believed to have proceeded in part through the recurrent deconstruction in independent lineages of an intricate ancestral ground plan (Chandler 2001; Parker 2016a, b). This groundplan comprises a suite of cuticular features, including sulci (canals), carinae (ridges), and foveae (pits), which decorate the ectoderm in a stereotypical pattern (Park 1942; Chandler 2001). Different components of this plesiomorphic pattern have been lost in descendent lineages, with the nature and degree of loss varying markedly between supraspecific groups (Grigarick and Schuster 1980; Chandler 2001). The pattern is most complete in the earliest diverging supertribe, Faronitae, while all groups of non-faronite pselaphine (so called “higher Pselaphinae” *sensu* Parker 2016b) have lost at least some components of the pattern. As noted by Chandler (2001) and Parker (2016a, b), a general trend is for myrmecophilous and termitophilous pselaphines to show the greatest losses of these primitive cuticular features. In extreme cases, the smooth tagmata of these symbiotic species have become highly convex and globose, and a reduction in setal vestiture and microsculpture gives a glabrous, shiny appearance, which in living specimens may be augmented by cuticular secretions. Species bearing this morphology commonly have antennae that are moniliform rather than clubbed. Some examples of taxa with this morphology are shown in Fig. 5.

Batriscydmaenus exemplifies this phenotype and prompted us to conduct a preliminary survey of Pselaphinae genera that are known or putative social insect symbionts, and which approach this “reductive” morphology to greater or lesser degrees. Table 1 summarizes our findings and shows that such taxa are found in a variety of tribes scattered across the subfamily. A number of these examples possess only partially reductive morphology. For example, at least some species of *Awas* Löbl (Arnyliini) retain a relatively prominent dorsal vestiture; *Liuyelis* Yin and Li (Trichonychini: Trimiina) has definite dorsal foveae, but they are very shallow, and the body surface is microgranulose and covered in short setae (Yin *et al.* 2011). Nevertheless, all genera in Table 1 appear to fit along a spectrum of degrees of abandonment of primitive cuticular features, with corresponding increases in the convexity of dorsal body surfaces. Given that multiple pselaphine lineages have independently converged upon this anatomy, we posit that an

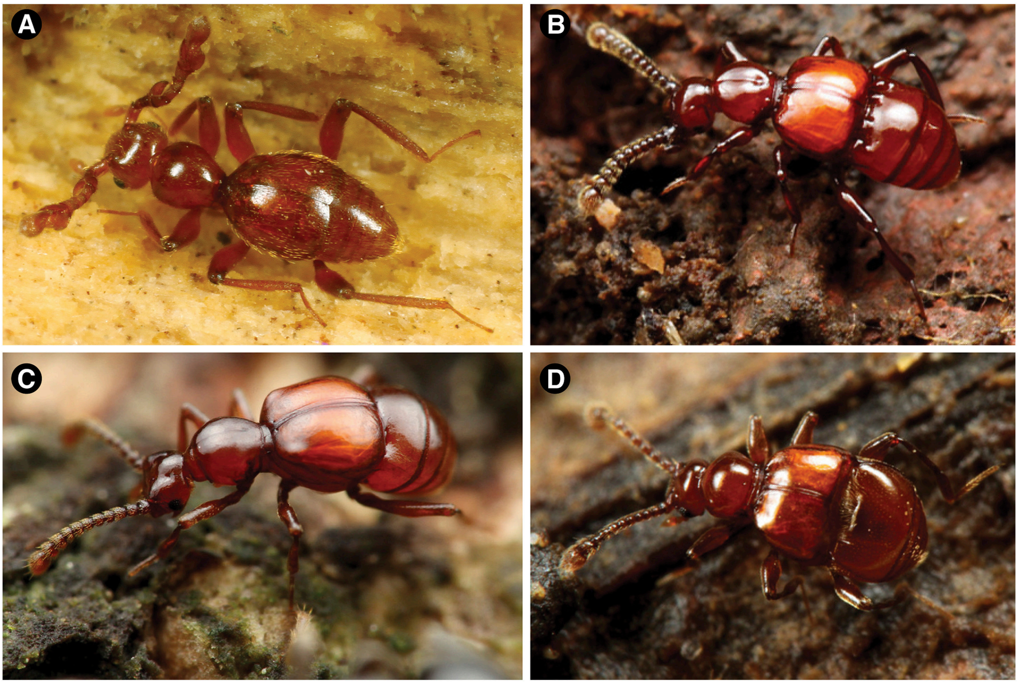

Fig. 5. Convergent examples of the reductive ecomorph in Pselaphinae. A) Batrisini: *Batrisopsis myrmecophila* Raffray, a myrmecophile of *Camponotus gigas* Latreille in Southeast Asia, B) Batrisini: *Batrisus politus*, a guest of *Lasius hayashi* Yamauchi and Hayashida in Japan, C) Batrisini: *Dendrolasiophilus nishikawai* Nomura, a guest of *Dendrolasius orientalis* Karavaiev in Japan, D) Brachyglutini: *Batraxis splendida* Nomura, associated with *Brachyponera chinesis* (Emery) in Japan. Photograph credits: Takashi Komatsu (A), Taku Shimada (B–D).

adaptive process of "reductive specialization" often accompanies the evolutionary transition to social parasitism in Pselaphinae. Reductive morphology thus constitutes a symbiotic "ecomorph"—a phenotype commonly associated with a certain organismal ecology, with adaptive utility for that specific way of life (Williams 1972).

The reason for this predictable shedding of cuticular features is presently mysterious. The biologies of reductive taxa inside nests are mostly unknown, and it is possible that symbiotic species lose these characters for different reasons. One general explanation might be that the features are energetically costly to produce, and only confer adaptive value to free-living species. Symbionts that lose them would thus be at an advantage, so the features are frequently allowed to degenerate in the absence of whatever selective forces sustain them in free-living taxa. Developmentally, the reductive ecomorph might evolve via loss of the patterning and morphogenetic signals that establish foveae or cause the epidermal folding or bending that produces striae and sulci (and paratergites in the more extreme taxa, such as *Batriscydmaenus*, that have lost them). By default, a more globular body morphology with smoothly rounded cuticular surfaces could develop this way. Cuticle microsculpturation may also be an actively controlled process that, when lost, would leave a smooth, glabrous integument. The potential ease by which reductive modifications might evolve, via loss of the underlying cuticle sculpting mechanisms, may represent a genetic path of least resistance for species inhabiting ant and termite nests. The reductive ecomorph may thus be expected to evolve with relative ease, leading to its observed convergent origins in independent lineages.

As shown in Table 1, the tribe in which the greatest number of reductive taxa appear to be found is Batrisini, and this list is certainly incomplete. These taxa are unlikely to form a monophyletic group. In our tree, for example (Fig. 4), *Batrisopsis* Raffray, a myrmecophile genus with strongly reductive morphology (Fig. 5A), is well separated from *Batriscydmaenus*. Moreover, the evolutionary development of the reductive ecomorph can be seen within a single genus of some batrisines. The *Lasius*-associated *Songius* Yin and Li includes species such as *Songius lasiuohospes* Yin and Li that are not especially modified, with well-impressed basal elytral foveae, a clear median longitudinal sulcus on the pronotum, and a relatively dense

Table 1. Inquilinous Pselaphinae genera proposed to possess or approach the reductive ecomorph and their hosts. The list is provisional and based on genera seen by us or discovered via literature search. Asterisks indicate genera where only a minority of species has been shown to be demonstrably inquilinous.

Pselaphinae Taxon	Host	Selected reference
Euplectitae		
Trichonychini		
Liuyelis Yin and Nomura	*Camponotus* Mayr	Yin *et al.* 2011
Trogastrini		
Zeasampa Nomura and Leschen	*Prolasius advenus* Smith	Nomura and Leschen 2015
Euplectini		
Capnites Raffray	*Pheidole oswaldi* Forel	Jeannel 1954
Goniaceritae		
Arnyliini		
Awas Löbl	*Ectomomyrmex* Mayr	Yin 2017
Harmophorus Motschulsky*	*Ectomomyrmex javanus* Mayr	Maruyama *et al.* 2013
Brachyglutini		
Batraxis Reitter *	Ants and termites	Raffray 1894a
Xenobryaxis Jeannel	Unidentified ants	Jeannel 1954
Cyathigerini		
Plagiophorus Motschulsky	Various ant species	Chandler 2001
Batrisitae		
Batrisini		
Batriscydmaenus Parker and Owens	Unknown; putative inquiline	This paper
Batrisopsis Raffray	*Camponotus gigas* Latreille	Raffray 1894b
Batrisus Aubé	*Lasius* Fabricius	Maruyama *et al.* 2013
Connodontus Raffray	Termites	Park 1949
Conogastridius Jeannel	Unidentified termites; *Odontomachus*	Jeannel 1959
Dendrolasiophilus Nomura	*Lasius* (*Dendrolasius*) Ruzsky	Yin and Li 2013b
Loeblibatrus Yin	*Ectomomyrmex* Mayr	Yin 2018
Mannoconnus Park	Termites	Park 1949
Ophelius Raffray	*Camponotus* (*Tanaemyrmex*)	Yin 2018
Pengzhongiella Yin and Li	*Odontomachus monticola* Emery	Yin and Li 2013a
Songius Yin and Li	*Lasius* Fabricius	Yin and Li 2015
Tangius Yin and Li	Unidentified ants	Yin and Li 2013c
Xenopygiella Jeannel	Unidentified termites	Jeannel 1959

vestiture of suberect setae on the dorsal surface. In contrast, species such as *Songius hlavaci* Yin and Li are extremely reductive, with an entirely smooth, glabrous, and glistening cuticle and an absence or at most weak traces of dorsal foveae, sulci, and striae (Yin and Li 2015). Species of *Batrisus* also sit on a spectrum from partially reductive (*Batrisus formicarius* Aubé) to fully so (*Batrisus politus* Sharp; Fig. 5B).

Many batrisines are inquilines, and the high frequency with which reductive morphology has evolved in Batrisini may be a consequence of the elevated occurrence of myrmecophily and termitophily relative to most other pselaphine tribes. It is possible that batrisines are especially preadapted for social parasitism due to their physically strengthened body plan that arises from a general thickening of the cuticle and fusion of the abdominal sternites and tergites (and corresponding loss or reduction of most or all paratergites) to create a rigid and compact cylindrical abdomen. Park observed how an individual of *Batrisodes* Reitter "slides out of the grasp of the ant's mandibles" when attacked by its host, and in this way "the beetles appear able to escape death" (Park 1947). Chandler (2001) proposed that pselaphine foveae fall into two categories: some are sensory (those on the thorax and elytra); others are structural (foveae on the head and abdomen). Carinae and sulci may likewise perform a structural role, acting as reinforcing struts that span cuticular sheets. Given the potential strengthening role of foveae, carinae, and sulci, reductive morphological changes may be expected to lessen the beetle's physical protection. Reductive symbiotic taxa may, therefore, represent species that are less invested in physical protection, but more advanced in their capacity to evade detection by behavioral or chemical means, perhaps via chemical insignificance or chemical mimicry (von Beeren *et al.* 2012). Hence, the reductive ecomorph may not just represent loss of structures, but also the gain of chemical strategies that enable the beetles to circumvent ant aggression. In Table 1, we excluded Clavigeritae, a supertribe composed exclusively of obligate myrmecophiles that also lack many foveae (Chandler 2001). We view Clavigeritae as having evolved a distinct ecomorph, one that is specialized for interacting intimately with host ants, equipped with trichomes and various other chemical/glandular, behavioral, and anatomical adaptations (Parker and Grimaldi 2014). However, we note that among the reductive taxa listed in Table 1, species of *Songius* and *Dendrolasiophilus* Nomura (both Batrisini) possess trichome-like structures that may produce appeasement compounds, approaching the clavigerite ecomorph. It seems plausible that reductive specialization could act in some cases as a stepping stone towards a more socially integrated ecomorph exemplified by the Clavigeritae.

Finally, we must point out that not all pselaphines with reductive morphology are demonstrably inquilinous. Such taxa occur principally in the tribes Iniocyphini (*e.g.*, *Auchenotropis* Raffray, *Globosulus* Jeannel, *Natypleurus* Newton and Thayer, and *Simplicorfa* Chandler) and Brachyglutini (a variety of genera, including *Araneabaxis* Chandler, *Booloumba* Chandler, and several from the subtribes Pselaptina and Eupseniina). Additionally, some reductive taxa, such as *Plagiophorus* Motschulsky and *Batraxis* Reitter, may not be obligately associated with ants and termites, since they are frequently collected away from colonies. However, the majority of all of these genera nevertheless inhabit tropical leaf litter where ant density and biomass can be extremely high (Fittkau and Klinge 1973; Hölldobler and Wilson 1990). It is possible that, in addition to living inside colonies, simply living in ant-rich leaf litter has contributed to the convergent evolution of this ecomorph.

ACKNOWLEDGMENTS

We are grateful to Chris Carlton for making this material available for study and for providing feedback on the manuscript, and to Don Chandler for searching in his collection for further specimens. We thank Zi-Wei Yin for contacting us about the similarity between *Batriscydmaenus* and *Loeblibatrus* and for sharing manuscripts prior to submission.

DISCLAIMER

In this publication, the name *Loeblibatrus yunnanus* Yin is to be excluded for purposes of zoological nomenclature.

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(Received 26 January 2018; accepted 19 April 2018. Publication date 20 June 2018.)