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Rainforest and cloud forest *Scolytodes* (Curculionidae, Scolytinae, Hexacolini) from the Arthropods of La Selva inventory in Costa Rica: new species, new synonymy, new records

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Abstract

Quantitative collecting efforts over the last several decades in Costa Rica have resulted in many new species of insects. The Arthropods of La Selva projects included collecting from a typical lowland Neotropical forest and up an altitudinal transect, and has provided many valuable samples of insects, spiders and mites potentially new to science. We describe 18 new species in the bark beetle genus *Scolytodes* Ferrari, 1867, 14 of which were collected during this project: *S. angulus* Jordal & Kirkendall, **sp. nov**., *S. sufflatus* Jordal & Kirkendall, **sp. nov**., *S. squamatifrons* Jordal & Kirkendall, **sp. nov.**, *S. comosus* Jordal & Kirkendall, **sp. nov.**, *S. spatulatus* Jordal & Kirkendall, **sp. nov.**, *S. seriatus* Jordal & Kirkendall, **sp. nov.**, *S. profundus* Jordal & Kirkendall, **sp. nov.**, *S. catinus* Jordal & Kirkendall, **sp. nov.**, *S. fimbriatus* Jordal & Kirkendall, **sp. nov.**, *S. sulcifrons* Jordal & Kirkendall, **sp. nov.**, *S. planifrons* Jordal & Kirkendall, **sp. nov.**, *S. porosus* Jordal & Kirkendall, **sp. nov.**, *S. mundus* Jordal & Kirkendall, **sp. nov.**, *S. callosus* Jordal & Kirkendall, **sp. nov.**, *S. parvipilus* Jordal & Kirkendall, **sp. nov.**, *S. plenus* Jordal & Kirkendall, **sp. nov.**, *S. niger* Jordal & Kirkendall, **sp. nov.**, and *S. simplex* Jordal & Kirkendall, **sp. nov.** One species, *Scolytodes minutissimus* Schedl, 1952, is redescribed to match the holotype. We give new Costa Rica records for *S. costabilis* Wood, 1974, which is the correct name for *S. obesus* Wood, 1975 (**syn. nov**.). We report Costa Rica as a new country record for six species: *Scolytodes clusiacolens* Wood, 1967, *S. crinalis* Wood, 1978, *S. culcitatus* (Blandford, 1897), *S. libidus* Wood, 1978, *S. reticulatus* (Wood, 1961), and *S. spadix* (Blackman, 1943). From a closely related genus, we provide the first record for Central America (and only the second collection) of *Pycnarthrum fulgidum* Wood, 1977.

Keywords
bark beetles, biodiversity survey, taxonomy, transect, weevils

Introduction

Modern biodiversity surveys of tropical arthropod faunas are discovering large numbers of new species and making them available to taxonomists. Good taxonomy, in turn, provides the cornerstones of biodiversity analyses. The Arthropods of La Selva projects (ALAS), supported by four NSF grants, ran from 1992 through 2005, with the aim of exhaustively sampling focal taxa in insects, mites and spiders from a Mesoamerican Neotropical forest (http://viceroy.eeb.uconn.edu/alas/history.html). The first three iterations (ALAS I–III) ran from 1992–2000 and concentrated on the lowland wet tropical forest of La Selva Biological Station run by the Organization for Tropical Studies on the Caribbean side of Costa Rica. ALAS IV was a five-year, 2000 m elevational gradient running SSW from La Selva up the north-eastern side of Volcan Barva to near the peak. The ALAS projects used a variety of quantitative sampling methods to survey both flying arthropods and those in vegetation or the leaf litter, including canopy sampling by UV light traps and canopy fogging (ALAS I–III only). Data from the ALAS project have contributed not only to our knowledge of the composition of hyperdiverse tropical arthropod communities but to ecological analyses of tropical biodiversity patterns as well (e.g., Longino and Colwell 1997, 2011; Colwell 2008; Kumar et al. 2011).

Kirkendall visited La Selva annually and participated in all the expeditions of the elevational gradient study (ALAS IV). He sampled bark beetles and pinhole borers by hand at all sites and has been identifying the large number of Scolytinae and Platypodinae collected. Many new species of these two weevil groups have been encountered in this material. Here, we describe 14 new species from *Scolytodes* Ferrari, 1867 that were collected during the ALAS projects, plus four other new species from Costa Rica.

Scolytodes Ferrari, 1867, is a highly diverse group of bark beetles distributed in the Neotropics from Florida and Mexico in the north, to subtropical Argentina in the south. There are many species at both low and high altitude; several species have been collected at close to 4000 m above sea level (Jordal 2018). Currently, 240 species are recognized, including the 18 new species described in this paper.

Scolytodes is of particular interest because of its wide range of breeding and feeding habits. Most species are typical monogynous bark beetles; a few species are harem polygynous (Wood 1982). Though many different host plants are recorded for *Scolytodes*, a strikingly high proportion breed in in *Cecropia* (Urticaceae) or *Clusia* (Clusiaceae) (Wood 1982; Jordal 1998b, 2013). Most species breed in inner bark, but several species groups reproduce in fallen leafstalks, some species breed in pith of twigs, and a few have only been found in vines and lianas. *Scolytodes unipunctatus* (Blandford, 1897) is an ambrosia beetle, whose larvae feed on symbiotic fungi growing in the parental tunnels in sapwood (Hulcr et al. 2007). Based on its atypical morphology, *S. culcitatus* (Blandford, 1897) could be a second, unrelated species with these habits (see below).

As is the case with many tropical bark beetles, most *Scolytodes* species are only known from a single collection and often only from a single specimen. Intensive arthropod field surveys in Neotropical forests have always found new species, especially those fogging canopy trees, but also from extracting insects from leaf litter, or using Malaise traps or flight intercept traps. *Scolytodes* is one of few scolytine genera that are found throughout the forest floor and canopy, in many host trees, and at all forested altitudes (Jordal 1998a, b, 2013, 2018).

Material and methods

Most of the material treated in this paper is based on collections made during the ALAS projects. In addition to the low altitude location at La Selva Biological Station, ALAS IV included sites on Volcan Barva at 300 m, 500 m, 1000 m, 1500 m, and 2000 m, thus covering all major forest types in Braulio Carrillo National Park.

Material originally deposited in INBio were transferred several years ago to the National Museum of Costa Rica (MNCR) and most of the types designated in this paper therefore belong to MNCR. These and other specimens studied are deposited in the following institutions:

CASC	California Academy of Sciences, San Francisco, California, USA.
CMNC	Canadian Museum of Nature (Entomology Div.), Ottawa, Ontario, Canada.
CNCI	Canadian National Collection of Insects, Ottawa.
EMEC	Essig Museum of Entomology, University of California, Berkeley, California, USA.
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA.
MNCR	Museo Nacional de Costa Rica, San José, Costa Rica.
NHMW	Naturhistorische Museum, Vienna, Austria.
USNM	United States National Museum, Washington D.C. (Smithsonian)
ZMBN	University Museum of Bergen, Norway.

All holotypes (or equivalent, e.g., Eggers 'types') of *Scolytodes* from USNM, NHMW, CNCI and MNHN and have been examined. One type is presumably lost (Budapest: *S. columbianus*). Type material of new species published by Bright (2019) was not examined directly but these have photos of the elytra and sufficiently detailed descriptions.

Measurements and morphological terminology are as used in previous papers on the genus (Jordal 1998b, 2018). *Scolytodes* is here treated as masculine as originally proposed and later corroborated by Alonso-Zarazaga and Lyal (2009). All female-amended names in Wood (2007) were therefore rejected.

Results

Scolytodes Ferrari

http://zoobank.org/0745C155-3489-4576-8A9B-8CA2026EFEE2

Diagnosis. *Scolytodes* is recognized by the sharply carinate lateral edges of the pronotum, separated procoxae, and protibiae that have two large lateral teeth near the distal end which appear unsocketed (but are actually socketed teeth embedded in cuticle; see fig. 8 in Jordal, 1998b). The eyes are entire or weakly sinuate, and the antennal funicle is 5- or 6-segmented (including the pedicel; see Wood 1982).

Scolytodes angulus Jordal & Kirkendall, sp. nov.

http://zoobank.org/24302CAD-3CF7-43CF-A093-C7D5A3FA8AA3
Figs 1, 4, 7

Type material. Holotype, female: Costa Rica, Puntarena, Monteverde, Estacion Biologica Monteverde, 10°19'10"N, 84°48'57"W, 1730 m, 12.VI.2001, R. Anderson, montane forest litter, 2001-107D. Holotype is deposited in USNM.

Diagnosis. Interstriae 10 sharply elevated to near apex; protibiae with an additional mesal socketed tooth near the mucro. Distinguished from the closely related *S. erineophilus* Wood, 1969, by the densely placed and confused setae on the sutural interstriae and on declivity, and by the acute posterior corners of the pronotum.

Description female. Length 1.7 mm, 2.4 × as long as wide; color brown, with densely placed white setae. ***Head.*** Eyes weakly sinuate, separated above by 1.6 × their width. Frons generally flattened, slightly bulging on central half; surface on bulging area glabrous, impunctate, transversely wrinkled, around this area densely punctured; vestiture consisting of median long setae in a circle around bulging area, a few more short setae at upper level of eyes. Antennal club with two obliquely procurved sutures marked by setae, segments 1 and 2 corneous, segment 3 setose. Funiculus 6-segmented. ***Pronotum*** parallel-sided except distinctly expanded laterally in posterior corners; surface reticulate, dull, with shallow tiny punctures on basal fourth, on anterior three-fourths densely asperous. Vestiture consisting of fine erect and recumbent setae (4–0–0). ***Elytra*** smooth, striae weakly impressed, punctures small, deep, subcontiguous; interstriae approximately 3–5 × as wide as striae, punctures similar to those in striae, strongly confused or in rows. Interstriae 10 sharply elevated to near apex. Vestiture consisting of regular rows of long fine setae on each interstria, becoming spatulate on sutural interstriae, mixed with shorter fine hair-like setae in striae and interstriae. ***Legs.*** Procoxae separated by 1.0 × and mesocoxae 1.1 × the width of one procoxa. Protibiae very narrow, lateral teeth 1 and 2 sub-equal, with 3–4 additional tiny granules along the edge towards base; an additional mesal socketed tooth near the mucro; protibial mucro short, straight. Meso- and metatibiae with 6 socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum bifid or plumose, on metasternum simple.

Figures 1–9. Dorsal, lateral and frontal view of the female holotype of **1, 4, 7** *S. angulus*, **2, 5, 8** *S. niger* and **3, 6, 9** *S. simplex*.

Male. Not known.

Key (Wood 1982). Keys to couplet 41, *S. erineophilus*, but distinguished as noted in the diagnosis.

Etymology. The Latin name *angulus* is a masculine noun in apposition meaning corner or angle, referring to the sharp hind corners of the pronotum.

Biology and distribution. This species is only known from the type locality in Costa Rica, in high altitude cloud forest.

Scolytodes niger Jordal & Kirkendall, sp. nov.

http://zoobank.org/C160D713-112C-45F3-8FCB-B3CE555CBA7C
Figs 2, 5, 8

Type material. Holotype, female: Costa Rica, Guanacaste prov., Rincon de La Vieja, Las Pailas, 18.II.1996-020A, R. Anderson, *Clusia rosea* forest litter. **Allotype male:** Costa Rica, Puntarenas, 11 km SW Est. Biol. Las Cruces, 1450 m, 08°46'43"N, 83°01'50"W, 9.VII.1999, R. Anderson, wet cloud forest litter, 99-124E. **Paratypes:** Prov. Heredia, 6 km ENE Vara Blanca, 1950–2050 m, 10°11'N, 84°07'W, 21 Feb. 2002, INBio–OET–ALAS transect, 20/TN/12/005 (INB0003223381) (1); San José prov., Zurquí de Moravia, 1600 m, 30.6.1997, L. Kirkendall, H. Lezama, flight intercept trap (1). Holotype and allotype deposited in CMNC, 1 paratype in MNCR, and 1 paratype in ZMBN.

Diagnosis. Interstriae 10 carinate to level of ventrite 2; protibiae with an additional mesal tooth near tarsal insertion. Metanepisternum covered with white plumose setae. Very similar to *S. clusiae* Wood, 1969, but differs by the smooth and shiny pronotum, the shorter setae in a smaller area in the female frons, and by the distinct, albeit tiny, interstrial punctures.

Description female. Length 1.5 mm, 2.1 × as long as wide; color black. ***Head.*** Eyes sinuate, separated above by 2.0 × their width. Frons weakly impressed from just above level of antennal insertion to epistoma; surface smooth, densely punctured in impressed area, scattered punctures above, shiny. Vestiture consisting of short setae in impressed area and on epistoma. Antennal club with two sutures marked by shorter setae, segment 1 and 2 corneous, sutures slightly constricted; funiculus 6-segmented. ***Pronotum*** shiny, with shallow, small, elongated punctures spaced by 2–3 × their diameter (length). Vestiture consisting of 8 erect long setae (4–2–2). ***Elytra*** generally smooth and shiny; striae not impressed, punctures shallow, tiny, appear elongated but composed by two punctures in one, each pair separated in rows by their length; interstriae 4 × as wide as striae, punctures of same size as in striae, much more separated, mainly in rows. Interstriae 10 carinate to level of ventrite 2. Vestiture consisting of regular rows of erect, interstrial setae of variable thickness, and regularly placed, fine, short, semi-recumbent setae in striae and interstriae, mainly on posterior half. ***Legs.*** Procoxae broadly separated by 0.9 × and mesocoxae 1.2 × the width of one procoxa. Protibiae slightly broadening distally, lateral teeth 1 and 2 of similar size, with a faint extension of cuticle between them, and with 3–4 additional small, sharp spines or granules along the lateral edge towards base; an additional mesal tooth present near tarsal insertion; protibial mucro obtuse. Meso- and metatibiae with 5 and 6 lateral, socketed, small teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum quadrifid to strongly plumose and densely placed, on mesanepisternum mainly trifid, on metasternum mainly simple, some bifid. Sclerolepidia scale-like or plumose.

Male. 1.4–1.6 mm long, 2.0–2.1 × as wide as long. Identical to female, except frons slightly more convex on lower part, with less dense vestiture.

Key (Wood 1982). Keys to couplet 25 with some uncertainty; *S. clusiae* in couplet 24 is a better match.

Etymology. The Latin name *niger* is a masculine adjective, meaning shining black, referring to the dark and shiny appearance of this species.

Biology and distribution. This species is known from four Costa Rican cloud forest localities – in the northern and southern slopes of Volcan Barva (Braulio Carrillo), the southern slope of Rincon de La Vieja, and close to the Panama border (Las Cruces). Two specimens were collected by flight intercept trapping, and two by leaf litter sifting, one of which from *Clusia* litter.

Scolytodes simplex Jordal & Kirkendall, sp. nov.

http://zoobank.org/7BFB9FF3-22E2-4529-B25C-A12FD0268B99
Figs 3, 6, 9

Type material. Holotype, female: Costa Rica, Cartago, km 89 PanAmHighway, Cerro de la Muerte, 3300 m, 10.II.1996-002A, R. Anderson, elfin bamboo forest litter. **Paratype:** same data as holotype, except Cerro Buenavista, 3200 m, 09°33'N, 83°45'30"W, 18.VI.1998, R. Anderson, elfin bamboo/ mixed subparamo litter 98-102D (1). Holotype and paratype deposited in USNM.

Diagnosis. Interstriae 10 carinate to level of metacoxae; protibiae broad with an additional mesal tooth near base of tooth 2. Similar to *S. venustulus* Wood, but is much larger, with shiny pronotum punctured to anterior margin, and finer elytral setae. Also rather similar to *S. radiatus* Wood, 1977, but differs by having much smaller punctures on pronotum and elytral striae, and the presence of setae in the female frons. Differs from *S. clusiae* Wood, 1969 by the smooth and shiny pronotum, the female frons is less setose without impressed area, and by the distinct, albeit tiny, interstrial punctures.

Description female. Length 1.9–2.0 mm, 2.1–2.2 × as long as wide; color black. ***Head.*** Eyes entire, separated above by 2.9–3.0 × their width. Frons convex, slightly bulging near upper level of eyes, flat below and level with epistoma; surface smooth, densely punctured on median half from just above level of antennal insertion to epistoma, shiny and impunctate above, with scattered punctures on vertex. Vestiture consisting of scant short fine setae on lower half. Antennal club with two slightly procurved sutures marked by short, coarse, setae, segment 1 and 2 rather large, corneous, suture 1 constricted; funiculus 5-segmented. ***Pronotum*** shiny, with deep, variably sized punctures spaced by 1–3 × their diameter. Vestiture consisting of 4 long, semi-erect, fine setae (4–0–0) and some fine, recumbent, setae along the anterior margin. ***Elytra*** generally smooth and shiny; striae not impressed, punctures shallow, tiny, appears elongated but composed by two punctures in one, each pair separated in rows by less than their length; interstriae 4 × as wide as striae, punctures of same size as in striae, much more and irregularly separated, mainly in rows. Interstriae 10 carinate to level of metacoxae. Vestiture consisting of about 20 erect setae of variable length on odd-numbered interstriae, and minute, recumbent setae in striae and interstriae. ***Legs.*** Procoxae separated by 0.5 × and mesocoxae 1.0 × the width of one procoxa. Protibiae broad distally, lateral teeth 1 and 2 of similar size, tooth 2 exposed, socketed, with 4–6 additional small, sharp spines or granules along the lateral edge towards base; an additional mesal tooth present near base of tooth 2; protibial mucro curved posterio-laterally. Meso- and metatibiae with 5 and 6 lateral, socketed teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum and metasternum simple, with some occasional bifid setae; on mesanepisternum strongly plumose. Sclerolepidia large, scale-like.

Male. Presumably similar to the female.

Key (Wood 1982). Keys to couplet 25a, *S. radiatus*, but differs as noted in the diagnosis.

Etymology. The Latin name *simplex* is an invariable adjective meaning plain or simple, in the sense of lacking ornaments, referring to the ordinary female frons.

Biology and distribution. This species is only known from two nearby locations at very high altitude in Costa Rica. Two specimens were sifted from mixed bamboo and elfin forest litter.

Scolytodes sufflatus **Jordal & Kirkendall, sp. nov.**

http://zoobank.org/83A5494B-EA63-4D05-B09E-A689400CDDBE
Figs 10, 13, 16

Type material. Holotype female: Costa Rica, Prov. Heredia, 6 km ENE Vara Blanca, 1950–2050 m, 10°11'N, 84°07'W, 21 Apr. 2002, INBio-OET-ALAS transect, 20/TN/17/030, INB0003223002. **Allotype male:** Alajuela, PN Volcan Poas, 2500 m, 10°11'30"N, 84°14'W, 6.VI.1997, R. Anderson, wet cloud forest litter, RSA 1997-003E. **Paratypes**: same data as holotype, except 22 Mar., 20/TN/08/011, INB0003222886 (1); San José, km 72, Int. Amer. Hwy, 3 km W. Ojo de Agua, 2950 m, 9°37'30"N, 83°50'30"W, 7.VI.1997, R. Anderson, oak for. Litter, 97-005B (1). Holotype and allotype in MNCR, 1 paratype in USNM, 1 paratype in ZMBN.

Diagnosis. Interstriae 10 sharply elevated to level of metacoxae, interstriae 9 sharply elevated from near base to near apex; protibiae with an additional socketed, thin tooth near the mucro, posterior surface of protibia sulcate and strongly reticulate. Distinguished from *S. radiatus* by the much smaller punctures on the pronotum, by the paired smaller punctures in elytral striae, and a much longer carinate interstriae 9.

Description female. Length 1.7–1.9 mm, 2.2–2.4 × as long as wide; color black. ***Head.*** Eyes entire, separated above by 3.1–3.3 × their width. Frons bulging on lower

Figures 10–18. Dorsal, lateral and frontal view of the female holotype of **10, 13, 16** *Scolytodes sufflatus* **11, 14, 17** *S. squamatifrons* **12, 15, 18** *S. comosus*.

two-thirds, transition to epistoma smooth; surface smooth and shiny, largely impunctate; vestiture consisting of 6–8 scattered long setae near epistoma and eyes. Antennal club with two obliquely procurved sutures densely marked by setae, corneous part of segments 1 and 2 barely visible. Funiculus 5-segmented. ***Pronotum*** smooth, strongly reticulate, dull, with scattered faint punctures reaching anterior margin. Vestiture consisting of two fine erect median setae along anterior margin (2–0–0), otherwise glabrous. ***Elytra*** smooth, striae 1 weakly, others not impressed, punctures small, in pairs of two subcontiguous punctures, each pair spaced by the length of each pair; interstriae 4–5 × as wide as striae, single punctures spaced by 5–10 × their diameter, in rows. Interstriae 10 sharply elevated to level of metacoxae; interstriae 9 sharply elevated from near base to near apex. Vestiture consisting of 10 erect long very fine setae, three on each interstria 3, two on each interstria 7. ***Legs.*** Procoxae separated by 0.4 × and mesocoxae 0.8 × the width of one procoxa. Protibiae broad, posterior surface of protibia sulcate and strongly reticulate; lateral teeth 1 and 2 of sub-equal size, cuticle extending around these, with 3 additional tiny granules along the edge towards base; an additional socketed, thin tooth present near the mucro; protibial mucro curved posteriorly. Meso- and metatibiae with 6–7 thin socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Scattered setae on metanepisternum and metasternum long and simple; sclerolepidia large round scales.

Male. Identical to female. The terminal tergite of two paratypes were examined and revealed separate tergites 7 and 8 (male), and a single broader tergite 7 (female).

Key (Wood 1982). Keys to couplet 23, but punctures on elytral declivity do not match. If not, it will key to couplet 25a, *S. radiatus*.

Etymology. The name *sufflatus* is a Latin masculine participle, meaning puffed up or inflated, referring to the swollen frons in both sexes.

Biology and distribution. This species is known from three localities above 2000 m altitude in Costa Rica.

Scolytodes squamatifrons Jordal & Kirkendall, sp. nov.

http://zoobank.org/B56E6C09-F0EB-4302-8BAA-D799C323B189
Figs 11, 14, 17

Type material. Holotype, female: Costa Rica, San José, km 68 PanAmHighway, Tres de Junio Bog, 2600 m, 10.I.1996-001C, R. Anderson, litter ex. Forest adjacent to *Sphagnum* bog. Holotype deposited in USNM.

Diagnosis. Interstriae 10 sharply elevated to level of metacoxa, interstriae 9 sharply elevated from the level of metacoxa to near apex; protibiae with an additional socketed, thin tooth near the mucro, posterior surface of protibiae sulcate and strongly reticulate. Distinguished from *S. sufflatus* by the impressed female frons, the broader eyes which are more closely situated above, by the narrower shape of the body, the shorter elytral setae, and by the shorter carinate part of interstria 9.

Description female. Length 1.5 mm, 2.4 × as long as wide; color black. ***Head.*** Eyes entire, separated above by 2.3 × their width. Frons generally flat, circularly impressed on median half; surface around impression smooth and shiny, impression with densely set punctures and tiny granules; vestiture in impressed area consisting of densely placed short scale-like setae, on epistoma and near antennal insertion with scant hair-like setae. Antennal club setose, with two obliquely procurved sutures barely discernible. Funiculus 5-segmented. ***Pronotum*** smooth, strongly reticulate, with scattered faint punctures reaching anterior margin. Vestiture consisting of two fine erect median setae along anterior margin (2–0–0), otherwise glabrous. ***Elytra*** smooth, striae 1 weakly, others not impressed, punctures small, in pairs of two subcontiguous punctures, each pair spaced by the length of each pair; interstriae 4–5 × as wide as striae, single punctures spaced by 5–10 × their diameter, in rows. Interstriae 10 sharply elevated to level of metacoxa, interstriae 9 sharply elevated from the level of metacoxa to near apex. Vestiture consisting of 4–6 short erect very fine setae, mainly on interstriae 3. ***Legs.*** Procoxae separated by 0.4 × and mesocoxae 0.8 × the width of one procoxa. Protibiae broad, posterior surface sulcate and strongly reticulate, lateral teeth 1 and 2 of sub-equal size, with cuticle extending between these, with 3 additional tiny granules along the edge towards base; an additional socketed, thin tooth present near the mucro; protibial mucro curved posteriorly. Meso- and metatibiae with 6–7 fine socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Scattered setae on metanepisternum and metasternum long and simple; sclerolepidia large round scales.

Male. Unknown.

Key (Wood 1982). As for *S. sufflatus*.

Etymology. The name *squamatifrons* is composed by the stem of the Latin adjective *squamatus*, meaning scaly, a linking vowel –i, and the noun *frons*, meaning forehead. It is invariable.

Biology and distribution. This species is known from the type locality at high altitude in Costa Rica.

Scolytodes comosus Jordal & Kirkendall, sp. nov.

http://zoobank.org/9575F9F8-16CE-45B0-946D-CE371D965F4E
Figs 12, 15, 18

Type material. Holotype: Costa Rica, Prov. Heredia, 9 km ENE Vara Blanca, 1450–1550 m, 10°14'N, 84°06'W, 11 Apr. 2005, INBio-OET-ALAS transect, ex *Cecropia* petiole, 050411. **Paratypes:** Same data as holotype (4); Alajuela Res. For. San Ramon, 25 km NE San Ramon, 20 Nov. 1993, L.R. Kirkendall, ex *Cecropia peltata* petiole (1). Holotype and 2 paratypes deposited in MNCR, 1 paratype in ZMBM, 2 in USNM.

Diagnosis. Interstriae 10 not elevated; protibiae without additional mesal tooth. Setae on pronotum, and elytral striae and interstriae very long. Distinguished from *S. punctiferus* Wood, 1976 and *S. punctatus* (Eggers, 1943) by the longer setae, by the broader body shape and more broadly separated eyes.

Description male and female. Length 1.2–1.4 mm, 1.9 × as long as wide; mature color dark brown. ***Head.*** Eyes entire, separated above by 2.8 × their width. Frons generally flat, surface impunctate and shiny on median fifth from epistoma to vertex, scattered deep punctures along this line; vestiture consisting of sparse long fine setae in punctured area, pointing medially. Antennal club setose, sutures not discernible, basal part of segment 1 corneous. Funiculus 5-segmented. ***Pronotum*** smooth, weakly reticulate, subshining, with deep large punctures reaching anterior margin, spaced on average by their diameter. Vestiture consisting of very long fine setae (0–0–0). ***Elytra*** smooth, striae not impressed, punctures large, deep, spaced by their diameter; interstriae difficult to distinguish from striae, occasionally in rows but largely confused with striae; all punctures on sides slightly raised on anterior margin, appearing granulated in dorsal profile. Interstriae 10 not raised. Vestiture consisting of very long fine setae on interstriae and striae. ***Legs.*** Procoxae separated by 1.0 × and mesocoxae 1.5 × the width of one procoxa. Protibiae broad, lateral teeth 1 and 2 of sub-equal size, tooth 2 exposed, both teeth extended distally, with a sharp serrated edge running from tooth 2 towards base; protibial mucro large, curved posterior-distally. Meso- and metatibiae with 6 and 7 coarse socketed lateral teeth on distal two-thirds and half, respectively. ***Ventral vestiture.*** Setae on metanepisternum bifid, on metasternum long and simple; sclerolepidia and setae on epimeron plumose.

Key (Wood 1982). Keys incorrectly to couplet 7 due to the mesal tooth on protibiae is missing. The same applies to *S. punctiferus*, which is nevertheless placed in couplet 20.

Etymology. The name *comosus* is a Latin masculine adjective, meaning long haired, referring to the confused rows of long strial, interstrial, and pronotal setae.

Biology and distribution. This species is known from two median altitude localities near Volcan Poas in Costa Rica. It was taken from *Cecropia* petioles in both sites. The species was recorded as *Scolytodes* sp. B by Jordal and Kirkendall (1998).

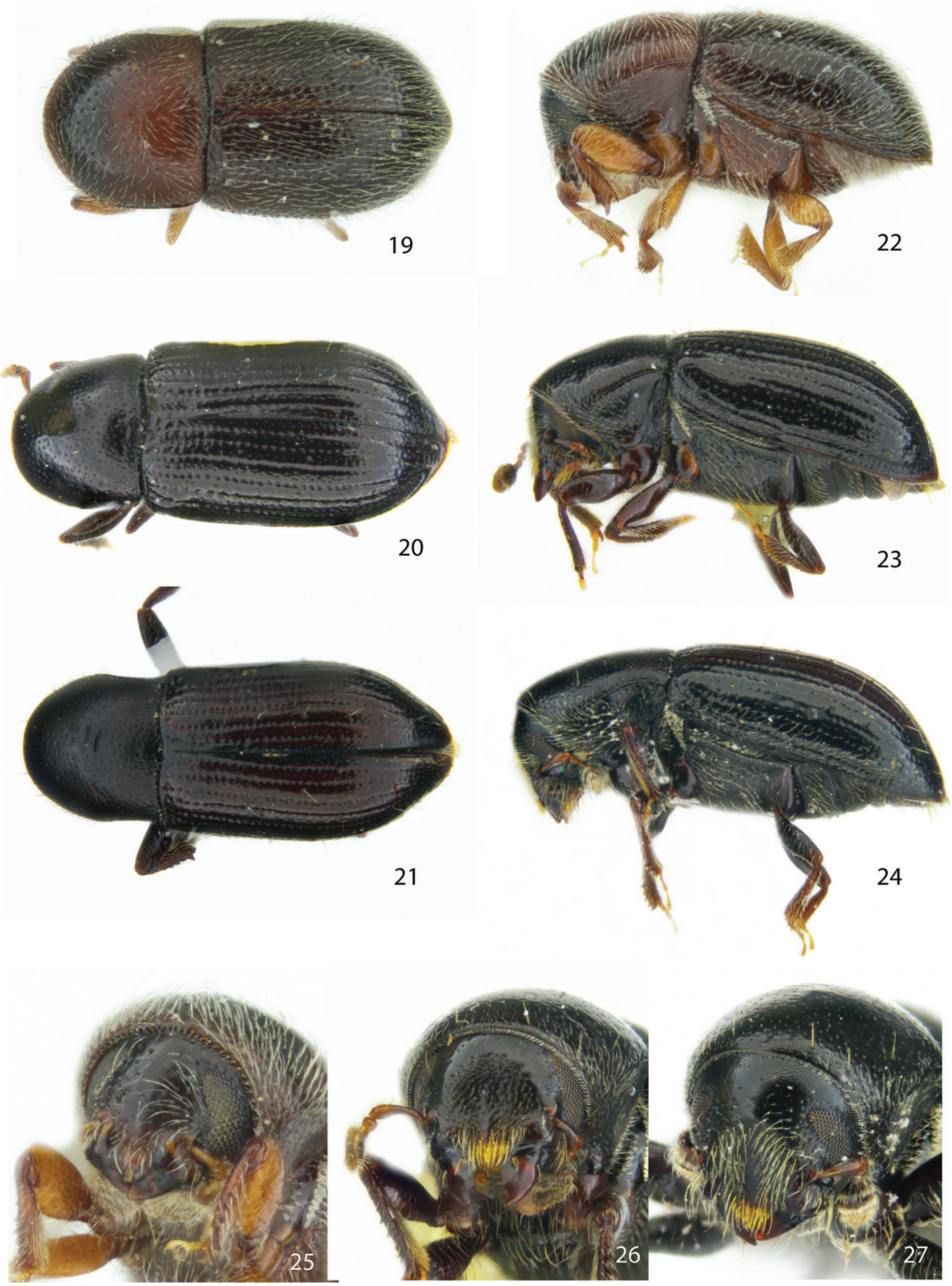
Scolytodes spatulatus Jordal & Kirkendall, sp. nov.

http://zoobank.org/D4ABB6CF-6F5B-463F-A351-3D1E24D1A676
Figs 19, 22, 25

Type material. Holotype: Costa Rica, Prov. Heredia, 11 km ESE La Virgen, 250–350 m, 10°21'N, 84°03'W, 21 Mar. 2004, INBio-OET-ALAS transect, Intercept trap 03/TN/14/017, INB0003619017. Holotype deposited in MNCR.

Diagnosis. Interstriae 10 weakly carinate to level of metacoxa, interstriae 9 carinate on posterior half; protibiae without additional mesal tooth. Distinguished from *S. comosus* by the long spatulate setae on each declivital striae, by the broader shape of the pronotum, the more narrowly separated eyes, and by the plumose setae on the metanepisternum.

Description, female(?) Length 1.3 mm, 2.1 × as long as wide; color dark brown. ***Head.*** Eyes entire, separated above by 2.1 × their width. Frons generally flat, narrowly impressed just above epistoma, surface irregularly punctured, reticulate; vestiture consisting of sparse long fine setae pointing medially. Antennal club setose, sutures not discernible, basal part of segment 1 corneous. Funiculus possibly 5-segmented. ***Pronotum***



Figures 19–27. Dorsal, lateral and frontal view of the female holotype of **19, 22, 25** *Scolytodes spatulatus* **20, 23, 26** *S. seriatus* **21, 24, 27** *S. profundus*.

smooth on posterior half, with shallow punctures spaced by 1–2 × their diameter, on anterior half replaced by low scattered asperities; surface reticulate, subshining. Vestiture consisting of long fine setae (0–0–0). ***Elytra*** generally smooth, but punctures crenulated; striae not impressed, punctures small, crenulated on the anterior margin, spaced by 1–2 × their diameter; punctures in interstriae similar and entirely confused with those in striae. Interstriae 10 weakly carinate to level of metacoxa, interstriae 9 carinate on posterior half. Vestiture consisting of long fine strial and interstrial setae, with additional spatulate long setae in each striae on declivity. ***Legs.*** Procoxae separated by 1.0 × and mesocoxae 1.2 × the width of one procoxa. Protibiae broad, lateral tooth 1 as long as 2, tooth 2 exposed and socketed, with additional 2–3 granules along the lateral edge towards base; protibial mucro large, and curved posteriorly. Meso- and metatibiae with 6 socketed lateral teeth on distal half. ***Ventral vestiture.*** Setae on metanepisternum trifid or plumose, on metasternum long and simple; sclerolepidia and setae on epimeron plumose.

Key (Wood 1982). Keys to couplet 6 with no match (see *S. comosus*, above). One should reach couplet 20, near *S. punctiferus*.

Etymology. The Latin name *spatulatus* is a masculine adjective, meaning spatula-like, referring to the broad tips of the longest setae on declivity.

Biology and distribution. This species is only known from the type locality in a lowland rain forest site south of La Selva Biological Station.

Scolytodes seriatus Jordal & Kirkendall, sp. nov.

http://zoobank.org/5CC0C3CB-F4C7-48C4-8B32-E2E735E86068
Figs 20, 23, 26

Type material. Holotype, female: Costa Rica, Prov. Heredia, 6 km ENE Vara Blanca, 1950–2050 m, 10°11'N, 84°07'W, 21 Feb. 2002, INBio-OET-ALAS transect, 20/TN/15/008, INB0003223280. **Allotype, male:** same data as holotype, except 9 Apr., transect 20/M/06/066, INB0003221635. **Paratypes:** same data as holotype except 21 Apr., transect 20/TN/15/028, INB0003223644 (1); 13 Apr., transect 20/RG/DBM/010, INB0003657266 (1). Holotype and allotype deposited in MNCR, 1 paratype in USNM, 1 paratype in ZMBN.

Diagnosis. Interstriae 10 sharply carinate to near apex; protibiae with a tiny, sharp, additional mesal tooth near tarsal insertion. Distinguished from *S. clusiacolens* Wood, 1967 and *S. prolatus* Jordal, 2018 by the stouter body shape and subobovate elytra, by the smaller body size, and by the regular placement of fine setae only on interstriae 3, 5, 7 and 9.

Description female. Length 2.1–2.3 mm, 2.3–2.4 × as long as wide; color black. ***Head.*** Eyes entire, separated above by 2.5–3.0 × their width. Frons impressed on a semi-circular area from just below upper level of eyes to epistoma, surface finely, densely punctured, finely reticulate; vestiture consisting of fine short setae. Antennal club with two obliquely procurved sutures marked by white setae, segment 1 and 2 mainly corneous, segment 3 setose. Funiculus 6-segmented. ***Pronotum*** smooth, finely reticulate, with fine punctures spaced by 1–2 × their diameter. Vestiture consisting of six erect long setae (4–2–0). ***Elytra*** smooth, shiny, striae distinctly impressed, punctures in rows spaced by 2 × their diameter; punctures in interstriae in irregular rows, shallow, smaller and more widely spaced. Interstriae 10 sharply carinate to near apex. Vestiture consisting of erect long setae, on interstriae 3, 5, 7 and 9. ***Legs.*** Procoxae separated by 0.5 × and mesocoxae 0.9 × the width of one procoxa. Protibiae narrow, lateral teeth 1 and 2 of sub-equal length, with 4–5 additional sharp small teeth along the lateral edge towards base; a tiny, sharp, additional mesal tooth present near tarsal insertion; protibial mucro short and curved, almost obtuse. Meso- and metatibiae with 6–7 small socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum trifid or bifid, on metasternum long and simple; sclerolepidia rounded scales.

Male. Similar to female except frons convex, with distinct abrupt impression on epistoma; eyes separated above by 3.3–3.6 × width of the eye; vestiture on frons consisting of few short setae.

Key (Wood 1982). Keys to couplet 6 but do not match due to the combination of a long interstriae 10 and the presence of a mesal protibial tooth. The same applies to *S. clusiacolens*, its closest relative.

Etymology. The Latin name *seriatus* is a Latin masculine adjective meaning seriate, referring to the deeply impressed rows of closely set punctures in the striae.

Biology and distribution. This species is only known from the type locality in Costa Rica at high altitude.

Scolytodes profundus **Jordal & Kirkendall, sp. nov.**

http://zoobank.org/EE501239-19BC-43E8-951F-EA32A31F2EB8
Figs 21, 24, 27

Type material. Holotype, female: Costa Rica, Guanacaste, Guanacaste cons. Area, Rincon de La Vieja, Las Pailas, 1650 m, 19.II.1996-021A, R. Anderson, windblown cloud forest ridge litter. **Allotype, male:** same data as holotype. **Paratypes:** Alajuela, PN Volcan Poas, 2500 m, 10°11'30"N, 84°14'W, 6.VI.1997, R. Anderson, wet cloud for. litter, 97-003 (4); wet mount. for. FIT 6-28.VI.97, S. & J. Peck, 97-16 (1); Hered. Prov, Cerro Chompipe, 2100 m 10km NNE Heredia, 12–27.VI.97, mont. for. FIT, S. & J. Peck, 97-21 (1); Prov. Heredia, 6 km ENE Vara Blanca, 1950–2050 m, 10°11'N, 84°07'W, 16 Mar. 2002, INBio-OET-ALAS transect, 20/WF/03/43, INB0003223948 (1); holotype, allotype and 1 paratype in FSCA, 2 paratypes in USNM, 2 paratypes in ZMBN, 2 paratypes in MNCR.

Diagnosis. Interstriae 10 sharply carinate to near apex; protibiae with a tiny, additional mesal tooth at the base of lateral tooth 2. Distinguished from *S. seriatus* by the more elongated shape and narrowly rounded apex of the elytra, by the reticulate pronotum that is constricted on basal one-fourth, and the different female frons.

Description female. Length 2.0–2.2 mm, 2.2–2.4 × as long as wide; color black. ***Head.*** Eyes entire, separated above by 3.3–3.6 × their width. Frons impressed on a semi-circular area from just below upper level of eyes to epistoma, surface densely punctured, except for a longitudinal median impunctate shiny glabrous band; vestiture consisting of fine short setae in punctured part of impressed area. Antennal club with two obliquely procurved sutures marked by short white setae, segment 1 and 2 mainly corneous, segment 3 setose. Funiculus 6-segmented. ***Pronotum*** slightly constricted laterally on basal on-fourth, surface smooth, reticulate, with fine punctures spaced by 2–3 × their diameter. Vestiture consisting of six erect long setae (4–2–0). ***Elytra*** smooth, shiny, striae distinctly impressed, punctures spaced by 2–3 × their diameter; punctures in interstriae confused, smaller and more widely spaced, intermixed with strial punctures. Interstriae 10 sharply carinate to near apex. Vestiture consisting of erect long acuminate setae on interstriae 3, 5, 7 and 9 only. ***Legs.*** Procoxae separated by 0.6 × and mesocoxae 0.9 × the width of one procoxa. Protibiae narrow, lateral teeth 1 and 2 sub-equal in length, with 5 small granules along the lateral edge towards base; a tiny, additional mesal tooth present at the base of lateral tooth 2; protibial mucro obtuse. Meso- and metatibiae with 6 small socketed lateral teeth on distal half and distal third, respectively. ***Ventral vestiture.*** Setae on metanepisternum bifid, on metasternum long and simple; sclerolepidia small rounded scales.

Male. Similar to female, except frons convex, with distinct abrupt impression on epistoma; eyes separated above by 3.9–4.1 × the width of eye; vestiture of frons consisting of a few short setae.

Key (Wood 1982). Keys to couplet 6 but does not match (long interstriae 10, presence of mesal protibial tooth). The same applies to *S. clusiacolens* and *S. seriatus*, presumably the closest relatives.

Etymology. The Latin name *profundus* is a masculine adjective, meaning deep or profound, referring to the deeply impressed striae comprising relatively small but densely placed punctures.

Biology and distribution. This species is known from several upper cloud forest localities in Costa Rica. One specimen was reared from sifted litter samples (miniWinkler method).

Scolytodes catinus Jordal & Kirkendall, sp. nov.

http://zoobank.org/91F7BCD1-0E37-4B71-A04B-624043DE576D
Figs 28, 31, 34

Type material. Holotype, female: Costa Rica, Heredia, near Virgen de Socorro, 10°14.4'N, 84°07.5'W, 1475 m, 11 Apr. 2005, L. Kirkendall #050411-1, 8 mm diameter *Clusia* branch. **Allotype, male:** same data as holotype. **Paratypes**: same data as holotype (3). Holotype, allotype, 1 paratype deposited in MNCR, 1 paratype in ZMBN, 1 paratype in USNM.

Diagnosis. Interstriae 10 weakly carinate to just before level of metacoxa; protibiae with a tiny, additional mesal tooth at the base of lateral tooth 2. Pronotum asperate on anterior third. Metanepisternum with a row of characteristic, broad, plumose setae.

Figures 28–36. Dorsal, lateral and frontal view of the female holotype of **28, 31, 34** *Scolytodes catinus* **29, 32, 35** *S. fimbriatus* **30, 33, 36** *S. sulcifrons*.

Distinguished from *S. pumilus* Wood, 1969, by the lack of interstrial punctures, less abundant vestiture of the female frons, and the different setae on the metanepisternum.

Description female. Length 1.7–1.8 mm, 2.6–2.7 × as long as wide; color black. ***Head.*** Eyes sinuate, separated above by 2.5–2.6 × their width. Frons weakly impressed on a semi-circular area on median half on lower two-thirds, surface in impressed area punctured, reticulate, dull, vertex shiny, with scant fine punctures; vestiture consisting of fine short setae in impressed area. Antennal club with two obliquely recurved sutures (posterior side procurved) marked by white setae, segment 1 and 2 corneous. Funiculus 5-segmented, segments very short, disc-like. ***Pronotum*** reticulate, with fine punctures on posterior two-thirds spaced by 3–4 × their diameter, replaced on anterior one-third by fine asperities. Vestiture consisting of six erect long setae (4–2–0). ***Elytra*** smooth, shiny, striae not impressed, punctures tiny, spaced by 2–3 × their diameter, with additional microscopic puncture associated near each main puncture; punctures in interstriae absent. Interstriae 10 weakly carinate to just before level of metacoxa. Vestiture consisting of ca 20 erect long setae on odd-numbered interstriae. ***Legs.*** Procoxae separated by 0.8 × and mesocoxae 1.1 × the width of one procoxa. Protibiae broadening apically, lateral teeth 1 and 2 of sub-equal size, with 3–6 additional small granules along the lateral edge towards base; a tiny, additional mesal tooth present at the base of lateral tooth 2; protibial mucro obtuse. Meso- and metatibiae with 6 and 5 small socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum broadly plumose, on metasternum long and simple; sclerolepidia small, round scales.

Male. Similar to female, except frons convex, with slight impression on epistoma; vestiture consisting of a few setae on epistoma.

Key (Wood 1982). Keys to couplet 53, *S. pumilus*, but differs as indicated in the diagnosis.

Etymology. The Latin name *catinus* is a masculine noun meaning plate or bowl, referring to the smoothly impressed female frons. It is invariable.

Biology and distribution. This species is only known from the type locality at medium altitude in Costa Rica. Specimens were collected from a thin dead branch on a live *Clusia* tree along with individuals of the smaller species *S. callosus* Jordal and Kirkendall (described below).

Scolytodes fimbriatus Jordal & Kirkendall, sp. nov.

http://zoobank.org/28003000-7A86-4107-B674-A1102D8B7289
Figs 29, 32, 35

Type material. Holotype, female: Costa Rica, Alajuela Province, N slope Volcan de Rincon, 2 km W. Dos Rios, 550 m, V-22-85. Blacklight. J.T. Doyen and P.A. Opler coll. [EMEC49554]. **Paratype female:** same data as holotype. The holotype is deposited in EMEC, 1 paratype in USNM.

Diagnosis. Interstriae 10 carinate to near apex; protibiae with a tiny, additional mesal tooth near base of mucro. Pronotum lightly wrinkled on anterior third, punctured from base to anterior margin. Distinguished from the most similar species *S. puer* (Schedl, 1952), *S. frontoglabratus* (Schedl, 1935) and *S. amoenus* Wood, 1967 by the long shiny median field on the female frons, the presence of exactly 6 erect setae on elytra, and by the presence of a minute additional mesal tooth on the protibia.

Description female. Length 2.0–2.1 mm, 2.2 × as long as wide; color light reddish brown to black, darkest on anterior half of pronotum, and near the elytral base and suture. ***Head.*** Eyes entire, separated above by 2.7 × their width. Frons weakly flattened between eyes, a longitudinal shiny impunctate area on median third on lower half, surrounded by fine medium-long curved setae. Antennal club setose, with two two strongly procurved sutures marked by longer setae, segment 1 and 2 darker, almost corneous. Funiculus 6-segmented. ***Pronotum*** reticulate, with fine punctures spaced by 1–2 × their diameter, anterior half with very fine asperities in front of each puncture. Vestiture consisting of six erect long setae (4–0–2). ***Elytra*** smooth, shiny; striae not impressed, punctures in row spaced by their diameter; interstriae broad, 4 × as wide as striae, punctures confused except almost seriate on interstriae 4. Interstriae 10 carinate to near apex. Vestiture consisting of 6 erect setae, one each at base of interstriae 7, one near declivity on interstriae 9 and 7. ***Legs.*** Procoxae separated by 0.6 × and mesocoxae 0.8 × the width of one procoxa. Protibiae parallel-sided, lateral teeth 1 and 2 of equal size, with 4 additional small granules along the lateral edge towards base; a tiny, additional mesal tooth present near base of mucro; protibial mucro very short curved posteriorly. Meso- and metatibiae with 5–6 small socketed lateral teeth on distal half. ***Ventral vestiture.*** Setae on metanepisternum and metasternum simple, on mesanepisternum trifid; sclerolepidia small round scales.

Male. Not known.

Key (Wood 1982). Keys to couplet 9, *S. amoenus*, but differs as indicated in the diagnosis.

Etymology. The Latin name *fimbriatus* is a masculine adjective, meaning fringed, referring to the broad circle of golden erect setae in the female frons, surrounding a large impunctate and shining area.

Biology and distribution. This species is only known from the lowland type locality in Costa Rica. Two individuals were attracted to UV light.

Scolytodes sulcifrons Jordal & Kirkendall, sp. nov.

http://zoobank.org/8F18E732-7AB0-4B0D-9597-7CD98E03541F

Figs 30, 33, 36

Type material. Holotype, female: Costa Rica, Prov. Heredia, 10 km SE La Virgen, 450–550 m, 10°20'N, 84°05'W, 14 Mar. 2003, #030314-3 [L. Kirkendall, leg]. **Allotype male and paratypes (2):** same data as holotype. Holotype and allotype deposited in MNCR, 1 paratype in USNM, 1 paratype in ZMBN.

Diagnosis. Interstriae 10 carinate to level of metacoxae; interstriae 9 carinate between level of metanepisternum and elytral apex; protibiae with an additional mesal tooth near tarsal insertion. Distinguished from the very similar species *S. planifrons* Jordal & Kirkendall (described below) and *S. clusiapraelatus* Jordal, 2013 by the sulcate female frons, the presence of several more and much longer elytral setae, and by the regularly sized and spaced strial punctures.

Description female. Length 1.3–1.4 mm, 2.0–2.1 × as long as wide; color dark brown to black. ***Head.*** Eyes entire, separated above by 2.5–2.6 × their width. Frons impressed on median third from just below upper level of eyes to epistoma, slightly elevated along margin of impressed area; impressed and elevated area with deep large punctures approximately in longitudinal rows. Vestiture consisting of sparse, fine setae associated with punctures. Antennal club setose, with two obliquely procurved sutures weakly marked by longer setae. Funiculus 5-segmented. ***Pronotum*** reticulate, with minute punctures spaced by 4–8 × their diameter. Vestiture consisting of two erect long setae along the median part of the anterior margin (2–0–0). ***Elytra*** smooth, shiny; striae not (or very weakly) impressed, small punctures spaced by 2–3 × their diameter; interstriae 3–4 × as wide as striae, scant punctures barely visible, confused. Interstriae 10 carinate to level of metacoxae; interstriae 9 carinate between level of metanepisternum and elytral apex. Vestiture consisting of 10–14 erect long setae on interstriae 3 and 7. ***Legs.*** Procoxae separated by 0.6 × and mesocoxae 1.0 × the width of one procoxa. Protibiae broadening slightly distally, lateral teeth 1 and 2 of sub-equal size, with 3–4 additional, small granules along the lateral edge towards base; all teeth, particularly 1 and 2 are connected by a thin, semi-transparent extension of the cuticle; an additional mesal tooth present near tarsal insertion; protibial mucro straight, short. Meso- and metatibiae with 7 and 6 lateral, socketed, small teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum and metasternum simple, on mesanepisternum trifid; sclerolepidia small, round scales.

Male. As in female, except frons convex, with scant short setae near epistoma.

Key (Wood 1982). Keys to couplet 22, with no further match.

Etymology. The Latin name *sulcifrons* is composed by the stem of the masculine adjective *sulcus*, meaning furrow, a linking vowel –i, and the noun *frons*, meaning forehead, referring to the broad longitudinal furrow in the female frons. It is invariable.

Biology and distribution. This species is only known from the lowland type locality in Costa Rica. Individuals were collected from the bark of a 9 cm-diameter standing dead tree that was covered with thick moss.

Scolytodes planifrons **Jordal & Kirkendall, sp. nov.**

http://zoobank.org/86558F26-7F63-4C40-BE9A-97AEB04C9897
Figs 37, 40, 43

Type material. Holotype, female: Costa Rica, Prov. Heredia, 9 km NE Vara Blanca, 1450–1550 m, 10°14'N, 84°06'W, 22 Mar. 2005, INBio-OET-ALAS transect, Finca Murillo, 15/WF/01/50, INB0003665427. **Allotype male:** same data as holotype,

Figures 37–45. Dorsal, lateral and frontal view of the female holotype of **37, 40, 43** *Scolytodes planifrons* **38, 41, 44** *S. porosus* **39, 42, 45** *S. mundus*.

INB0003665426. **Paratype:** same data as holotype, INB0003665425 (1f); 6 km ENE Vara Blanca, 1950–2050 m, 10°11'N, 84°07'W, 17 Feb. 2002, INBio-OET-ALAS transect, 20/WF/01/22, INB0003223047 (1f). Holotype and allotype deposited in MNCR, 1 paratype in USNM, 1 paratype in ZMBN.

Diagnosis. Interstriae 10 carinate to level of metacoxae; interstriae 9 carinate between level of metanepisternum and elytral apex; protibiae with an additional mesal tooth near tarsal insertion. Distinguished from the the very similar species *S. sulcifrons* and *S. clusiapraelatus* Jordal, 2013 by the flat lower frons of females, the small elytral setae, and by the paired strial punctures.

Description female. Length 1.4–1.5 mm, 2.0–2.1 × as long as wide; color dark brown to black. ***Head.*** Eyes entire, separated above by 2.8–3.0 × their width. Frons convex on upper half, entirely flat with scant fine punctures below. Vestiture consisting of sparse fine setae associated with punctures. Antennal club setose, with two transverse sutures weakly marked by longer setae. Funiculus 6-segmented. ***Pronotum*** shiny, very weakly reticulate, with small punctures spaced by 2–3 × their diameter. Vestiture consisting of two erect long setae along the median part of the anterior margin (2–0–0). ***Elytra*** smooth, shiny; striae not impressed, small punctures in rows, two and two in longitudinal pairs, each pair spaced by the length of a pair; interstriae 3–4 × as wide as striae, punctures of same size as in striae, widely spaced, mainly in rows. Interstriae 10 carinate to level of metacoxae; interstriae 9 carinate between level of metanepisternum and elytral apex. Vestiture consisting of 2–4 short erect interstrial setae, minute recumbent setae elsewhere. ***Legs.*** Procoxae separated by 0.5 × and mesocoxae 0.9 × the width of one procoxa. Protibiae broadening slightly distally, lateral teeth 1 and 2 of sub-equal size, with 2–3 additional small teeth along the lateral edge towards base; an additional mesal tooth present near tarsal insertion; protibial mucro, short, slightly curved posteriorly. Meso- and metatibiae with 7 and 6 small socketed lateral teeth on distal half. ***Ventral vestiture.*** Setae on metanepisternum and metasternum simple; sclerolepidia small round scales.

Male. Nearly identical to female, frons slightly more rounded on lower half, body length 1.3–1.4 mm.

Key (Wood 1982). Keys to couplet 22, with no further match.

Etymology. The Latin name *planifrons* is composed by the stem of the masculine adjective *planus*, meaning flat, the linking vowel –i, and the noun *frons*, meaning forehead, referring to the completely flat and shiny lower frons of the female (and almost so in male). It is invariable.

Biology and distribution. This species is only known from two high altitude localities in Costa Rica. The four individuals were reared from sifted litter samples (miniWinkler method).

Scolytodes porosus Jordal & Kirkendall, sp. nov.

http://zoobank.org/CEC1D42A-A771-4F6B-99C6-089CF14D080D
Figs 38, 41, 44

Type material. Holotype, presumably female: Costa Rica, Prov. Heredia, 9 km NE Vara Blanca, 1450–1550 m, 10°14'N, 84°06'W, 6 Apr. 2005, INBio-OET-ALAS transect, #050406-3 [ex *Clusia*, L. Kirkendall, leg]. **Paratype** female: same data as holotype, except 8 Mar. 2005, 15/M/15/040, Finca Murillo, INB0003669571. Holotype deposited in MNCR, 1 paratype in USNM.

Diagnosis. Interstriae 10 carinate to level of metacoxae; protibiae with an additional mesal tooth near tarsal insertion. Similar to *S. minutus* Wood, 1981, with the combination of deep large punctures on pronotum and elytra, and spatulate shape of elytral setae, but differs from *S. minutus* by the larger size, black color, and the smooth and more elongated pronotum.

Description female(?) Length 1.5–1.6 mm, 2.7 × as long as wide; color dark brown to black. ***Head.*** Eyes entire, separated above by 2.6–2.7 × their width. Frons convex, with few shallow tiny punctures, surface shiny, reticulate on epistoma and vertex. Vestiture consisting of sparse fine setae on lower frons, denser on epistoma. Antennal club with two transverse sutures marked by short setae, segments 1 and 2 corneous, segment 3 setose. Funiculus 6-segmented. ***Pronotum*** shiny, with large deep punctures spaced by less than their diameter. Vestiture consisting of 8 longer erect setae (4–2–2), on the anterior part additional fine short setae. ***Elytra*** smooth, shiny; striae not impressed, punctures large, deep, separated in rows by less than their diameter, smaller on declivity; interstriae as broad as striae, punctures much smaller than in striae, widely spaced. Interstriae 10 carinate to level of metacoxae. Vestiture consisting of erect interstrial setae which are bristle-like near base of elytra and spatulate on posterior part and declivity, and fine short recumbent setae in striae. ***Legs.*** Procoxae separated by 0.4 × and mesocoxae 0.6 × the width of one procoxa. Protibiae broadening distally, lateral teeth 1 and 2 of equal size, tooth 2 socketed and exposed, with 2–3 additional small teeth along the lateral edge towards base; an additional mesal tooth present near tarsal insertion; protibial mucro obtuse. Meso- and metatibiae with 6 and 5 small socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum trifid to broadly plumose, on metasternum mainly simple, bifid near episternal suture; sclerolepidia broad plumose scales.

Male(?). Presumably identical to the female. Sex of holotype is not determined but is identical to the female paratype with one elytron (exposing seven visible tergites).

Key (Wood 1982). Keys to couplet 25, with no further match.

Etymology. The Latin name *porosus* is a masculine adjective, meaning porous, referring to the densely and deeply punctured pronotum and elytra.

Biology and distribution. This species is only known from the high altitude type locality in Costa Rica. One individual was collected in a Malaise trap, the other was dissected from a *Clusia* branch.

Scolytodes mundus Jordal & Kirkendall, sp. nov.

http://zoobank.org/AD4DA531-187D-4450-A4B1-959D69F1001D
Figs 39, 42, 45

Type material. Holotype, female: Costa Rica, Prov. Heredia, 11 km SE La Virgen, 450–550 m, 10°20'N, 84°05'W, 17 Mar. 2003, INBio-OET-ALAS transect, 05/F/02/30, INB0003605900. **Allotype, male:** same data as holotype, 05/F/02/30 (INB0003605847). **Paratypes:** same data as holotype, 05/F02/13 (INB0003605727) (1); same data except

16 Feb., 05/F/01/24 (1); same data except 12 Apr., 05/F/03/37 (INB0003605900) (1). Holotype and 2 paratypes are deposited in MNCR, 1 paratype in ZMBN, 1 in USNM.

Diagnosis. Interstriae 10 carinate to level of ventrite 1; protibiae with an additional mesal tooth near base of tooth 2. Distinguished from the very similar *S. callosus* Jordal & Kirkendall (described below) by the convex female frons which lacks a callus above epistoma, by the abundance of confused interstrial micro-punctures, and the entire eyes which are more broadly separated above.

Description, female. Length 1.3–1.5 mm, 2.7 × as long as wide; color black. ***Head.*** Eyes entire, separated above by 2.8–3.1 × their width. Frons convex, short; surface weakly reticulate, more strongly so on vertex, with large punctures intermixed with micro-punctures on lower half. Vestiture consisting of fine setae from below upper level of eyes to epistoma. Antennal club and funiculus not clearly visible on specimens. ***Pronotum*** shiny, with shallow small punctures spaced by 3–4 × their diameter; faint asperities present on anterior fifth. Vestiture consisting of 8 erect long setae (4–2–2). ***Elytra*** smooth and shiny, cuticle slightly wrinkled at interstriae 1 and 2; striae 1 and 2 weakly impressed, others not, punctures small, deep, associated with a micro-puncture and together appears like one elongated puncture, each pair separated in rows by less than their length; interstriae 3–4 × as wide as striae, with abundant, confused micro-punctures, particularly abundant on interstriae 1–5. Interstriae 10 carinate to level of ventrite 1. Vestiture consisting of about 40 erect setae regularly distributed on odd-numbered interstriae. ***Legs.*** Procoxae separated by 0.4 × and mesocoxae 0.9 × the width of one procoxa. Protibiae narrow, lateral teeth 1 and 2 of equal size, with 3 additional small teeth along the lateral edge towards base; an additional mesal tooth present near base of tooth 2; protibial mucro obtuse. Meso- and metatibiae with 6 and 5 small socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum and metasternum simple, on mesanepisternum bifid. Sclerolepidia very small elongated scales.

Male. Near identical to female.

Key (Wood 1982). Keys to couplet 25, with no further match.

Etymology. The Latin name *mundus* is a masculine adjective, meaning clean, pure, or neat, referring to the small size of the species, with few, very fine, setae on elytra and in the female frons, and the generally shiny appearance.

Biology and distribution. This species is only known from the type locality at 500 m altitude in Costa Rica. Specimens were collected from three different fogging events (http://viceroy.eeb.uconn.edu/alas/canopy03.html). The species is morphologically very similar to other small *Scolytodes* species breeding in *Clusia*.

Scolytodes callosus Jordal & Kirkendall, sp. nov.

http://zoobank.org/1CE53A64-A4CE-4D1D-9A3E-7B03D0CD9B3E
Figs 46, 49, 52

Type material. Holotype, female: Costa Rica, Prov. Heredia, 16 km SSE La Virgen, 1050–1150 m, 10°16'N, 84°05'W, 19 Feb. 2001, INBio-OET-ALAS transect, #010219-5, ex dead branch of *Clusia* [L. Kirkendall, leg]. **Allotype male:** same data as holotype. **Paratypes:** same data as holotype (2); Heredia, near Virgen de Socorro, 10°14.4'N, 84°07.5'W, 1475 m, 11 Apr. 2005, #050411-1, ex *Clusia* 8 mm dia. [L. Kirkendall, leg] (4); Prov. Heredia, 16 km SSE La Virgen, 1050–1150 m, 10°16'N, 84°05'W, 21 Mar. 2001, INBio-OET-ALAS transect, 11/TN/16/016 and 11/TN/06/011 (2); Prov. Heredia, 9 km NE Vara Blanca, 1450–1550 m, 10°14'N, 84°06'W, 6 Apr. 2005, INBio-OET-ALAS transect, #050406-3, ex dead branch of *Clusia* [L. Kirkendall, leg] (1); 17 Apr. 2005, 15/TN/08/024 (1); 20 Mar. 2005, 15/TN/11/016 (1); 20 Feb. 2001, 15/TN/04/002 (1); Prov. Heredia, 10 km SSE La Virgen, 450–550 m, 10°20'N, 84°05'W, 16 Mar. 2003, INBio-OET-ALAS transect, #030316-2 ex *Clusia* 2 cm dia. [L. Kirkendall, leg] (2); 11 km SSE La Virgen, 250–350 m, 10°21'N, 84°03'W, 11 Apr. 2004, INBio-OET-ALAS transect, #040411-1 [L. Kirkendall, leg] (1). Holotype, allotype and 8 paratypes are deposited in MNCR, 4 paratypes in ZMBN, 4 paratypes in USNM.

Diagnosis. Interstriae 10 carinate to level of ventrite 1; protibiae with an additional mesal tooth near base of tooth 2. Distinguished from the very similar *S. mundus* by the impressed lower female frons which has a small median callus just above epistoma, by the sparse, but regular, interstrial punctures, by the more broadly separated pro- and mesocoxae, and by the slightly emarginated eyes which are less broadly separated above.

Description female. Length 1.2–1.5 mm, 2.4–2.5 × as long as wide; color dark brown. ***Head.*** Eyes weakly emarginated along anterior margin, separated above by 2.4–2.6 × their width. Frons weakly impressed on a semi-circular area from just below upper level of eyes to near epistoma, surface strongly reticulate, with dense small punctures; a short median vertically elongated callus just above epistoma. Vestiture consisting of a mixture of fine short setae, and longer semi-erect setae, in impressed area. Antennal club with two recurved sutures on anterior face marked by short setae, on posterior side procurved, forming two oblique rings around the club; funiculus not clearly visible, likely 5-segmented. ***Pronotum*** strongly reticulate, with shallow tiny obscure punctures spaced by 3–5 × their diameter; faint asperities present on anterior fifth. Vestiture consisting of 8 erect long setae (4–2–2). ***Elytra*** generally smooth and shiny, sub-rugose on interstriae 1–3; striae 1 impressed, others not, punctures small, deep, associated with a micro-puncture and together appears like one elongated puncture, each pair separated in rows by less than their length; interstriae 3–4 × as wide as striae, with few small scattered punctures. Interstriae 10 carinate to level of ventrite 1. Vestiture consisting of about 25 erect setae regularly distributed on odd-numbered interstriae. ***Legs.*** Procoxae separated by 0.7 × and mesocoxae 1.1 × the width of one procoxa. Protibiae narrow, lateral teeth 1 and 2 of equal size, with 1–2 additional small granules along the lateral edge towards base; an additional mesal tooth present near base of tooth 2; protibial mucro obtuse. Meso- and metatibiae with 7 and 6 small socketed lateral teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum and mesanepisternum bifid, on metasternum and part of metanepisternum simple. Sclerolepidia large, plumose-like scales.

Male. Similar to female, except frons convex, flattened just above (and level with) epistoma, with fine punctures and scant fine setae.

Figures 46–54. Dorsal, lateral and frontal view of the female holotype of **46, 49, 52** *Scolytodes callosus* **47, 50, 53** *S. parvipilus* **48, 51, 54** *S. plenus*.

Key (Wood 1982). Keys to couplet 25, with no further match.

Etymology. The Latin name *callosus* is a masculine adjective, meaning hard, thick skin, referring to an elevated median callus just above the epistoma in females.

Biology and distribution. This species is known from rainforest localities on the northern slopes of Braulio Carrillo in Costa Rica. Specimens were dissected from thin branches and twigs of *Clusia*, or collected by flight intercept traps (TN). The majority were collected in cloud forest. Some specimens were from the same twig as the larger species *S. catinus*.

Scolytodes parvipilus Jordal & Kirkendall, sp. nov.

http://zoobank.org/420406F4-6583-4EF9-9BAC-D065EC221143

Figs 47, 50, 53

Type material. Holotype, female: Costa Rica, Prov. Heredia, 16 km SSE La Virgen, 1050–1150 m, 10°16'N, 84°05'W, 20 Feb. 2001, INBio-OET-ALAS transect, 11/TN/16/006, INB0003209608. **Allotype male:** Tapanti, Cartago, 4000 ft, IX-17-1963, S.L. Wood, ex unknown branch, #180, *Scolytodes* sp. det. S. L. Wood. **Paratype** (1 female): same data as allotype. Holotype deposited in MNCR, allotype and paratype in USNM. **Other material.** Same data as holotype, INB0003209621; only abdomen with elytra on point.

Diagnosis. Interstriae 10 carinate to apex; protibiae without additional mesal tooth. The combination of few erect interstrial setae, and ground vestiture consisting of fine recumbent strial and interstrial setae, distinguish this species from several species related to *S. chapuisi* Wood, 1977 or *S. pseudopiceus* Wood, 1969, and further from *S. venustus* Wood, 1969 by the long abundant setae in the female frons.

Description female. Length 1.7–1.8 mm, 2.3–2.4 × as long as wide; color light brown. ***Head.*** Eyes entire, separated above by 1.8–1.9 × their width. Frons flattened from vertex to epistoma, surface shiny, median fifth impunctate and very weakly elevated, punctured elsewhere at base of setae. Vestiture consisting of long, golden setae arising from vertex and upper lateral areas of flattened area, tips of setae reaching level of antennal insertion. Antennal club setose, two procurved sutures weakly marked by shorter setae; funiculus not clearly visible, likely 6-segmented. ***Pronotum*** strongly reticulate, with shallow, obscure punctures spaced by 1–2 × their diameter; faint asperities present on anterior third. Vestiture consisting of 8 erect long setae (4–2–2). ***Elytra*** generally smooth and shiny; striae not impressed, punctures shallow, separated in rows by their diameter, confused with interstriae on declivity; interstriae on average 2 × as wide as striae, with confused punctures slightly smaller than in striae. Interstriae 10 carinate to apex. Vestiture consisting of about 15–20 erect setae on odd-numbered interstriae, and fine recumbent ground vestiture in both striae and interstriae. ***Legs.*** Procoxae narrowly separated by 0.2 × and mesocoxae 0.7 × the width of one procoxa. Protibiae narrow, parallel-sided, lateral teeth 1 slightly as long as 2, with 3–5 additional small rugae or granules along the lateral edge towards base; protibial mucro obtuse. Meso- and metatibiae with 7 and 6 lateral, socketed, small teeth on distal half and third, respectively. ***Ventral vestiture.*** Setae on metanepisternum and metasternum simple, on mesanepisternum bifid. Sclerolepidia very small, scale-like.

Male. Similar to female, except size 1.6 mm; frons more convex, with a very weakly formed carina from epistoma to near upper level of eyes, punctures obscure, surface strongly reticulate, nearly glabrous except epistoma.

Key (Wood 1982). Keys to couplet 17, with no close match to *S. venustus* or *S. pseudopiceus*.

Etymology. The Latin name *parvipilus* is composed by the stem of the adjective *parvus*, meaning small, the linking vowel –i, and the noun *pilus*, meaning fine hair, referring to the small curly or recumbent fine setae on the elytra, with only a few erect, longer, setae. It is invariable.

Biology and distribution. This species is known from two Costa Rican cloud forest localities – the northern slopes of Braulio Carrillo, and Tapanti. Two specimens were collected in the same flight intercept trap, and two specimens were dissected from an unidentified branch.

Scolytodes plenus Jordal & Kirkendall, sp. nov.

http://zoobank.org/C0E3C083-60DF-4C78-AB40-48C5CBDFAE70
Figs 48, 51, 54

Type material. Holotype, female: Costa Rica, Prov. Heredia, 16 km SSE La Virgen, 1050–1150 m, 10°16'N, 84°05'W, 21 Mar. 2001, INBio-OET-ALAS transect, 11/TN/18/008, INB0003210556. **Allotype, male:** Prov. Heredia, 9 km NE Vara Blanca, 1450–1550 m, 10°14'N, 84°06'W, 20 Mar. 2005, INBio-OET-ALAS transect, 15/TN/04/012, INB0003675744. **Paratypes:** same data as allotype, except 15/TN/20/020 (INB0003675955) (1); same data as allotype except 17 Apr. 2005, 15/TN/04/022 (INB0003676180) (1); Costa Rica, Puntarenas, 5 km SW Est. Biol. Las Cruces, 1425 m, 08°46'59"N, 82°59'18"W, 22 VI. 1998, R. Anderson, wet cloud forest litter, 98-108B (2); Costa Rica, S. J., Zurquí de Moravia, 1600 m, IX-1-9-1998, FIT, C.W. & L.B. O'Brien (1). Holotype and allotype deposited in MNCR, 2 paratypes in FSCA, 1 paratype in USNM, 1 paratype in CASC, 1 paratype in ZMBN.

Diagnosis. Interstriae 10 carinate to level of metacoxa; protibiae without additional mesal tooth. Unique female frons with silky white, soft setae, and one of few species bearing 10 erect pronotal setae where the additional pair is close to the center of the pronotum. Only distantly related to species such as *S. banosus* (Hagedorn, 1909) and *S. hagedorni* (Schedl, 1962); more similar to *S. obovatus* Jordal, 2013 but the new species differs by having a short interstriae 10.

Description female. Length 1.4–1.7 mm, 1.9–2.0 × as long as wide; color brown to dark brown. ***Head.*** Eyes weakly sinuate, separated above by 2.0–2.5 × their width. Frons flattened between eyes from vertex to epistoma, more deeply impressed at level of antennal insertion; surface shiny, smooth, median third impunctate, with dense punctures elsewhere associated with setae. Vestiture consisting of short, soft, silky setae from vertex to epistoma, except in central impunctate area. Antennal club setose, particularly on anterior face, on posterior face with two obliquely procurved sutures, segment 1 large, corneous; funiculus 6- or 7-segmented, segments very thin and disc-like. ***Pronotum*** shiny, very weakly reticulate, with shallow, medium-sized punctures spaced on average by their diameter. Vestiture consisting of 10 erect long setae (4–2–2–2), and short, fine, recumbent setae on anterior half. ***Elytra*** generally smooth and shiny; striae not impressed, punctures shallow, tiny, in longitudinal pairs, each pair separated in rows by their length; interstriae 5 × as wide as striae, punctures of same size as in striae, mainly in rows. Interstriae 10 carinate to level of metacoxa. Vestiture consisting of irregularly placed, erect, interstrial setae of variable length and thickness, and densely placed, fine, short, partly curled, semi-recumbent setae in both striae and interstriae. ***Legs.*** Procoxae separated by 0.6 × and mesocoxae 0.9 × the width of one procoxa. Protibiae narrow, oval-parallel-sided, lateral teeth 1 and 2 long and sharp, 2 as long as 1, with 3–4 additional small, sharp spines or granules along the lateral edge towards base; protibial mucro obtuse. Mesotibiae with 6–9 lateral, socketed, small teeth on distal half, the apical 3–4 teeth smaller, forming a dense comb; metatibiae with 5–6 lateral, small, socketed teeth on distal half. ***Ventral vestiture.*** Setae on metanepisternum and metasternum simple, on mesanepisternum trifid. Sclerolepidia very small, scale-like.

Male. Similar to female, except frons slightly more convex, with fewer and shorter setae distributed near inner margin of eyes and antennal insertion.

Key (Wood 1982). There is a mismatch in couplet 6 (short interstriae 10, but no mesal tooth on protibiae).

Etymology. The Latin name *plenus* is a masculine adjective, meaning plump or chubby, referring to the stout body shape.

Biology and distribution. This species is known from four Costa Rican cloud forest localities – in the northern and southern slopes of Volcan Barva (Braulio Carrillo) and close to the Panama border (Las Cruces). Two specimens were collected by leaf litter sifting, and four specimens by flight intercept trapping.

Redescription

Scolytodes minutissimus Schedl

Figs 55, 56, 57

Scolytodes minutissimus Schedl, 1952: 355.

Material examined. Holotype, female: Costa Rica, Limón, Hamburgfarm on Reventazón. [NHMW]. **New records**: Costa Rica, Heredia, Est. Biol. La Selva, 50–150 m, 10°26'N, 84°01'W, May 2000, INBio-OET; 09 May 2000, *Goethalsia meiantha* FOT/47/29 (INBIOCRI002730681), FOT/49/26 (INBIOCRI002731590), FOT/49/23 (INBIOCRI002731568).

Diagnosis. Interstriae 10 elevated to near apex; protibiae without an additional mesal tooth. Recognized by the presence of exactly two erect setae on the median an-

Figures 55–57. Dorsal, lateral and frontal view of a female *Scolytodes minutissimus*.

terior margin of the pronotum, and one erect setae on each interstriae 3 on the elytral disc, and by the broad longitudinal callus in a sparsely setose female frons.

Description female. Length 1.3 mm, 2.0 × as long as wide; color brown. ***Head.*** Eyes entire, separated above by 1.6 × their width. Frons impressed in a hoof-shaped fashion, from broadly impressed on epistoma to more narrowly impressed near upper level of eyes, a longitudinal, broad callus in the middle of impressed area; surface shiny, punctured in impressed area only; vestiture consisting of fine, short setae in impressed area. Antennal club densely pubescent, without sutures, posterior face partly corneous on basal median half. Funiculus 5-segmented. ***Pronotum*** shiny, small punctures spaced by 3–4 × their diameter. Vestiture consisting of two erect setae at the middle of frontal margin (2–0–0). ***Elytra*** smooth, striae generally not impressed, punctures minute and barely visible, close to each other in irregular rows; interstriae approximately 4–6 × as wide as striae, punctures as small as in striae, in rows, separated by 5–10 × their diameter. Interstriae 10 carinate to near apex. Vestiture consisting of two erect setae on disc, one on each interstriae 3. ***Legs.*** Procoxae separated by 0.8 × and mesocoxae 1.0 × the width of one procoxa. Protibiae narrow, teeth 1 and 2 equal, with 3–4 additional tiny granules along the edge towards base; protibial mucro tiny, curved posteriorly. Mesotibiae with 6 socketed lateral teeth on distal half, metatibiae with 4 small socketed teeth on distal fourth. ***Ventral vestiture.*** Setae on metasternum and metanepisternum simple.

Male. Similar to female except frons convex, slightly impressed just above epistoma having scant setae; surface shiny, with few punctures.

Biology and distribution. This species is only known from two nearby sites in the lowland of eastern Costa Rica. Three specimens were collected by fogging of a *Goethalsia meiantha* tree (Malvaceae).

Note. The holotype is a light-colored teneral specimen. The mature color is very dark brown. Wood (1982) did not note the peculiar pattern of setae with two erect frontal setae on pronotum, and two erect setae on the elytral disc (one each on interstriae 3).

Scolytodes costabilis **Wood, 1974**

Scolytodes obesus Wood, 1975, new synonymy

New Costa Rica records. San José, Zurquí de Moravia, 1600 m, 11 July 1997, L. R. Kirkendall, 4 cm dia. *Cecropia insignis* branch (14); Prov. Heredia, 16 km SSE La Virgen, 1050–1150 m, 10°16'N, 84°05'W, 20 Feb. 2001, INBio-OET-ALAS transect, 11/TN/19/009, INB0003210610 (1); Heredia, Est. Biol. La Selva, 50–150 m, 10°26'N, 84°01'W, 15 May 2000, FOT/50/34, fogging *Goethalsia meiantha*, INBIOCRI002731022 (1); [Puntarenas] La Gamba, Piedras Blancas NP, Esquinas rainforest, 18–28 May 2006, 8°42'/-83°12', 90–200 m, leg. Erwin Holzer (1).

Scolytodes obesus was described from a single teneral specimen from the Canal Zone in Panama (Wood 1975). This specimen is slightly stouter than the holotype of *S. costabilis* (2.1 vs. 2.3 × as long as wide), and the declivity of the elytra is slightly more gradual. Slight variation observed among populations and even within series of the new collections argue for there being just a single species.

Scolytodes costabilis is recorded for the second time from Costa Rica (see Jordal 2018), from three additional localities. With the four records reported here, this species is regarded as broadly distributed, ranging from Veracruz, Mexico (holotype of *S. costabilis*) to central Panama, from near sea level to cloud forest.

New country records for Hexacolini

Six species of *Scolytodes* and one of the related genus *Pycnarthrum* were recorded from Costa Rica for the first time (Table 1).

Scolytodes clusiacolens Wood was previously known from Mexico and Honduras. The collection of this large species comprises three pairs just starting galleries in 8–10 mm thick *Clusia* branches.

Scolytodes crinalis Wood, 1978, another *Clusia*-associated species, was previously known only from Venezuela. It was collected in two different traps.

Scolytodes libidus Wood, 1978, another Venezuelan species, was collected by traps and from leaf litter samples from several Costa Rican localities.

Scolytodes reticulatus Wood, 1961 was originally recorded from *Ficus* in Mexico and the Costa Rica collection from a fallen *Ficus jimenezii* tree suggests it might be widely distributed fig tree specialist.

Scolytodes culcitatus (Blandford), was known only from the holotype collected in Panama, despite being one of the three first described species in the genus (Blandford 1897). This distinctive species is unique in the genus in for having a large patch of dense long setae on the anterolateral area of the pronotum, obscuring a large impression there. The impression with long setae is likely to be a repository for fungal spores, but nothing is known of the biology of this elusive species.

Scolytodes spadix (Blackman, 1943) seems to be common in Costa Rica based on the multiple collections reported here, though all are from the Caribbean side of Costa Rica; it was previously known from a single specimen taken from a mahogany log thought to have originated in Guatemala. The two host records reported here are from unrelated tree species in the families Meliaceae and Urticaceae.

Pycnarthrum fulgidum Wood, 1977 was known only from the original series collected from a broken log of *Guarea* (Meliaceae) in lowland Colombia. The new record for Costa Rica is based on a male found in a Malaise trap collection in secondary forest at La Selva Biological Station.

Table 1. Species of *Scolytodes* not previously found in Costa Rica. Coll=collection. FIT=flight intercept trap, FOG=canopy fogging, MAL= Malaise trap, WFL=Winkler funnel litter samples. Full specimen data are given in Suppl. material 1: Table S1.

Species	Sites (specimens)	Previous range	Costa Rica province	Altitude	Host or Coll. Method
S. clusiacolens Wood	1 (6)	Mexico, Honduras	Heredia	1450–1550 m	*Clusia*, small branch
S. crinalis Wood	2 (2)	Venezuela	Heredia	1450–2050 m	FIT, MAL
S. culcitatus (Blandford)	1 (2)	Panama	Cartago	2800–3000 m	unknown
S. libidus Wood	4 (5)	Venezuela	Cartago, Heredia	1950–2600 m	FIT, MAL, WFL
S. reticulatus (Wood)	1 (3)	Mexico	San José	1200 m	*Ficus* branch
S. spadix (Blandford)	7 (10)	Guatemala? (see text)	Heredia	50–550 m	*Carapa*, *Coussapoa*, FOG, MAL

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Supplementary material 1

Table S1

Authors: Bjarte H. Jordal, Lawrence R. Kirkendall

Data type: occurrences

Explanation note: New records of Scolytodes and Pycnarthrum from Costa Rica. Species marked in bold are new country records, see Table 1 in text.

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Unexpected palaeodiversity of omaliine rove beetles in Eocene Baltic amber (Coleoptera, Staphylinidae, Omaliinae)

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Abstract

Fossil records of the subfamily Omaliinae are fragmentary and most of them are less informative compression fossils. Baltic amber from the mid-Eocene of northern Europe is one of the most important sources of insect fossils, but only two reliably placed omaliines have been described. Here, we provide a general overview of this subfamily in Baltic amber. In total, five new extinct species of four genera in three tribes are described and illustrated: *Geodromicus balticus* **sp. nov.** (Anthophagini), *Eusphalerum kanti* **sp. nov.** (Eusphalerini), *Paraphloeostiba morosa* **sp. nov.**, *Phyllodrepa daedali* **sp. nov.**, and *Ph. icari* **sp. nov.** (Omaliini). Additionally, we report on four species belonging to *Eusphalerum*, which remain unnamed, from the same amber deposit. The records of *Eusphalerum* include the first fossils of the tribe Eusphalerini, while that of *Geodromicus* may represent the second and the first definitive fossil record of the genus and tribe Anthophagini. Our discoveries highlight the unexpected palaeodiversity of Omaliinae in Baltic amber, further reinforcing the coexistence of thermophilous and temperate-loving beetles in Baltic amber and potentially indicating wetland and riparian habitats of amber-producing forests.

Keywords

Anthophagini, Eusphalerini, Omaliini, fossil, micro-CT

Introduction

With 1639 species in 117 extant and 14 extinct genera (Thayer 2016; A.F. Newton unpublished database 17 Jan. 2019), the rove beetle subfamily Omaliinae (Staphylinidae) is a relatively large group, currently composed of seven tribes: Anthophagini Thomson, 1859, Aphaenostemmini Peyerimhoff, 1914, Corneolabiini Steel, 1950, Coryphiini Jakobson, 1908, Eusphalerini Hatch, 1957, Hadrognathini Portevin, 1929 and Omaliini W.S. MacLeay, 1825. However, McKenna et al. (2015) recently demonstrated the non-monophyly of Omaliinae with respect to three other subfamilies (i.e., Empelinae Newton & Thayer, 1992, Glypholomatinae Jeannel, 1962, and Microsilphinae Crowson, 1950) in the "Omaliine group of subfamilies based on two molecular markers. Their result supports the earlier results of Thayer (2000) based on larval morphology (although larvae of Empelinae are still unknown and therefore were not included in her study). These four subfamilies combined formed a monophyletic clade, sister to Proteininae (McKenna et al. 2015). Members of the Omaliinae are distributed worldwide, with the greatest diversity in the Holarctic and Oriental regions, predominantly in montane areas. A revision and clear diagnosis of Omaliinae still do not exist, and thus, the status of many supraspecific taxa is still unclear due to the difficulties of formally placing them within tribes (Newton and Thayer 1992, 1995). Omaliinae, or even the Omaliine group, have often been considered to be plesiomorphy-rich among Staphylinidae (Thayer 2016). However, this was not supported by the comprehensive molecular phylogenetic study by McKenna et al. (2015). The presence of paired ocelli in most taxa of Omaliinae has often been regarded as one of the most important characters to define the subfamily. Nevertheless, it is unclear whether ocelli should be interpreted as primitive or even apomorphic (Newton and Thayer 1995; Leschen and Beutel 2004; Cai et al. 2013; Thayer 2016). The extant omaliines are further characterized by having antennae inserted under the lateral margins of the frons, tarsal formula 5-5-5 (except Corneolabiini, 4-4-4; Steel 1950), procoxal cavities opened behind, well-developed prosternal and post-procoxal processes, procoxae conical and prominent, abdomen with six visible sternites, abdominal intersegmental membranes attached apically and with brick-wall-like pattern of sclerites, all spiracles well developed and functional, presence of wing-folding patches of microtrichia on some abdominal tergites, and anterior projection of abdominal sternite VIII with well-developed defensive glands (e.g. Klinger 1980; Dettner and Reissenweber 1991), as well as some features of genitalia and genital segments of both male and female (Thayer 1985; Newton et al. 2000; Peris et al. 2014; Zanetti et al. 2016).

A brief history of fossil Omaliinae was recently provided by Chatzimanolis (2018). Fossil records of omaliines are relatively prevalent. Compared to the high diversity and abundance of extant Omaliinae, however, the records of extinct omaliines are still significantly fragmentary. Many of them are described with short descriptions, incomplete illustrations and problematic systematic placements (Chatzimanolis 2018). Hence, it prevents a comparison of these fossils to each other and to recent taxa. In addition, several extinct genera are known as "tribe *incertae sedis*" and not placed in any of the tribes mainly because of their poor preservation or difficulty in interpreting their morphology (Schaufuss 1890; Tikhomirova 1968; Ryvkin 1985, 1990; Herman 2001). Chatzimanolis (2018) listed five Jurassic omaliine genera (Tikhomirova 1968; Ryvkin 1985): †*Archodromus* Tikhomirova, †*Globoides* Tikhomirova, and †*Porrhodromus* Tikhomirova from the Upper Jurassic of Karatau, Kazakhstan; †*Eophyllodrepa* Ryvkin from the Middle-Upper Jurassic of Novospasskoe, Russia; and †*Morsum* Ryvkin from the Middle Jurassic of Kubekovo, Western Siberia. Two genera †*Daiodromus* Ryvkin and †*Prodaia* Ryvkin are known from the Upper Jurassic of Daya, Russian Transbaikalia, although Chatzimanolis et al. (2012) regarded them as Lower Cretaceous taxa. Later, Cai and Huang (2013) added the extinct genus †*Sinanthobium* Cai & Huang from the Middle Jurassic of Inner Mongolia, China. Compared to Jurassic compressions, only a handful of fossils are known from the Cretaceous, with only a single compression fossil, genus †*Mesodeliphrum* Ryvkin, described from the Lower Cretaceous of Turga, Transbaikalia (Ryvkin 1990). In addition, Peris et al. (2014) recently reported the first Mesozoic amber genus †*Duocalcar* Peris & Thayer (Omaliini) from opaque Lower Cretaceous French (Charentes) amber and visualized the beetle fossil by using phase-contrast Synchrotron Radiation x-ray microtomography (PPC-SR X-ray μCT).

The Cenozoic omaliine fauna is also far from well understood. Scudder (1900) described the compression fossil species *Geodromicus abditus* Scudder (Anthophagini), from the Upper Eocene of Florissant, USA, although the preservation is not adequate to assess its systematic position. For example, the whole head was lost prior to description (Scudder 1900), which makes its generic identification highly doubtful or impossible. Nevertheless, according to the original description, the general body shape of *G. abditus* is similar to that of *Geodromicus* or some other related genera (for example *Microedus*), but there is no information about structure of the head and mouthparts. Another fossil species, *Omalium antiquorum* Wickham (Omaliini), with *Proteinus*-shaped body (Wickham 1913: pl. 5 fig. 3), is described from the same horizon (Wickham 1913), but again, the preservation of this fossil is insufficient to justify its taxonomic placement. Although the description is too short for final conclusions (Wickham 1913), this taxon may not belong to *Omalium* due to the proportions of the markedly transverse pronotum and wide elytra, which are consistent with many *Proteinus* (Proteininae) species. Other pre-Quaternary records include *Anthophagus giebeli* Heyden & Heyden (Anthophagini) from the Oligocene of Germany (Heyden and Heyden 1866), *Omalium protogaeae* Heer from the Miocene of Croatia (Heer 1847) and some unnamed fossils (e.g. Hopkins et al. 1971; Archibald and Mathewes 2000; Kiselev and Nazarov 2009). All these compression fossils need re-examination as generic assignments by the early paleontologists are doubtful. For example, *A. giebeli* can be assigned neither to *Anthophagus* nor Anthophagini. Based on the small body with two darkened spots in middle of the pronotum, it may belong to *Eusphalerum* or a small Omaliini (*Phloeonomus*-like) considering the shape of the very wide abdomen (Heyden and Heyden 1866). Schaufuss (1890) described *Pseudolesteua insinuans* Schaufuss from the mid-Eocene Baltic amber (ca 44 Ma) but this fossil may not even belong to Omaliinae (Zanetti et al. 2016). Unfortunately, Schaufuss's material was likely to be lost or scattered during World War II (Vitali 2006); thus, it is probably impossible to re-examine the type specimen. The only definitive omaliines in Baltic amber were recently described by Zanetti et al. (2016), representing two Omaliini species: *Paraphloeostiba electrica* Zanetti et al. and *Phyllodrepa antiqua* Zanetti et al. They were visualized with the PPC-SR X-ray µCT method, illuminating fine morphological details. Further, Hieke and Pietrzeniuk (1984) noted an "*Anthobium*" from Baltic amber identified by E. Reitter; however, this species has not been formally described (see also the history of confusion between *Anthobium*, *Lathrimaeum* and *Eusphalerum* in Tottenham (1939) and Shavrin and Smetana (2017)).

The present paper provides an overview of the remarkable and unexplored palaeofauna of Omaliinae in Baltic amber. We report at least 18 fossil beetles in seven amber pieces, with the descriptions of five new extinct species in four extant genera from the tribes Anthophagini, Eusphalerini and Omaliini. The new species and unnamed specimens of *Eusphalerum* Kraatz represent the first definitive fossil of Eusphalerini, while that of *Geodromicus* Redtenbacher may represent the second and the first definitive fossil record of the genus and Anthophagini. These discoveries are significant for future phylogenetic and paleontological studies of the subfamily Omaliinae and related taxa.

Materials and methods

Eighteen adults in seven Baltic amber pieces were used in our study. Nearly all studied material is deposited in the Gantz Family Collections Center, Field Museum of Natural History (FMNH), Chicago, USA, with the assigned specimen numbers from FMNHINS-3260628 to FMNHINS-3260632 with addition of FMNHINS-3965993, but a single amber piece is derived from the private collection of V.I. Alekseev (Kaliningrad, Russia), under the registration number AWI-045. Each piece of amber is placed in a small transparent rectangular plastic envelope with the labels within. The age of Baltic amber is of great debate, with estimates from the Lower Eocene to Lower Oligocene (e.g. Perkovsky et al. 2007; Weitschat and Wichard 2010; Alekseev 2013; Bogri et al. 2018), although it is generally accepted as middle to upper Eocene. Here we tentatively follow the mid-Eocene (Lutetian: 44.1 ± 1.1 Ma) age based on the most recent estimations obtained by the absolute dating analyses of glauconites from Sambia Peninsula (Wappler 2005). The staphylinid fauna in Baltic amber is diverse and abundant, with the following 12 extant subfamilies recorded: Aleocharinae, Euaesthetinae, Omaliinae, Oxyporinae, Paederinae, Piestinae, Proteininae, Pselaphinae, Scydmaeninae, Staphylininae, Steninae, and Tachyporinae (e.g. Chatzimanolis and Engel 2011; Alekseev 2013; Cai et al. 2017; Yamamoto and Maruyama 2017). The amber pieces originate from the Baltic Sea Coast: Yantarny, Kaliningrad, Russia (FMNHINS-3965993, FMNHINS-3260629, FMNHINS-3260632, AWI-045); Wisła River, Gdańsk, Poland (FMNHINS-3260628); and the Baltic Sea Coast without further information (FMNHINS-3260630). The second author (SY) further prepared two specimens (FMNHINS-3260628 and FMNHINS-3260629) by polishing with emery papers of different grain sizes and a plastic buffing cloth.

The following measurements are used in this paper and abbreviated as follows:

HW	maximum width of head including eyes;
HL	length of head (from base of labrum to neck constriction along head midline in dorsal view or from apical margin of mentum to neck constriction in ventral view (*G. balticus* sp. nov.));
OL	ocular length (longitudinal);
PLL×PLW (II, III)	length×width of segments II and III of labial palpi;
PML×PMW (III, IV)	length×width of segments III and IV of maxillary palpi;
AL	length of antenna;
PL	length of pronotum;
PW	maximum width of pronotum;
ESL	sutural length of elytra (length of elytra from the apex of scutellum to the posterior margin of sutural angle);
EW	maximum width of elytra together;
MTbL	length of metatibia;
MTrL	length of metatarsus;
AW	maximum width of abdomen (at segment IV);
TL	total length (from anterior margin of clypeus to apex of abdomen).

All measurements are given in millimeters and were made with a stereoscopic microscope equipped with an ocular micrometer. Some measurements of the body were difficult to do because of the specimen's partial visibility and orientation within the amber pieces; the resulting approximate values are marked with “~”, and the cases when measurements were not possible are marked with “?”. The description of the preservation of the material is given below the type material listing in a separate paragraph. The type labels are cited in inverted commas and separated from each other by a comma, different lines in labels of the types and historic labels are separated with ‘|’; explanations of the type labels are given in square brackets, necessary notes within the label are given in angle brackets.

Specimens were examined using Nikon SMZ 745T and Nikon Eclipse E200 stereomicroscopes. A digital camera (Sony Alpha DSLR-A300) was used for photographs of habitus of *Geodromicus balticus* sp. nov. Other photographs were produced using a Canon 80D digital camera with a Canon MP-E 65 mm macro lens (F2.8, 1–5×), equipped with a Canon MT-24EX macro twin lite flash as light source. Then, image stacks were carried out using CombineZM software (Alan Hadley, Sheffield, UK). All figures were modified using Adobe Photoshop software. For one paratype (FMNHINS-3260630) of *Eusphalerum kanti* sp. nov., images were generated using x-ray micro-computed tomography (μ-CT), acquired with a micro-focus x-ray CT system (inspeXio SMX-100CT; Shimadzu) through the courtesy of Shimadzu Corp. (Kyoto, Japan). It was scanned at 60 kV under 60 μA, resulting in a voxel size of 5.0 μm. Specific settings of the scan are confidential and retained by the company. Rendering of the image volume was carried out using VGstudio max v. 2.2 (Volume Graphics, Heidelberg, Germany).

Systematic Palaeontology

Order Coleoptera Linnaeus, 1758
Family Staphylinidae Latreille, 1802
Subfamily Omaliinae MacLeay, 1825

Systematic placement of fossils. The characters of the subfamily by which the fossil specimens describe here are unambiguously referred to Omaliinae are: shape of the body is variable but in general more or less wide, with short and less flexible abdomen than most staphylinids; elytra are variable in length and sometimes distinctly elongate and covering the entire abdomen (Newton and Thayer 1995); dorsal surface of the head, more or less close to hind margin, usually with ocelli (e.g. Hatch 1957; Moore and Legner 1979; Newton et al. 2000; Leschen and Beutel 2004; Thayer 2016), reduced in some taxa (see below); apical maxillary palpomere as wide as penultimate segment, but in Coryphiini and some taxa of Anthophagini and Omaliini it can be distinctly narrower; antennae attached under lateral margins of frons, filiform, moniliform or clavate; coxal cavities usually open; postcoxal process well developed (with some exceptions; see Newton et al. 2000); procoxae conical and prominent; epistomal suture absent, posterior face of metacoxa vertical (Newton and Thayer 1995; Thayer 2016); tarsal formula 5-5-5 (4-4-4 in Corneolabiini); abdomen with six visible sternites; abdominal tergites three to seven, usually with one pair of paratergites; intersegmental membranes attached apically and with brick-wall structures (e.g. Hammond 1971).

Tribe Anthophagini Thomson, 1859

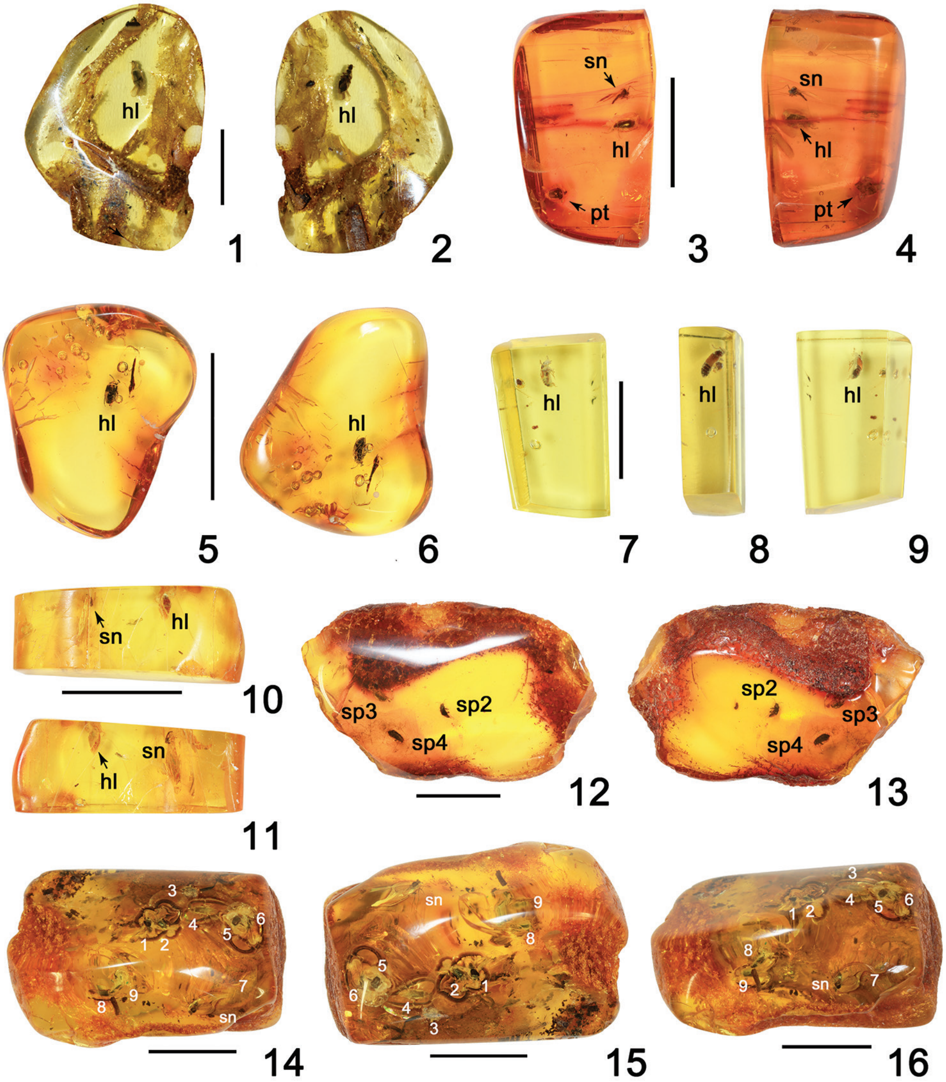
Genus *Geodromicus* Redtenbacher, 1857

Type species. *Staphylinus plagiatus* Fabricius, 1798

†*Geodromicus balticus* Shavrin & Yamamoto, sp. nov.

http://zoobank.org/16755333-4CBD-4485-B51A-6B64459253B3
Figures 1, 2, 17–20

Type materials examined. Holotype: female, FMNHINS-3965993, complete specimen as inclusion in a piece of light yellow Baltic amber, 3.4 cm × 2.4 cm × 0.5 cm in size (Figs 1, 2), with glued small paper on plastic envelope labeled "6083", with three colour photographs of habitus of the beetle (two of dorsal and one of ventral view) with rectangular stamp on the back of each labeled "Certificate 6083 [handwritten in blue] | Natural Baltic Amber with Inclusions | expert Jonas Damzen | International Amber Association | Names of Inclusions: | Staphylinidae [handwritten in blue] | Rove beetle [handwritten in blue]" <with additional round stamp on the left



Figures 1–16. Amber specimens with inclusions of Omaliinae: **1, 2** *Geodromicus balticus* sp. nov. **3, 4** *Eusphalerum kanti* sp. nov. **5, 6** *Paraphloeostiba morosa* sp. nov. **7–9** *Phyllodrepa daedali* sp. nov. **10, 11** *Ph. icari* sp. nov. **12, 13** *Eusphalerum* sp. 2 (sp2), *Eu.* sp. 3 (sp3) and *Eu.* sp.4 (sp4) **14–16** *Eu.* sp. 1 (specimens 1 to 9 (in the text: no. 1 to no. 9). Abbreviations: hl = holotype, pt = paratype, sn = syninclusion. Scale bars: 1.0 cm (**1–6, 10–16**), 0.5 cm (**7–9**).

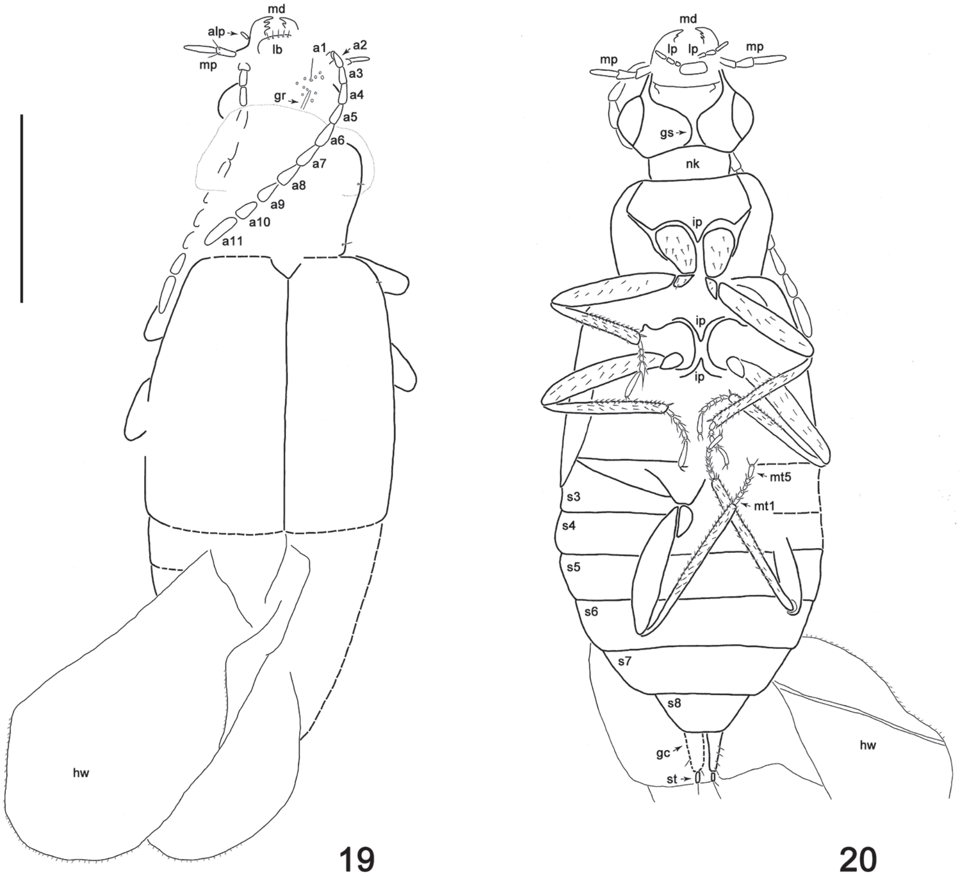
side: "+SOCIETAS SVCCINORVM+INTERNATIONALIS"]>, with the following labels: "Baltic amber | Yantarny, Kaliningrad | Russia | (S. Yamamoto Coll.) | ?Geodromicus | Omaliinae, Anthophagini | Protobiae with minute | hairs | tarsi with long hairs" <rectangular label; handwritten on both sides of the label>, "HOLOTYPE | *Geodromicus* | *balticus* sp. nov. | Shavrin A. & Yamamoto S. des. 2019" <red rectangular label, printed> (FMNH).

Figures 17, 18. Habitus photographs of *Geodromicus balticus* sp. nov. **17** Dorsal view **18** Ventral view. Scale bars: 1.0 mm.

Preservation. The specimen is poorly visible because it is partially covered with white cloud of microbubbles created by decay products interacting with resin, a characteristic of authentic Baltic amber (Cai and Huang 2013). This is especially noticeable on the anterior half of the body, under the apical and basal portions of the head, including the usual location of ocelli, and most of the pronotum. The abdominal tergites are not visible dorsally, as they are covered by the hind wings. The ventral side of the specimen is visible in detail except for the basal portion of the thoracic sclerites.

Locality and horizon. Baltic amber from Yantarny, Kaliningrad, westernmost Russia; mid-Eocene (ca 44 Ma; Wappler 2005).

Description. Measurements: HW (ventral): 0.76; HL (ventral): ~0.40; OL (ventral): 0.25; PLL×PLW (II, III): II: 0.05 × 0.03, III: 0.08 × 0.02; PML × PMW (III, IV): III: 0.10 × 0.06, IV: 0.16 × 0.05; PL (ventral): ~0.47; PW (ventral): ~0.87; ESL: 1.40;



Figures 19, 20. Habitus drawings of *Geodromicus balticus* sp. nov. **19** Dorsal view **20** ventral view. Abbreviations: a1–a11 = antennomeres 1–11; alp = apical labial palpomere; gc = gonocoxite; gr = groove; gs = gular suture; hw = hind wing; ip = intercoxal process; lb = labrum; lp = labial palpi; md = mandibles; mp = maxillar palpus; mt1, mt5 = metatarsomeres; nk = neck; s3–s8 = sternites 3–8; st = stylus. Scale bar: 1.0 mm.

EW: 1.51; MTbL: 1.00; MTrL: 0.36 (I–IV: 0.20; V: 0.16); AW (IV): 1.41; TL: 3.80 (head of specimen slightly out of pronotum, thus the total length likely to be slightly shorter). Antennomeres with lengths × widths: 1: ? × 0.07; 2: 0.16 × 0.06; 3: 0.11 × 0.06; 4–5: 0.15 × 0.05; 6–7: 0.15 × 0.07; 8: 0.14 × 0.07; 9–10: 0.12 × 0.07; 11: 0.25 × 0.07.

Body elongate; forebody convex. Specimen dark-brown and glossy, with antennomeres brown, mouthparts reddish-brown, legs yellow-brown with a somewhat darkened tibia. Habitus as in Figures 17–20.

Head transverse, slightly elevated in middle, about twice as wide as long, with short temples, moderately strongly narrowing toward neck, with diagonal moderately deep grooves (visible only apical part of left groove), reaching level of apical third of eye; gular sutures slightly separated at narrowest point on level of basal third of length of eyes (Fig. 20). Eyes large and widely convex, with medium-sized facets. Medioapical portion with irregular, dense and moderately deep, small punctation, without microsculpture, basal portion of head between eyes and gular sutures with dense diagonal mesh. Middle portion of swollen neck (ventral view) with dense isodiametric microsculpture (Fig. 18). Labrum transverse, with moderately widely rounded apical margin and elongate apical setae, without visible median emargination. Mandibles with strongly curved acute apex; left mandible with two elongate subapical teeth on inner side of cutting edge; distal third of cutting edge of right mandible not clearly visible, with elongate tooth somewhat shorter than that in left mandible. Maxillary palpi moderately long, with several long setae on apical margins of palpomeres 2 and 3; palpomere 2 narrower basally, gradually and slightly widened apicad; palpomere 3 distinctly longer than broad, narrow basally, markedly widened apicad; apical palpomere elongate, 1.8 times as long as penultimate segment one and visibly narrower at base than apex of penultimate one, somewhat parallel-sided in middle, slightly narrowed toward moderately acute apex (Figs 17–20). Labial palpomeres 2 and 3 distinctly longer than their width, apical palpomere 1.6 times as long as preceding segment, gradually narrowing toward apex from middle. Antenna reaching basal third length of elytra, with moderately wide antennomeres, with short dense setation; antennomere 2 slightly narrower than 1; antennomere 3 slightly shorter than antennomere 2, narrow basally and slightly widened apicad; antennomeres 4 and 5 three times as long as broad; antennomeres 6 and 7 slightly longer and distinctly wider than antennomere 5; antennomere 8 twice as wide as long; antennomeres 9 and 10 slightly shorter than antennomere 8; apical antennomere elongate, twice as long as penultimate segment and more than three times as long as broad (Figs 17, 19).

Pronotum transverse, about 1.3 times as wide as long, slightly wider than head, widest slightly in front of middle, markedly more narrowed posterad than anterad, indistinctly emarginate laterally; anterior angles widely rounded, posterior angles obtuse. Lateral portions of pronotum with small irregular punctation, without microsculpture. Pubescence appears regular, accumbent. Pronotal hypomeron and postcoxal process well developed; intercoxal process almost reaching basal third of length of procoxae, with acute sharp apex; pronotosternal suture distinct; mesoventrite with acute intercoxal process, reaching basal third of mesocoxae; metaventrite broad, with moderately acute apex of intercoxal process, not reaching mesosternal process (Figs 18, 20). Median part of prosternum with very sparse, irregular, small punctation; metaventrite with dense small punctation (Fig. 18); prosternal process with dense isodiametric microsculpture.

Elytra slightly broader than long, reaching apical margin of abdominal tergite III, markedly more than twice as long as pronotum, gradually widened apicad, with straight hind margin (Figs 17, 19). Punctation dense, small and deep, markedly smaller in basal portion, near scutellum and along suture. Pubescence regular, accumbent. Hind wings fully developed (Figs 17, 18).

Legs of moderately similar length, slender and moderately long; procoxae wide, protruding ventrad; mesocoxae large and oval, contiguous; metacoxae strongly transverse; protrochanter narrow, elongate; mesotrochanter relatively small, semioval; metatrochanter elongate; femora widest about middle; pro- and mesotibiae about as long as femora, slightly widened from narrowest basal portions toward middle, covered with regular moderately short pubescence and elongated setae on lateral margins (more visible in protibiae); metatibia markedly longer than metafemora and more than twice as long as metatarsus; apical metatarsomere slightly shorter than preceding tarsomeres together; tarsal claws simple and moderately long, without modifications (Figs 18, 20).

Abdomen slightly narrower than elytra (Figs 17–20). Abdominal tergite III to IV similar in width, beginning from segment V gradually narrowed apicad; tergite VII strongly narrowed to truncate apex (Figs 18, 20).

Male unknown.

Female. Apical margin of abdominal sternite VIII straight (Figs 18, 20). Genital segment with elongate gonocoxites, and moderately small, narrow styli (Fig. 20).

Etymology. The specific epithet is the Latinized adjective derived from the name of the Baltic Sea.

Remarks. Based on the shape of elongate antennomeres 8–10, the general shape of the apical maxillary palpus with elongate apical palpomere not dramatically narrower than the penultimate one, and on the length of tarsomeres 1–4 together distinctly longer than apical tarsomere, the studied specimen undoubtedly belongs to the tribe Anthophagini (Moore and Legner 1979; Newton and Thayer 1995; Newton et al. 2000). Judging from the combination of visible morphological details of the fossil, such as shapes of the forebody, maxillary palpomeres, gonocoxites, and mandibles with developed large teeth on inner side of the cutting edge, as well as by presence of distinct grooves in front of ocelli, the species belongs to the *Hygrogeus* complex of genera (Zerche 1992, 2003). The representatives of these taxa are widespread in the Holarctic Region and contain several genera reaching their greatest diversity in Central and East Asia (Shavrin 2017a). Unfortunately, the condition of the specimen described here does not allow the observation of the presence of neither the anteocellar impressions nor the ocelli. The presence of impression between ocelli depends on the degree of convexity of head and can be significantly variable among genera and even among species of a species group, from indistinct to very deep. Regarding ocelli, these structures can be large and very convex, small, flattened, and indistinct, or reduced (sometimes in one genus) as in the tribe Anthophagini, but also in Coryphiini, Eusphalerini, and Omaliini (Zerche 1990, 1992; Shavrin 2016). Besides proportions of the forebody, internal and external structure of the aedeagus, genera of the *Hygrogeus* complex can vary by the shape of the apical two maxillary palpomeres (Coiffait 1981; Zerche 1992). The fossil cannot be member of *Altaiodromicus* Zerche, 1992, *Hygrodromicus* Tronquet, 1981, *Liophilydrodes* Nakane, 1983, *Microedus* LeConte, 1874, or *Philydrodes* Bernhauer, 1929, because members of these taxa share a short and very narrow apical maxillary palpomere. The new species cannot be placed in *Trichodromeus* Luze, 1903, species of which share a moderately small apical conical-shaped maxillary palpomere, shorter than an indistinctly widened apicad penultimate segment, or *Paratrichodromeus* Zerche, 1992, species of which have an apical maxillary palpomere distinctly narrower and shorter than the preceding segment. Additionally, from all these taxa the new species differs by the following: from *Altaiodromicus*, *Hygrodromicus*, and *Trichodromeus* by the larger eyes, less transverse head and pronotum, and elongate elytra gradually widened apicad; from *Liophilydrodes* and *Microedus* by longer elytra and absence of microsculpture between punctures on the head; from *Philydrodes* by the smaller head, larger pronotum, wider and longer elytra; from *Paratrichodromeus* by the wider pronotum and elytra and shorter antennae. The elongate apical and penultimate segment of the maxillary palpomere in this fossil are somewhat like that of some Asian species of the genus *Hygrogeus* Mulsant & Rey, 1880, especially the narrowed apical portion of the apical segment as in European *H. aemulus* (Rosenhauer, 1847). In general, the fossil differs from *Hygrogeus* by the slightly convex body, distinctly larger eyes and shorter temples, significantly shorter labial palpomeres and markedly wider pronotum. The relatively small body and its coloration, slightly convex dorsal side of the head, similar location of grooves and shape of mandibles are like some species of the genus *Anthophagus* Gravenhorst, 1802. However, it differs from *Anthophagus* by the shape of the apical maxillary palpomere (in *Anthophagus* significantly narrowed apicad and shorter than preceding palpomere), wider pronotum with markedly transverse prosternum and distinctly elongate mesosternal process (*Anthophagus* with a small mesosternal process extending short distance between coxae; Moore and Legner 1979), and, more importantly, different shape and structure of metatarsi: the first metatarsomere very short as opposed to markedly elongate as in *Anthophagus* (sometimes slightly shorter than apical tarsomere) and absence of modifications at base of tarsal claws (*Anthophagus* with two membranous patches at the base).

Based on the general shapes of the forebody, eyes, gular sutures, preapical and apical maxillary palpomeres, and antennomeres, as well as characters of the punctation and microsculpture of the body, shapes of thoracic sclerites, and length of basal metatarsomere, the new species can be placed as a putative *Geodromicus*. The extant representatives of the genus are widely distributed in the Holarctic Region, reaching their greatest diversity in Asia. The genus includes more than 120 species, the majority of which are distributed in the eastern Palaearctic Region and strongly associated with mountain regions (Herman 2001; Schülke and Smetana 2015; Shavrin 2018). According to the observed morphological data, it is rather difficult to place the new species into one of the subgenera (*Geodromicus* sensu stricto or *Brachydromicus* A. Bordoni, 1993) or any species group because the subgeneric subdivision seems to be artificial and species group placements were provided only for some taxa of the western (Bordoni 1984) and eastern (Shavrin 2018) Palaearctic and based on external and internal morphology of the aedeagus. The species can be tentatively compared with the smallest specimens (about 4.00 mm length, known to the first author) of the Palaearctic species *G. plagiatus* (Fabricius, 1798).

From all species of the genus, *G. balticus* sp. nov. differs by the markedly elongate apical segment of maxillary palpi. It highlights the need to revise the supraspecific taxonomy of the *Hygrogeus* complex, some of which have unclear status.

Tribe Eusphalerini Hatch, 1957

Genus *Eusphalerum* Kraatz, 1857

Type species. *Anthobium triviale* Erichson, 1839 (synonym of *Eusphalerum primulae* Stephens, 1834)

†*Eusphalerum kanti* Shavrin & Yamamoto, sp. nov.

http://zoobank.org/7C377BF2-1233-4E7D-AFDB-CDF6E0EDD22B

Figures 3, 4, 21–44

Type materials examined. Holotype (male) and paratype (female), FMNHINS-3260630, complete specimens as inclusions in a piece of dark yellow to reddish orange Baltic amber, 21.6 mm × 12.7 mm × 6.3 mm in size (Figs 3, 4), with the following labels: “SYAC 0027 | Baltic | prob. Anthobium” <rectangular small label, handwritten>, “07[printed] 09 [handwritten] | Baltic / ~~Dominican~~ | ~~Larva~~/Adult (× 2) [printed] [handwritten] | ? Anthobium [handwritten] | ~~Axel Niggeloh~~ | ~~Schalksmuehle~~” <large rectangular label, printed>, “15[printed]01[handwritten] – SYAC 00[printed] 27[handwritten] | Baltic / ~~Burmite~~ | ~~Other:~~ | ~~Larva /~~ Adult | prob. Anthobium [handwritten] | 2 in amber [handwritten] | Baltic Sea coast [handwritten] | Shûhei Yamamoto’s | Amber Collection” <large rectangular label, printed>, “[FMNH barcode at left side of label] FMNHINS | 3965993 | FIELD MUSEUM | AMBER” <small rectangular label, printed>, “HOLOTYPE | *Eusphalerum* | *kanti* sp. nov. | Shavrin A. & Yamamoto S. des. 2019” <red rectangular label, printed>, “PARATYPE | *Eusphalerum* | *kanti* sp. nov. | Shavrin A. & Yamamoto S. des. 2018” <red rectangular label, printed> (FMNH).

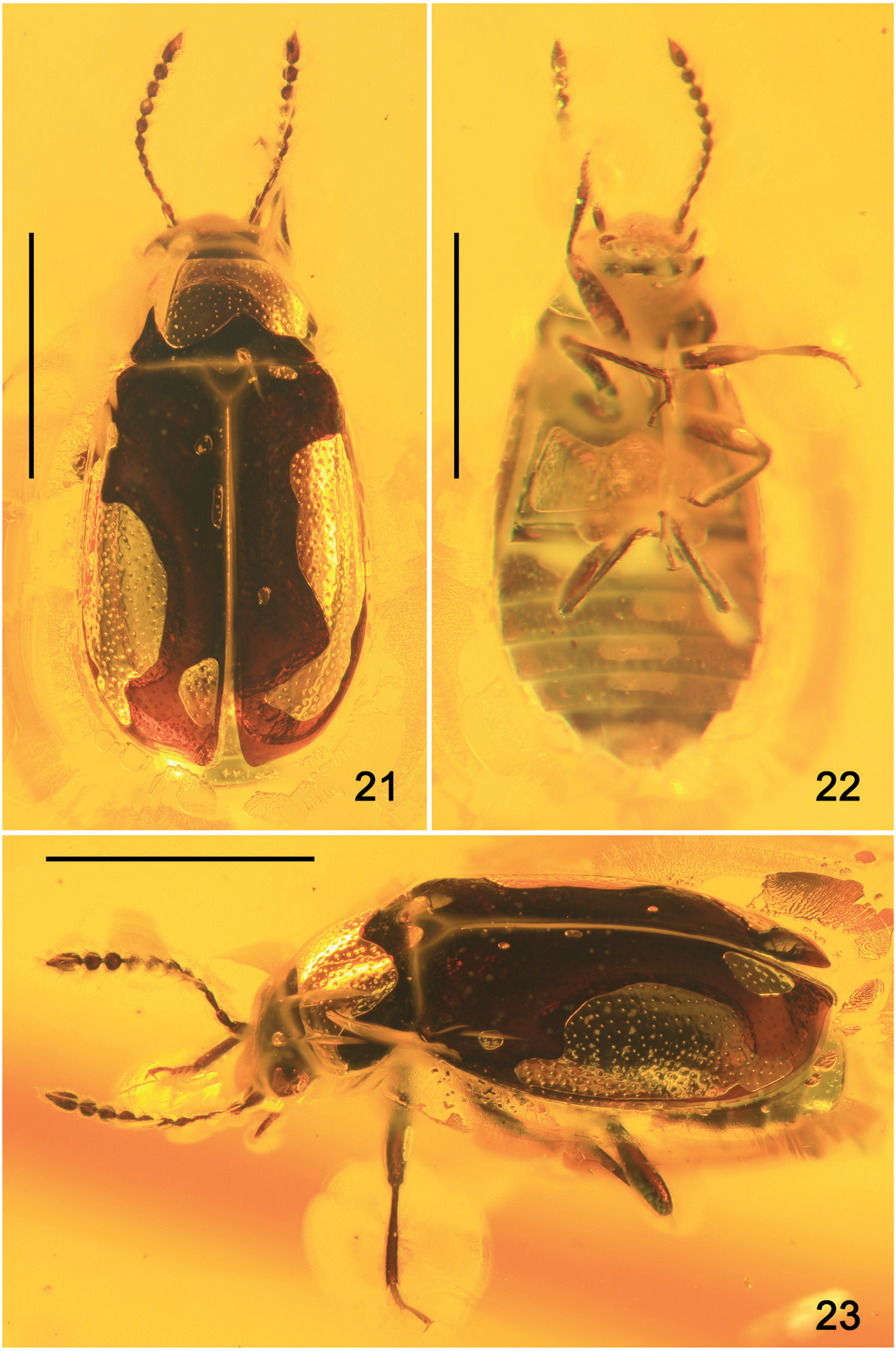
Preservation. The holotype is best observed on its dorsal side, close to the surface of the amber piece and with apical part of the body somewhat deeper (Fig. 3): head, pronotum and basal portion of elytra are visible from the lateral edge of the amber. The paratype is oriented dorsolaterally and located close to the outer surface of the amber piece (Fig. 3). Syninclusion: imago of Diptera about 2.00 mm length, including wings.

Locality and horizon. Baltic amber from Baltic Sea Coast, further details unknown; mid-Eocene (ca 44 Ma; Wappler 2005).

Description. Measurements (n = 2): HW (holotype): 0.47; HL (holotype): 0.33; OL (paratype): 0.18; AL (paratype): 0.75; PML × PMW (III, IV): III: 0.05 × 0.02, IV: 0.11 × 0.02; PL (holotype): 0.42; PW: 0.77; ESL (paratype): 1.25; EW (paratype): 1.15; MTbL (paratype): 0.42; MTrL (paratype): 0.24 (I–IV: 0.12; V: 0.12); AW: ?; TL: 2.60 (holotype)–2.70 (paratype). Antennomeres with lengths × widths (paratype): 1: 0.12 × 0.04; 2: 0.06 × 0.02; 3: 0.07 × 0.02; 4: 0.06 × 0.02; 5–6: 0.06 × 0.03; 7: 0.05 × 0.04; 8: 0.05 × 0.05; 9–10: 0.05 × 0.06; 11: 0.12 × 0.06.

Body elongate, convex (Figs 21, 24, 34, 37); body laterally as in Figure 36; body dorsolaterally as in Figure 23; body ventrally as in Figures 22, 25, 35. The specimens appear black, with mouthparts, antennae and legs yellow-brown; tarsi and basal portion of apical maxillary palpomere yellow. Body glossy and glabrous, without visible setation; antennomeres with elongate setae (Fig. 28).

Head about 1.4 times as wide as long (Figs 29, 39); middle portion of head slightly flattened, without visible grooves in front of ocelli, median impressions and occipital line; postocular carina smooth and indistinct. Head laterally as in Figure 42 and dorsolaterally as in Figure 28. Head with moderately irregular, dense and small punctation, markedly denser on posterior portion; middle part of neck with sparse small punctures (Fig. 43); infraorbital ridges with indistinct diagonal small meshes between punctures.



Figures 21–23. Habitus of *Eusphalerum kanti* sp. nov. (paratype) **21** dorsal view **22** ventral view **23** dorsolateral view. Scale bars: 1.0 mm.

Eyes large, widely convex (Figs 35, 37). Ocelli large, situated at level of posterior margins of eyes (Figs 28, 37), distance between ocelli distinctly longer than distance between ocellus and posterior margin of eye. Apical segment of maxillary palpi elongate, twice as long as preceding segment, about same width in middle as preceding segment, from middle gradually narrowed apicad (Figs 22–23, 28). Gular sutures with rounded apical parts, widely separated from each other (Figs 35, 38). Antenna (Figs 21–23, 25, 28, 29) moderately long, slightly exceeding shoulders of elytra, with elongate setae; basal antennomere wide and oblong, antennomere 2 slightly swollen and elongate, antennomere 3 thin and long, antennomere 4 slightly wider than antennomere 3, antennomeres 5 and 6 twice as long as wide, antennomeres 7 and 8 slightly and antennomeres 9 and 10 distinctly transverse, apical antennomere twice as long as wide, strongly narrowed in apical third toward acute apex.

Pronotum slightly convex, moderately short and transverse, 1.8 times as wide as long, 1.6 times as wide as head, widest at about middle, distinctly more narrowed posterad than anterad (Figs 21, 24, 37); apical margin straight, distinctly narrower than posterior margin; anterior angles widely rounded and distinctly protruded anterad (Figs 39, 43); posterior angles widely rounded; lateral margins distinctly emarginate, without crenulation on lateral edges (Figs 37, 39); pronotum with moderately widely elevated middle portion (Fig. 37), with very indistinct small transverse impression in mediobasal third; lateral portions narrowly but distinctly explanate, each with distinct moderately deep semioval impression at middle (Fig. 39). Pronotum with irregular small punctation like that on head but slightly deeper, markedly sparser in mediobasal and lateral portions; median portion with very indistinct transverse microsculpture. Prosternum with moderately wide intercoxal process (Figs 25, 26, 35, 38). Mesoventrite with thin, elongate and acute intercoxal process indistinctly reaching apical third of mesocoxae (Figs 35, 41). Scutellum large and wide, with several very small punctures in basal portion (Figs 21, 23, 24). Metaventrite convex (Fig. 36), with wide and deep metacoxal cavities and moderately wide metaventral process, reaching middle of mesocoxae, not contacting with apex of mesosternal process (Figs 25, 35, 41). Median part of prosternum and metaventrite with moderately dense small punctation (Figs 25, 35).

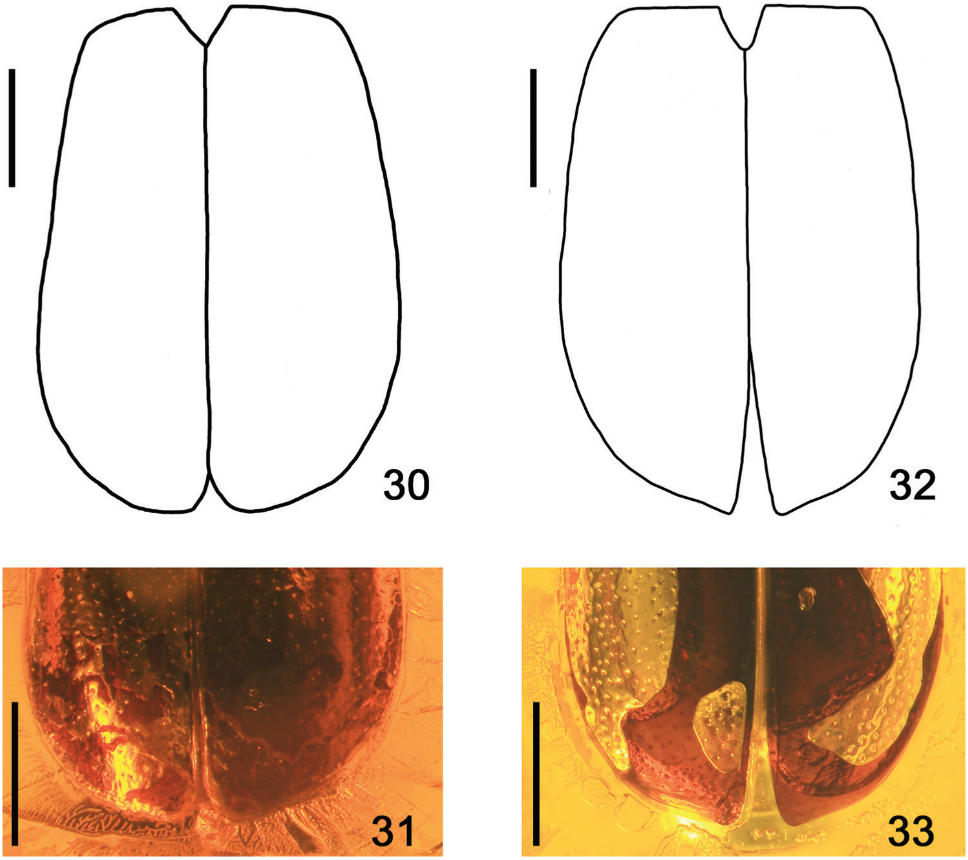
Elytra sexually dimorphic (male: Figs 30, 31; female: Figs 32, 33), distinctly longer than wide (Figs 21, 23, 24, 34) and more convex behind middle; in lateral view (Fig. 36) very long, about three times as long as pronotum, distinctly widened apicad from middle, reaching middle of abdominal tergite VI, with widely rounded apical angles (Fig. 40). Punctation of elytra larger and significantly denser than that on pronotum, markedly smaller on parascutellar portion and along suture, sparser on apical portion, larger and coarser in lateroapical and medioapical portions (Figs 21, 23, 24, 31, 33).

Legs with relatively wide femora (Figs 22, 23, 25, 26, 35, 36), tibiae thin, gradually widened apicad, about as long as femora, covered by elongate setae, markedly stronger on lateral margin (Figs 22, 23, 29, 36, 44); tarsomeres 1–4 with dense distinctly elongate setae ventrally; apical metatarsomere long, as long as previous tarsomeres together (excluding tarsal claws) (Figs 23, 27–29, 36).

Figures 24–29. *Eusphalerum kanti* sp. nov. (holotype: **24–26, 29** paratype: **27, 28**) **24** habitus, dorsal view **25** habitus, ventral view **26** thoracic sclerites and legs, ventral view **27** apical part of elytra, abdomen and hind legs, posterodorsal view **28** head and antennae, dorsolateral view **29** head, antennae and forelegs, dorsal view. Abbreviations: a1–a11 = antennomeres; amp = apical maxillary palpomere; gc = gonocoxite; gs = gular suture; ip = intercoxal process; nk = neck; mtf = metafemur; mtt = metatibia; mtv = metaventrite; oc = ocellus; prt = protibia; pt1, pt5 = protarsomeres 1 and 5; s3–s8 = sternites III–VIII; sc = scutellum; st = stylus; t4–t8 = tergites IV–VIII. Scale bars: 1.0 mm (**24, 25**), 0.3 mm (**26–29**).

Abdomen distinctly narrower than elytra (Figs 27, 40); apical margin of tergite VII with indistinct brick-wall sculpture; abdominal tergites with sparse small punctures and no visible microsculpture (Fig. 27); sternites VII and VIII of both males and females without modifications (Fig. 44).

Male. Elytra as in Figure 24; apical margin of elytra widely rounded (Figs 30, 31). Apical margin of abdominal tergite VIII somewhat straight. Apical margin of abdominal sternite VIII widely rounded (Fig. 27).

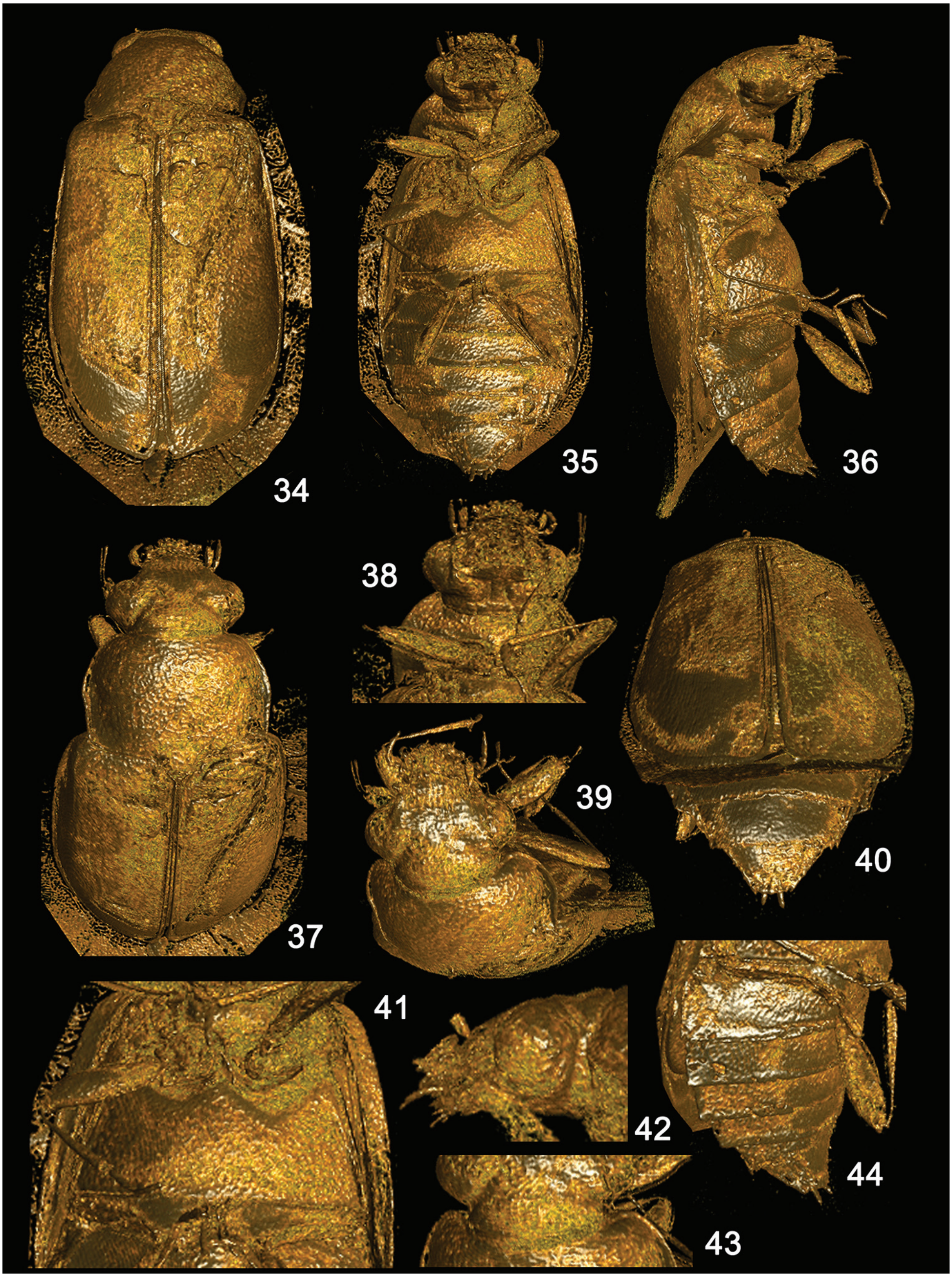


Figures 30–33. *Eusphalerum kanti* sp. nov. (holotype, male: **30, 31** paratype, female: **32, 33**): **30, 32** elytra (schematic drawings) **31, 33** apical part of elytra. Scale bars: 0.3 mm.

Female. Elytra as in Figure 21; apical margin of elytra distinctly prolonged at sutural apex (Figs 32, 33). Apical margin of abdominal tergite VIII and sternite VIII (Figs 27, 40) straight. Genital segment with markedly elongate gonocoxites and very small styli (Figs 27, 40).

Etymology. Patronymic, the species is named in honour of the great German philosopher Immanuel Kant (1724–1804), the author of the doctrine of transcendental idealism.

Remarks. The paratype of *Eu. kanti* sp. nov. was visualised three-dimensionally using a micro-CT scan. Although the result was not very satisfactory, we could observe the fossil from multiple additional angles (Figs 34, 44). Based on this scan, we could describe more characters that were not visible with light microscopy. The fossil was assigned to the tribe Eusphalerini and genus *Eusphalerum* based on the general shape of the body, shapes and length of short and slightly widened tarsomeres 1–4, with dense and elongate ventral setae, together about as long as apical tarsomere, and shape of the elytra of female slightly longer than that of male, with prolonged portion at sutural apex (Figs 32, 33). This floricolous genus contains 260 valid species (Zanetti 2014)



Figures 34–44. *Eusphalerum kanti* sp. nov., paratype, reconstructions from x-ray micro-computed tomography (µ-CT) **34** habitus, dorsal view **35** habitus, ventral view **36** habitus, lateral view **37** forebody, dorsal view **38** head and prothorax, ventral view **39** head and pronotum, anterodorsal view **40** elytra and abdomen, posterodorsal view **41** pterothoracic sclerites, ventral view **42** head, lateral view **43** neck and anterior portion of pronotum, dorsal view **44** abdomen, lateroventral view. Copyright 2015 Shimadzu Corporation.

distributed in the Holarctic Region. Earlier, the genus was subdivided into two subgenera: *Eusphalerum* and *Pareusphalerum* Coiffait, 1959 (Zanetti 1987), but because several species of sensu stricto and *Pareusphalerum* were overlapping in some morphological characters, the latter was synonymized with the nominotypical taxon (Tronquet and Zanetti 2008). Based on general morphological features of the aedeagus, female accessory sclerite and, in some cases, shapes of the modified apical abdominal sternites, several species groups have been erected for many species of the genus (e.g. Zanetti 1987, 1993, 2014). However, to date, this diverse genus remains insufficiently studied globally and is in need of further phylogenetic revision because of unclear relations between both species groups and the tribe Eusphalerini with related Omaliini.

The new species is difficult to compare with extant species as they typically differ from each other by the morphology of the aedeagus and female genital structures. However, based on the shape of the strongly elongate and dimorphic elytra, *Eu. kanti* sp. nov. is like members of the following species groups: North American *convexum* (Zanetti 2014; four species distributed in Canada and USA) and western Palaearctic *amplipenne* (Zanetti 1993; one species known from Turkey), *longipenne* (Zanetti 1987; six species distributed in Middle and South Europe), *montivagum* (Zanetti 1987, 1992, 1993, 2004, 2012a; 10 species distributed in Central and Southern Europe and Turkey) and *anale* (Tronquet and Zanetti 2001; three species from the central-western part of Europe). The new species differs from the *convexum* group by the presence of the postocular carina, by the dorsal portion of head without visible impressions, by the shape of the apical tarsomere slightly longer than that in species of *convexum* group and by the abdominal sternite VII of male without modifications. It differs from the *amplipenne* group by its somewhat smaller and darker body, sparser punctation of the forebody and shape of metatarsus of male, slightly curved in *Eu. amplipenne* (see Zanetti 1993: fig. 13). The new species shares similar length of the body and postocular carina with some species of the *longipenne* group, but differs by the darker body and longer apical tarsomeres. Based on the dark body, general characters of punctation and microsculpture of head and pronotum, *Eu. kanti* sp. nov. is somewhat like some species of the *montivagum* and *anale* groups, for example Southern European *Eu. schatzmayri* (Koch, 1938), *Eu. anale* (Erichson, 1840), *Eu. brandmayri* (Zanetti, 1981), and *Eu. coiffaiti* Nicolas, 1974, but it differs by the larger body (body length of members of the *montivagum* and *anale* groups varies from 1.50 to 2.50 mm) and more transverse pronotum. From all these groups, *Eu. kanti* sp. nov. differs by the absence of distinct grooves in front of the ocelli and elongate antennomeres 2–4 (Fig. 28).

Tribe Omaliini MacLeay, 1825

Genus *Paraphloeostiba* Steel, 1960

Type species. *Paraphloeostiba marianicola* Steel, 1960.

†*Paraphloeostiba morosa* Shavrin & Yamamoto, sp. nov.

http://zoobank.org/722E3364-B487-4F94-8BA6-5A38BD4A1C00
Figures 5, 6, 45–53

Type materials examined. Holotype (female), FMNHINS-3260632, complete specimen as inclusion in a piece of small yellow Baltic amber, 15.6 mm × 13.1 mm × 4.0 mm in size (Figs 5, 6), with the following labels: "14[printed] 11[handwritten]- SYAC 00 [printed]06 [handwritten] | Baltic / ~~Burmite~~ | ~~Other:~~ | ~~Larva~~ / Adult | Omaliinae [handwritten] | Kalini[n]grad [handwritten] | Shûhei Yamamoto's | Amber Collection" <large rectangular label, printed>, "Kaliningrad, RUSSIA | Shûhei Yamamoto's | Amber Collection | (SYAC0006)" <small rectangular label, printed>, "[FMNH barcode at left side of label] FMNHINS | 3260632 | AMBER [handwritten] | FIELD MUSEUM | Wet" <small rectangular label, printed>, "HOLOTYPE | *Paraphloeostiba* | *morosa* sp. nov. | Shavrin A. & Yamamoto S. des. 2019" <red rectangular label, printed> (FMNH).

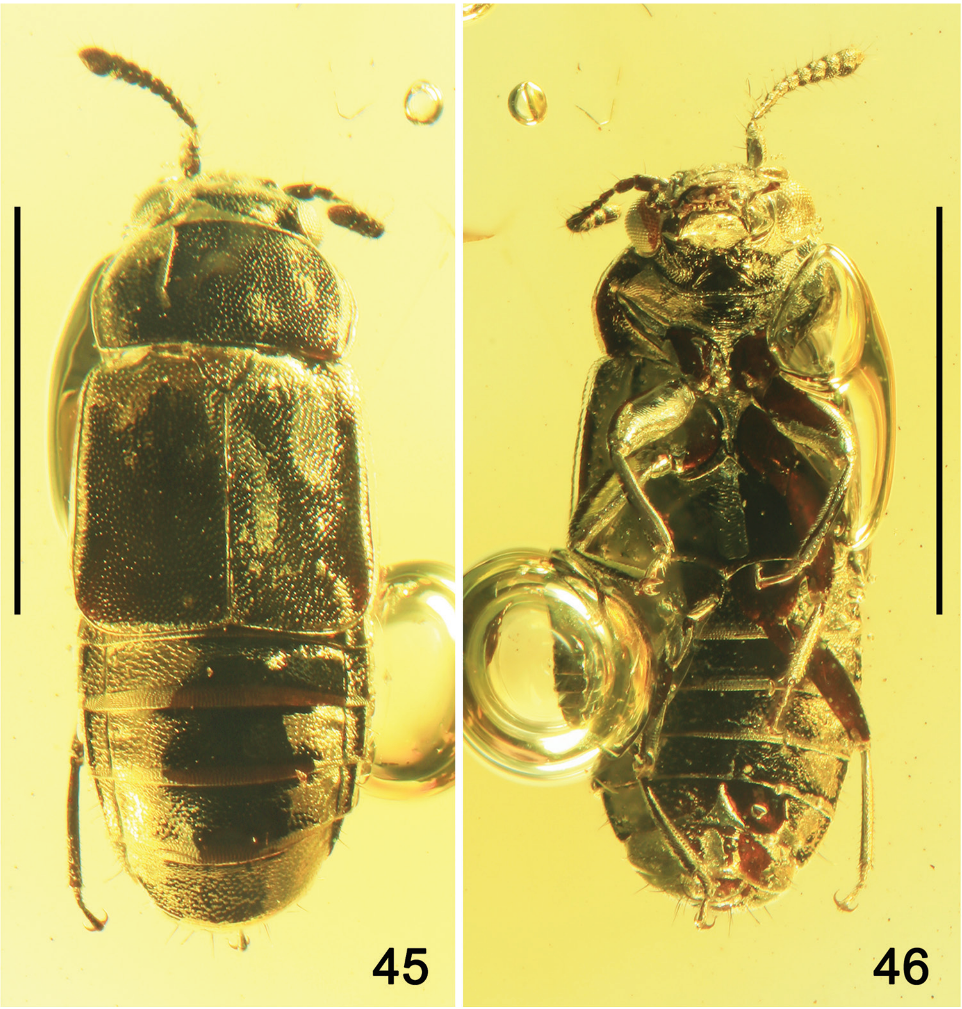
Preservation. The specimen is located at an angle with the head somewhat deeper in the amber piece (Figs 5, 6); the specimen is clearly visible from both dorsal and ventral sides. Syninclusions: round and elongate air bubbles near the specimen on from the ventral side of its body, and elongate piece of plant material located close to the dorsal surface of amber piece near the beetle.

Locality and horizon. Baltic amber from Yantarny, Kaliningrad, westernmost Russia; mid-Eocene (ca 44 Ma; Wappler 2005).

Description. Measurements: HW: 0.36; HL: 0.29; OL: 0.17; AL: 0.51; PML × PMW (III, IV): III: 0.03 × 0.03, IV: 0.06 × 0.02; PL: 0.31; PW: 0.74; ESL: 0.52; EW: 0.77; MTbL: 0.38; MTrL: 0.15 (I–IV: 0.07; V: 0.08); AW: 0.75; TL: ~1.80. Antennomeres with lengths × widths: 1: 0.07 × 0.03; 2: 0.05 × 0.02; 3: 0.05 × 0.01; 4: 0.03 × 0.02; 5: 0.04 × 0.02; 6–7: 0.03 × 0.03; 8: 0.03 × 0.04; 9–10: 0.04 × 0.05; 11: 0.10 × 0.05.

Body moderately wide, glossy (Fig. 45), black, with mouthparts, femora, and apical parts of abdominal tergites reddish-brown, and tarsi yellow-brown. Body laterally as in Figures 47 and 48. Body without visible microsculpture and setation except of paratergites and abdominal tergite VIII with long erect setae (Fig. 48).

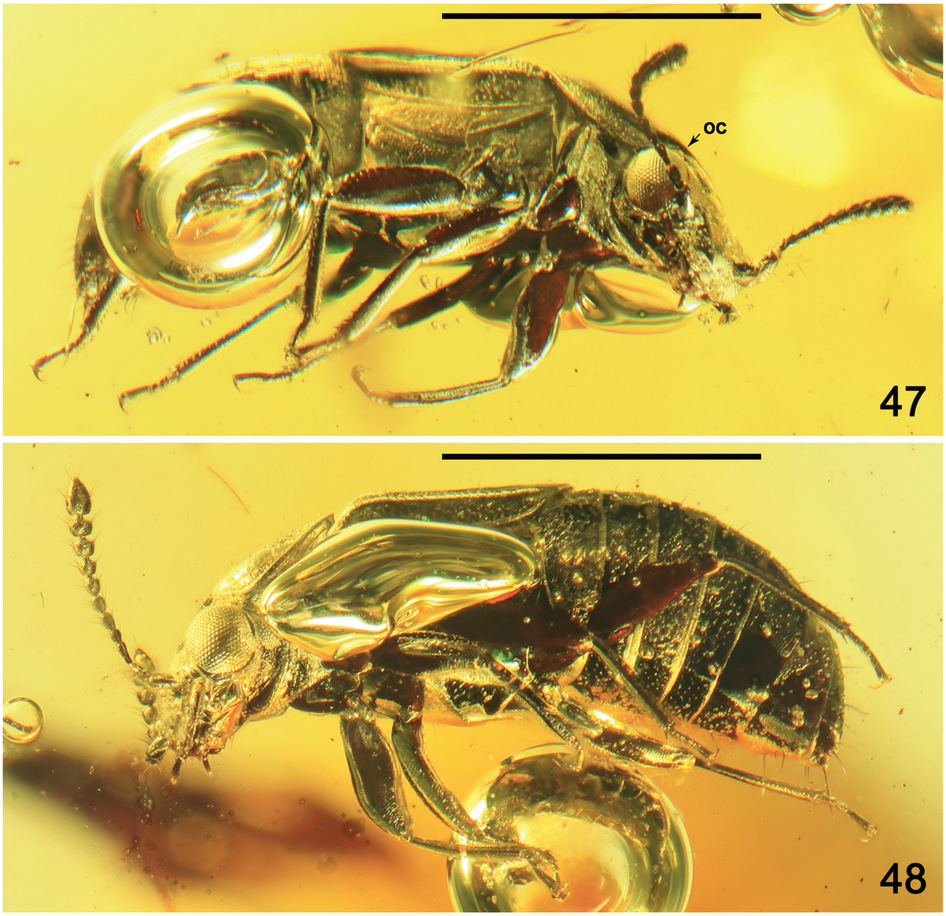
Head 1.2 times as wide as long, with slightly convex posterior portion, dense and small punctation and postocular carina (Fig. 49). Head laterally as in Figure 49, anteroventrally as in Figure 50, and ventrally as in Figure 51. Eyes large, with medium-sized facets, broadly convex, with distinct infraorbital carina (Figs 49–51). Ocelli moderately large, situated at level of posterior third of eyes, distance between ocelli about twice as long as distance between ocellus and medial margin of eye (Fig. 45). Labrum with widely rounded apical margin (Figs 46, 51). Apical maxillary palpomere distinctly longer and slightly narrower than penultimate, swollen in middle and elongate, from middle gradually narrowing toward rounded apex (Figs 49–51). Submentum large, trapezoidal; apical labial palpomere elongate, from middle narrowing apicad (Fig. 49). Gular sutures with markedly rounded posterior parts widely separated from each other below level of posterior margins of eyes (Figs 50, 51). Gena with rugose isodiametric microsculpture (Figs 50, 51). Antenna moderately short, exceeding basal portion of pronotum, with



Figures 45, 46. Habitus of *Paraphloeostiba morosa* sp. nov. **45** dorsal view **46** ventral view. Scale bars: 1.0 mm.

sparse elongate setation; basal antennomere swollen, more than twice as long as wide, antennomere 2 elongate, slightly widened apicad, 3 thin, as long as 2, 4, and 5 markedly widened apicad, 6 and 7 as long as wide, 8–10 slightly transverse, apical antennomere wide, from apical third slightly narrowing toward rounded apex (Figs 45–49).

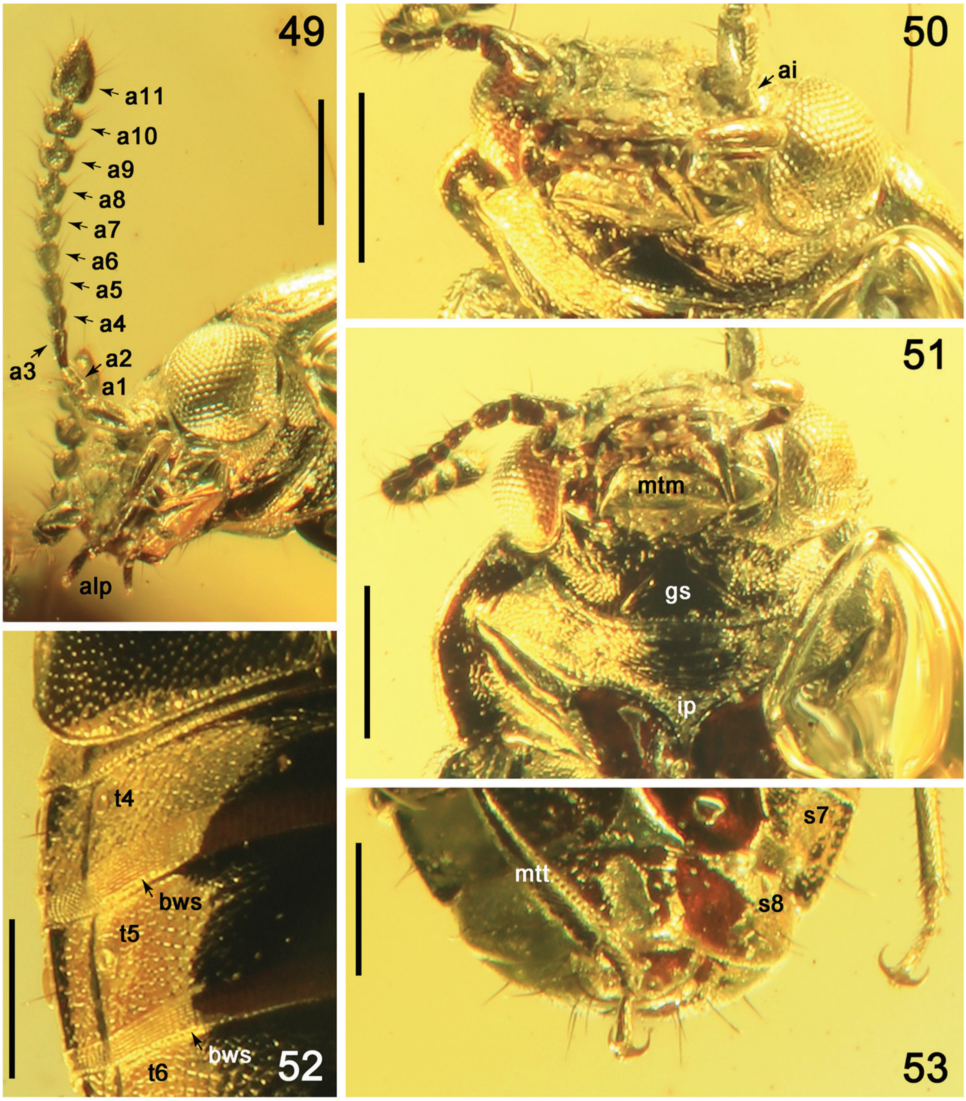
Pronotum with slightly convex surface, markedly transverse, more than twice longer than broad, twice wider than head, from middle slightly more narrowed anterad than posterad, with widely rounded anterior and scarcely rounded posterior angles; apical margin widely rounded, distinctly shorter than somewhat concave posterior margin; paramedian longitudinal impressions indistinct, wide and long, occupying most of middle portion; lateral margins narrowly emarginate, with indistinctly concave laterobasal margins; posterior angles without depressions (Fig. 45). Dorsal surface of pronotum with more or less regular small and dense punctation, distinctly denser than in posterior portion of head



Figures 47, 48. Habitus of *Paraphloeostiba morosa* sp. nov., lateral view. Abbreviation: oc = ocellus. Scale bars: 1.0 mm.

(Fig. 45). Prosternum with widely open procoxal fissures, exposing trochantins, and very long intercoxal process, with acute apex reaching apical part of procoxae (Figs 46, 51). Median part of mesoventrite somewhat convex, with very long acute intercoxal process, reaching more than halfway along the length of the mesocoxae and moderately wide apex of metaventral process (Fig. 46). Scutellum large and triangular, with rounded apex and dense punctation in apical part (Fig. 45). Metaventrite with moderately wide metacoxal cavities (Fig. 46). Median part of prosternum and metaventrite with indistinct and sparse small punctures; mesanepisternum with diagonal microsculpture; median portions of prosternum and metaventrite, including intercoxal processes, with transverse meshes (Fig. 46).

Elytra evidently flattened, 1.4 times as wide as long, 1.6 times as long as pronotum, with moderately parallel lateral sides (Fig. 45), with widely rounded apical angles (Fig. 52), reaching apical margin of abdominal tergite III, with apical margins slightly oblique toward suture (Fig. 45). Punctation as that in pronotum, slightly sparser in basal portion and near scutellum.



Figures 49–53. *Paraphloeostiba morosa* sp. nov. **49** head and antenna, lateral view **50** head, anteroventral view **51** head and prothorax, ventral view **52** apical part of elytron and abdominal tergites IV–V, dorsal view **53** apex of abdomen and hind legs, ventral view. Abbreviations: a1–a11 = antennomeres 1–11; ai = antennal insertion; alp = apical labial palpomere; bws = brick-wall sculpture on intersegmental membrane; gs = gular suture; ip = intercoxal process; mtm = mentum; mtt = metatibia; s7–s8 = sternites VII–VIII; t4–t6 = tergites IV–VI. Scale bars: 0.2 mm.

Legs moderately long and slender, with wide femora and slender tibiae, gradually widened apicad, covered by elongate setae on both inner and outer margins and with a few strong setae on outer margins (Figs 46–48); tarsi short, with small setae on tarsomeres 1–4, apical metatarsomere slightly longer than preceding tarsomeres together; tarsal claws simple, widely curved and elongate (Figs 46, 53).

Abdomen convex, slightly narrower than elytra, with wide brick-wall sculpture on intersegmental membranes between tergites III–VI (Fig. 52) and sternites III–VI (Fig. 45). Abdominal tergites with moderately dense and deep small punctation and distinct net-like microsculpture (Fig. 52); abdominal sternites with indistinct sparse punctation, with shallow isodiametric microsculpture (Figs 45, 52).

Male unknown.

Female. Apical margin of abdominal tergite VIII rounded. Apical margin of abdominal sternite VIII broadly concave (Fig. 53). Genital segment with moderately wide apical portions of gonocoxites; shape and length of styli invisible, each with very long seta (Figs 47, 48).

Etymology. The specific epithet is the Latin adjective *morosus*, *-a*, *-um* (strange). It refers to somewhat broad body with markedly transverse pronotum of the new species.

Remarks. Based on the shape of body and maxillary palpomeres (see also Zanetti 2012: fig. 55l), slightly convex pronotum, punctation and microsculpture of the surface of body, the fossil presumably belongs to the genus *Paraphloeostiba*. The genus was erected by Steel (1960a) and was compared with *Phloeostiba* Thomson, 1858 and *Phloeonomus* Heer, 1839. It differs from *Phloeostiba* by the shape of short maxillary palpomere 3 and relatively elongate apical palpomere, and from *Phloeonomus* by a different shape of ligula and maxillary palp (for details see Steel 1960a). *Paraphloeostiba* includes more than 30 species distributed in the Palaearctic, Madagascan, Nearctic, and predominantly in Oriental, Australian, and Oceanic regions (Steel 1960a; Herman 2001; Shavrin and Smetana 2016; Shavrin 2017b); one species, *P. gayandahense* (W.J. MacLeay, 1873) is widely adventive around the world to New Zealand, several countries of Europe, and the USA (Herman 2001). The new species is difficult to compare reliably with known species as these mostly differ by the structure of the aedeagus, and shapes of accessory sclerite and spermatheca. The apical antennomeres of *P. morosa* sp. nov. are slightly transverse, beginning with antennomere 8 (Figs 48, 49) while other known species have transverse antennomeres beginning with 6 or 7. Based on the punctation and microsculpture of the pronotum and shape of antennomere 10 (Fig. 49), the new species is similar to *P. specularis* (Bernhauer, 1915), known from New Britain (Bismarck Archipelago of Papua New Guinea) but differs by the somewhat larger and wider body, the absence of laterobasal pronotal depressions, and the more transverse pronotum (Fig. 45). Based on the shape and coloration of the body, similar punctation, pronotum without depressions on basal portions, and somewhat convex mesoventrite, *P. morosa* sp. nov. is also similar to *P. electrica* Zanetti et al., 2016, recently described from Baltic amber, from which it differs by the wider body with more transverse pronotum, as well as elongate antennomeres 4–7, and wide apical and penultimate palpomeres.

Paraphloeostiba requires revision due to unclear morphological boundaries between described species and related genera, as well as many undescribed species from the Oriental and Australian regions deposited in institutional and private collections. The new species is tentatively attributed to this genus, making it the second extinct representative of the genus after *P. electrica*.

Genus *Phyllodrepa* Thomson, 1859

Type species. *Staphylinus floralis* Paykull, 1789

†*Phyllodrepa daedali* Shavrin & Yamamoto, sp. nov.

http://zoobank.org/BDE372B6-F773-433D-B98E-C0E272FB8FA7
Figures 7–9, 54–64

Type materials examined. Holotype (male), FMNHINS-3260629, complete specimen as inclusion in very small piece of light yellow Baltic amber, 9.3 mm × 5.9 mm × 2.9 mm in size (Figs 7–9), with the following labels: "16 [printed] 02 [handwritten] SYAC 0 [printed] 294 [handwritten] | Baltic / ~~Burmite~~ | ~~Other:~~ | ~~Larva~~ / Adult | Omalium sp. [handwritten] | Omaliinae [handwritten] | Yantarny, Kaliningrad [handwritten] | Shûhei Yamamoto's | Amber Collection" <large rectangular label, printed>, "[FMNH barcode at left side of label] FMNHINS | 3260629 | AMBER [handwritten] | FIELD MUSEUM | Wet" <small rectangular label, printed>, "HOLOTYPE | *Phyllodrepa* | *daedali* sp. nov. | Shavrin A. & Yamamoto S. des. 2019" <red rectangular label, printed> (FMNH).

Preservation. The specimen is relatively well preserved and many details are visible, from the dorsal, ventral and lateral sides (Figs 7–9). However, most body parts, except the dorsal surface of the head, are covered with cloud of milky substance, especially most of the ventral side.

Locality and horizon. Baltic amber from Yantarny, Kaliningrad, westernmost Russia; mid-Eocene (ca 44 Ma; Wappler 2005).

Description. Measurements: HW: 0.32; HL: 0.22; OL: 0.11; AL: 0.52; PML × PMW (III, IV): III: 0.02 × 0.02, IV: 0.07 × 0.02; PL: 0.35; PW: 0.48; ESL: 0.56; EW: 0.51; MTbL: 0.31; MTrL: 0.20 (I–IV: 0.08; V: 0.12); AW: 0.50; TL: ~1.80. Antennomeres with lengths × widths: 1: 0.08 × 0.03; 2: 0.06 × 0.02; 3–4: 0.05 × 0.02; 5: 0.04 × 0.02; 6: 0.04 × 0.03; 7: 0.03 × 0.03; 8–10: 0.03 × 0.04; 11: 0.08 × 0.04.

Body elongate and slightly convex, glossy (Fig. 54), reddish-brown, with darker head and abdomen; mouthparts, antennae, legs and apical margins of abdominal sclerites yellow-brown. Body lateroventrally as in Figure 55 and laterally as in Figure 56. Lateral margins of pronotum (Figs 54, 57), paratergites and abdominal tergite VIII (Fig. 64) with several long erect setae.

Head 1.4 times as wide as long, with slightly convex median portion and slight oval lateroapical impressions (Fig. 57), with sparse, small and moderately deep punctation, with shallow postocular carina. Eyes large and broadly convex (Figs 55–57, 60). Ocelli large and convex, situated at level of posterior margins of eyes, distance between ocelli much more than twice as long as distance between ocellus and posterior margin of eye; grooves in front of ocelli present, moderately deep and short (Fig. 57). Apical segment of maxillary palp significantly longer than small penultimate segment, from swollen middle gradually narrowing apicad (Figs 56, 57, 63). Antenna moderately short, just surpassing basal margin of pronotum, with sparse very long setae on antennomeres

Figures 54–56. Habitus of *Phyllodrepa daedali* sp. nov. **54** dorsal view **55** lateroventral view **56** lateral view. Abbreviation: mds = modified setae. Scale bars: 1.0 mm.

5–11; basal and antennomere 2 swollen and elongate, 3 and 4 narrow and elongate, 5 ovoid, 6 and 7 slightly transverse and 8–10 distinctly transverse, apical antennomere large, strongly narrowing from about middle apicad (Figs 54–58).

Pronotum slightly convex, without longitudinal impressions, 1.3 times as wide as long, 1.5 times as wide as head, from middle distinctly more narrowed posterad than apicad, with widely rounded anterior and obtuse posterior angles; apical margin widely rounded, slightly shorter than somewhat straight posterior margin; lateral margins slightly sinuate posteriorly, narrowly emarginate and finely crenulate; lateroposterior portions with indistinct, moderately wide impressions (Figs 54, 57). Dorsal surface of pronotum without visible microsculpture between punctures, with dense, very large and deep punctation, markedly sparser in lateral and smaller in apical and basal portions (Figs 54, 57). Prosternum with wide procoxal fissures and moderately short prosternal process, with acute apex (Fig. 60). Scutellum moderately large, triangular, with somewhat rounded apex, without visible punctures or microsculpture (Fig. 54).

Elytra slightly convex, longer than wide, 1.6 times as long as pronotum, reaching basal margin of abdominal tergite IV, with somewhat parallel lateral sides and widely rounded lateroapical angles, with sutural apices truncate to very oblique (Fig. 54). Punctation as that in pronotum, but shallower and somewhat smoothed on apical portion, smaller and sparser on basal and apical portions. Surface between punctures with shallow dense isodiametric microsculpture.

Legs long and slender, similar in shape, with moderately wide femora; tibiae slender, gradually widened apicad, covered by elongate setae, denser and stronger on inner margins, and with a few strong spines near apex and additional spine on outer margin in apical third (Figs 55, 56, 59); tarsi long, with apical metatarsomere distinctly longer than previous tarsomeres together (Figs 59, 61, 62); protarsus as in Figure 61, with long tenent setae (probably only in males); tarsal claw simple (Figs 61, 62).

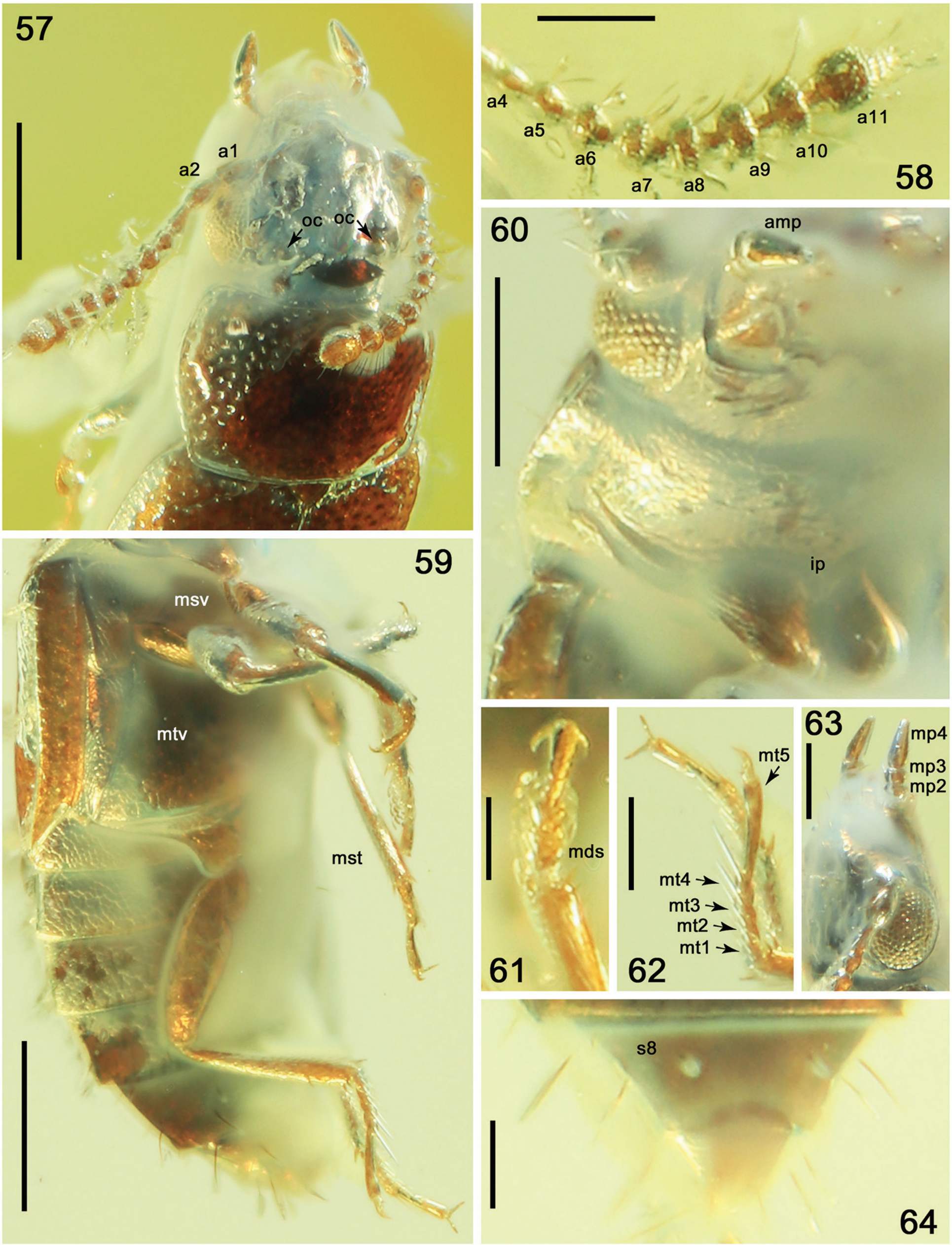
Abdomen markedly convex, slightly narrower at base than elytra; wing-folding patches in middle of tergite IV and/or V not visible; intersegmental membranes between tergites IV–VII with brick-wall sculpture, apical margin of tergite VII with indistinct very narrow palisade fringe (Fig. 54). Abdominal tergites without visible punctation, with large distinct transverse microsculpture.

Male. First four protarsomeres wide (Figs 55, 59, 61); ventral surface of protarsomeres 1–4 with several rows of modified tenent setae (not all details visible) consisting of internal rows formed by markedly elongate setae with leaf-shaped apical parts (Figs 55, 56, 59, 61); ventral surface of mesotarsomeres 1–4 with two rows of elongate setae with broadened apical parts as that in protarsomeres 1–4 but without additional internal rows (Figs 55, 56); metatarsi as in Figure 62. Apical margin of abdominal tergite VIII straight.

Female unknown.

Etymology. The specific epithet is the Latinized name of *Daedalus*, *-i*, *m*, the Greek architect of the times of Theseus and Minos, and father of Icarus.

Remarks. In external characters such as proportions of the body, antennomeres, and maxillary palpomeres, and, more substantially, by the proportions of tarsi with elon-



Figures 57–64. *Phyllodrepa daedali* sp. nov. **57** head and pronotum, laterodorsal view **58** left antenna, ventral view **59** thorax, legs and abdomen, lateroventral view **60** head and prothorax, ventral view **61** protarsus, dorsal view **62** hind tarsi, lateral view **63** head and maxillar palpi, dorsolateral view **64** apex of abdomen, ventral view. Abbreviations: a1–a11 = antennomeres 1–11; amp = apical maxillary palpomere; ip = intercoxal process; mp2–mp4 = maxillary palpomeres 2–4; mds = modified setae; mst = mesotibia; msv = mesoventrite; mt1–mt5 = metatarsomeres 1–5; mtv = metaventrite; oc = ocellus; s8 = sternite VIII. Scale bars: 0.1 mm (**58, 61–63**), 0.2 mm (**57, 60, 64**), 0.3 mm (**59**).

gate apical tarsomere, the fossil undoubtedly belongs to the tribe Omaliini. Based on the triangular and elongate apical maxillary palpomere, shape of slightly convex head and slightly transverse antennomere 7, presence of two small depressions between bases of antennae, short grooves (dorsal tentorial pits) in front of the ocelli, and shape of the moderately convex pronotum with slightly sinuate lateral margins in front of obtuse posterior angles, the new species belong to the *Phyllodrepa* complex, specifically to the genus *Phyllodrepa*. *Phyllodrepa* includes about 30 species distributed in Palaearctic, Nearctic, and Neotropical regions (Newton et al. 2000; Herman 2001; Schülke and Smetana 2015). The genus requires a worldwide revision and apparently includes some taxa that belong to other related genera (Shavrin 2016; Zanetti et. al. 2016). *Phyllodrepa daedali* sp. nov. and *Ph. icari* sp. nov., described below, are species with a very small and pale body that reminds of some Palaearctic species of the genus *Dropephylla* Mulsant & Rey, 1880, that for a long time had been regarded as a subgenus of *Phyllodrepa*. Nevertheless, species of *Dropephylla* differ by the absence of grooves in front of ocelli and microsculpture on the elytra, wider apical maxillary palpomere, oval antennomere 4, by the presence of moderately defined short and rounded temples, shorter apical tarsomere, and other morphological characters that were considered in the revision of the Palaearctic fauna of the genus by Jászay and Hlaváč (2006). Although faintly crenulate lateral margins of the pronotum (Fig. 57) are similar to those in *Dialycera* Ganglbauer and *Hapalaraea* Thomson (Zanetti 1987, 2012b; Zanetti et al. 2016), they are also known to the first author in European *Phyllodrepa puberula* Bernhauer, 1903 and some little-known species distributed in the eastern Palaearctic Region. Despite this, the new species can not be reliably associated with any extant species of the genus due to its unique morphological characters and the fact that most species differ only by the external structure of the aedeagus. Both new species of *Phyllodrepa* described herein differ from the more ancient Transbaikal †*Eophyllodrepa* Ryvkin from the Middle-Upper Jurassic of Novospasskoe (Ryvkin 1985) and †*Daidromus* Ryvkin from the Upper Jurassic of Daya (Ryvkin 1990), by the same morphological characters as in *Ph. electrica* (see Zanetti et al. 2016). Based on the small body, shape of head, general shape of apical antennomeres, and pronotum with finely crenulate lateral margins, *Ph. daedalum* sp. nov. is similar to *Ph. antiqua* Zanetti, Perreau & Solodovnikov, 2016, which was recently described from Baltic amber (Zanetti et. al 2016). It is also similar to *Ph. icari* sp. nov. (see below), based on the crenulate lateral pronotal margins, pale body, and large and deep punctation of the elytra. It differs from *Ph. antiqua* by the smaller, paler and slightly more convex body (Figs 54, 56), coarser and deeper punctation of pronotum (Figs 54, 57) and elytra (Fig. 54), and elongate antennomeres 2–5 (Fig. 58), and from *Ph. icari* sp. nov. by the darker abdomen, wider apical maxillary palpomere (Fig. 57), shape of anterior angles of the pronotum not protruded apicad (Fig. 57), denser punctation of the pronotum, less transverse head and pronotum (Fig. 57), and longer antennomeres 4–5 and 11 (Fig. 58). From both these species it differs by longer elytra, and from *Ph. antiqua* by the presence of modified setae on tarsomeres 1–4 of front and middle legs of the male.

A remarkable morphological feature of *Ph. daedali* sp. nov. is the presence of modified rows of elongate setae (Figs 55, 56, 61) with leaf-shaped apical parts on ventral surface of pro- and mesotarsomeres 1–4, described earlier as disco-setae (Stork 1980) or clavate adhesive setae (Smetana 1987). Similar structures were observed in species of the Oriental genera *Xanthonomus* Bernhauer by Steel (1955: fig. 6), *Prosopaspis* Smetana (Smetana 1987: fig. 22), *Duocalcar* Peris & Thayer, 2014 (at least protarsi), and *Paraphloeostiba* (Steel 1960a).

†*Phyllodrepa icari* Shavrin & Yamamoto, sp. nov.

http://zoobank.org/C1EC61D0-CD67-48CC-92C0-07489AE05B8A

Figures 10, 11, 65–72

Type materials examined. Holotype (female), FMNHINS-3260628, complete specimen as inclusion in small rectangular light yellow Baltic Amber, 19.2 mm × 7.9 mm × 5.1 mm in size (Figs 10, 11), with the following labels: "15[printed]04[handwritten] – SYAC 00[printed]94[handwritten] | Baltic / ~~Burmite~~ | ~~Oher:~~ | ~~Larva~~ / Adult | Omaliinae[handwritten] | Baltic Sea Coast, [handwritten] | close to the Wisla Riv. | Estuary, Poland[handwritten] | Shûhei Yamamoto's | Amber Collection" <large rectangular label, printed>, Nadewca / Sender: | Artur Michalski" <large light yellow rectangular label, handwritten>, "[FMNH barcode at left side of label] FMNHINS | 3260628 | AMBER [handwritten] | FIELD MUSEUM | Wet" <small rectangular label, printed>, "HOLOTYPE | *Phyllodrepa* | *icari* sp. nov. | Shavrin A. & Yamamoto S. des. 2019" <red rectangular label, printed> (FMNH).

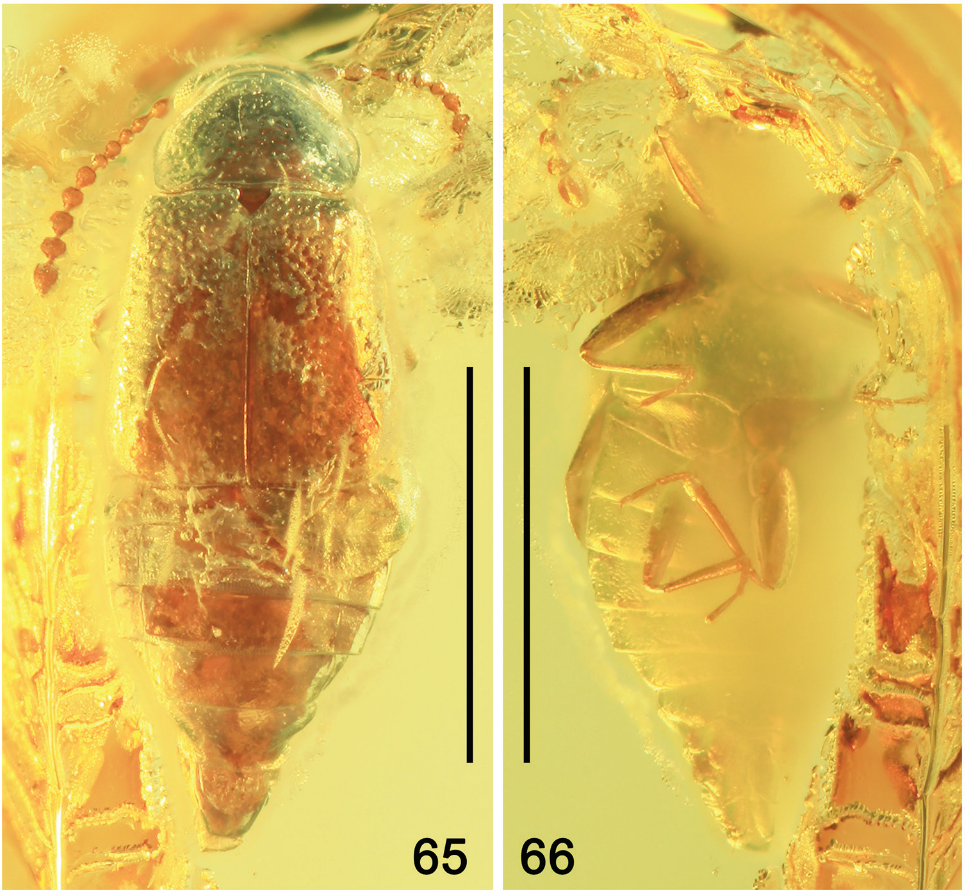
Preservation. The specimen is in relatively good condition and best visible from the dorsal side of the body, except the head and right antennomeres 9–11, and with head visible from the narrow side of the amber piece (Fig. 10). The details of the ventral side of inclusion are not visible except for the apical antennomeres, middle and hind legs, and a part of the mesothoracic segment and abdominal sternites (Figs 66, 69, 72). Syninclusion: imago of small Diptera about 1.20 mm in length.

Locality and horizon. Baltic amber from Baltic Sea Coast, close to the estuary of Wisła River, Gdańsk, Poland; mid-Eocene (ca 44 Ma; Wappler 2005).

Description. Measurements: HW: 0.31; HL: 0.18; OL: 0.11; AL: 0.50; PML × PMW (III, IV): III: 0.03 × 0.02, IV: 0.05 × 0.01; PL: 0.25; PW: 0.46; ESL: 0.58; EW: 0.66; MTbL: 0.16; MTrL: 0.11 (I–IV: 0.05; V: 0.06); AW: 0.66; TL: ~1.80. Antennomeres with lengths × widths: 1: 0.08 × 0.03; 2: 0.05 × 0.02; 3: 0.04 × 0.02; 4–5: 0.03 × 0.02; 6: 0.02 × 0.02; 7: 0.04 × 0.03; 8: 0.04 × 0.04; 9: 0.05 × 0.05; 10: 0.05 × 0.06; 11: 0.07 × 0.06.

In general appearance, body (Fig. 65) and legs as in *Ph. daedali* sp. nov., reddish-brown, with darker head and pronotum; mouthparts, antennae and legs yellow-brown. Body ventrally as in Figure 66.

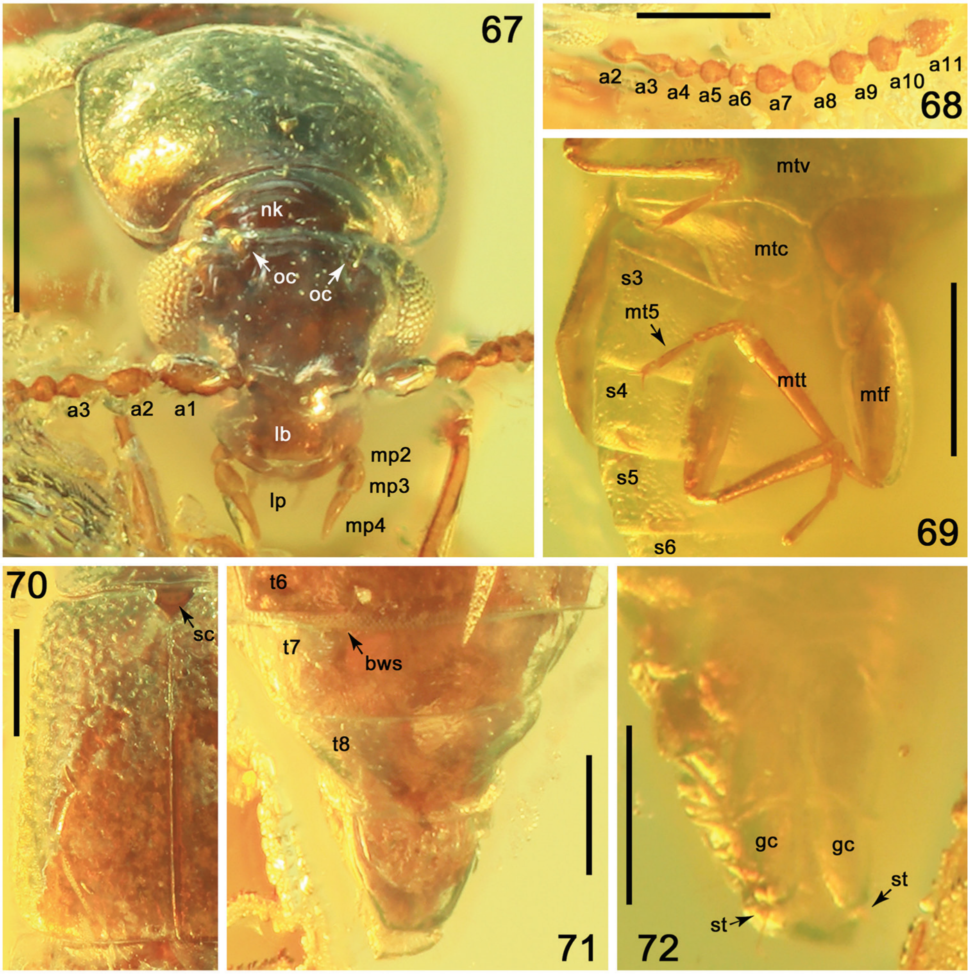
Head transverse, 1.7 times as wide as long, with slightly convex median portion (Fig. 67); punctation and postocular carina invisible. Eyes very large and broadly convex (Fig. 67). Ocelli large and convex, situated almost at level of posterior margins of eyes, distance between ocelli about twice as long distance between ocellus and medial



Figures 65, 66. Habitus of *Phyllodrepa icari* sp. nov. **65** dorsal view **66** ventral view. Scale bars: 1.0 mm

margin of eye; grooves in front of ocelli very short and moderately deep (Fig. 67). Labrum wide and transverse, with slightly rounded apical margin (Fig. 67). Apical segment of maxillary palp narrow, narrowing from base toward moderately acute apex, distinctly longer and narrower than swollen penultimate segment (Fig. 67). Antenna moderately long, reaching basal third of elytra; antennomeres 1 and 2 swollen and elongate, 3 with very narrow elongate base, 4–6 ovoid, 7–9 slightly and 10 distinctly transverse, apical antennomere slightly longer than wide, strongly narrowed from about apical third (Figs 65, 68).

Pronotum transverse, 1.8 times as wide as long, 1.4 times as wide as head, from middle more narrowed posterad than anterad, with widely rounded slightly protruding anterior and obtuse posterior angles (Fig. 67); apical margin moderately widely concave, distinctly shorter than posterior margin; lateral margins narrowly marginate and slightly crenulate, more distinct posteriorly; laterobasal portions with indistinct wide impressions (Figs 65, 67). Dorsal surface of pronotum with moderately sparse, large and deep punctation, distinctly sparser in basal and apical portions, with nar-



Figures 67–72. *Phyllodrepa icari* sp. nov. **67** head and pronotum, anterodorsal view **68** left antenna, dorsal view **69** hind legs and abdomen, ventral view **70** left elytron, dorsal view **71** apex of abdomen, dorsal view **72** apex of abdomen, ventral view. Abbreviations: a1–a11 = antennomeres 1–11; bws = brick-wall sculpture on intersegmental membranes; gc = gonocoxite; lb = labrum; lp = labial palpi; mp2–mp4 = maxillary palpomeres 2–4; mt5 = metatarsomere 5; mtf = metafemur; mtt = metatibia; mtc = metacoxa; mtv = metaventrite; nk = neck; oc = ocellus; s3–s6 = sternites III–VI; sc = scutellum; st = stylus; t6–t8 = tergites VI–VIII. Scale bars: 0.2 mm.

row impunctate longitudinal area (Figs 65, 67). Scutellum large, with triangular apex, without punctures or microsculpture (Fig. 65).

Elytra 1.2 times as long as wide, reaching apical margin of abdominal tergite III, slightly widened apicad, with widely rounded apicolateral angles and apical margins truncate at suture (Figs 65, 70). Punctation denser, markedly larger and deeper than that on pronotum, smaller in basal and apical, and sparser in lateral portions. Surface between punctures with dense isodiametric microsculpture.

Tarsi long, with apical tarsomere markedly longer than previous tarsomeres together (Figs 66, 69).

Abdomen slightly convex, as wide as elytra or slightly wider, intersegmental membranes between tergites IV–VII with brick-wall sculpture (Fig. 65). Abdominal tergites with indistinct small and very sparse punctation and microsculpture, and with sparse and short pubescence, wing-folding patches not visible.

Male unknown.

Female. First four mesotarsomeres 1–4 without modified setae (Figs 66, 69). Apical margin of abdominal tergite VIII slightly rounded (Fig. 71). Apical margin of abdominal sternite VIII widely concave (Fig. 72). Genital segment with markedly elongate and wide gonocoxites, with very small narrow styli, each with very long seta (Fig. 72).

Etymology. The specific epithet is the Latinized name of Icarus (Ikaros), son of Deaedalus in Greek mythology.

Remarks. Despite the shape of antennomere 3 and the posterior angles of the pronotum, which are usual in members of the genus *Acrolocha* Thomson, in other external characters (see details above), the new species belongs to the genus *Phyllodrepa*. The fossil shares with that genus slightly protruded anterior angles of the pronotum with impressed laterobasal portions (Fig. 67), similar to those of extant North European *Ph. sahlbergi* Luze, in addition to similar coloration of the body and proportions of antennomeres 4 and 5 (Fig. 68). However, the fossil differs from that species by the significantly smaller and slightly more convex body (Fig. 65), with more prominent eyes (Fig. 67), coarser punctation of the elytra and pronotum, pronotum with less sinuate lateral margins (Figs 65, 67), less transverse antennomeres 6–10 (Fig. 68), and longer elytra (Fig. 70). Based on the shape of its small and pale body, and large and deep punctation of the elytra (Figs 65, 70), *Ph. icari* sp. nov. is similar to *Ph. daedali* sp. nov., from which it differs by the paler abdomen, narrow apical maxillary palpomere (Fig. 67), the shape of anterior angles of the pronotum protruding apicad, sparser punctation of the pronotum, distinctly transverse head and pronotum (Fig. 67), shorter antennomeres 4, 5, and 11 (Fig. 58), and shorter elytra.

Unnamed species

Eusphalerum sp. 1

Figures 14–16, 73–80

Materials examined. 2 males (no. 6, no. 9), 2 females (no. 3, no. 7), 5 unsexed specimens (no. 1, no. 2, no. 4, no. 5, no. 8), FMNHINS-3260631, complete specimens as inclusions in yellow Baltic amber 31.3 mm × 20.6 mm × 12.6 mm in size (Figs 14–16), with the following labels: "15[printed]03[handwritten]-SYAC 00[printed]8[handwritten] | Baltic / ~~Burmite~~ | ~~Other:~~ | ~~Larva~~ / Adult | Omaliinae 11 exs, [handwritten] | Baltic Sea Coast [handwritten] | Axel (Germany) [handwritten] | Shûhei Yamamoto's | Amber Collection" <large rectangular label, printed>, "Axel Niggeloh" <rectangular label, printed>, "[FMNH barcode at left side of label] FMNHINS | 3260631 | AMBER

Figures 73–75. Habitus of *Eusphalerum* sp.1: **73** forebody, dorsal (specimen no. 5) and lateral (specimen no. 6) view **74** pronotum and elytra of specimens no. 1 and no. 2, dorsal view **75** body, lateral view (specimen no. 6). Scale bars: 1.0 mm.

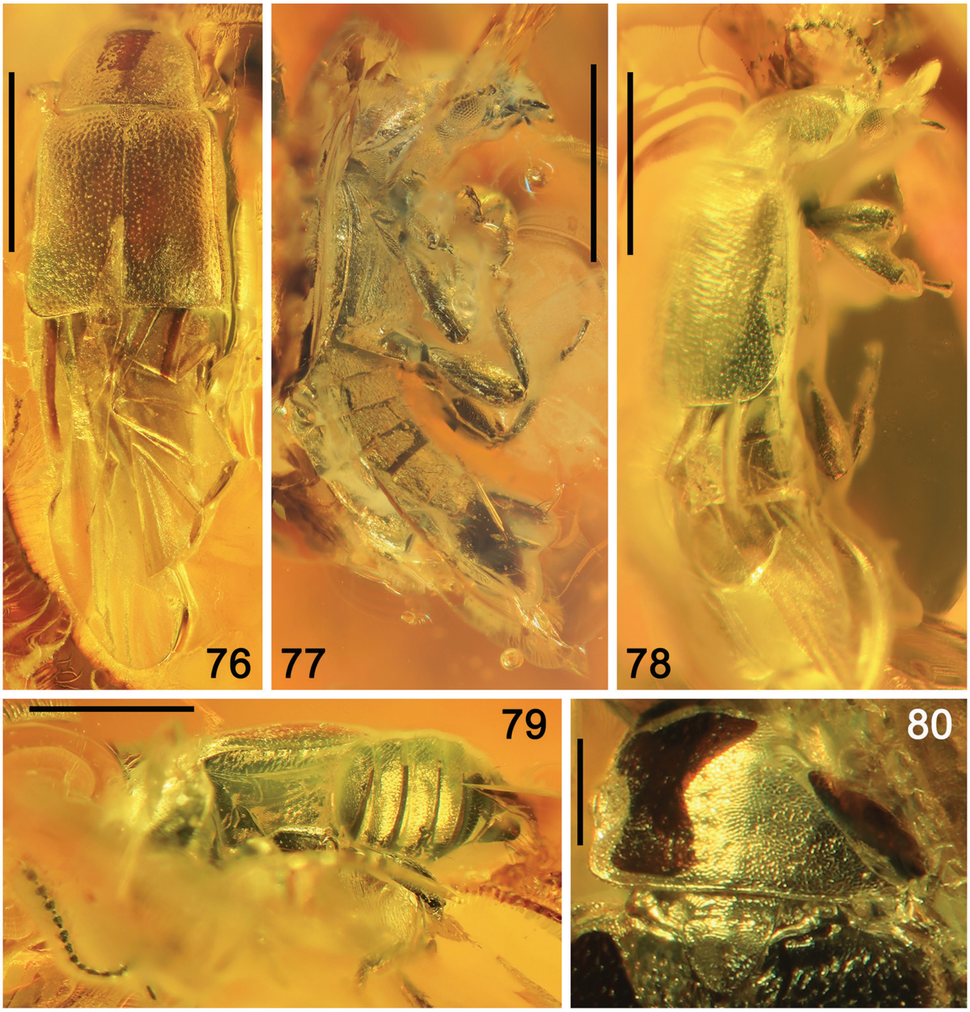
[handwritten] | FIELD MUSEUM | Wet" <small rectangular label, printed>, "*Eusphalerum* | sp. 1 | Shavrin A.V. det. 2018" <rectangular label, printed> (FMNH).

Preservation. The specimens are visible from one surface of the piece of amber (specimens were numbered as in Figs 14–16). One of the best preserved specimens (male, no. 6) is located dorsolaterally: the surface of the body, left antenna, and part of the abdomen in lateral view are clearly visible. Eight other specimens are present with differing degrees of visible details. A male (no. 9) is located deep in the piece of amber at the level of its median convexity; its pronotum, elytra, and abdomen are clearly visible dorsolaterally, and the antennae, mouthparts, legs and parts of the thoracic segments and abdomen are visible ventrally. A female (no. 3) is laterally oriented close to the outer surface of the amber piece; its basal antennomeres of the right antenna are partly visible, and the mouthparts, including maxillary and labial palpi, lateral side of the elytra, and partly thoracic sclerites, and legs relatively are visible. Another female (no. 7) is located laterally deep in the piece of amber and, therefore, the dorsal side of its body is visible but strongly cloudy and distorted; details of the structure of maxillary palpus, right antenna, five legs partly, some details of the thorax and abdomen, including apical portion with the genital segment are more or less visible from lateral view. An unsexed specimen (no. 1) is located dorsally near the outer surface of the piece of amber; only the pronotum and elytra are partly visible. Another unsexed specimen (no. 2) is located dorsally near the outer surface of the piece of amber near specimen no. 1; the apical segments of its right antenna, pronotum, and elytra are clearly visible. An unsexed specimen (no. 4) is located a little deeper in the piece of amber, close to specimen no. 3; its hind wings are extended and cover the entire abdomen. The body is not clearly visible except for the pronotum and elytra. An unsexed specimen (no. 5) is located dorsally near specimen no. 6, with the left antenna, posterior portion of head, pronotum, and elytra partially visible. Another unsexed specimen (no. 8) is located deep in the piece of amber, near specimen no. 9, and has its hind wings extended so as to cover the dorsal side of the abdomen; there is a milky covering on the lateral side of the body, and, therefore, the middle and hind legs are only partly visible in lateral view and the pronotum and elytra are partly visible in dorsal view. Syninclusion near outer surface of the piece of amber close to its margin: imago of Diptera about 2.80 mm length, including wings (Fig. 14).

Description. Measurements (n = 9): HW: 0.67 (no. 5); HL: ?; OL: 0.18 (no. 6); AL (no. 6): 0.74; PML × PMW: ?; PL: 0.41–0.46; PW: 0.87 (no. 5); ESL: 0.83–0.96; EW: 0.71–0.77; MTbL (no. 8): 0.40; MTrL (no. 8): 0.28; AW: 0.68–0.74; TL: ~2.50–3.20. Antennomeres with lengths × widths (no. 6): 1: 0.15 × 0.05; 2: 0.08 × 0.04; 3: 0.06 × 0.03; 4–6: 0.05 × 0.03; 7: 0.05 × 0.04; 8: 0.06 × 0.04; 9 0.05 × 0.05; 10: 0.06 × 0.05; 11: 0.08 × 0.05.

Body moderately wide, convex (Figs 73–76). Body laterally as in Figures 77 and 79, dorsally as in Figs 73, 74, and 76 and dorsolaterally as in Figure 78. The specimens appear brown to black. Body glabrous, without visible setation.

Head transverse, with slightly convex middle portion, without grooves in front of ocelli (Fig. 75); punctation of posterior portion of head irregular, small, and sparse; surface between punctures with relatively large transverse fine microsculpture, distinctly larger and coarser on neck. Eyes large, widely convex (Figs 75, 77). Ocelli relatively small, slightly convex (Figs 73, 75). Apical segment of maxillary palp elongate, slightly narrower and distinctly longer than penultimate segment, from middle gradually narrowed apicad, with moderately acute apex (Fig. 77). Antenna reaching basal margin of elytra; basal antennomere markedly wide, antennomere 2 swollen and slightly elongate, 3 with thin basal portion, slightly widened apicad, antennomeres 4–6 slightly shorter than 3, 7 slightly wider than 6 and 8, 10 slightly transverse in apical portion, apical antennomere wider than penultimate segment, from apical third gradually narrowed apicad (Figs 73, 75, 78, 79).



Figures 76–80. *Eusphalerum* sp. 1 **76** habitus, dorsal view (specimen no. 4) **77** habitus, lateral view (specimen no. 3) **78** habitus, dorsolateral view (specimen no. 8) **79** habitus, lateral view (specimen no. 9) **80** pronotum and scutellum, dorsal view (specimen no. 1). Scale bars: 1.0 mm (**76–79**), 0.2 mm (**80**).

Pronotum slightly convex and distinctly transverse, about twice as wide as long, distinctly broader than head, widest in middle, more narrowed posterad than anterad; apical margin slightly rounded, about as broad as posterior margin, anterior (Fig. 75) and posterior angles (Fig. 80) widely rounded; laterobasal margins slightly concave; lateral margins in middle narrowly marginate; median disc of pronotum with very indistinct transverse and laterobasal portions with indistinct wide impressions (Figs 73–76, 80). Pronotum with more or less regular small and sparse punctation, sometimes with wide impunctate longitudinal area on disc, with distinct and moderately large transverse and diagonal microsculpture (Figs 73–76, 80). Scutellum without visible punctures, with distinct isodiametric microsculpture (Figs 73, 74, 76, 80).

Elytra slightly convex, distinctly longer than broad, twice as long as pronotum, from middle slightly widened apicad, reaching apical margin of abdominal tergite IV, with widely rounded apical angles and straight apical margin truncated at suture (Figs 73–76, 78). Punctation markedly denser and deeper than that on pronotum, smaller on basal and apical margins and near scutellum; microsculpture as that on pronotum (Figs 73, 74, 76, 78).

Abdomen slightly narrower than elytra, with small, moderately sparse punctation and fine indistinct microsculpture.

Male. Apical margin of abdominal tergite VIII rounded. Apical margin of abdominal sternite VIII slightly sinuate.

Female. Details of shapes of apical abdominal segment not visible.

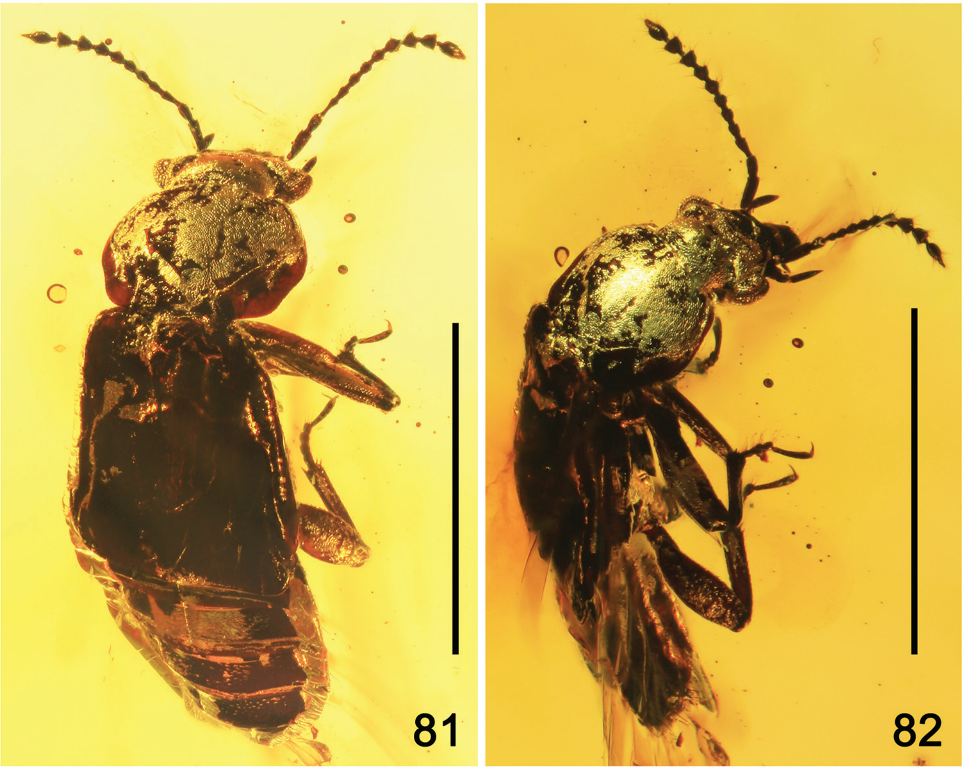
Remarks. The present unique piece of amber contains an interesting and rare aggregation of omaliine specimens which apparently belong to one species. Based on the shape of the body and other structures (antennae, maxillary palpus), features of punctation and microsculpture, etc., the species belongs to Eusphalerini or Omaliini. Tarsi of fore- and middle legs are partly visible in one specimen (Fig. 77); tarsi of this specimen has long and indistinctly dense setae on lateral portions of tarsomeres 1–4 that are common in species of the genus *Eusphalerum*. Based on the shape of the body and other morphological details, and lack of additional morphological data, we have not found similar species among extant representatives of the genus, so we here treat this taxon as *Eusphalerum* sp. 1. We did not observe sexual dimorphism in the shape of apical portions of the elytra, which often occurs in *Eusphalerum*, as was observed for *Eu. kanti* sp. nov. above. Furthermore, the morphology of the aedeagus should be studied, as species of the genus are reliably distinguished by the shapes of the median lobe of the aedeagus and the parameres.

***Eusphalerum* sp. 2.**

Figures 12, 13, 81–85

Materials examined. One male, complete specimen as an inclusion in a piece of yellow Baltic amber 35.4 mm × 21.5 mm × 7.5 mm in size (Figs 12, 13), with glued very small quadrate paper on plastic bag labeled "AWI | 045", with the following labels: "AWI-045 | Phyllodrepa (?) | 3 spec." <rectangular handwritten label>, "Dr. Vitalii Alekseev's | Collection" <rectangular handwritten label>, "*Eusphalerum* sp. 2 | Shavrin A.V. det. 2018" <rectangular label, printed>. The specimen is deposited in the private collection of Vitalii I. Alekseev (Kaliningrad, Russia), registered as AWI-045.

Preservation. The single specimen is a male located close to the outer surface of the piece of amber, with many details visible in both dorsal and ventral surfaces. The elytra are somewhat deformed and seem flattened, and the right elytron is depressed into the thorax. Additionally, the piece of the amber contains two males of *Eu.* sp. 3 and *Eu.* sp. 4 (see below), and a syninclusion located near the narrowest side of the amber: nymph of small mite about 0.50 mm in length (Figs 12, 13).

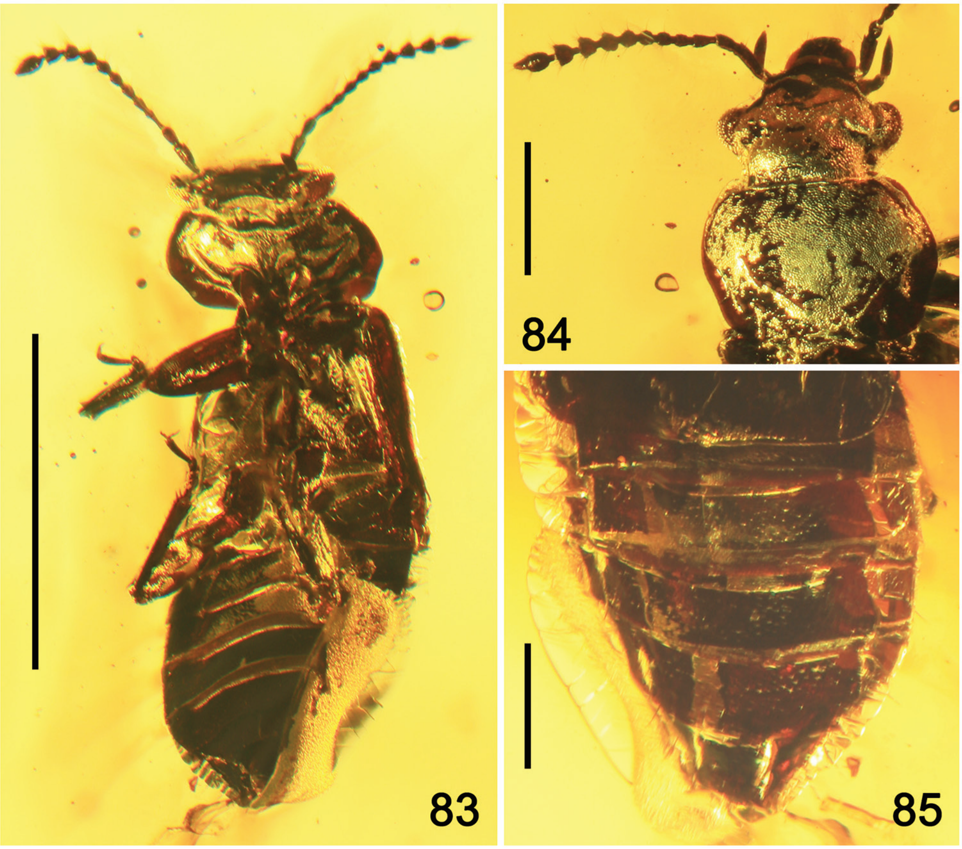


Figures 81, 82. Habitus of *Eusphalerum* sp. 2 **81** oblique dorsal view **82** dorsolateral view. Scale bars: 1.0 mm.

Description. Measurements: HW: 0.53; HL: 0.20; OL: 0.11; AL: 0.69; PML × PMW (III, IV): III: 0.03 × 0.01, IV: 0.07 × 0.02; PL: 0.43; PW: 0.67; ESL: 0.85; EW: 0.81; MTbL: 0.36; MTrL: 0.27 (I–IV: 0.14; V: 0.13); AW: 0.79; TL: 2.06. Antennomeres with lengths × widths: 1: 0.12 × 0.02; 2: 0.07 × 0.02; 3: 0.06 × 0.02; 4: 0.05 × 0.02; 5–6: 0.05 × 0.03; 7: 0.04 × 0.04; 8: 0.05 × 0.04; 9–10: 0.05 × 0.05; 11: 0.10 × 0.04.

Body elongate, somewhat flattened (Fig. 81), glossy and glabrous, without visible setation. Body appears dark-brown, with basal portions of pronotum and legs reddish-brown. Body dorsolaterally as in Figure 82 and ventrally as in Figure 83.

Head strongly transverse, distinctly more than twice as wide as long, with slightly convex middle portion and posterior parts of infraorbital ridges, without visible grooves in front of ocelli and postocular carina (Fig. 84). Head with indistinct, small and sparse punctation, with moderately coarse and large isodiametric microsculpture between punctures becoming more transverse toward middle part of neck. Eyes large, strongly protruding laterad. Ocelli small, convex, situated very close to infraorbital ridges at level of about middle length of eyes, distance between ocelli about twice as long as distance between ocellus and margin of eye (Figs 82, 84). Labrum transverse. Apical segment of maxillary palp elongate, slightly wider in middle than penultimate segment, from apical third gradually narrowed toward moderately acute apex (Figs 82,



Figures 83–85. *Eusphalerum* sp. 2 **83** habitus, ventral view **84** left antenna, head and pronotum, dorsal view **85** abdomen, dorsal view. Scale bars: 1.0 mm (**83**), 0.4 mm (**84, 85**).

84). Gular sutures not fully visible, widely separated from each other (Fig. 83). Antenna moderately long, distinctly exceeding shoulders of elytra, with elongate setae, distinctly longer on antennomeres 6–11; basal antennomere wide, gradually widened apicad, antennomere 2 similar in width, swollen and elongate, 3 with thin basal portion, slightly widened apicad, 4 slightly shorter than 3, 5, and 6 slightly wider than 4, 7 short and moderately rounded, 8–10 slightly transverse, apical antennomere more than twice as long as broad, from about middle strongly narrowed toward acute apex (Figs 81–84).

Pronotum 1.5 times as wide as long, slightly broader than head, widest in middle, markedly more narrowed posterad than anterad; apical margin slightly and widely rounded, about as broad as posterior margin, anterior and posterior angles widely rounded; laterobasal margins slightly concaved, with very indistinct small crenulation; lateral margins narrowly explanate; lateral portions with indistinct semioval impression about middle (Figs 81, 84). Pronotum with somewhat regular small and sparse punctation and with isodiametric ground sculpture slightly coarser than that on head (Figs 81, 84). Prosternum with moderately wide and protruded prosternal process (Fig. 83). Scutellum large and wide (Fig. 81).

Elytra little longer than wide, about twice as long as pronotum, gradually widened apicad, reaching basal to apical margins of abdominal tergite IV, with widely rounded apicolateral angles; shoulders moderately widely rounded; lateral edges narrowly explanate (Fig. 81). Punctation of elytra invisible in details but appears slightly denser and deeper than that on pronotum.

Legs moderately long and slender, femora markedly widened in middle, tibiae moderately short and thin, gradually widened apicad, slightly shorter than femora, covered by elongate setae, with a few strong setae on apical margins near apex; tarsomeres 1–4 distinctly wide, with dense and long setae; apical metatarsomere long, yet slightly shorter than length of preceding tarsomeres together; tarsal claws simple, elongate (Figs 81–83).

Abdomen (Fig. 85) slightly narrower than elytra; abdominal tergites with sparse and moderately small punctures, no wing-folding patches are visible.

Male. Apical margin of abdominal tergite VIII slightly rounded. Apical margin of abdominal sternite VIII slightly sinuate.

Female unknown.

Remarks. As in the previous species, this specimen has very long and moderately dense setae on lateral portions of tarsomeres 1–4, distinctly deformed body (especially elytra) and unusually strongly protruded eyes.

***Eusphalerum* sp. 3**

Figures 12, 13, 86, 89

Materials examined. One male, an inclusion in the same piece of the Baltic amber that contains a specimen of *Eu.* sp. 2 and *Eu.* sp. 4, with an additional label: "*Eusphalerum* sp. 3 | Shavrin A.V. det. 2018" (private collection of Vitaly Alekseev (Kaliningrad, Russia), registered as AWI-045).

Preservation. The specimen is located dorsolaterally close to the margin of the piece of amber (Figs 12–13). Antennae, lateral potion of the pronotum and elytra with details of the structure of punctation and microsculpture, abdomen and legs (partly) are visible in a dorsal view of the body (Fig. 86); eyes, antennae, some details of thorax, legs and abdomen are relatively visible in a lateral view of the body (Fig. 89).

Remarks. This specimen is about 2.30 mm long (Figs 86, 89). It is similar to *Eu. kanti* sp. nov. and *Eu.* sp. 4 in the shape of the body, eyes and antennomeres. Because some morphological details of head, pronotum, thoracic sclerites, and legs, as well as punctation and microsculpture, are not visible, we leave this specimen unnamed.

***Eusphalerum* sp. 4**

Figures 12, 13, 87–88, 90

Material examined. One male, as an inclusion in the same piece of the Baltic amber that contains *Eu.* sp. 2 and *Eu.* sp. 3, with an additional label: "*Eusphalerum* sp. 4 |

Figures 86–90. *Eusphalerum* spp. (**86, 89** *Eu.* sp. 3; **87, 88, 90** *Eu.* sp. 4) **86** habitus, dorsolateral view **87** habitus, oblique dorsal view **88** habitus, ventral view **89** habitus, lateral view **90** abdominal apex, ventral view. Scale bars: 1.0 mm (**86–89**), 0.2 mm (**90**).

Shavrin A.V. det. 2018" (private collection of Vitaly Alekseev (Kaliningrad, Russia), registered as AWI-045).

Preservation. The specimen is located with its dorsal side near the widest outer margin of the piece of amber (Figs 12, 13). It is relatively clouded with many details not visible both dorsally (Fig. 87) and ventrally (Fig. 88).

Remarks. This specimen is about 2.30 mm long (Figs 87, 88). Based on the relatively narrow body and shapes of antennomeres, as well as the punctation and microsculpture of the forebody, it is similar to *Eu.* sp. 2. However, we consider this specimen belongs to a different species, because the eyes of this specimen are widely rounded as in *Eu. kanti* sp. nov. and *Eu.* sp. 3, and because some details of the body such as dorsal portion of the head and shapes of front and middle tarsi are poorly visible. Apical part of the abdomen (ventral view) as in Figure 90, with sternite VII distinctly emarginated medioapically.

Discussion

Here we report on a remarkable, unexpected palaeodiversity of the Omaliinae fauna in Baltic amber. The discovery of five new species and four additional unnamed taxa is noteworthy for several reasons. First of all, the fossil records of Omaliinae in general are fragmentary, resulting in a significant lack of fossil information for this group. So far, omaliines seem to be relatively "prevalent" in the available fossil record but these only reflect a tiny fraction of the complete diversity of Omaliinae. Furthermore, many of these fossils may not be correctly placed systematically, especially for older records. Therefore, there are only few reliable omaliine fossils known so far. Even from Baltic amber, which is one of the most famous and long-studied fossil deposits, only two definitive omaliine species in the tribe Omaliini have been described (Zanetti et al. 2016), with another doubtful taxon considered (Schaufuss 1890). Our discovery of multiple, well-preserved omaliine fossils in Baltic amber adds new insight into the species composition and diversity of Omaliinae during the Eocene. Second, we found several fossils of the genera *Geodromicus* (Anthophagini), *Eusphalerum* (Eusphalerini), *Paraphloeostiba*, and *Phyllodrepa* (Omaliini). Excluding older, doubtfully placed taxa, our fossils of *Eusphalerum* represent the first definitive records of the genus and its monobasic tribe. *Geodromicus balticus* represents the second and the first definitive fossil record of Anthophagini, with the Eocene *G. abditus* from Florissant, USA, and a probable Jurassic anthophagine from Daohugou, China (Cai and Huang 2013). They extend the origin of each genus at least to the mid-Eocene (ca 44 Ma) and provide several fossil calibration points for future divergence dating of phylogenies. It is highly likely that *Paraphloeostiba* and *Phyllodrepa* had diversified by the mid-Eocene, and our study illuminates the diversity of omaliine assemblages in amber-producing Baltic forests. Third, we describe these fossils using modern photography and used micro-CT imaging for one inclusion. There are only a few examples of micro-CT scanning for staphylinid inclusions in Baltic amber (e.g., Yamamoto and Maruyama 2018; Jałoszyński et al. 2018), although there are additional examples in using PPC-SR X-ray mCT (Zanetti et al. 2016). The techniques applied in this study enable us to systematically place fossil taxa much more precisely and allow for the detailed comparison with other taxa based on concrete evidence. The palaeobiogeogaphy of *Paraphloeostiba* and *Phyllodrepa* was previously discussed based on occurrence of these genera in Baltic amber (Zanetti et al. 2016). Unlike most Omaliinae, *Paraphloeostiba* is a rare example of a thermophilous taxon, while *Phyllodrepa*, in the restricted sense, is more typically temperate loving (Zanetti et al. 2016). Notably, *Paraphloeostiba morosa* sp. nov. is externally similar to *P. specularis*, which is known from the tropical Bismarck Archipelago, Papua New Guinea. It is interesting to understand the reason behind such a puzzling mixture of thermophilous and temperate beetle elements in Baltic amber (Zanetti et al. 2016). The occurrence of *Paraphloeostiba* potentially indicates a higher diversity of thermophilic rove beetles than is currently known (e.g. Brunke et al. 2017) and further supports distinctly warm palaeoclimatic conditions for the Eocene amber forest of Europe. Several examples of palaeodistributions for Baltic amber beetles are discussed by Alekseev (2017). Together with the work of Zanetti et al. (2016), our study forms a foundation for study of the Baltic amber Omaliinae.

A preliminary generic placement of some described fossil species was necessary based on an absence of modern phylogenetic revisions, which would provide clear morphological limits between genera. This applies to the genus *Geodromicus* and other related taxa of the *Hygrogeus* complex, some genera of which were described based on limited morphological characters, such as proportions of the body, shapes of maxillary palpomeres and aedeagus (e.g. Tronquet 1981; Zerche 1992). Some of these characters are distinctly variable and character states overlap. This is also true for *Paraphloeostiba*, which was erected by Steel (1960a) for very diverse groups of Omaliini related to *Phloeostiba* and based on a limited number of characters. Besides *Paraphloeostiba*, several related genera were described from the Oriental Region (e.g. Steel 1959, 1960a, 1960b). However, all of them need revision and a clarification of their limits and phylogenetic relationships based on analysis of both morphological, and molecular data would be extremely desirable. Members of the diverse anthophilous genus *Eusphalerum* and the tribe Eusphalerini are also in need of similar studies and are relevant for higher classification. The morphological data extracted here from extinct species, in some sense, can be useful in the future for understanding boundaries of extant taxa.

Among the extinct species of Omaliinae described here, *G. balticus* sp. nov. raised the most interest as it is the first representative of the tribe Anthophagini recorded in Baltic amber. All the known species of *Geodromicus* are strongly temperate, mostly rheophilous, and inhabit alluvial and other communities connected to rivers, streams, and other water courses. Species of *Geodromicus* and related genera are predators of various small invertebrates, which is reflected in the morphological features of the body, such as elongated legs, antennae, and mouthparts, development and strengthening of teeth on inner margin of each mandible. The newly described species appear to have potentially lived in riparian areas or wet biotopes with mosses and hygrophilous plants, which were distributed in ancient amber-producing forests. Rheophilous and even water beetles are insufficiently known from Baltic amber (see the list of described Coleoptera from the European ambers in Alekseev 2017). Unlike *Geodromicus*, species of the genus *Eusphalerum* are pollen-feeding species, attracted to flowers of various plants (e.g. Zanetti 2014), and very often representatives of this genus aggregate in flowers in huge numbers. The extant species of the other two genera, *Paraphloeostiba* (some species) and *Phyllodrepa* inhabit litter, mosses, decaying plant debris, and sometimes hygrophilous and hygromesophilous communities or nests of birds and mammals (some species of *Phyllodrepa*). It is interesting that some species such as the widespread *Ph. floralis* (Paykull), *Ph. nigra* (Gravenhorst) and some other species are attracted to flowers and known as pollen-feeders (Steel 1970). It can be assumed, hypothetically, that together with *Eusphalerum*, these pollen-feeding species were widely distributed in Cenozoic amber forests, and to the present time are fragmentary preserved in the Holocene fauna with an overwhelming number of species distributed in the mountain regions of the Holarctic Region.

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RESEARCH ARTICLE

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Cirrhilabrus wakanda, a new species of fairy wrasse from mesophotic ecosystems of Zanzibar, Tanzania, Africa (Teleostei, Labridae)

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Abstract

Cirrhilabrus wakanda **sp. nov.** is described on the basis of the holotype and four paratypes collected between 50 and 80m depth over low-complexity reef and rubble bottoms at the east coast of Zanzibar, Tanzania, Africa. The new species belongs to a group of fairy wrasses from the western Indian Ocean, sharing a combination of characters that include: short pelvic fins (not or barely reaching anal-fin origin); relatively unmarked dorsal and anal fins; males with a strongly lanceolate caudal fin (except in *C. rubrisquamis*); both sexes with a pair of prominent facial stripes above and below the orbit; and both sexes with prominent purple scales and osseus elements that persist, and stain purple, respectively, even in preservation. This group of fairy wrasse is part of a larger complex that includes related species from the western Pacific Ocean. In addition to meristic and morphometric comparisons, we also compare mitochondrial DNA sequence data to the aforementioned, putatively related species.

Keywords

Coral reefs, deep reefs, Indian Ocean, rebreather diving, reef fish

Introduction

The labrid fish genus *Cirrhilabrus* Temminck & Schlegel, 1845 consists of small, colourful, planktivorous fishes found mostly on rubble slopes adjacent to coral reefs. Allen et al. (2015) listed 51 valid species in the genus. Eight other species have subsequently been described: *Cirrhilabrus isosceles* Tea et al., 2016, *C. hygroxerus* Allen & Hammer, 2016, *C. rubeus* Victor, 2016, *C. efatensis* Walsh et al., 2017, *C. shutmani* Tea & Gill, 2017, *C. greeni* Allen & Hammer, 2017, and *C. cyanogularis* Tea et al., 2018, bringing the valid species count to 59.

Members of this genus occur exclusively within the Indo-Pacific, attaining their highest diversity in the western Pacific Ocean and eastern Indian Ocean. In contrast, only seven nominal species have been reported from the western Indian Ocean, just slightly more than 10% of the genus. These are: *Cirrhilabrus exquisitus* Smith, 1957, *C. blatteus* Springer & Randall, 1974, *C. rubriventralis* Springer & Randall, 1974, *C. rubrisquamis* Randall & Emery, 1983, *C. sanguineus* Cornic, 1987, *C. africanus* Victor, 2016, and *C. rubeus* Victor, 2016. Of these, *C. sanguineus*, *C. blatteus*, and *C. rubrisquamis* are common only in mesophotic ecosystems, at depths greater than 40 m (Randall and Emery 1983; Springer and Randall 1974; Tea et al. 2018)

Mesophotic coral ecosystems (MCEs) characterise the deeper portions of coral reefs, found between 30 and 150 m (Rocha et al. 2018). While the number of studies conducted in MCEs of the Atlantic, Pacific, and northern Red Sea has increased in recent years (Loya et al. 2016), few researchers have investigated deep reefs of the western Indian Province. In a recent expedition organised by the California Academy of Sciences' "Hope for Reefs" initiative, we had the opportunity to study the fish biodiversity in MCEs of Zanzibar, western Indian Ocean. While exploring deep reefs through technical rebreather diving, the authors discovered a new species of fairy wrasse belonging to the genus *Cirrhilabrus*. We herein describe *Cirrhilabrus wakanda* sp. nov., the 60th recognised species of the genus and the eighth species recorded from the western Indian Ocean.

Materials and methods

Specimens of the new species were collected using hand nets while diving on mixed-gas, closed-circuit rebreathers (Hollis Prism 2). Methods of counting and measuring follow Randall and Masuda (1991). Gill raker counts follow Tea and Gill (2017) and are presented as upper (epibranchial) + lower (ceratobranchial); the angle raker is included in the second count. Data are presented as the range of all specimens examined, followed by data for the holotype in parentheses. Where counts were recorded bilaterally, both counts are given and separated from each other by a slash; the first count presented is the left count. Morphometric values are presented in Table 1, expressed as percentage of standard length. Institutional codes follow Sabaj (2016) and are as follows:

CAS	California Academy of Sciences.

DNA extraction and PCR amplification of the mitochondrial cytochrome c oxidase subunit I (COI) were performed following protocols detailed in Weigt et al. (2012). Forward and reverse contigs were aligned and trimmed separately using Geneious Prime 2019.1.1. (Biomatters, Auckland, New Zealand). Uncorrected pairwise distances for the COI marker were calculated in Geneious Prime. We compared the DNA sequences from four specimens of the new species to putatively related species of *Cirrhilabrus* with publicly available sequence data in GenBank (*Cirrhilabrus sanguineus*: MH780162; *Cirrhilabrus rubrisquamis*: MH780161; *Cirrhilabrus blatteus*: MF123821).

Taxonomy

Cirrhilabrus wakanda sp. nov.

http://zoobank.org/2E9018A1-A98F-4F8C-AEA9-89D18BC69162
Vibranium fairy wrasse
Figures 1–4, 5A, 6A; Table 1

Holotype. CAS 246395 (field code: HTP 900), 70.3 mm SL male, GenBank MN010585, east coast of Zanzibar, Tanzania, Africa (GPS coordinates: 6°10'30"S; 39°32'28"E), 75 m, collected by H.T. Pinheiro, B. Shepherd, and L.A. Rocha, 14 December 2018; Figure 1.

Paratypes. CAS 246396 (HTP 883), 56.8 mm SL female, GenBank MN010586, east coast of Zanzibar, Tanzania, Africa, 70 m, 07 December 2018; CAS 246397 (HTP 901), 61.3 mm SL male, GenBank MN010587, east coast of Zanzibar, Tanzania, Africa, 75 m, 14 December 2018; Figure 2 (A1, A2); CAS 246398 (HTP 902), 57.4 mm SL female, GenBank MN010588, east coast of Zanzibar, Tanzania, Africa, 75 m, 14 December 2018; Figure 2 (B1, B2); CAS 246399 (HTP 903), 54.3 mm SL female, east coast of Zanzibar, Tanzania, Africa, 75 m, 14 December 2018; Figure 2 (C1, C2). All type specimens collected by H.T. Pinheiro, B. Shepherd, and L.A. Rocha.

Diagnosis. *Cirrhilabrus wakanda* shares similar meristic characters to other members of this genus. However, it is readily distinguished from all other *Cirrhilabrus* in having the following combination of colouration and morphological characters: caudal fin strongly lanceolate in males; both sexes with a series of purple scales (in life and in preservation) arranged in a chain-link pattern across dorsal two-thirds of body.

Description. Dorsal-fin rays XI,9; anal-fin rays III,9; dorsal and anal-fin soft rays branched except first ray unbranched in two individuals; last dorsal and anal-fin ray branched to base; pectoral-fin rays 14–15 (15/15), upper two unbranched; pelvic-fin rays I,5; principal caudal-fin rays 7+6, uppermost and lowermost unbranched; upper procurrent caudal-fin rays 6, lower procurrent caudal-fin rays 6; lateral line interrupted, with dorsoanterior series of pored scales 16–19 (17/17) and midlateral posterior peduncular series 8–9 (9/9); scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 4–5 (4); median prepelvic scales 5; rows of scales on cheek 2; circumpeduncular scales 15–16 (15); gill rak-

Figure 1. *Cirrhilabrus wakanda* sp. nov., freshly euthanized male holotype (CAS 246395), 70.3 mm SL, male, collected at a depth of 75 m, east coast of Zanzibar, Africa (above). Note the pair of facial stripes above and below orbit. Photograph by H.T. Pinheiro and B. Shepherd.

Table 1. Proportional measurements of type specimens of *Cirrhilabrus wakanda* sp. nov. expressed as a percentage of the standard length.

	Holotype	Paratypes			
	CAS 246395	CAS 246397	CAS 246398	CAS 246399	CAS 246396
Sex	male	male	female	female	female
Standard length (mm)	70.3	61.3	57.4	54.3	56.8
Body depth	30.9	31.7	29.8	31.9	31.8
Body width	11.8	12.9	12.6	13.9	14.5
Head length	31.0	30.6	31.2	30.1	27.7
Snout length	8.0	8.9	7.9	8.2	7.4
Orbit diameter	6.6	8.0	7.2	9.0	7.7
Interorbital width	8.5	9.6	7.7	9.3	9.1
Upper jaw length	6.9	8.2	6.5	7.4	8.2
Caudal-peduncle depth	15.1	16.3	14.8	16.3	16.5
Caudal-peduncle length	12.8	16.5	14.1	14.9	14.8
Predorsal length	32.6	33.8	31.9	31.7	33.7
Preanal length	60.4	59.5	59.6	58.5	61.4
Prepelvic length	34.4	33.1	31.5	35.7	36.4
Dorsal-fin base	58.2	56.6	55.3	63.2	57.0
First dorsal spine	5.4	6.5	6.2	5.2	6.4
Longest dorsal spine	11.9	14.3	12.4	13.6	12.7
Longest dorsal ray	19.0	18.3	16.8	16.7	17.2
Anal-fin base	26.1	25.3	25.4	27.6	24.6
First anal spine	6.0	6.4	5.2	5.7	6.4
Second anal spine	9.1	9.3	9.3	9.4	10.1
Third anal spine	10.5	11.1	10.8	10.9	11.4
Longest anal ray	16.8	17.8	14.5	15.1	17.9
Caudal-fin length	28.2	28.6	25.4	28.0	31.6
Pectoral-fin length	19.6	21.8	20.6	18.3	20.3
Pelvic spine length	11.2	12.1	11.7	11.0	11.3
Pelvic fin length	18.0	17.9	16.2	15.5	18.8

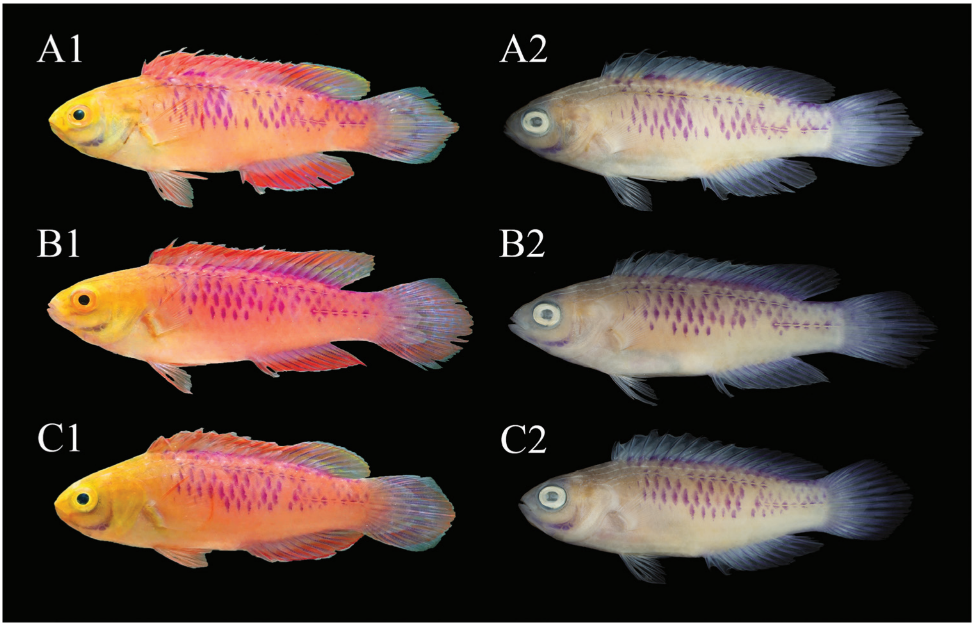

Figure 2. Paratypes of *Cirrhilabrus wakanda* sp. nov., not to scale **A1** CAS 246397, 61.3 mm SL, male, freshly euthanized **A2** CAS 246397, male in preservation **B1** CAS 246398, 57.38 mm SL, female, freshly euthanized **B2** CAS 246398, female in preservation **C1** CAS 246399, 54.32 mm SL, female, freshly euthanized **C2** CAS 246399, female in preservation. Photographs by H.T. Pinheiro and B. Shepherd (**A1, B1, C1**), and J. Fong (**A2, B2, C2**).

ers 8–9 (8) + 8–9 (8) = 16–18 (16); pseudobranchial filaments 8–10; vertebrae 9+16; epineurals 13 (Figure 3).

Body moderately elongate and compressed, depth 3.1–3.4 (3.2) in SL, width 2.1–2.6 (2.6) in depth; head length 3.2–3.6 (3.2) in SL; snout pointed, its length 3.4–3.9 (3.9) in HL; orbit diameter 3.6–4.7 (4.7) in HL; depth of caudal peduncle 1.7–2.1 (2.1) in HL. Mouth small, terminal, and oblique, with maxilla almost reaching vertical at front edge of orbit; dentition typical of genus with three pairs of canine teeth present anteriorly at side of upper jaw, first forward-projecting, next two strongly recurved and outcurved, third longest; an irregular row of very small conical teeth medial to upper canines; lower jaw with a single stout pair of canines anteriorly which protrude obliquely outward and are slightly lateral to medial pair of upper jaw; no teeth on roof of mouth.

Posterior margin of preoperculum with 30–32 (32) very fine serrated; margins of posterior and ventral edges of preoperculum free to about level of middle pupil. Anterior nostril in short membranous tube, located nearer to orbit than snout tip; posterior nostril larger, roughly ovoid to rectangular, located just medial and anterior to upper edge of eye. Scales cycloid; head scaled except snout and interorbital space; four large scales on opercle; a broad naked zone on membranous edge of preopercle; a row of large, elongate, pointed scales along base of dorsal fin, one per element, scales progressively shorter posteriorly on soft portion of fin; anal fin with a similar basal

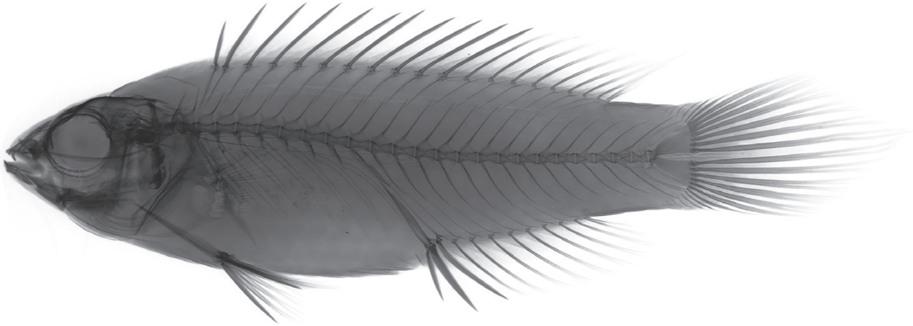

Figure 3. *Cirrhilabrus wakanda* sp. nov., CAS 246395, 70.3 mm SL, male holotype, x-ray. Radiograph by J. Fong.

row of scales; last pored scale of lateral line (posterior to hypural plate) enlarged and pointed; one scale above and below last pored scale also enlarged; a horizontal series of greatly enlarged scales extend two-thirds distance to central posterior margin of caudal fin; pectoral fins naked except for a few small scales at extreme base; a single large scale at base of each pelvic fin, about three-fourths length of pelvic spine.

Origin of dorsal fin above third lateral-line scale, predorsal length 3.0–3.2 (3.1) in SL; first 1–4 dorsal-fin spines progressively longer, fifth to sixth subequal, eighth to tenth longest, 2.1–2.6 (2.6) in HL; interspinous membranes of dorsal fin in males extend beyond dorsal-fin spines, with each membrane extending in a pointed filament beyond spine; fifth dorsal-fin soft ray longest, 1.6–1.9 (1.6) in HL, remaining rays progressively shorter; origin of anal fin below base of ninth dorsal-fin spine; third anal-fin spine longest, 2.4–3.0 (3.0) in HL; interspinous membranes of anal fin extended as on dorsal fin; anal-fin soft rays relatively uniform in length, sixth longest, 1.5–2.1 (1.8) in HL; dorsal and anal-fin rays barely reaching caudal-fin base; caudal fin of males lanceolate; pectoral fins short, reaching vertical between bases of fifth or sixth dorsal-fin spines, longest ray 1.4–1.6 (1.6) in HL; origin of pelvic fins below lower base of pectoral fins; pelvic fins short, not reaching past anal fin origin, longest ray 1.5–1.9 (1.7) in HL.

Colouration of males in life. Based on colour photographs and specimens when freshly dead, and field photos of live individuals (Figures 1; 2A1; 4A; 4B; 5A): head ochreous yellow; lower part of head whitish to pale pink (yellowish when freshly dead), purple stripe present from mid-upper lip to mid-upper edge of orbit; second stripe of similar colour present from lower edge of maxilla to mid-lower edge of orbit; interorbital and upper part of snout yellowish, with a series of very fine white stripes; preoperculum prominently purple on outer edge; iris bright yellow, greenish on the upper edge, with orange ring around pupil; body pale mauve to purplish-pink, with a faint region of paler yellowish-pink below middle part of dorsal fin; body with a network of dark purple scales arranged in a chain-link pattern from just after dorsal fin origin

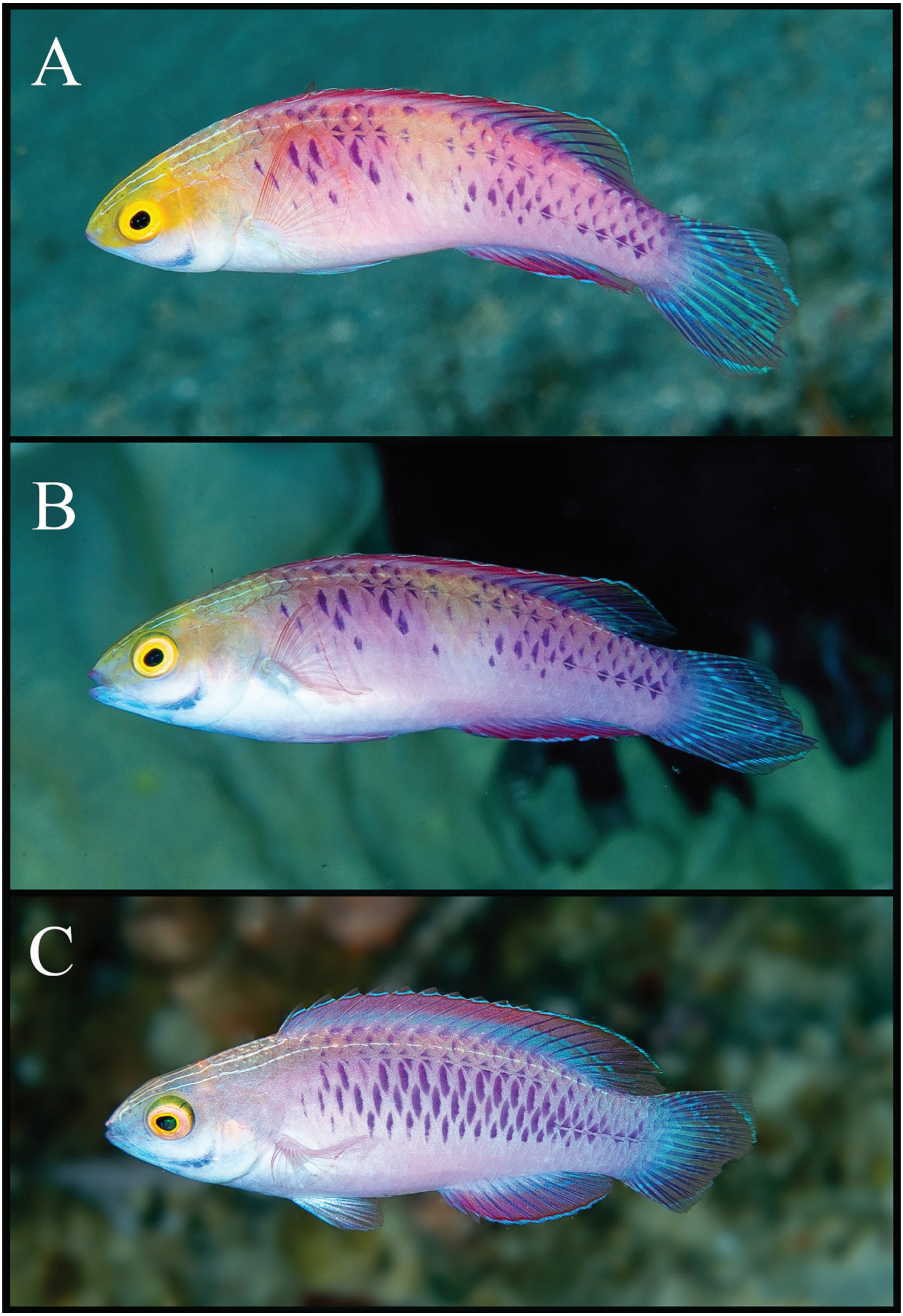

Figure 4. *Cirrhilabrus wakanda* sp. nov., in situ photographs at 75 m depth, in the east coast of Zanzibar, Tanzania, Africa. Specimens not retained. Note intensity of yellow on the heads of males (**A**), transitioning males (**B**), and females (**C**). Photographs by L.A. Rocha.

to edge of caudal peduncle, absent from lower third of body; dorsal-fin bluish-purple, bright fuchsia on distal half; posterior dorsal fin yellowish hyaline with a faint blue medial band, sometimes broken into spots; distal edge of dorsal fin narrowly bright blue; caudal fin bluish hyaline with a pair of concentric bright blue chevrons converging at lanceolatus terminus; coloured portion of chevron marking bright fuchsia to magenta; anal-fin similar to dorsal fin, distal edge narrowly bright blue; pelvic fins hyaline to translucent magenta; pectoral fins pinkish hyaline.

Colouration of females and juveniles in life. Similar to males described above. Head and body more subdued in colouration, pinkish-purple to lilac (Figure 4C), deepening to yellow post mortem (Figures 2B1; 2C1).

Colouration in preservative. (Figures 2A2; 2B2; 2C2; 6A): head and body pale tan; fine white stripes on interorbital and nape remain; infraorbitals, frontals, and premaxilla weakly purple; preoperculum, dentary, angular, and articular bones strongly purple; scales in chain-link formation deep purple; median fins translucent, except rays weakly purple; pelvic and pectoral fins translucent hyaline.

Etymology. The specific epithet refers to the fictional East African nation of Wakanda, home of the superhero Black Panther, as is the case for the new species, which has remained hidden from the world for a long time. To be treated as a noun in apposition. The common name refers to the fictional metal vibranium, a rare substance found on Wakanda that is woven into Black Panther's suit. The purple chain-link scale pattern of the new species is reminiscent of this detail.

Distribution and habitat. *Cirrhilabrus wakanda* is presently known only from the east coast of Zanzibar, Tanzania. The species inhabits deep shelves consisting of small patch reefs dominated by rhodolith and sponge beds, at depths between 50 and 80 m.

Comparisons. Pairwise comparison of mitochondrial sequence data suggests that *Cirrhilabrus wakanda* is most closely related to *C. rubrisquamis* Randall & Emery (1983), differing by 0.6% in mitochondrial COI (uncorrected pairwise distance). Such marginal differences in sequence data between closely related sister species is not uncommon in *Cirrhilabrus*, even when stark morphological differences are present (Tea et al., 2016; Victor, 2016; Allen & Hammer, 2017). It also appears to be closely related to *C. blatteus* Springer & Randall (1974) (1.9% difference in COI) and *C. sanguineus* Cornic (1987) (1.5% difference in COI). These four species share the following character combination: short pelvic fins (not or barely reaching anal-fin origin); relatively unmarked dorsal and anal fins; males with a strongly lanceolate caudal fin (except in *C. rubrisquamis*); both sexes with a pair of prominent facial stripes above and below the orbit; and both sexes with prominent purple scales and osseus elements that persist, and stain purple, respectively, even in preservation.

In *Cirrhilabrus wakanda* the purple scale pattern presents as a scattered, chain-link motif (Figure 1; 2; 4; 5A). In the other related species, the purple scales are manifested as: two rows dorsally and laterally in *C. blatteus* (Figure 5B); an oblique mid-dorsal saddle in *C. sanguineus* (Figure 5C); a crosshatch network anteriorly in *C. rubrisquamis* (Figure 5D). Aside from details in live colouration, *Cirrhilabrus wakanda* differs from: *C. blatteus* in having a higher number of pored lateral line scales (24–28 vs. 21–24); *C. sanguineus* in having one fewer median prepelvic scale (5 vs. 6) and fewer

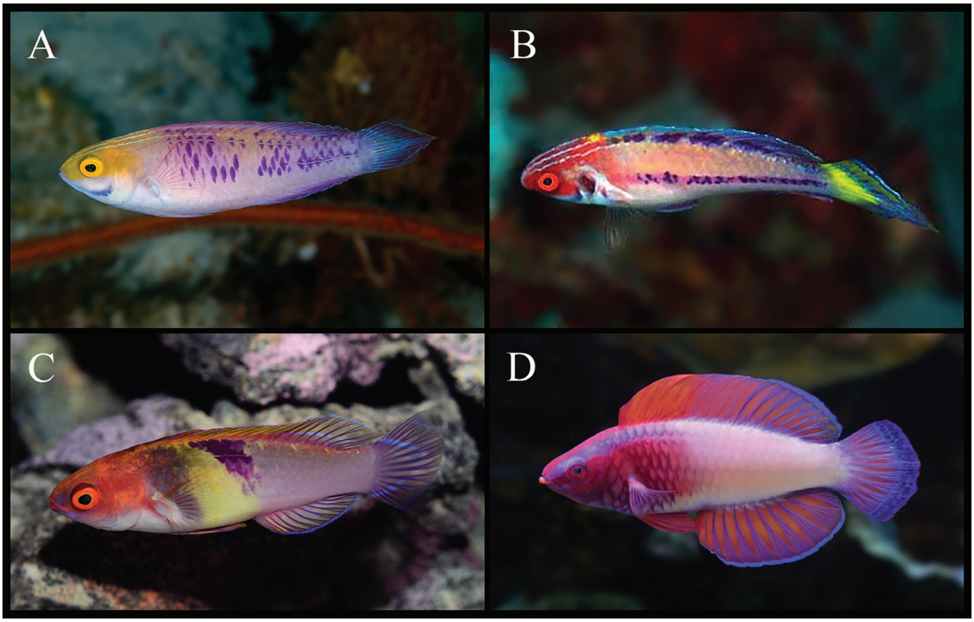

Figure 5. A selection of *Cirrhilabrus* species from the western Indian Ocean group of the *Cirrhilabrus jordani* complex **A** *Cirrhilabrus wakanda* sp. nov., in situ photograph from the east coast of Zanzibar, Africa **B** *Cirrhilabrus blatteus*, *in situ* photograph from the Red Sea, off the coast of Eilat; **C**: *Cirrhilabrus sanguineus*, aquarium photograph of a specimen from Mauritius **D** *Cirrhilabrus rubrisquamis*, aquarium photograph of a specimen from the Maldives. Photographs by L.A. Rocha (**A**); E. Brokovich (**B**), and Y.K. Tea (**C, D**).

pseudobranchial filaments (8–10 vs. 11), and further from *C. rubrisquamis* in having a lanceolate caudal fin.

The four species are part of a larger complex of fairy wrasses that includes five other species from the western Pacific Ocean: *Cirrhilabrus jordani*, *C. earlei*, *C. roseafascia*, *C. lanceolatus*, and *C. shutmani*. Together, these nine species form the *Cirrhilabrus jordani* complex. Previous morphological and molecular studies have also shown support for this grouping (Tea and Gill 2017; Tea et al. 2018).

Remarks. *Cirrhilabrus wakanda* possess several osseus elements and fin rays that stain naturally purple in ethanol (Figure 6A). Only a handful of other *Cirrhilabrus* share this character. Springer and Randall (1974) first noted this occurrence in *Cirrhilabrus blatteus* (Figure 6B). Subsequently, Randall (1995) made note of its reoccurrence in *Cirrhilabrus rubrisquamis* and *Cirrhilabrus sanguineus*. Tea et al. (2018) expanded this list to include *Cirrhilabrus earlei* (Figure 6C). Incidentally, these species are all closely related members of the *jordani* complex, with *C. wakanda*, *C. rubrisquamis*, *C. sanguineus* and *C. blatteus* occurring in the western Indian Ocean, and *C. earlei* occurring in the western Pacific Ocean. However, since the purple post-preservation staining is not found in the other Pacific Ocean species (*C. jordani*, *C. shutmani*, *C. roseafascia*, and *C. lanceolatus*), the distribution of this character within the *jordani* complex sensu lato is paraphyletic and is therefore not synapomorphic for this group of fairy wrasses.

Figure 6. A selection of *Cirrhilabrus* species in preservation showing the purple staining qualities. Not to scale **A** *Cirrhilabrus wakanda* sp. nov., 70.3 mm SL, male holotype, CAS 246395 **B** *Cirrhilabrus blatteus*, 65.1 mm SL, male, CAS 235080 **C** *Cirrhilabrus earlei*, 56.5 mm SL, male paratype, CAS 213114. Photographs by L.A. Rocha (**A**) and B.W. Frable (**B, C**).

Material examined. *Cirrhilabrus blatteus* – Red Sea, off Saudi Arabia: CAS 235080, 56.2 mm SL; 63.4 mm SL; 65.1 mm SL; *Cirrhilabrus earlei* – Palau: CAS 213114, 56.5 mm SL.

Acknowledgements

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RESEARCH ARTICLE

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Liopropoma incandescens sp. nov. (Epinephelidae, Liopropominae), a new species of basslet from mesophotic coral ecosystems of Pohnpei, Micronesia

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Abstract

A new species of the genus *Liopropoma* Gill found on the lower mesophotic coral ecosystem of Pohnpei, Micronesia, is herein described. *Liopropoma incandescens* **sp. nov.** differs from its congeners in coloration, number of lateral-line scales, number of pectoral fin rays, body depth, and snout length. *Liopropoma incandescens* **sp. nov.** is the 31st species in the genus. It was collected from a small rocky crevice in a steep slope at 130 m depth. Water temperature was 20 °C and benthic habitat was dominated by gorgonians, sponges and tunicates.

Keywords

closed-circuit rebreather, coral-reef twilight zone, reef fish, SubCAS, taxonomy

Introduction

Despite significant recent growth on research in mesophotic coral ecosystems (MCEs, 30–150 m depth), exploration at these depths is still yielding high rates of new species discovery worldwide (Rocha et al. 2017, Pinheiro et al. 2018, Pyle et al. 2018, Shepherd et al. 2018a, Arango et al. 2019). Through rebreather technical diving to depths up to 150 m, the Hope for Reefs Initiative of the California Academy of Sciences is advancing the knowledge ca. the biodiversity and ecology of MCEs conducting on average four expeditions per year. MCEs shelter unique communities, and much like their shallow coral ecosystem counterparts, are being affected by overfishing, pollution and climate change (Rocha et al. 2018).

Coral reefs of the Central Pacific are home to a high fish diversity, with over 2,300 species (Kulbicki et al. 2013). Pohnpei, one of the four states in the Federated States of Micronesia, has well-developed shallow coral reefs and MCEs, which also harbor diverse mesophotic fish communities (Coleman et al. 2018, Rocha et al. 2018). Technical diving exploration in Pohnpei MCEs has yielded the recent descriptions of species in the genera *Luzonichthys* Herre (e.g., Copus et al. 2015) and *Tosanoides* Kamohara (e.g., Pyle et al. 2018). Although overall richness decreases significantly along the depth gradient, high betadiversity, driven mainly by species turnover, differentiates shallow from deep reefs in the region (Coleman et al. 2018, Rocha et al. 2018).

The serranid genus *Liopropoma* Gill is a typical inhabitant of MCEs, with the most recent species being described from the Caribbean (Baldwin and Robertson 2014; Baldwin and Johnson 2014). It is characterized by VIII, 11–14 dorsal fin rays, III, 8–11 anal rays, weak ctenoid scales on the body, a complete lateral line (highly arched over pectoral fin) with 44–66 pored scales, and a band of villiform teeth in both jaws lacking canines (Kon et al. 1999). According to Eschmeyer and Fong (2018), *Liopropoma* currently contains 30 recognized species, 22 of which are distributed in the Indo-Pacific region, with a further eight species in the Western and Eastern Atlantic. These authors consider *Liopropoma danae* (Kotthaus) as a doubtful species, almost certainly a synonym of a valid species, described based on juvenile specimens. During our latest expedition to Pohnpei in August of 2017, we discovered a new species of *Liopropoma* at 130 m depth at Ahnd (Ant) Atoll. Here we describe *Liopropoma incandescens* sp. nov. as the 31st species of the genus.

Materials and methods

The specimen was collected with hand nets during a deep dive using mixed-gas, closed-circuit rebreathers, and brought to the surface alive in the SubCAS submersible fish decompression chamber (Shepherd et al. 2018b). It was placed in a 1 L plastic bag filled with seawater and pure oxygen in equal ratios, packed inside a Styrofoam box with a cardboard outer liner, and transported alive via air cargo to San Francisco, where it was photographed and euthanized following California Academy of Sciences institutional animal care and use committee (IACUC) guidelines. Counts were performed with a stereo microscope, and morphological characters were measured to the nearest 0.01 mm with digital calipers following the conventions described in Baldwin and Robertson (2014). Body proportions are expressed as percentage of standard length (SL). Comparative material included *Liopropoma africanum* (Smith) (CAS 32371), one specimen 37.67 mm SL, from Comoros Islands, collected 25–30 m depth; *Liopropoma collettei* Randall & Taylor (CAS 228952), one specimen 54.55

mm SL, from Honolulu, Hawaii, collected ca. 15 m depth; *Liopropoma fasciatum* Bussing (CAS 46579), one specimen 117.30 mm SL, from Galapagos, Ecuador, collected ca. 20 m depth; *Liopropoma latifasciatum* (Tanaka) (CAS 243779), one specimen 54.06 mm SL, from Okinawa, Japan; *Liopropoma longilepis* Garman (CAS 86404), one specimen 145.52 mm SL, from Galapagos, Ecuador, collected from a submersible down to 200 m; *Liopropoma mitratum* Lubbock & Randall (CAS 27698), one specimen 41.06 mm SL, from Raroia Atoll, French Polynesia, collected ca. 10 m depth; *Liopropoma mowbrayi* Woods & Kanazawa (CAS 56894), one specimen 43.40 mm, from U.S. Virgin Islands; and *Liopropoma susumi* (Jordan & Seale) (CAS 214155), one specimen 52.01 mm SL, from the American Samoa, collected ca. 15 m depth; along with a revision of the genus by Randall and Taylor (1988). The holotype was deposited at the California Academy of Sciences (CAS) ichthyological collection.

Results

Liopropoma incandescens sp. nov.

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Figures 1, 2
Incandescent Basslet

Type locality. Ant Atoll, Pohnpei, Micronesia.

Holotype. CAS 246199, 54.15 mm SL, Federated States of Micronesia, Pohnpei, Ahnd (Ant) Atoll, west side, 6.75589N, 157.91933E, 29 August 2017, B. D. Greene, hand nets, 130 m depth.

Diagnosis. *Liopropoma incandescens* sp. nov. can be distinguished from all of its congeners by the yellow to orange body color (Figure 1A), with two distinctive black blotches on the upper and lower caudal fin lobes (Figure 1A, B), and by the following combination of characters: dorsal fin VIII,13; anal fin III, 9; pectoral fin 14; total gill rakers on first arch 15; lateral-line scales 62; length of first dorsal-fin spine 5% SL; depth at origin of dorsal fin 22% SL; least depth of caudal peduncle 15% SL; orbit diameter 9% SL.

Description. Dorsal-fin rays VIII, 13 (spines not embedded into the skin, and the last two soft rays are associated with a single complex pterygiophore; Figure 1C); anal-fin rays III, 9 (last two soft rays associated with a single complex pterygiophore); pectoral-fin rays 14, dorsal-fin-most ray unsegmented; pelvic-fin rays I, 5; principal caudal-fin rays 8+7=15; rudimentary and procurrent caudal-fin rays 10+9=19; pored lateral-line scales 62; scales from lateral line to dorsal fin origin 6; scales from lateral line to anal fin origin 22; gill rakers on first arch, including rudiments, 6+9; vertebrae 8+15 (Figure 1C).

Measurements presented as percentage of standard length (SL): body depth at origin of dorsal fin 21.8; body width just behind gill opening 14.9; head length 38; snout length 9.5; orbit diameter 8.6; bony interorbital width 6.4; upper-jaw length 14.7;

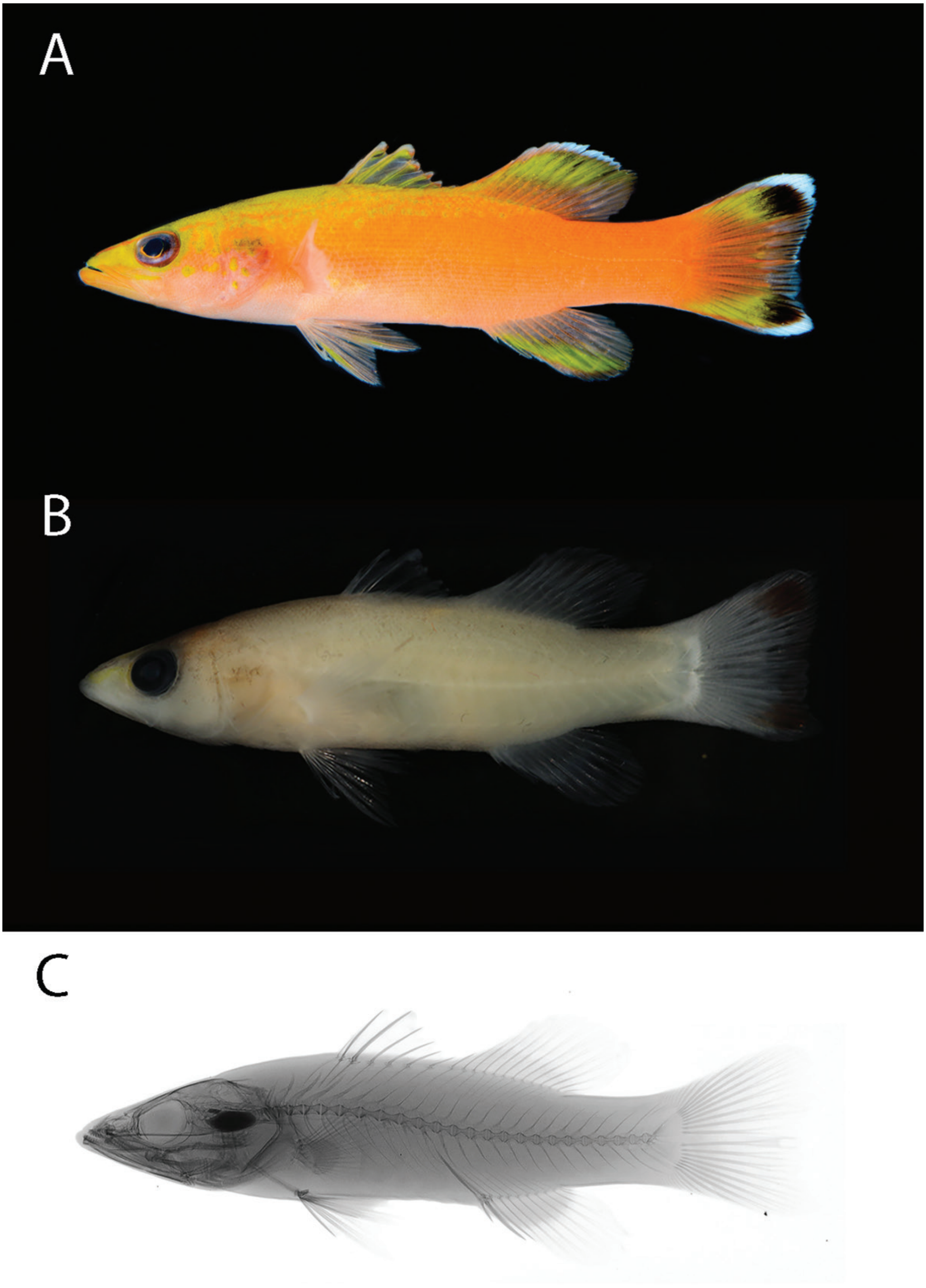

Figure 1. Holotype of *Liopropoma incandescens* (CAS 246199), 54.15 mm SL, collected at a depth of 130 m off Ahnd (Ant) Atoll, Pohnpei, Federated States of Micronesia. Photographs by L. A. Rocha and J. Fong.

maxillary length 12.7; least caudal-peduncle depth 14.6; caudal-peduncle length 13.5. Fin lengths: dorsal-fin spines: (I) 4.6; (II) 9.9; (III) 10.7; longest dorsal-fin soft ray the 10th, length 17.4; lengths of anal-fin spines: (I) 3.9; (II) 10.1; (III) 11.3; longest anal soft ray the 5th, length 18.1; caudal-fin length 23.2; pectoral-fin length 26, fin short, not reaching vertical between anus and dorsal fin; pelvic-fin length 19, fin reaching vertical slightly posterior to base of 5th dorsal-fin spine.

Interorbital region flat; mouth oblique, maxilla almost reaching vertical crossing posterior border of pupil; prominent bony projection on posteroventral corner of maxilla; lower jaw projected. Anterior nostril in thin, membranous tube, situated close to tip of snout; posterior nostril a simple opening, situated close to orbit. Lateral line strongly arched above pectoral fin, highest point below fourth dorsal-fin spine. Trunk covered with ctenoid scales, scales becoming weakly ctenoid anteriorly and cycloid on head. Head fully scaled except over branchiostegal area. Short membrane covered by scales anteriorly to first dorsal-fin spine, six rows of scales covering basal anterior portion of soft dorsal fin, decreasing uniformly to two scales at posterior basal portion of soft dorsal fin. Anal fin with two to five rows of scales basally (more rows between second and fourth spine. Caudal fin almost completely scaled, except for distal tips of rays. Scales present on pectoral-fin base, pelvic-fin base, and on proximal portion of pelvic fin. Jaw teeth small; upper and lower jaws with bands of villiform teeth, bands slightly wider anteriorly. Vomer oval patch of small teeth. Palatines with several rows of small teeth in long and narrow bands at each side of mouth. Opercle with one conspicuous middle spine. Margin of upper and lower limb of preopercle smooth.

Color in life. Alive and freshly euthanized holotype (Figures 1A, 2) with coloration as follows: snout, top of head and trunk yellow, grading to vivid orange on a diagonal around upper two-thirds of body to caudal fin. Pale pink checks with yellow blotches behind eye, on operculum, and on dorsal-most part of body from head to base of soft dorsal fin. Indistinct orange line from tip of snout, across top of eye, continuing to above preopercle edge. Pupil black with yellow outer margin; eye pale purple and orbit with orange ring along margin. Pale pink-orange to peach-colored throat, continuing below pectoral fins, and across belly. Dorsal fin with yellow-orange tipped spines and mostly translucent inter-spinous membranes; base of soft dorsal-fin rays (ventral third, scaled region) orange; soft dorsal fin central upper region yellow from first to eighth ray; margin of the first soft dorsal-fin ray orange, transitioning to white from second to eighth; dorsal portion between eighth and twelfth soft ray light orange, with no white margin and no yellow. Pectoral fin light orange, yellow anteriorly (first ray). Upper two-thirds of anal fin orange, distal region yellow from second to ninth ray; anal-fin margin white along second to ninth ray with a pale orange sub-border, translucent along tenth to twelfth ray. Central portion of caudal fin with orange rays and membranes, with white pigments in the distal posterior third; upper and lower portions of caudal fin yellow with orange base; two pronounced oval-shaped black spots with posterior white margins, approximately the same size as orbit, on outer upper and lower caudal lobes.

Figure 2. Holotype of *Liopropoma incandescens* (CAS 246199), 54.15 mm SL, shown alive in an aquarium. Photograph by L. A. Rocha.

Color in alcohol. In alcohol (Figure 1B), body light beige, pigment only present on a small patch of yellow on the snout, and the two pronounced dark spots on distal upper and lower caudal fin lobes.

Distribution. *Liopropoma incandescens* sp. nov. is known based on one specimen collected at a depth of 130 m in Ahnd (Ant) Atoll, Pohnpei, Federated States of Micronesia. The lack of records for the species in other MCEs of the Pacific Ocean is probably due to its cryptic habits combined with the lack of sampling at those depths across the wider region.

Habitat and behavior. *Liopropoma incandescens* sp. nov. has a cryptic habit and was discovered and collected in a small rocky crevice along a steep limestone coral reef drop-off at a depth of 130 m (Figure 3). A second individual (~10 cm length) was sighted in the same area, together with species such as *Tosanoides annepatrice* Pyle, Greene, Copus & Randall, *Centropyge abei* Allen, Young & Colin, *Odontanthias* sp. and *Roa* sp., but was not collected.

Etymology. The specific name is a noun in apposition from the Latin, *incandescens*, to glow. The vivid yellow to orange incandescent coloration of the species prompted us to select this name.

Comparisons. The color of *Liopropoma incandescens* sp. nov. sets it apart from all other species in the genus: the gradient from yellow to orange and the two black spots on the upper and lower caudal fin lobes are unique. The only other species with black spots on upper and lower caudal fin lobes is *Liopropoma carmabi* (Randall), from

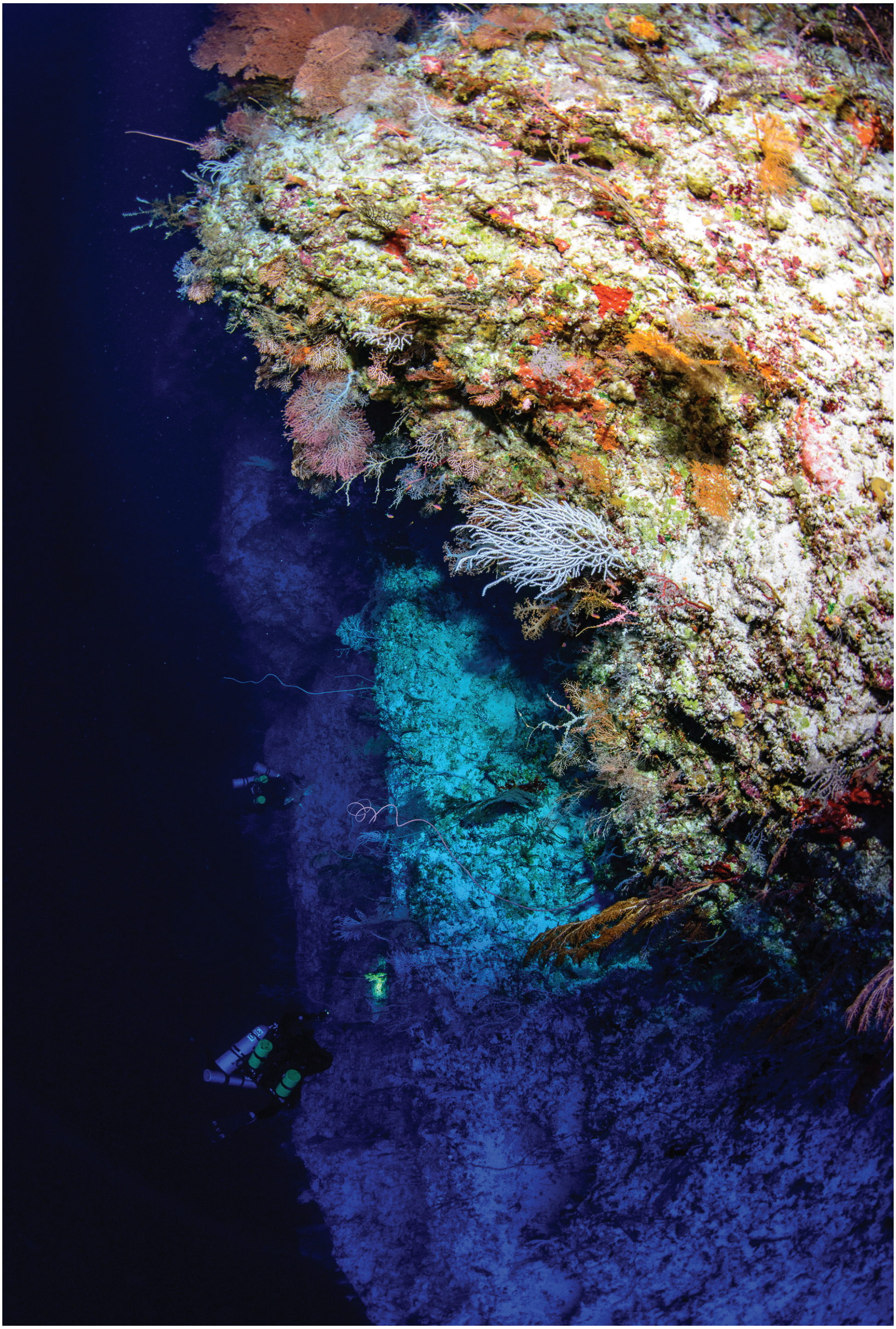

Figure 3. Coral reef wall at a depth of 130 m, the habitat where *Liopropoma incandescens* was discovered in Ahnd (Ant) Atoll, Pohnpei. Photograph by L. A. Rocha.

the Western Atlantic, which has alternating orange and pink horizontal lines running from the snout to the caudal fin. Moreover, most species of *Liopropoma* have between 44 and 54 lateral-line scales, whereas *L. incandescens* sp. nov. shares a high number of lateral-line scales (62) exclusively with *Liopropoma maculatum* (Döderlein) (Randall and Taylor 1988, Kon et al. 1999, Wirtz and Schliewen 2012, Baldwin and Johnson 2014, Baldwin and Robertson 2014). *Liopropoma incandescens* sp. nov. differs from *L. maculatum* by the lower number of pectoral fin-ray counts (14 vs 15–16), the presence of two black spots on outer upper and lower lobes of the caudal fin, a more slender body (body depth 4.6 vs 3.2–4 in SL), and shorter snout (4 vs 3.3–3.7 in HL).

Discussion

The shallow coral reefs of Micronesia are known to shelter a high diversity of reef fishes (Myers 1999, Kulbicki et al. 2013), and the clear waters of central Pacific seem also to favor biodiverse communities at mesophotic depths. However, communities change considerably along the shallow to mesophotic gradient. When studying shallow and deep reefs of Pohnpei, both Coleman et al. (2018) and Rocha et al. (2018) found shifts in species composition and abundance as depth increases, showing high abundances of serranid fishes at deeper depths. In general, *Liopropoma* are cryptic, and most species have their depth range spanning mesophotic depths (Randall and Taylor 1988, Baldwin and Robertson 2014). Therefore, continued exploratory work on mesophotic coral ecosystems is poised to reveal additional new species within this genus.

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RESEARCH ARTICLE

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Taxonomy, systematics and geographic distribution of ground frogs (Alsodidae, *Eupsophus*): a comprehensive synthesis of the last six decades of research

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Abstract

The genus *Eupsophus* (ground frogs) inhabits exclusively the temperate forests of southern South America (Chile and Argentina). The current delimitation of the genus was reached in the late 1970s, when only two species were recognized, but since then the number of described species steadily increased, reaching a maximum of 11 by 2012. Subsequent studies that applied explicit species delimitation approaches decreased the number of species to six in 2017 and raised it again to 11 the following year, including an undescribed putative species. Despite these taxonomic changes, the two species groups traditionally recognized, *roseus* and *vertebralis*, have been maintained. Another recent contribution to the taxonomy of the genus was the explicit recognition of the extremely high level of external phenotypic variation exhibited by species of the *roseus* group, which undermines the utility of some diagnostic characters. Here we provide a critical review of the extensive taxonomic and systematic literature on the genus over the last six decades, to examine the evidence behind the recurrent taxonomic changes and advances in its systematics. We also update and complete a 2017 review of geographic information, provide additional qualitative observations of external characters commonly used in the diagnoses of species of the *roseus* group, and reassess the phylogenetic position of a putative new species from Tolhuaca (Chile), which was not included in the last species delimitation study. The present review shows that: 1) there is no congruence between the patterns of phenotypic and genetic/phylogenetic differentiation among species of both groups; 2) in the *roseus* group, the intraspecific variation in some external characters is as high as the differences described among species; 3) there is little morphological and bioacoustic differentiation within species groups, and inconsistencies in the chromosomal evidence at the genus level; 4) under the latest taxonomic proposal (2018), species of the *roseus* group still lack consistent and reliable diagnoses and their distribution limits are poorly defined; and 5) the population from Tolhuaca represents an additional undescribed species under the most recent taxonomic framework. Finally, we discuss the implications of these findings for the taxonomy and biogeography of the genus, pointing out some areas that require further research to understand their patterns and processes of diversification.

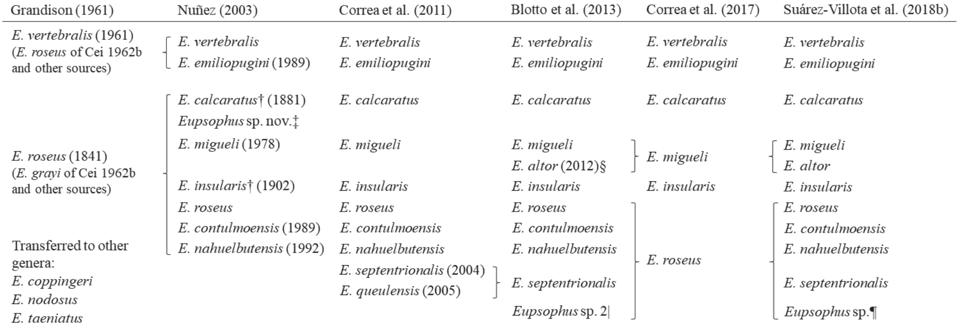
Keywords

Biogeography, diagnoses, ground frogs, literature review, southern South America, species groups

Introduction

Temperate forests of southern South America (Chile and Argentina) are home to a reduced but evolutionarily diverse group of amphibians (Formas 1979, Cei 1980, Correa et al. 2006, Blotto et al. 2013, Streicher et al. 2018). The most diversified anuran lineage of these forests is the family Alsodidae, which currently is represented there by two sister genera, *Alsodes* Bell, 1843 (19 species; Blotto et al. 2013, Frost 2019) and *Eupsophus* Fitzinger, 1843 (11 species; Suárez-Villota et al. 2018b). Only *Eupsophus* (members commonly referred to as "ground frogs") is found exclusively in temperate forests, inhabiting mainly the forest floor (Rabanal and Nuñez 2008). Recently, a controversy about the number of species of *Eupsophus* has emerged in the literature (Correa et al. 2017, Suárez-Villota et al. 2018b), according to which there are six or eleven species, respectively. The 11 species of the last taxonomic proposal (Suárez-Villota et al. 2018b) are arranged into the two species groups traditionally recognized (Fig. 1): *roseus* (*E. roseus* (Duméril & Bibron, 1841), *E. calcaratus* (Günther, 1881), *E. insularis* (Philippi, 1902), *E. migueli* Formas, 1978, *E. contulmoensis* Ortiz, Ibarra-Vidal & Formas, 1989, *E. nahuelbutensis* Ortiz & Ibarra-Vidal, 1992, *E. septentrionalis* Ibarra-Vidal, Ortiz & Torres-Pérez, 2004, *E. altor* Nuñez, Rabanal & Formas, 2012, and a putative new species from Villarrica, Chile) and *vertebralis* (*E. vertebralis* Grandison, 1961 and *E. emiliopugini* Formas, 1989) (Formas 1991, Nuñez 2003, Blotto et al. 2013, Suárez-Villota et al. 2018b).

The genus *Eupsophus* has a long and complex taxonomic history. Among the currently valid species, the first two were described in the nineteenth century under other genera: *Cystignathus roseus* and *Cacotus calcaratus* (see the dates of description in Fig. 1). Subsequently, several species were described under now disused generic names (*Borborocoetes*, *Borborocoetus*, *Cystignathus*; e.g., Philippi 1902), among which only *Borborocoetus* (*Cystignathus*) *insularis* is currently recognized. The use of the name *Eupsophus*, coined by Fitzinger (1843), only became widespread in the first half of the twentieth century, when it included species from other currently valid genera (*Alsodes*, *Batrachyla*, *Phrynopus*, *Thoropa*; e.g., Capurro 1958, Grandison 1961, Cei 1962a, 1962b, Lynch 1971). The current delimitation of the genus was achieved in



Grandison (1961)	Nuñez (2003)	Correa et al. (2011)	Blotto et al. (2013)	Correa et al. (2017)	Suárez-Villota et al. (2018b)
E. vertebralis (1961) (*E. roseus* of Cei 1962b and other sources)	*E. vertebralis*	*E. vertebralis*	*E. vertebralis*	*E. vertebralis*	*E. vertebralis*
	E. emiliopugini (1989)	*E. emiliopugini*	*E. emiliopugini*	*E. emiliopugini*	*E. emiliopugini*
E. roseus (1841) (*E. grayi* of Cei 1962b and other sources)	*E. calcaratus*† (1881)	*E. calcaratus*	*E. calcaratus*	*E. calcaratus*	*E. calcaratus*
	Eupsophus sp. nov.‡				
	E. migueli (1978)	*E. migueli*	*E. migueli*	*E. migueli*	*E. migueli*
			E. altor (2012)§		*E. altor*
	E. insularis† (1902)	*E. insularis*	*E. insularis*	*E. insularis*	*E. insularis*
	E. roseus	*E. roseus*	*E. roseus*	*E. roseus*	*E. roseus*
	E. contulmoensis (1989)	*E. contulmoensis*	*E. contulmoensis*		*E. contulmoensis*
Transferred to other genera: *E. coppingeri* *E. nodosus* *E. taeniatus*	*E. nahuelbutensis* (1992)	*E. nahuelbutensis*	*E. nahuelbutensis*		*E. nahuelbutensis*
		E. septentrionalis (2004)	*E. septentrionalis*		*E. septentrionalis*
		E. queulensis (2005)			
			Eupsophus sp. 2|		*Eupsophus* sp.¶

Figure 1. Composition of the genus *Eupsophus* between 1961 and 2018 according to several reviews and studies. Year of species description is provided in parentheses. Capurro (1958) and Cei (1958, 1960, 1962a, 1962b) recognized the same two species of Grandison (1961), but with different names (see comment in Cei 1962b). †Revalidated by Formas and Vera (1982) (removed from the synonymy of *E. roseus*). ‡Undescribed species from Isla Wellington (Chile), sister to *E. calcaratus*. §It appears as *Eupsophus* sp. 1 in Blotto et al. (2013). |Probable undescribed species from Tolhuaca (Chile), sister to *E. roseus*. ¶Putative species from Villarrica (Chile), sister to *E. roseus*.

the late seventies (Lynch 1978), when only two species were recognized (*E. roseus* and *E. vertebralis*). Since 1978, when *E. migueli* was described (Formas 1978a), the number of species progressively increased to 11 (*E. calcaratus* and *E. insularis*, both revalidated by Formas and Vera 1982, *E. contulmoensis*, *E. emiliopugini*, *E. nahuelbutensis*, *E. septentrionalis*, *E. queulensis* and *E. altor*), but one of them, *E. queulensis*, was synonymized with *E. septentrionalis* by Blotto et al. (2013). The number of species was reduced to six by Correa et al. (2017), but the more recent proposal (Suárez-Villota et al. 2018b) restored the previous taxonomy, adding an additional species not described; so currently the genus is composed of ten nominal species plus an undescribed one (see the taxonomic changes since 1961 in Fig. 1).

During the last six decades, morphometric, immunological, chromosomal, bioacoustic and molecular (allozymes, RFLPs and DNA sequences) approaches have been applied, separately or in combination, to the taxonomy and systematics of these frogs (reviewed by Nuñez 2003). Phylogenetic analyses with DNA sequences only have been performed since Nuñez (2003), but they have had a profound influence on the estimation of species diversity and evolutionary patterns of the genus, particularly of the *roseus* group. Two of these studies (Nuñez et al. 2011, Blotto et al. 2013) suggested that the species diversity of that group may be underestimated. Nuñez et al. (2011) indicated that *E. calcaratus* would represent a species complex composed of six groups of mitochondrial haplotypes "diagnostic of species lineages", and at least one of them would represent a new species (Villarrica population, foothills of Chilean Andes, 39° 20'S). Blotto et al. (2013) tested the monophyly of the genus and its species groups and investigated the relationships among species, including all the species recognized at that time. They synonymized *E. queulensis* with *E. septentrionalis* and suggested that the population from Tolhuaca, also located in the Chilean Andean foothills (38°13'S), would correspond to an undescribed species related to *E. roseus*. More recently, Correa et al. (2017), applying several unilocus species delimitation analyses with mitochondrial sequences, proposed a new arrangement that reduced the species of the genus to six. Suárez-Villota et al. (2018b) rejected this arrangement using new samples, different molecular markers and several species delimitation analyses (unilocus and multilocus). They considered as valid the ten species recognized before 2017 and found support for recognizing the population of Villarrica as a putative species, although they did not include specimens from Tolhuaca. All these hypotheses, including the species status of Villarrica and Tolhuaca populations, have been supported exclusively by molecular phylogenetic evidence, without explicitly incorporating phenotypic characters.

The application of molecular approaches and integrative taxonomy to the discovery and delimitation of species has drastically changed our estimates of amphibian diversity at global and local levels (Catenazzi 2015). Recent systematic research on *Eupsophus* frogs illustrates this trend, as shown by the putative new species mentioned above (Nuñez et al. 2011, Blotto et al. 2013), the description of *E. altor*, where an integrative taxonomy approach was applied (Nuñez et al. 2012a), and the most recent taxonomic proposals (Correa et al. 2017, Suárez-Villota et al. 2018b), based on explicit species delimitation analyses. However, descriptions and diagnoses of *Eupsophus* have historically been based primarily on external and internal phenotypic characters (Nuñez 2003) and molecular data have been included in only two cases (*E. septentrionalis* and *E. altor*, both considered invalid by Correa et al. 2017). Correa et al. (2017) pointed out some weaknesses of the diagnoses of the species of the *roseus* group, recognizing also that there are no known phenotypic characters to support their own taxonomic proposal. Moreover, they reviewed the chromosome and bioacoustic evidence published for the genus, finding a scarce differentiation in the karyotypes and advertisement calls among species of the *roseus* group, which was one of the decisive arguments for choosing a conservative delimitation (i.e., fewer species) in this group. On the other hand, the taxonomic proposal by Suárez-Villota et al. (2018b) rests exclusively on species delimitation approaches with DNA sequences, assuming that such a proposal is completely consistent with the numerous previous taxonomic and systematic studies of the genus based on non-molecular evidence.

The last complete review of the taxonomy and systematics of the genus *Eupsophus* was Nuñez (2003), a doctoral dissertation that was not published in a peer-reviewed journal. That review presented a rather stable and uncontroversial view of the taxonomy of the genus, which at that time comprised eight species. Since that date, there have been several changes in the composition of the genus, specifically in the *roseus* group (summarized in Fig. 1). Correa et al. (2017) reviewed partially the taxonomy and geographic information of the genus, with a focus on the *roseus* group. These authors not only noted the weaknesses of the diagnoses of the species of that group, but also the problems that arise when comparing all the published chromosomal, bioacoustic and geographic information on the genus.

In this study, we synthesize the vast taxonomic and systematic literature of the genus to identify the evidence supporting the recurrent taxonomic changes. We extend the review of Correa et al. (2017) to the whole genus, adding other lines of evidence that have been applied to the *Eupsophus* taxonomy, and provide a more complete compilation of geographic information. We also add new qualitative observations of external characters of live adults of selected populations and reassess the phylogenetic position of a putative new species from Tolhuaca (Andean foothills of Chile; Blotto et al. 2013), which was not included in the last species delimitation study (Suárez-Villota et al. 2018b). We aim not only to provide a complete and updated summary of the taxonomic, systematic and geographic information of the genus, but also to highlight the incongruences among different lines of evidence that should be addressed by future taxonomic and systematic studies.

Materials and methods

Literature sources

Taxonomy and systematics

Our literature review was focused on (but not restricted to) taxonomic, genetic and phylogenetic studies in which phenotypic and/or genetic variation within and among *Eupsophus* species is described. As starting point, we considered the first reviews exclusively dedicated to the taxonomy of Chilean *Eupsophus*, Cei (1960), Grandison (1961) and Cei (1962a), because they combined several problematic taxa (e.g., the forms described by Philippi 1902) under that genus name. Although those reviews (and some previous ones, such as Capurro 1958 and Cei 1958) included some species currently considered members of other South American genera (*Alsodes*, *Batrachyla*, *Phrynopus*, *Thoropa*), information about the genus, in its current definition (e.g., Lynch 1978), is easily retrievable. The last complete review of the taxonomy and systematics of *Eupsophus* is the unpublished doctoral dissertation of Nuñez (2003), but recently Correa et al. (2017) partially reviewed the chromosome, bioacoustic and geographic information on the genus. Other taxonomic and/or systematic studies with wider taxonomic coverage (but that include several species of *Eupsophus*) are Díaz (1986), Correa et al. (2006), and Blotto et al. (2013). The latter also contains a synthesis of the recent systematics of *Eupsophus* and was the most comprehensive molecular phylogenetic study of the genus until Correa et al. (2017) and Suárez-Villota et al. (2018b). Descriptions and redescriptions of the ten nominal species recognized by Suárez-Villota et al. (2018b) are included in Duméril and Bibron (1841) (*E. roseus* as *Cystignathus roseus*), Günther (1881) (*E. calcaratus* as *Cacotus calcaratus*), Philippi (1902) (*E. insularis* as *Borborocoetus* (*Cystignathus*) *insularis*), Grandison (1961) (*E. vertebralis* and *E. roseus*, the latter as *E. grayi*), Capurro (1963) (who proposed to recognize *E. insularis* as subspecies of *E. grayi*), Formas (1978a) (*E. migueli*), Formas and Vera (1982) (revalidation of *E. calcaratus* and *E. insularis*), Formas (1989) (*E. emiliopugini*), Ortiz et al. (1989) (*E. contulmoensis*), Ortiz and Ibarra-Vidal (1992) (*E. nahuelbutensis*), Nuñez (2003) (which includes somewhat different descriptions of the aforementioned eight species), Ibarra-Vidal et al. (2004) (*E. septentrionalis*), Veloso et al. (2005) (*E. queulensis*, synonymized with *E. septentrionalis* by Blotto et al. 2013), and Nuñez et al. (2012a) (*E. altor*). Other studies of *Eupsophus* with a taxonomic and/or systematic focus have used different approaches: Capurro (1963) (morphology), Formas (1978b) (karyotypes), Formas (1980) (karyotypes), Iturra and Veloso (1981) (karyotypes), Formas et al. (1983) (allozymes), Formas (1985) (calls), Fernández de la Reguera (1987) (morphometrics), Iturra and Veloso (1989) (karyotypes), Formas (1991) (karyotypes), Formas et al. (1991) (allozymes), Formas et al. (1992) (allozymes and morphometrics), Formas (1992) (karyotypes), Formas and Brieva (1992) (immunology), Formas (1993) (allozymes and morphometrics), Formas and Brieva (1994) (calls), Cuevas and Formas (1996) (karyotypes), Nuñez et al. (1999) (morphometrics and RFLPs), Cárdenas-Rojas et al. (2007) (larval morphology), Nuñez and Úbeda (2009) (larval morphology), Opazo et al. (2009) (calls), Lavilla et al. (2010) (morphology), Nuñez et al. (2011) (phylogeography using mitochondrial sequences), and Vera Candioti et al. (2011) (larval morphology).

Geographic distributions

We compiled literature records to define the geographic ranges of the 11 species recognized by Suárez-Villota et al. (2018b) and compared them with the most recent maps (Nuñez 2003, Rabanal and Nuñez 2008, Correa et al. 2017, and IUCN 2019). Locality data were obtained from the publications in which the species were described (see above) and from other sources (e.g., Webb and Greer 1969, Formas and Vera 1980, 1982, Formas et al. 1991, Nuñez et al. 1999, Úbeda 2000, Díaz-Páez and Nuñez 2002, Méndez et al. 2005, Ortiz and Ibarra-Vidal 2005, Asencio et al. 2009, Nuñez et al. 2011, Blotto et al. 2013, Núñez and Gálvez 2015, Correa et al. 2017, Suárez-Villota et al. 2018b). Distribution data and/or maps of older reviews (Cei 1960, 1962a, 1962b, Grandison 1961, Formas 1979) were carefully considered because the delimitations of the species at that time were quite different from the present. In addition, we reviewed all biological studies of the genus and other relevant sources about Chilean amphibians to collect additional geographic data.

Phenotypic observations

Correa et al. (2017) showed that the four characters most frequently included in the diagnoses of the species of the *roseus* group (body coloration pattern, iris color, lateral and dorsal snout profile, and shape of the end of the xiphisternum) vary at the intrapopulation level. Here, we provide additional examples of intrapopulation variation in the first three characters. The observations were made in two undescribed and two type localities (Valdivia, *E. roseus*, and Mehuín, *E. migueli*), including less than 20 live specimens per locality. All specimens were released at the same capture site after being photographed.

Phylogenetic analyses

Blotto et al. (2013) identified one specimen from Tolhuaca (foothills of Chilean Andes, ~38°S) as a probable undescribed species, sister to *E. roseus*. Correa et al. (2017) included the same specimen and other samples from near Villarrica (as representatives of the area where there would be another undescribed species according to Nuñez et al. 2011) in their phylogenetic and species delimitation analyses, finding support for the inclusion of all of them into a redefined *E. roseus*. Suárez-Villota et al. (2018b) included specimens from Villarrica, but not from Tolhuaca in their species delimitation analyses, so the reciprocal relationships between both populations and the taxonomic status of the latter currently are not clear. Here we address both issues, using the two coding mitochondrial fragments included in common by Blotto et al. (2013), Suárez-Villota et al. (2018a, b): cytochrome b (cytb) and cytochrome c oxidase subunit I (COI). We concatenated the sequences of both fragments, totaling 147 specimens representing the ten currently recognized species and the two undescribed taxa (Villarrica and Tolhuaca). The sequences of both genes differ in length between studies, so an initial alignment was obtained with blocks of gaps at the ends of the genes. We obtained an alternative alignment by cutting those extremes. Two schemes to apply nucleotide evolution models were used in both alignments: considering each gene fragment as a partition or each position of the codons as a distinct partition within each fragment (six partitions). Sequences were aligned with Muscle v3.5 (Edgar 2004) and then inspected by eye. Phylogenetic relationships were estimated through a Bayesian inference (BI) method with a Markov Chain Monte Carlo algorithm, performed with the program MrBayes v3.2.6 (Ronquist et al. 2012). A General Time Reversible, plus gamma and proportion of invariable sites model was independently applied to each fragment/partition, using also a reversible jump method. Two independent BI analyses (each consisting of two groups of four chains that ran independently) applying that method were run for 10 million generations, sampling every 1000th generation. The first 25% of generations were conservatively discarded as burn-in after observing the stationarity of ln-likelihoods of trees in Tracer v1.7 (Rambaut et al. 2018). Convergence and mixing of chains were assessed examining values of average standard deviation of split frequencies, and expected sampling sizes and potential scale reduction factors for all parameters. One specimen of *Alsodes norae* of Suárez-Villota et al. (2018b) was used as outgroup (MK180951, cytb; MK181499, COI).

Results

Literature review

Changes in the content of the genus and species groups

The reviews by Cei (1960, 1962a) and Grandison (1961) are fundamental for the recent taxonomy of *Eupsophus*, because they combined several invalid (for example, several forms of *Cystignathus* and *Borborocoetus* of Philippi 1902) and now valid species (*E. calcaratus* and *E. insularis*) into two taxa, which represent the two species groups currently recognized (Fig. 1; see below). However, since the description of *E. migueli* (Formas 1978a), the number of species increased from three to eleven (with *E. altor*), most of them derived from or closely related to *E. roseus*. One additional species from Isla Wellington (southern Chile), closely related to *E. calcaratus*, was proposed by Nuñez (2003), though it was never named or formally described (Fig. 1; Blotto et al. 2013 included specimens from Isla Wellington, showing that they belong to *E. calcaratus*). All descriptions and revalidations (in the case of *E. calcaratus* and *E. insularis*) were primarily motivated by observations of differences in external morphological characters and in some cases also internal ones. Other types of characters were added in some descriptions and diagnoses (see Table 1), but only exceptionally additional evidence was obtained subsequently to reinforce the distinction of some species (e.g., the karyotype of *E. migueli*, Iturra and Veloso 1981). Another important change was the synonymization of *E. queulensis* with *E. septentrionalis* (Blotto et al. 2013), which resulted in ten formally recognized species until 2017. That year, Correa et al. (2017) proposed to synonymize *E. contulmoensis*, *E. nahuelbutensis* and *E. septentrionalis* with *E. roseus*, and *E. altor* with *E. migueli*, thus reducing from ten to six the species of the genus (Fig. 1). These authors suggested that part of the diversity of species previously recognized was due to the excessive importance attributed to non-fixed morphological differences in certain populations. These last synonymizations were reverted by Suárez-Villota et al. (2018b), who revalidated the same ten species recognized by 2017 plus one not described from Villarrica, Chile (Fig. 1), although they did not include specimens from Tolhuaca, Chile (*Eupsophus* sp. 2 of Blotto et al. 2013, Fig. 1). The division of *Eupsophus* into two species groups, *roseus* and *vertebralis* (Fig. 1), already implicit in the reviews of Cei (1960, 1962a) and Grandison (1961), it was first formally proposed by Formas (1991) based on karyotype differences. This division has been supported by cumulative morphological (Fernández de la Reguera 1987, Nuñez 2003), chromosomal (Formas 1980, Formas 1991), bioacoustic (advertisement calls; Formas 1985, Formas and Brieva 1994), genetic (allozymes; Formas et al. 1983) and immunological evidence (Formas and Brieva 1992). More recently, molecular phylogenetic analyses with DNA sequences have ratified the reciprocal monophyly and high genetic divergence between those groups (Nuñez 2003, Correa et al. 2006, Blotto et al. 2013, Correa et al. 2017, Suárez-Villota et al. 2018a, b).

Diagnostic characters

Correa et al. (2017) summarized the diagnostic characters of nine species of the *roseus* group (the eight species currently recognized plus *E. queulensis*). They extracted the information mainly from the original diagnoses, but also used other two sources for *E. roseus*, *E. calcaratus* and *E. insularis*, since the original descriptions and diagnoses of these species are very brief and were made under generic names no longer used. The two additional sources are Formas and Vera (1982), where *E. calcaratus* and *E. insularis* are revalidated, and Nuñez (2003), which contains partially different diagnoses for the eight species recognized at that date. The summary of Correa et al. (2017) highlighted several general deficiencies of the diagnoses of the species of the *roseus* group: 1) in some cases, characters that varied in the type series were used; 2) the great heterogeneity in number and type of characters used, which makes it difficult to identify the differences among the species; and 3) the four characters most frequently included in the diagnoses vary widely at the intraspecific level. Here (Table 1), we expand the summary table of Correa et al. (2017) to include the species of the *vertebralis* group and reorder the species according to the taxonomy and phylogenetic hypothesis of Suárez-Villota et al. (2018b). Table 1 allows to compare the diagnostic differences between species within groups, showing that the diagnoses are heterogeneous in the number of characters and level of detail, so they are scarcely comparable, regardless of the taxonomic scheme used (Correa et al. 2017 or Suárez-Villota et al. 2018b). In particular, diagnoses of sister species do not contain characters in common (*E. migueli* and *E. altor*) or these could be differentiated only by the body coloration pattern (*E. contulmoensis* and *E. nahuelbutensis*, *E. vertebralis* and *E. emiliopugini*), which has been described as variable in most species (see Correa et al. 2017 and the section Phenotypic observations).

Variation in diagnostic characters

Correa et al. (2017) showed, using literature information and observations of live specimens, that the four characters most frequently included in diagnoses (body coloration, color of upper part of iris, shape of snout and shape of the end of the xiphisternum) vary within species. Here we summarize the information used by those authors and add some additional details from the literature. The first comprehensive reviews of the genus (Cei 1960, 1962a, Grandison 1961) already mentioned, although briefly, that body coloration patterns vary at intrapopulation level in species of the *roseus* group. However, these type of observations did not prevent the coloration pattern (dorsal and/or ventral) from being later included as a diagnostic character for several species of the group (Table 1). Moreover, according to their descriptions, body coloration varies in *E. calcaratus* (Formas and Vera 1982), *E. emiliopugini* (Formas 1989) and *E. altor* (Nuñez et al. 2012a; see their fig. 5). Another characteristic that contributes to the variation of the dorsal coloration patterns is a mid-dorsal (vertebral) line of whitish or yellowish color, which may be present or absent, and vary in length and width. This vertebral line is more frequent in the two species of the *vertebralis* group (Cei 1962b, Grandison 1961, Formas 1989), but also has been reported in some specimens of *E. migueli* (Formas 1978a), *E. calcaratus* (Formas and Vera 1982), *E. contulmoensis* (Ortiz et al. 1989), *E. nahuelbutensis* (Ortiz and Ibarra-Vidal 1992) and *E. septentrionalis* (Ibarra-Vidal et al. 2004, Veloso et al. 2005; see also Fig. 4B). Correa et al. (2017) discussed the possible causes and practical consequences of the variation of the body coloration patterns, adding several examples with live specimens of the *roseus* group (see their Supporting Information). There are also previous literature records of variation in the other three characters mentioned. The coloration of the

Table 1. Phenotypic, karyotypic and genetic characters included in the diagnoses of the ten nominal species of *Eupsophus* currently recognized (Suárez-Villota et al. 2018b; Fig. 1). This is a modified version of the table of Correa et al. (2017) with two main changes: the two species of the *vertebralis* group were added, and the diagnoses of *E. queulensis* and *E. septentrionalis* were combined. Species are ordered by species group and then by their phylogenetic affinities according to the hypothesis of Suárez-Villota et al. (2018b). Empty cells indicate that character was not included in the respective diagnosis. The V in parentheses indicates that the character was described as variable in the type series. Character states are described such as they appear in the original sources. Diagnoses of *E. roseus*, *E. calcaratus* and *E. insularis* include characters of their original descriptions and/or later redescriptions (see the text).

character	*E. calcaratus*	*E. roseus*	*E. contulmoensis*	*E. nahuelbutensis*	*E. septentrionalis*† (including *E. queulensis*)	*E. insularis*	*E. migueli*	*E. altor*	*E. vertebralis*‡	*E. emiliopugini*§
Body coloration		body with brown tones on a pink background; transparent or whitish ventral area	dark purple dorsal pigmentation and bright yellow belly (V)	white belly with dark brown marmorino (V)	dark brown to blackish on a light gray to leaden background (V); *E. queulensis*: two melanic dots on dorsal region and reddish ventral surfaces (V)	dark brown with irregular yellow spots on the dorsum and legs (V)	dark venter and white brilliant irregular spots (V)		usually with a vertebral band which may be as broad as the distance between the nares (V)	a distinctive olive-green band between the eyes
Color of upper part of iris	bronze-yellow	orange	bronze-yellow		light yellow; *E. queulensis*: yellow		bronze-yellow			
Shape of snout	pointed in dorsal and lateral view, noticeably protruding over the lower jaw|			sloping in lateral view (V)	*E. queulensis*: truncate in lateral view				broadly rounded	
Xiphisternum				ample in its middle portion and rounded at its extreme	*E. queulensis*: without a notch	truncated and slightly notched	notched			
Canthus rostralis		thin and short		ample and extended						
Cloacal fold				marked						
Relative position of epicoracoids		right over left			*E. queulensis*: left epicoracoid superimposed to the right one					
Carpal tubercles			inner palmar tubercle prominent		*E. queulensis*: prominent external and internal tubercles				subarticular tubercles prominent	
Tips of toes	rounded and prominent									

character	***E. calcaratus***	***E. roseus***	***E. contulmoensis***	***E. nahuelbutensis***	***E. septentrionalis*†** **(including *E. queulensis*)**	***E. insularis***	***E. migueli***	***E. altor***	***E. vertebralis*‡**	***E. emiliopugini*§**
Other osteological characters¶	prevomers in narrow contact	vomerine teeth arranged in a transverse row			skull morphology#	prevomerine teeth below the choanae			vomerine teeth in two, only slightly curved groups	
Karyotype		eight pairs of biarmed chromosomes			*E. queulensis*: heteromorphic sexual chromosomes, and secondary constriction at the fourth pair		16 acrocentric chromosomes			
Allozymes					allozyme pattern# (V)					
Reproductive traits								early winter breeding season and terrestrial tadpoles		
Advertisement call								spectral elements reaching 20 kHz		mating call with two notes
Genetic divergence								nine nucleotide site substitutions in the mitochondrial control region from *E. migueli*#		

†We add the diagnosis of *E. queulensis* because it includes a greater number of characters.

‡The original diagnosis of *E. vertebralis* (Grandison 1961) is very extensive, but based exclusively on external morphology (e.g., characteristics of the skin, ears, and limbs), so here we only included those characters comparable with other species; Nuñez (2003) indicated that the diagnosis of Grandison (1961) also included specimens of *Alsodes*, but he did not provide further details to support this assertion.

§Formas (1989) included the adult size in its diagnosis to differentiate it from its sister species *E. vertebralis*; however, there is a high degree of superposition in male and female sizes between both species (Table 1 of Formas 1989).

|Formas and Vera (1982) used this character to differentiate *E. calcaratus* from *E. roseus*, but they did not describe the snout profile of *E. roseus* (they only showed a drawing of the head in lateral profile).

¶To simplify the table, we reunite in this miscellaneous category a series of osteological details of the skull that have been included occasionally in the diagnoses.

#These are not character states, but we transcribed them as they appear in the original diagnosis.

iris has been included recurrently in the descriptions and diagnoses of the species of the *roseus* group, so it was considered a useful character to distinguish certain species (Table 1). In contrast, the iris of both species of the *vertebralis* group is very similar, uniformly reticulated in black and yellowish (Nuñez 2003). Iris coloration appears to be a less variable trait, because there are only a couple of references of intraspecific variation in the literature. Nuñez (2003) suggested indirectly that there is variation in this trait: the iris color of *E. calcaratus* and *E. nahuelbutensis* is "generally" yellow, whereas that of *E. roseus*, *E. migueli,* and *E. contulmoensis* "can be" orange. Moreover, Nuñez et al. (1999) mentioned that the typical copper-colored upper part of the iris of *E. roseus* is also observed occasionally in specimens of *E. calcaratus*, which otherwise is bronze-yellow. The snout profile also has been included in several diagnoses of species of both groups (Table 1). For example, the snout profile, both in dorsal and lateral view, was one of the few characters used by Formas and Vera (1982) to differentiate *E. calcaratus* from *E. roseus*. Only in the case of *E. nahuelbutensis* this character was described as variable in the type series (some paratypes had the snout rounded, Ortiz and Ibarra-Vidal 1992). Another instance of intraspecific variation stems from the synonymy of *E. queulensis* with *E. septentrionalis*, since the shape of the snout was described as truncate in the former (Veloso et al. 2005) and short and rounded in lateral profile in the latter (Ibarra-Vidal et al. 2004; Table 1). Correa et al. (2017) gave examples of intrapopulation variation of iris coloration and snout profile in live specimens of several populations, including individuals of the type localities of *E. roseus* and *E. altor*, showing that these characters are not useful to diagnose the species of the *roseus* group. We provide additional examples of variation of body and iris coloration and snout profile with specimens of four localities, including the type localities of *E. roseus* and *E. migueli* (section Phenotypic observations). The shape of the distal end of the xiphisternum is the osteological character most frequently included in descriptions and diagnoses (Table 1), where it has been implicitly considered as fixed. According to the literature, the xiphisternum of most species is rounded and unnotched (*E. roseus*, *E. calcaratus*, *E. vertebralis*, *E. contulmoensis*, *E. nahuelbutensis*, *E. septentrionalis*, *E. queulensis,* and *E. altor*), but in *E. insularis* it is truncated and slightly notched (Capurro 1963, Formas and Vera 1982; although in this last study it was drawn as unnotched), and in *E. migueli* it is notched (Formas 1978a) (this character has not been described in *E. emiliopugini*). However, one study (Díaz 1986) examined the form of the xiphisternum in a significant number of specimens from the type localities of *E. roseus* (Valdivia, $N = 37$) and of *E. migueli* (Mehuín, $N = 45$), finding four types of xiphisternum (rounded, pointed, notched and seminotched) in *E. migueli* and three in *E. roseus* (notched condition was not found). Although in both species the rounded xiphisternum was the most frequent condition, this example demonstrates that intrapopulational variation in osteological characters may be detected when a large number of specimens is examined. Nuñez (2003) mentioned that some osteological characters vary at intra- and interspecific levels (for example, the relative position of epicoracoids, which has been included in the diagnoses of two species, Table 1), though which species display the variation were not specified by the author.

Morphometric studies

Morphometric approaches have usually been used to infer, implicitly or explicitly, the relationships among species or to discriminate (or validate) them. Also, they have been used in conjunction with allozymes (see below) to evaluate explicitly the agreement between morphological and genetic evolution in the genus (Formas et al. 1983, Formas et al. 1992, Formas 1993). The first comprehensive reviews (Grandison 1961, Cei 1962a) contain measurements and/or indices (ratios) of body, head and hind legs of adults of only two species of *Eupsophus* (equivalent to the two species groups) and the other species (*Alsodes* spp., *Batrachyla taeniata*) that the genus contained at that time. Cei (1962a) described morphometric differences between continental and insular (Chiloé Island) populations of *E. grayi* (equivalent to the current *roseus* group), but in those groups of populations he mixed several species that were described later. Subsequent studies on adults have applied multivariate statistical techniques (mainly principal components and discriminant analyses), but they have been carried out with a small number of species (no more than four species per study; *E. nahuelbutensis* and *E. septentrionalis* have not been included in any study) and populations (no study included more than one population per species). Despite these limitations, morphometric differences have been observed between the species groups (Fernández de la Reguera 1987), and not within them (Formas et al. 1983, Díaz 1986, Fernández de la Reguera 1987, Formas et al. 1992, Formas 1993, Nuñez et al. 1999, Nuñez et al. 2012a). In particular, some species of the *roseus* group are morphometrically indistinguishable from each other (*E. roseus*, *E. migueli,* and *E. altor*; Díaz 1986, Nuñez et al. 2012a). Similarly, the only comparative morphometric study of tadpoles, Nuñez and Úbeda (2009), showed a clear differentiation between species groups (*E. vertebralis* and *E. emiliopugini* versus *E. roseus* and *E. nahuelbutensis*), but scarce differences within them.

Chromosomal studies

The karyotypes of nine of the ten species of *Eupsophus* currently recognized are shown in Table 2, ordered by species group and date of description (that of *E. nahuelbutensis* has not been described, although Nuñez 2003 pointed out that it has 30 chromosomes). Species groups are characterized by different numbers of chromosomes (30 in the *roseus* group, 28 in the *vertebralis* group; Nuñez 2003, Veloso et al. 2005) and three species present heteromorphic sex chromosomes (*E. migueli*, Iturra and Veloso 1981; *E. insularis*, Cuevas and Formas 1996; and *E. septentrionalis*, Veloso et al. 2005). In *E. roseus* the sex chromosomes do not differ in form, but can be distinguished by their constitutive heterochromatin patterns (Iturra and Veloso 1989). Correa et al. (2017) noted that different authors described different karyotypes for the same population in several species, without reporting variation among the specimens used, even though in most studies more than one was included (in some cases more than ten, e.g., Formas

Table 2. Summary of karyotypes described in *Eupsophus*. Species are ordered by group (*roseus* and *vertebralis*) and then by year of description and locality, considering the current taxonomy (Suárez-Villota et al. 2018b; Fig. 1). Number of samples (f: females, m: males, j: juveniles) for obtaining the karyotypes are indicated (when specified), although in some studies is not clear how many specimens were used (indicated with a question mark). Reported morphology of each chromosome (pairs 1–15; m: metacentric; sm: submetacentric; st: subtelocentric; t: telocentric), diploid number (2n) and fundamental number (*FN*) are also indicated. An asterisk indicates the chromosome bearing the secondary constriction. In several cases, chromosomal morphology was not described in the text or was described with ambiguity, so this information was inferred from the original figures (indicated with a question mark). Heteromorphic chromosomes (pair 14) have been described for three species and imply different chromosome morphology and fundamental number between sexes (both telocentric in females, *FN* = 44; metacentric and telocentric in males, *FN* = 45). Veloso et al. (2005) summarized the information of the karyotypes of the genus without specifying the source or the number of samples.

species	source	locality	sample size	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	2n	*FN*
roseus	Formas (1978b)	Valdivia (city)	12m, 6f	m	sm	st*	t	t	m	m	t?	sm?	t	t?	m?	t	m	t	30	46
roseus	Formas (1978a)	near Valdivia (city)	2m, 14f	m	st*	st	t	t	m	m	m	t	m	t	t	m	t	t	30	46
roseus	Iturra and Veloso (1989)	Valdivia (city)	4m, 4f?	m	sm*	st	t	t	t	m	m	m	t	t	m	t	m	t	30	46
roseus	Formas (1978b)	Fundo San Martín	12m, 11f	m	st	st	t	t*	t	m	m	m	t	t	t	m	t	m	30	46
roseus	Veloso et al. (2005)	not specified	–	m	sm*	st	t	t	t	m	m	m	t	t	m	t	m	t	30	46
calcaratus†	Barrio and Rinaldi de Chieri (1971)	Puerto Blest (Río Negro, Argentina)	3m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–
calcaratus†	Veloso et al. (1974)	P.N. Vicente Pérez Rosales	5m, 2f, 1j	m	st*	st	t	t	t	m	m	m	t	t	m	t	m	t	30	46
calcaratus	Formas (1980)	La Picada, Cordillera Pelada and P.N. Puyehue	3m, 7f; 11m, 1f; 2m	m	sm*	st	t	m	t	m	m	t	m	t	t	m	t	t	30	46
calcaratus	Veloso et al. (2005)	not specified	–	m	sm	st*	t	m	t	m	m	t	m	t	t	m	t	t	30	46
insularis	Cuevas and Formas (1996)	Isla Mocha	11m, 9f	m	sm*	st	m	t	m	t	t	m	t	m	t	t	m/t	t	30	45/44
insularis	Veloso et al. (2005)	not specified	–	m	sm	st*	m	t	m	t	t	m	t	m	t	t	m/t	t	30	45/44
migueli†	Bogart (1970)	Mehuín	2m, 1f	m	st*	st	t	t	t	m	m	m	t	t	m	t	t	t	30	44
migueli†	Formas (1978b)	Mehuín	23m, 4f	m	sm*	st	t?	t?	m	m	m	t?	m	t	t	t	t	t	30	44
migueli	Formas (1978a)	Mehuín	7m, 3f	m	st*	st	t	m	m	t	m	t?	t	t	t	t	t	t	30	44
migueli	Iturra and Veloso (1981)	Mehuín	14m, 10f	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	45/44
migueli	Iturra and Veloso (1989)	Mehuín	4m, 4f?	m	sm*	st	t	t	t	m	m	m	t	t	m	t	m/t	t	30	45/44
migueli	Veloso et al. (2005)	not specified	–	m	sm*	st	t	t	t	m	m	m	t	t	m	t	m/t	t	30	45/44
contulmoensis	Formas (1992)	M.N. Contulmo	5m, 3f?	m	st	sm*	t	t	m	m	t	t	m	m	t	t	m	t	30	46
contulmoensis	Veloso et al. (2005)	not specified	–	m	st	st*	t	t	m	m	t	t	m	m	t	t	m	t	30	46
septentrionalis‡	Veloso et al. (2005)	R.N. Los Queules	1m, 1f	m	st	st	t*	t	m	t	m	sm	t	t	m	t	m/t	t	30	45/44
altor	Nuñez et al. (2012a)	not specified	1h	m	sm*	st	t	m	t	t	t	m	m	m	t	t	t	t	30	44
vertebralis	Bogart (1970)	Mehuín	2m	sm	m	t	st	st	st	sm	m	m	m	sm	sm	m	m		28	–

species	**source**	**locality**	**sample size**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**2n**	***FN***
vertebralis	Formas (1991)	Mehuín	9m, 1f	m	st	m	st	st*	st	sm	m	m	m	m	m	t	m		28	54
vertebralis	Veloso et al. (2005)	not specified	–	m	st	m	st	st	st	sm	m	m	m	m	m	t	m		28	56§
emiliopugini|	Veloso et al. (1974)	P.N. Vicente Pérez Rosales	1m, 1f	m	m	st	st	st	t	sm	sm	sm	m	m	sm	m	m		28	54
emiliopugini	Formas (1991)	Puntra	4m, 2f	m	st	m	st	st*	st	sm	m	m	m	m	m	m	m		28	56
emiliopugini	Veloso et al. (2005)	not specified	–	m	st	m	st	st	st	sm	m	m	m	m	m	m	m		28	56

†As *E. roseus*.

‡As *E. queulensis*.

§According to the chromosomal morphology, it should be 54, but here the original figure of the Table 2 from Veloso et al. (2005) is reported.

|As *E. vertebralis*.

1978a, 1978b, Cuevas and Formas 1996). Correa et al. (2017) argued that these differences are due to observer biases, which is consistent with the information of the karyotypes summarized in Table 2, where karyotypes of the same species obtained by several authors, from the same (e.g., *E. roseus*, *E. migueli*) or several localities (e.g., *E. roseus*, *E. calcaratus*) can be compared. Almost all karyotypes of the same species described by different authors differ in chromosomal morphology and position of the secondary constriction, and even in the presence or absence of this last structure (*E. vertebralis* and *E. emiliopugini*), so that intrapopulation and/or intraspecific variation is revealed only when different studies are compared. The levels of variation in chromosome morphology and position of the secondary constriction within a same species (considering all studies by different authors) are as high as the levels of variation observed among species of the same group (e.g., between *E. migueli* and *E. insularis*, or between *E. roseus* and *E. contulmoensis*; Table 2). The discovery of heteromorphic sex chromosomes in *E. migueli* (Iturra and Veloso 1981) is another example of inconsistent descriptions of karyotypes of the same population and species, since they were not observed in previous studies of the species (Bogart 1970, Formas 1978a, 1978b; Table 2). Differences in chromosome morphology are not due to methodological issues, since all studies followed Levan et al. (1964) to determine the position of the centromere and Bogart (1970, 1973) to determine the relative lengths of the chromosomes, so we agree with the suggestion of Correa et al. (2017) that many of the differences among studies are observer-dependent.

Bioacoustic studies

Vocalizations of nine nominal species of both species groups have been described (Table 3; summarized by Nuñez 2003 and Correa et al. 2017). The vocalizations emitted more frequently by males are advertisement calls (called type A or short calls; Formas 1985, Formas and Brieva 1994, Penna and Veloso 1990), which have been described for most species. The difference in the temporal and spectral (frequencies) structure of the advertisement calls is one of the lines of evidence that has been used to support the division of the genus into two groups (Formas 1985, Formas and Brieva 1994, Nuñez 2003). Also, long calls (> 2.7 seconds; type B of Formas 1985) are emitted by males of some species of the *roseus* group, which could correspond to territorial or encounter calls (Formas 1985, Penna and Veloso 1990), but these calls have been described only in *E. migueli* (Formas 1985, Penna and Veloso 1990) and *E. roseus* (Penna and Veloso 1990) (Table 3). Another type of call described in the *roseus* group is an aggressive call recorded occasionally in *E. calcaratus* and *E. roseus* (Márquez et al. 2005). Short advertisement calls are structurally very similar among species of the *roseus* group: all calls consist of only one note and ranges of temporal and spectral parameters overlap extensively among species (Table 3; see comments in Formas and Brieva 1994 and Correa et al. 2017). Formas and Brieva (1994) noted only differences in the intervals among harmonics among species of the *roseus* group: *E. contulmoensis* and *E. insularis* have harmonics at about 500 Hz, while *E. calcaratus*, *E. migueli* and *E. roseus* show harmonics at about 1000 Hz intervals. Instead, the advertisement calls of both species

Table 3. Parameters most commonly used to describe the vocalizations of nine of the ten species of *Eupsophus* currently recognized (see Fig. 1; vocalizations of *E. nahuelbutensis* has been not described). Species are ordered by group (*roseus* and *vertebralis*) and then by year of description. Mean and/or range (in parentheses after the means) of each parameter (N/C: notes per call; RR: repetition rate; CL: call length; PPN: pulses per note; FF: fundamental frequency; DF: dominant frequency) are given.

species	source	locality	N/C	RR (calls/min)	CL (ms)	PPN	FF (Hz)	DF (Hz)
E. roseus	Formas and Vera (1980)	Huachocopihue	1	64 (60-72)	200 (190-210)	17 (15-20)	-	2200 (1600-2900)
E. roseus	Penna and Veloso (1990)	Valdivia	1	25.1 (11.1-60)	105 (70-160)	-	-	1291 (1250-1350)
E. roseus (long call)	Penna and Veloso (1990)	Valdivia	32.1 (8-47)	10.2 (9.3-11.2)	2730 (650-4000)	-	-	1390 (1220-1470)
E. roseus	Márquez et al. (2005)	Lago Tinquilco	1	-	158 (124-235)	-	633 (346-1019)	1871 (1503-2167)†
E. calcaratus	Formas (1985)	Puntra	1	19 (16-25)	190 (150-210)	-	-	1100-2700‡
E. calcaratus	Márquez et al. (2005)	La Picada	1	-	192 (112-262)	-	776 (447-1104)	2157 (1805-2407)†
E. insularis	Formas and Brieva (1994)	Isla Mocha	1	7.8 (4-12)	160 (140-180)	-	-	1500-2100
E. migueli	Formas (1985)	Mehuín	1	6 (3-8)	240 (200-350)	-	450 (390-987)§	1835§ (1500-2500)
E. migueli (long call)	Formas (1985)	Mehuín	24 (19-33)	6 (5-8)	3400 (2700-4400)|	4-7¶	-	900-1500
E. migueli	Penna and Veloso (1990)	Mehuín	1	4.2 (2.4-6.6)	208 (160-260)	-	-	1633 (1170-1820)
E. migueli (long call)	Penna and Veloso (1990)	Mehuín	12.3 (4-23)	5.4 (2.4-8.4)	1072 (300-2160)	-	-	1532 (1210-2000)
E. contulmoensis	Formas and Brieva (1994)	M.N. Contulmo	1	23.3 (15-34)	180 (150-200)	-	-	1100-2000
E. septentrionalis#	Opazo et al. (2009)	R.N. Los Queules	1	-	135 (46-182)	-	-	1818 (1464-2326)†
E. altor	Nuñez et al. (2012a)	Parque Oncol	1	-	336 (290-360)††	-	756 (304-1298)††	1882 (1317-2098)
E. vertebralis‡‡	Formas and Vera (1980)	Mehuín	5 (4-6)	4 (2-10)	600 (400-800)	15 (11-23)	-	1900 (1100-2500)
E. vertebralis	Formas (1989)	Mehuín	5 (4-6)	-	89 (62-187)	15.9 (11-23)	-	1154 (600-1680)
E. vertebralis	Penna and Veloso (1990)	Mehuín	5.6 (3-8)	27.8 (18.6-36.6)	641 (400-880)	-	-	932 (700-1110)
E. emiliopugini	Formas (1989)§§	Puntra	2	-	203 (132-250)	25.45 (17-34)	85-633	1132 (500-2000)
E. emiliopugini	Penna and Solís (1999)	La Picada	1?	-	255 (181-314)	-	-	1062 (636-1459)
E. emiliopugini	Penna et al. (2005)	La Picada	1-2	-	255 (177-342)||	-	-	1053 (723-1401)
E. emiliopugini	Nuñez (2003)¶¶	not specified	2	-	640 (400-880)	-	-	507-1320

†Authors indicated that the second or third harmonic is dominant in *E. roseus*, *E. septentrionalis* and *E. calcaratus*, so here we reported the high frequency of the third harmonic for these three species.
‡Formas (1985) gave two inferior limits for this range: 1900 in the text, and 1100 in his Table 1.
§These values were extracted from Table 2 of Nuñez et al. (2012a), who cited as source to Formas (1985) (where these values do not appear).
|Formas (1985) gave two inferior limits for this range: 2700 in the text, and 3300 in his Table 1.
¶Formas and Brieva (1994) gave a different range for this species (6-7), citing Formas (1985).
#As *E. queulensis*.
††These values were extracted from the text of Nuñez et al. (2012a), but in their Table 2 appear different range limits.
‡‡As *E. vittatus*.
§§The values of the parameters were extracted from his Table 2, except the range of fundamental frequencies, which appears in the text; in the text there is also a different mean of pulses per note (27) and a different range of dominant frequencies (729-1320).
||CL of the single-note call.
¶¶Nuñez (2003) compiled the N/C, CL and range of DF for the eight species known at that time, but their values differ in some cases from the cited sources; here only included the values of *E. emiliopugini* reported in his Table 4, whose values of CL and DF are different of the original source (Formas 1989).

of the *vertebralis* group differ in notes per call, although the other parameters show a high degree of overlap (Formas 1989, Nuñez 2003). Table 3 contains the parameters most commonly used in the descriptions of *Eupsophus* vocalizations, but other parameters have been reported in some species: for example, pulses per second in *E. roseus* and *E. vertebralis* (as *E. vittatus*, Formas and Vera 1980), and notes per second and note duration in *E. vertebralis* and for long calls of *E. roseus* and *E. migueli* (Penna and Veloso 1990). More recently, the maximum frequency was included in the diagnosis of *E. altor* (Nuñez et al. 2012a) to differentiate it from *E. roseus* and *E. migueli*: this parameter surpasses 20 kHz in *E. altor*, while in the other two species it does not exceed 15 kHz. Correa et al. (2017) argued that this parameter would be the only diagnostic difference to distinguish *E. altor* from *E. migueli*, but they considered it insufficient to support the validity of *E. altor*. Variation in frequency modulation patterns of short advertisement calls have been described in *E. calcaratus* (Márquez et al. 2005), *E. roseus* (Márquez et al. 2005) and *E. septentrionalis* (as *E. queulensis*; Opazo et al. 2009).

Immunological, allozyme and RFLPs studies

Since the mid-1970s, several immunological techniques and enzymatic systems (e.g., lactate dehydrogenases, hepatic hexokinases) were used to solve taxonomic and systematic problems of the anurans of the temperate forests of South America, including the genus *Eupsophus*. However, the earliest studies with enzymes (Díaz and Veloso 1979, Díaz 1981, 1986) had a more systematic orientation at the genus level and included only a few species of *Eupsophus*. Here we consider only those molecular studies focused on estimating genetic differentiation and relationships among the species of the genus. Similarly to morphometric analyses, allozyme studies revealed greater genetic differentiation between species groups (Formas et al. 1983) than within groups (Formas et al. 1983; Díaz 1986; Formas et al. 1992; Formas 1993; Ibarra-Vidal et al. 2004). In fact, some species such as *E. roseus* and *E. migueli* (Díaz 1986), and *E. contulmoensis* and *E. nahuelbutensis* (Ibarra-Vidal et al. 2004) are almost genetically indistinguishable according to this technique. The comparative studies of morphometry and allozymes showed that in general there is more disagreement (Formas et al. 1983; Formas et al. 1991, within *E. roseus*; Formas et al. 1992) than concordance (Formas 1993) between the morphological and genetic differentiation within the genus. Ibarra-Vidal et al. (2004) was the last study in which these markers were used in the genus, where two diagnostic loci between *E. septentrionalis* and *E. roseus* (among 19 putative loci), and less differentiation between *E. septentrionalis* and its geographically closest congeners, *E. contulmoensis* and *E. nahuelbutensis*, were reported. These allozyme patterns, particularly the almost fixed differences between *E. septentrionalis* and *E. roseus*, were used to support the specific status of *E. septentrionalis* (Ibarra-Vidal et al. 2004; Table 1). Only one study investigated intraspecific genetic variation using these markers: Formas et al. (1991) analyzed the allozyme variation among seven populations of *E. roseus*, representing a substantial part of its distribution. These authors found low levels of genetic differentiation among populations and interpreted that in support of its taxonomic status. It should be noted that in that study, the population of P.N. Nahuelbuta (type locality of *E. nahuelbutensis*; Ortiz and Ibarra-Vidal 1992) was included as part of *E. roseus*. The only immunological study focused exclusively on the relationships of the genus *Eupsophus* was Formas and Brieva (1992), who used precipitin tests in agar-gel. Although the focus of that study was mainly to examine the relationships of *Eupsophus* with other genera, they found a great affinity among some species of the *roseus* group and ratified the differentiation of the genus into two groups previously observed with chromosomal (Formas 1991) and bioacoustic (Formas 1985) evidence. Regarding RFLP markers, a single taxonomic study (Nuñez et al. 1999) used this technique to distinguish between the morphologically similar species *E. calcaratus* and *E. roseus*. They found identical restriction patterns of mitochondrial DNA within each species (two localities each) using two restriction enzymes.

Studies with DNA sequences

These studies have aimed to estimate the phylogenetic relationships within *Eupsophus*, its phylogenetic position with respect to other anuran groups, the phylogeographic history of one of its species (*E. calcaratus*) and its species diversity with species delimitation approaches (Fig. 2). Nuñez (2003) was the first study in which DNA sequences were incorporated to investigate the phylogenetic relationships of the genus. Nuñez (2003) included only one specimen per species (eight), obtaining a high support for the monophyly of the genus and its division into two groups, with *E. calcaratus* as sister of the rest of the species of the *roseus* group (Fig. 2A). Two later studies including more than one species (but still only one specimen of each) defined the phylogenetic position of the genus with respect to other anuran taxa. Correa et al. (2006), although including only five species of the genus, obtained a topology within *Eupsophus* congruent with that of Nuñez (2003) and found a close relationship of this genus with *Alsodes*, while Pyron and Wiens (2011) also recovered a well-supported sister relationship between *Eupsophus* and *Alsodes*, but with specimens wrongly labeled as *Batrachyla* and *Hylorina* nested within a monophyletic *Eupsophus* (confusion clarified by Blotto et al. 2013). Subsequent studies have included more than one specimen per species, so they have also allowed to assess the phylogenetic relationships among populations. Nuñez et al. (2011) reconstructed the phylogeographic history of *E. calcaratus* with mitochondrial sequences, including samples of most of its distribution range. They considered the six main groups identified in their phylogenetic analyses (labeled A to F) as "diagnostic of species lineages" (Fig. 2B), highlighting the great divergence between lineage A (locality of Villarrica) and the rest of the lineages (which they recovered as the sister taxon to *E. calcaratus*; see comment below). Nuñez et al. (2012a), in the description of *E. altor*, performed a phylogenetic analysis with a fragment of the control region (including samples of *E. calcaratus*, *E. roseus* and *E. migueli*), in which a sister relationship between *E. altor* (samples only from the type locality) and *E. migueli* was recovered (not included in Fig. 2). They included the molecular divergence between both species in the diagnosis of *E. altor* (nine nucleotide substitutions, according to the paper), but an examination of the sequences of Nuñez et al. (2012a) shows that this figure is higher (22 sites with fixed differences between both species

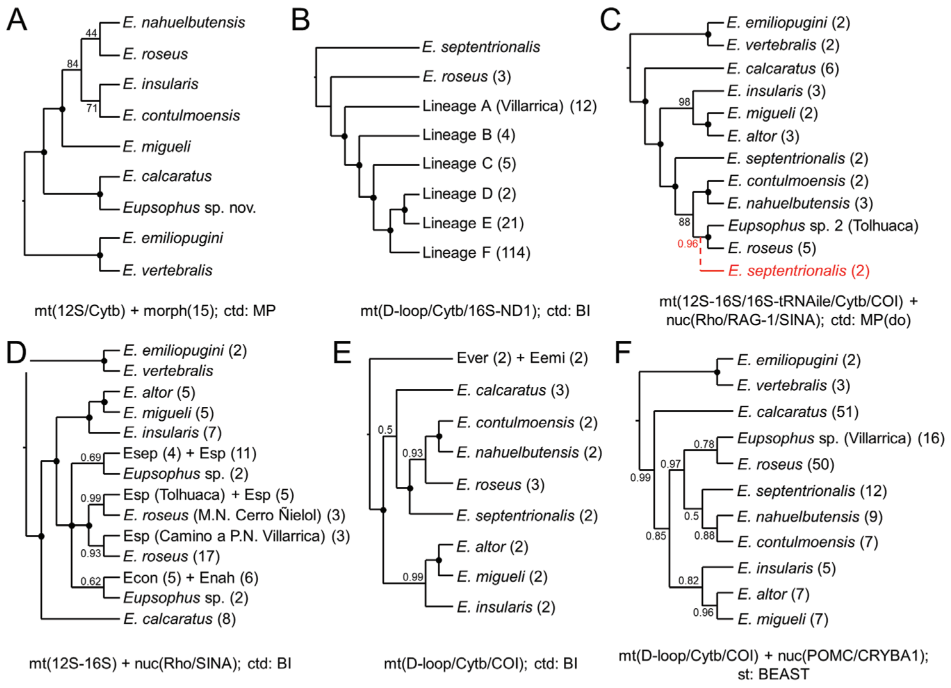


Figure 2. Phylogenetic hypotheses of *Eupsophus* obtained with DNA sequences. In some of these studies several phylogenetic analyses were made but here we show the hypotheses preferred by the authors. The trees were simplified by merging the terminal nodes by species or other relevant groupings and uniforming the branch lengths, but maintaining the original topologies. The numbers next to the nodes indicate the bootstrap or jackknife support values for the maximum parsimony (MP) analyses or posterior probability for those of Bayesian inference (BI). Black circles over the nodes indicate maximum support. The number of specimens included for each taxon or population is indicated in parentheses (omitted when only one was included). When relevant, the localities of origin of some specimens are indicated in parentheses. For simplicity, some names were abbreviated (for example, Esep = *E. septentrionalis*; Esp = *Eupsophus* sp.). Below the trees are indicated the gene fragments used, whether they are mitochondrial (mt) or nuclear (nuc), the analysis strategy (concatenated: ctd; species tree: st) and the phylogenetic reconstruction method used. **A** Nuñez (2003); this is the only tree of those shown where morphological characters (15) were included to build it **B** Nuñez et al. (2011); the only one of these studies where not all species of the genus were included; lineages A-F were considered a priori as *E. calcaratus* **C** Blotto et al. (2013); the alternative position of *E. septentrionalis* (with its respective support value) obtained with a Bayesian analysis of the same data set is shown in red; the method used was MP with direct optimization (do); the support values correspond to jackknife absolute frequencies **D** Correa et al. (2017); note that several undescribed populations (*Eupsophus* sp. = Esp) appear intermixed with some nominal species of the *roseus* group; in this analysis *E. contulmoensis* (Econ) and *E. nahuelbutensis* (Enah) make up a clade but they are not reciprocally monophyletic **E** Suárez-Villota et al. (2018a); in this analysis *E. vertebralis* (Ever) and *E. emiliopugini* (Eemi) are not reciprocally monophyletic **F** Suárez-Villota et al. (2018b); they obtained a different topology within the *roseus* group in maximum likelihood and BI analyses of the same concatenated data set (not shown).

and seven additional variable sites within *E. altor*; see comment in Correa et al. 2017). Blotto et al. (2013) performed a phylogenetic analysis of *Eupsophus* and *Alsodes* with mitochondrial and nuclear genes, including the 11 nominal species of *Eupsophus* recognized at that time, and in some cases more than one locality per species (Fig. 2C). They recovered the two species groups and ten of the eleven species as well-supported lineages, except for *E. queulensis* and *E. septentrionalis*, which were sympatric and had an extremely low sequence divergence (and consequently they were synonymized). Blotto et al. (2013) also suggested that one specimen from Tolhuaca probably represents an undescribed taxon, sister to *E. roseus* (Fig. 1). Correa et al. (2017) reassessed the species diversity of *Eupsophus*, specifically of the *roseus* group (see the next section), and estimated the phylogenetic relationships within the genus, using mitochondrial and nuclear sequences and including a greater number of specimens and localities than Blotto et al. (2013). Correa et al. (2017) found support for both species groups and for a topology within the *roseus* group consistent with that of Blotto et al. (2013) (although reduced to only four species; Fig. 2D). Suárez-Villota et al. (2018a) used a novel combination of mitochondrial sequences for reconstructing the relationships within the genus with a few specimens per species, but following the same taxonomy of Blotto et al. (2013). They obtained a high support for both species groups and recovered *E. calcaratus* in a different position with respect to previous studies (Nuñez 2003, Blotto et al. 2013, Correa et al. 2017; Fig. 2E). More recently, Suárez-Villota et al. (2018b) used a set of mitochondrial and nuclear genes and several phylogenetic approaches to reconstruct the relationships within the genus and estimate its species diversity with species delimitation approaches (see next section). They included an even greater number of specimens than Correa et al. (2017) (although a similar number of localities), obtaining a strong support for the species groups, but different positions for *E. calcaratus* depending on the analysis: the same position as in the hypothesis of Suárez-Villota et al. (2018a) (in a maximum likelihood analysis with concatenated sequences) or as the sister species of all the other species of the *roseus* group (in their species tree analyses). They also obtained a weak support for an alternative position of *E. septentrionalis*, which is congruent with previous hypothesis (Blotto et al. 2013, Suárez-Villota et al. 2018a), and strong support for recognizing the Villarrica lineage as a new putative species, although as the sister taxon to *E. roseus* (differing from the position found by Nuñez et al. 2011). Furthermore, Suárez-Villota et al. (2018b) estimated diversification times within the genus, finding that their delimited species diverged from 0.396 to 0.023 Mya (means). In summary, the relationships among the most of nominal species of the *roseus* group are well-supported by several studies (the clades *E. insularis* + (*E. migueli* + *E. altor*) and *E. contulmoensis* + *E. nahuelbutensis*, the position of *E. calcaratus* as sister taxon of all the other species of the *roseus* group), with the notable exception of *E. septentrionalis*, whose position fluctuates between studies (e.g., Blotto et al. 2013, Suárez-Villota et al. 2018a, b). Also, the position of the two putative species with respect to *E. roseus* (Villarrica and Tolhuaca populations) is uncertain, since both have not been included simultaneously in any study (Correa et al. 2017 included specimens from the surroundings of Villarrica, but not from the exact location where the new species would be found). Finally, a series of populations included by Correa et al. (2017) (*Eupsophus* sp. = Esp of Fig. 2D), whose geographic and phylogenetic position is intermediate with respect to *E. roseus*, *E. septentrionalis*, *E. contulmoensis* and *E. nahuelbutensis*, currently cannot be assigned to any of these species since they were not included in the species delimitation analyses of Suárez-Villota et al. (2018b). With respect to the two species of the *vertebralis* group, they show a very low degree of genetic divergence and are not always recovered as reciprocally monophyletic groups (Suárez-Villota et al. 2018a) or with high support values (Blotto et al. 2013). This low degree of divergence is reflected in the estimated time of separation of both species, which is the lowest in the genus (mean of 23 kya).

Species delimitation studies

Recently, two studies have focused explicitly on the delimitation of species, particularly in the *roseus* group (Correa et al. 2017, Suárez-Villota et al. 2018b). These two studies present contrasting views of the diversity of the genus (six and eleven species, respectively), so it is pertinent to review the evidence and methodology that supports both proposals, and their taxonomic and biogeographic implications. Correa et al. (2017) used one mitochondrial and two nuclear fragments of relatively conserved genes to reassess the species diversity of the *roseus* group, applying three unilocus species delimitation approaches. The sampled populations, many of them not described, cover the whole distribution of the genus, but are concentrated between 36 and 40°S, where the greatest diversity of species of the *roseus* group is found. In addition, they reviewed the chromosomal and bioacoustic evidence of the genus, which was used to choose between different delimitation scenarios. The proposal of Correa et al. (2017) represents a novel view of the diversity of species of the genus, recognizing only four species in the *roseus* group (Fig. 1). The proposed synonymizations were also supported by non-molecular arguments. Biogeographically, these changes imply a more simplified scenario since three of the synonymized species (*E. contulmoensis*, *E. nahuelbutensis* and *E. altor*) had distributions surrounded by populations of other species according to literature records. On the other hand, Suárez-Villota et al. (2018b) used three mitochondrial fragments (more variable) and two nuclear regions analyzed with several unilocus and multilocus species delimitation methods. The number of samples was double, but the number of localities was roughly the same as that of Correa et al. (2017). Their sampling scheme also covered the entire distribution range of the genus, but most of sampled populations are located between 39 and 46°S (and half of the localities included belong to *E. calcaratus*). Although Suárez-Villota et al. (2018b) used more sophisticated methods (multilocus), making use of mitochondrial and nuclear sequences, they did not explicitly consider non-molecular evidence to support their proposal. From a taxonomic point of view, Suárez-Villota et al. (2018b) reverted the changes proposed by Correa et al. (2017), returning to the previous classification of ten species, to which a new one not described would be added (Fig. 1). Biogeographically, this proposal implies that several species of the *roseus* group have restricted distributions, maintaining the same pattern of overlap between some species that is derived from the accumulated information of the literature (see fig 2 of Correa et al. 2017, and the collection of localities below).

Genomic studies

The recent description of the mitochondrial genomes of two species (*E. vertebralis* and *E. emiliopugini*) (Suárez-Villota et al. 2018a) marks the beginning of the genomic studies in the genus. Both species exhibit the same mitochondrial gene order as other neobatrachian frogs, and their mitogenomes are composed by 13 protein-coding genes, two ribosomal RNA genes, 22 transfer RNA genes, and a non-coding control region. Both genomes share 94.5% identity, which agrees with the low genetic divergence observed between the two species in several phylogenetic studies (e.g., Blotto et al. 2013, Correa et al. 2017, Suárez-Villota et al. 2018b).

Geographic distributions

The genus is distributed approximately between 35°28'S (Núñez and Gálvez 2015) and 49°25'S (Asencio et al. 2009) in Chile, and between 39°20'S and 43°S in Argentina (Úbeda 2000, Vaira et al. 2012, Blotto et al. 2013) (Fig. 3). The distribution range of the *roseus* group is the same as that of the genus (Fig. 3A–C), but that of the *vertebralis* group is more restricted (37°19' to 45°30'S, approximately; Fig. 3D). The most recent sources of range maps of *Eupsophus* species are Nuñez (2003), Rabanal and Nuñez (2008), Correa et al. (2017) and IUCN (2019). Nuñez (2003) and Rabanal and Nuñez (2008) contain highly congruent maps of eight species (*E. roseus*, *E. calcaratus*, *E. insularis*, *E. vertebralis*, *E. migueli*, *E. contulmoensis*, *E. emiliopugini,* and *E. nahuelbutensis*) generated with point occurrences and areas, respectively. Correa et al. (2017) reviewed the geographic information of the genus and compiled literature records to define the distribution ranges of the ten species recognized until that date, with an emphasis on the *roseus* group and the Chilean portion of the distribution. However, their maps (their fig. 2) were only intended to represent the boundaries among species that can be inferred by combining all the occurrence points collected from the literature. Correa et al. (2017) showed that the eight species of the *roseus* group exhibited a high degree of overlap, including several cases of the presence of more than one species in the same locality reported in the same or different publications (see details in S4 File of Correa et al. 2017 and Appendix 1). These instances of sympatry were not considered in the previous reviews or map sources, where a general pattern of allopatry among species of the same group was assumed

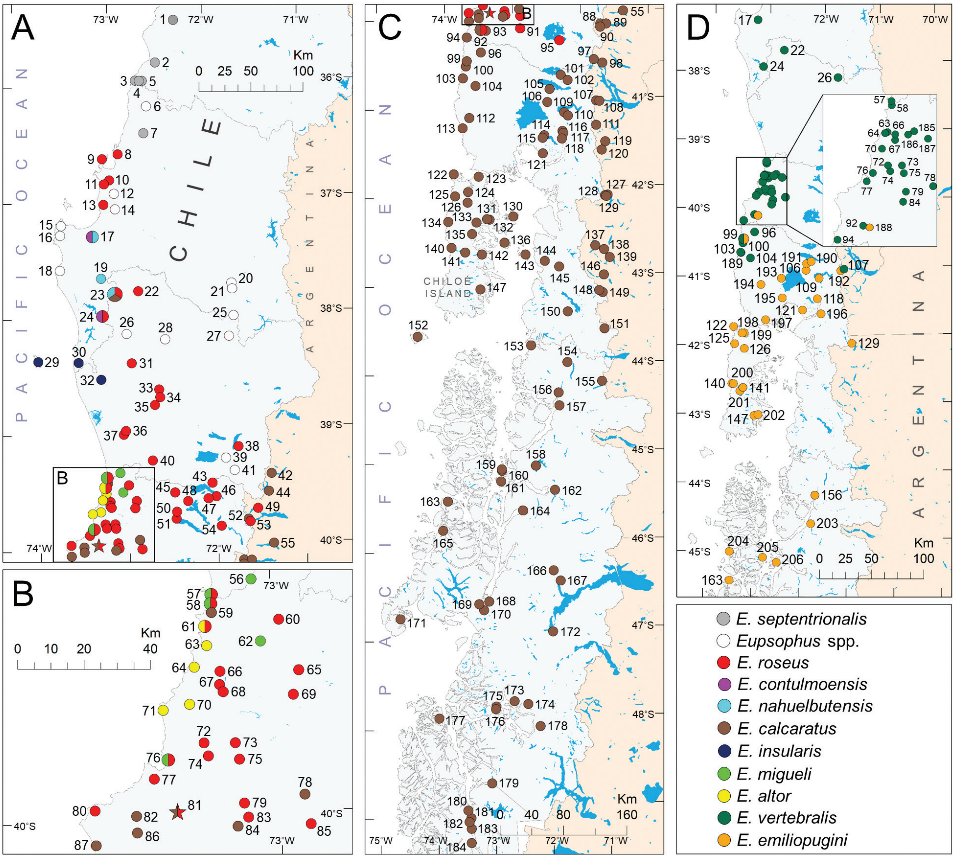


Figure 3. Compilation of localities of Eupsophus species gathered from the literature (see the complete list of localities in Appendix 1). Multicolored circles and the star indicate localities where two or three species of the same group have been reported in the same or different sources. White circles indicate the localities where two undescribed species have been identified (Villarrica and Tolhuaca), two undetermined populations included in this study (Fig. 4) and several ones considered by Correa et al. (2017) as E. roseus, whose taxonomic status is uncertain according to the current taxonomy (Suárez-Villota et al. 2018b). Thin gray lines within Chile represent boundaries of Administrative Regions.

(e.g., Formas 1989, Formas and Brieva 1994, Nuñez et al. 1999). Recently, the IUCN (2019) updated the assessments of *Eupsophus* species, adopting the taxonomy of Correa et al. (2017) (six species, Fig. 1), so its maps (areas representing the extent of occurrence) incorporated the synonymizations proposed by those authors. Despite being the most recent, the maps of IUCN (2019) do not adequately reflect the distribution limits of some species according to the literature (see details below). Here we update and complement the compilation of localities made by Correa et al. (2017) (Fig. 3 and Appendix 1), considering the current taxonomy (ten nominal species plus several undescribed populations), and highlight the inconsistencies that arise when all the available geographic information of the genus is compared.

Eupsophus septentrionalis

Fig. 3A

Type locality. R.N. Los Queules (Ibarra-Vidal et al. 2004); the same of *E. queulensis* (Veloso et al. 2005); locality 4 of Fig. 3A.

Geographic distribution. One of the six species of the *roseus* group considered endemic to Chile, which currently presents a restricted distribution according to Suárez-Villota et al. (2018b). Its distribution range covers a narrow strip of the Coastal Range between 35°28' and 36°27'S (Ibarra-Vidal et al. 2004, Núñez and Gálvez 2015). Here we included a record omitted by Correa et al. (2017) (locality 1 of Fig. 3 and Appendix 1) that extends its distribution range almost 45 km to the north (Núñez and Gálvez 2015). Currently, this record constitutes the northern limit of the genus, which was incorporated in the new map of the IUCN (2019) as part of *E. roseus* (as well as all localities attributed to *E. septentrionalis*).

Eupsophus roseus

Fig. 3A–C

Type locality. Valdivia (Cei 1962a, b); locality 72 of Fig. 3B.

Geographic distribution. The distribution range of this species is the most difficult to define from the literature, because its distribution limits differ among sources and four species were described within its range in Chile (*E. migueli*, *E. contulmoensis*, *E. nahuelbutensis* and *E. altor*), without clarifying the level of sympatry between them. In fact, *E. roseus* has been recorded in the type localities of some of these species: M.N. Contulmo (Ortiz et al. 1989, although Nuñez 2003 discarded its presence there), P.N. Nahuelbuta (Nuñez et al. 1999) and Mehuín (Formas et al. 1980, Puga 1986, Méndez et al. 2005). The maps of Nuñez (2003) and Rabanal and Nuñez (2008) are not very useful either, because they do not coincide in the northern and southern limits and restrict this species only to Chile. According to Formas (1979) and Formas et al. (1991), its northern limit in Chile is Concepción City (36°50'S), but subsequent sources limit it to Nahuelbuta Range (approximately 37°50'S; Nuñez et al. 1999, Rabanal and Nuñez 2008) or further south (Tolhuaca, 38°13'S; Nuñez 2003), ignoring several older records (e.g., Tomé, Cei 1962a, 1962b, as *E. grayi*; Tumbes, Grandison 1961; Fig. 3A). In contrast, the map of the IUCN (2019) extends its northern limit to ~35°28'S, encompassing completely the distribution range of *E. septentrionalis* (see above), and includes the few confirmed localities from Argentina (see below). Also, this map covers completely the distribution ranges of *E. migueli* and *E. altor*, and the continental area where *E. insularis* has been recorded (see below). According to Nuñez et al. (1999), the southern limit of *E. roseus* in Chile would be the Calle-Calle River basin (approximately 39°50'S), from where would be replaced by *E. calcaratus* southwards. The map of the IUCN (2019) is concordant with this pattern of allopatry between these species, though there are literature records of both species that surpass that limit (reviewed by

Correa et al. 2017; Fig. 3B, C). Here we added an old literature record that implies the presence of *E. roseus* further south, until Cordillera Pelada (Puga 1986; locality 92 of Fig. 3C). Correa et al. (2017) discovered, using molecular evidence, a locality where *E. roseus* and *E. calcaratus* coexist (Naguilán, ~40°S, locality 81 of Fig. 3B, represented by a star), which would be the only confirmed site where two species of the *roseus* group live in sympatry. More recently, Suárez-Villota et al. (2018b) extended the distribution range of *E. roseus* further south on the western foothills of Andes in Chile (Los Mañíos, ~40°20'S) and demonstrated that effectively there are populations of *E. calcaratus* north of some localities of *E. roseus*. Taken together, these last two studies show that both species are present in Chile between 39°55' and 40°20'S approximately, although the degree of sympatry between them is currently unknown. Until 1996 (see account of *E. calcaratus*), *E. roseus* was considered as the only species of the genus in Argentina (e.g., Cei 1980), but recently its presence in that country has been debated (e.g., Vaira et al. 2012), where some populations have been unsteadily assigned to *E. roseus* and/or to *E. calcaratus* (discussed in Blotto et al. 2013). Blotto et al. (2013) confirmed the presence of *E. roseus* in that country (around 39°50'S, Fig. 3A), which suggests that the populations of Argentina north of that latitude, which were previously considered as *E. calcaratus* (Úbeda 2000), might correspond to *E. roseus*. Moreover, the finding of *E. roseus* in Los Mañíos (see above) shows that this species reaches further south through the Chilean Andes, which suggests the need to reevaluate the taxonomic status of the populations located in Argentina at the same latitude.

Eupsophus nahuelbutensis

Fig. 3A

Type locality. P.N. Nahuelbuta (Ortiz and Ibarra-Vidal 1992); locality 23 of Fig. 3A.

Geographic distribution. Another of the six species of the *roseus* group endemic to Chile, which would have a restricted distribution according to Suárez-Villota et al. (2018b). Together with *E. contulmoensis*, they are the two species of the genus endemic to the Nahuelbuta Range. *Eupsophus nahuelbutensis* has been recorded in only two additional localities (Nuñez 2003): Ramadillas (where also *E. contulmoensis* was reported by Ortiz and Ibarra-Vidal 2005) and Rucapehuén. The map of Nuñez (2003) includes these three records, but that of Rabanal and Nuñez (2008) shows an area that exceeds the limits defined by those localities.

Eupsophus contulmoensis

Fig. 3A

Type locality. M.N. Contulmo (Ortiz et al. 1989); locality 24 of Fig. 3A.

Geographic distribution. Another of the six species of the *roseus* group endemic to Chile, specifically to the Nahuelbuta Range, which would have a restricted distribution according to Suárez-Villota et al. (2018b). There are few records of this species in the literature (see Appendix 1). However, Ortiz and Ibarra-Vidal (2005) pointed out that this species has a wider distribution on the western slopes of the Nahuelbuta Range, between the south of the Biobío River (~37°10'S) and the latitude of the town of Tirúa (~38°20'S). On the other hand, the maps of Nuñez (2003) and Rabanal and Nuñez (2008) restrict the distribution of this species to its type locality and surroundings.

Eupsophus insularis

Fig. 3A

Type locality. Isla Mocha (Philippi 1902, Formas and Vera 1982); locality 29 of Fig. 3A.

Geographic distribution. Another of the six species of the *roseus* group endemic to Chile, which would have a restricted distribution according to Suárez-Villota et al. (2018b). Correa et al. (2017) reported its presence in two localities on the southern part of the Nahuelbuta Range, one of them in front of Isla Mocha (Primer Agua), which were not included in the species delimitation study of Suárez-Villota et al. (2018b). We recognize these populations as *E. insularis* because of their close phylogenetic relationship with specimens from Isla Mocha and because they clearly belong to a clade other than the one that includes the geographically closest species (*E. contulmoensis*, *E. nahuelbutensis* and *E. roseus*; Correa et al. 2017). The map of IUCN (2019) coincides with previous representations (Nuñez 2003, Rabanal and Nuñez 2008) that restrict the species only to Isla Mocha. However, the continental populations assigned to this species by Correa et al. (2017) would be within the distribution range of *E. roseus* according to IUCN (2019).

Eupsophus migueli

Fig. 3B

Type locality. Mehuín (Formas 1978a); locality 58 of Fig. 3B.

Geographic distribution. Another of the six species of the *roseus* group endemic to Chile, restricted to a narrow coastal strip between 39°23' and 39°51'S (Fig. 3B). *Eupsophus migueli* was described from two coastal localities in Chile, Mehuín and Los Molinos (39°25' to 39°51'S; Formas 1978a), but later its distribution was expanded eastward to a few nearby localities, like San José de la Mariquina (Méndez et al. 2005) and Colegual Alto (Nuñez et al. 2012a) (Fig. 3B). Cumulative literature records imply the sympatry of *E. migueli* and *E. roseus* at Mehuín, Queule and Los Molinos (Appendix 1 and Fig. 3B). Available maps restrict its distribution to its type locality and surroundings (Nuñez 2003, Rabanal and Nuñez 2008), ignoring the other locality of the original description, Los Molinos. The map of IUCN (2019), by including the entire range of *E. altor*, extends the distribution of *E. migueli* further south, but it does not include Los Molinos either. To the north, this map surpasses the northernmost record of the species by about 20 km, but does not include the locality of San José de la Mariquina, which extends its distribution significantly to the east (compare with the map of Correa et al. 2017). Moreover, the map of *E. roseus* of the IUCN (2019) implies that both species are completely sympatric across the entire distribution range of *E. migueli*.

Eupsophus altor

Fig. 3B

Type locality. Parque Oncol (Nuñez et al. 2012a); locality 70 of Fig. 3B.

Geographic distribution. Another of the six species of the *roseus* group endemic to Chile, which presents a restricted distribution according to Suárez-Villota et al. (2018b). *Eupsophus altor* was reported originally from four localities (39°29' to 39°42'S, Nuñez et al. 2012a), but a map by Nuñez et al. (2012b) shows six points without mentioning the localities (not included in Fig. 3B). In any case, all these localities are between the two original ones of *E. migueli*, Mehuín and Los Molinos (localities 58 and 76 of Fig. 3B). In one of the original localities, Alepúe, *E. roseus* has also been recorded (Blotto et al. 2013). This last record can be added to the others mentioned above, which indicate the presence of *E. roseus* in several coastal locations where *E. migueli* and *E. altor* are found, but the map of the IUCN (2019) shows a continuous distribution of *E. roseus* that completely covers those of both species.

Eupsophus calcaratus

Fig. 3A–C

Type locality. Chiloé Island (locality not specified; Günther 1881, Formas and Vera 1982); localities 122-126, 131-135, 140-142 and 147 of Fig. 3C.

Geographic distribution. This is the species with the widest distribution of the genus, slightly surpassing the 49°20'S toward the south (Fig. 3C). However, its northern limit cannot be clearly defined from the literature since there are three records north of the Calle-Calle River basin, the limit defined by Nuñez et al. (1999) (around 39°50'S): P.N. Nahuelbuta (locality 23 of Fig. 3A), Villarrica (39) and Mississipi (59). Its presence in P.N. Nahuelbuta (Ortiz and Ibarra-Vidal 1992; Fig. 3A) was questioned by Nuñez (2003) and the inclusion of the populations around Villarrica in this taxon was challenged by Nuñez et al. (2011), Correa et al. (2017) and Suárez-Villota et al. (2018b). Thus, the record of the species in Mississipi would remain, but this population would be entirely surrounded by populations of *E. migueli* and *E. roseus* according to all the available information. The populations near Reumén (39°57'S), recently reported by Suárez-Villota et al. (2018b), would also be surrounded by populations of *E. roseus*, but in this case these findings are supported by molecular evidence. Together with Naguilán (locality 81, where *E. roseus* also is present, Correa et al. 2017) these localities constitute the northern limit confirmed by molecular phylogenetic analyses. All these findings do not coincide with the limits that appear on the maps of IUCN (2019), where *E. calcaratus* is replaced to the north by *E. roseus* around 40°S in Chile. In Argentina, the presence of this species was first reported by Christie and Úbeda (1996), but later, all the populations of the *roseus* group in that country were considered as *E. calcaratus* (39°34' to 43°S; Úbeda 2000; see comment in Vaira et al. 2012). However, the phylogenetic analyses of Blotto et al. (2013) (ratified by Correa et al. 2017) imply that two localities in Argentina correspond to *E. roseus* (Fig. 3A), which would be flanked to the north and south by populations of *E. calcaratus*. The maps of Rabanal and Nuñez (2008) and IUCN (2019) show that *E. calcaratus* reaches further north on the Argentine side, assuming that all the populations included in Úbeda (2000) and others that extend their distribution about 30 km further north belong to this species.

Eupsophus vertebralis

Fig. 3D

Type locality. Valdivia (Grandison 1961); locality 72 of Fig. 3D.

Geographic distribution. It is known mainly in the coastal zone of Chile, between the north of the Nahuelbuta Range (37°19'S) and the Osorno coast (40°49'S). Only two localities outside this area are known, Tolhuaca (locality 26), on the western margin of the Andes, and Puerto Blest in Argentina (107; Basso and Úbeda 1999, Úbeda and Basso 2012a), on the other side of the Andes. However, this last point is closer to the records of *E. emiliopugini*. *Eupsophus vertebralis* and *E. emiliopugini* would have allopatric distributions according to Formas (1989) and Nuñez (2003), but two relatively recent records of *E. emiliopugini* (Raulintal and Pucatrihue, Olivares et al. 2014 and Suárez-Villota et al. 2018b, respectively; Fig. 3D) imply the sympatry of both species in the southern end of the distribution of *E. vertebralis*. The maps of Rabanal and Nuñez (2008) and IUCN (2019) also imply sympatry areas in Chile, but in different zones: on the Coastal Range according to Rabanal and Nuñez (2008) and on the western foothills of the Andes according to IUCN (2019). None of those sympatry areas is supported by the review of the literature records (Fig. 3D).

Eupsophus emiliopugini

Fig. 3D

Type locality. La Picada (Formas 1989); locality 106 of Fig. 3D.

Geographic distribution. *Eupsophus emiliopugini* would be distributed both on the coast and the Andean zone, mainly in Chile, between 40°11' and 45°30'S, although it would be in sympatry with *E. vertebralis* in a small area of the Chilean Coastal Range (see above). In Argentina, it is present on the northwest and southwest coasts of Lago Puelo (Úbeda and Basso 2012b), where Arroyo Melo (Úbeda et al. 1999; locality 129) is located.

Eupsophus spp.

Fig. 3A

Geographic distribution. The two undescribed species mentioned in the recent literature (Fig. 1) are known from one locality each: Tolhuaca (*Eupsophus* sp. 2 of Blotto et al. 2013) and Villarrica (*Eupsophus* sp. of Suárez-Villota et al. 2018b) (both considered as *E. roseus* by Correa et al. 2017). Also, a series of populations located between 36°10' and 38°15'S, assigned to *E. roseus* by Correa et al. (2017), should be included here since they occupy intermediate phylogenetic and geographic positions among the species recognized by Suárez-Villota et al. (2018b). Almost all these localities are within the latitudinal limits defined for *E. roseus* according to historical records (see above), but as Correa et al. (2017) indicated, these populations cannot identify unambiguously to species level by their external characters. Other southernmost undetermined populations included in Correa et al. (2017) (Santa Amelia, Pumalal, Puringue and Malalhue) are considered here as *E. roseus* because they make up a well-supported monophyletic group with specimens from the type locality of that species (where the specimen from Naguilán is also included). The two new localities where phenotypic observations were done for this review (see below) are also included here.

Phenotypic observations

One of the contributions of Correa et al. (2017) was the explicit recognition of the high level of intrapopulation variation in external characters considered diagnostic in the taxonomy of the genus. Here we show additional examples of intrapopulation variation in the three external characters most frequently included in the diagnoses of *Eupsophus* species (dorsal and ventral color patterns, iris color, and lateral and dorsal snout profile; Table 1; see also Correa et al. 2017), in live animals of two undescribed populations (Fig. 4) and two type localities (Fig. 5). Figure 4 illustrates the variation in dorsal coloration patterns in specimens from Pidenco (A, four adults randomly selected, from a total of 13, to show also the typical cryptic coloration of the genus and the variation of iris color and snout profile) and Las Lianas (B, five specimens chosen among 19 to represent contrasting dorsal coloration patterns, including one with a thin vertebral line). Most of specimens from Las Lianas had uniform brown eyes and only one had the upper part of the iris yellowish. Moreover, the length and profile of the snout varied among these specimens (data not shown). Figure 4 shows the variation of body coloration patterns (dorsal and ventral), iris coloration and shape of snout (both in dorsal and lateral profile) in the type localities of *E. roseus* (A, Valdivia, where it is the only species of the *roseus* group that has been reported; see Fig. 3) and *E. migueli* (B, Mehuín, where also *E. roseus* would be present, see above and Fig. 3). The six specimens of *E. roseus* were selected from 16, collected in two sessions, in order to exemplify the variation of iris color, which ranges from reddish to pale orange, and shape of the snout, which varies in length and form in lateral and dorsal profile. The three specimens of *E. migueli* (Fig. 5B) were collected in two sessions (14 in total) and differ notably in dorsal and ventral coloration patterns and in snout profile. They also differ in coloration from the holotype, which had the dorsum grayish with two dark paravertebral areas and a thin light vertebral line (Formas 1978a). At Mehuín, where *E. migueli* and *E. roseus* supposedly coexist (see above), no specimens with the iris orange like *E. roseus* were observed.

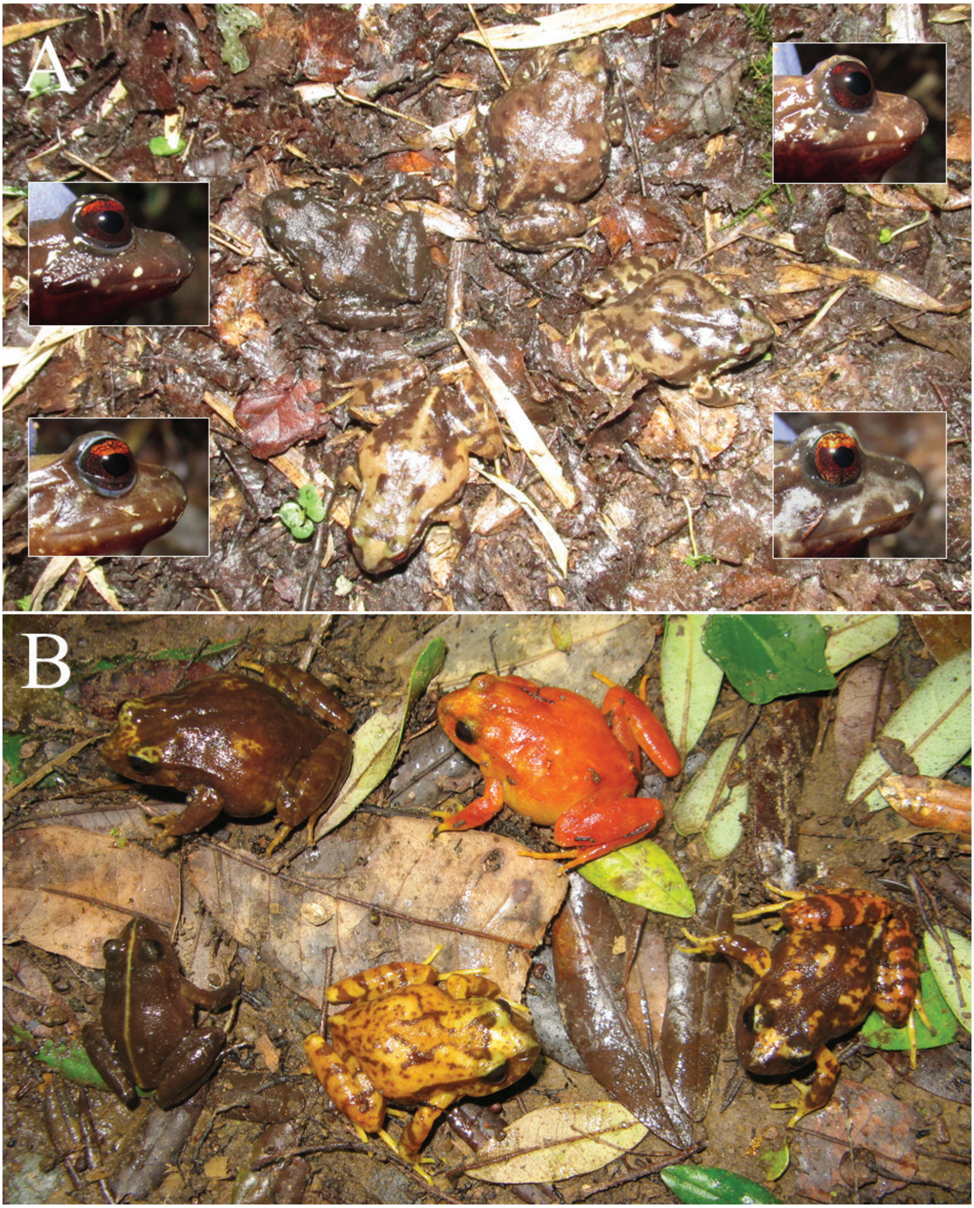


Figure 4. Cryptic coloration and variation of coloration patterns in two undetermined populations of the *Eupsophus roseus* group **A** adult females from Pidenco, showing cryptic coloration resembling the forest ground; insets show head profiles of the same individuals **B** adults and juveniles from Las Lianas exemplifying variation in coloration patterns. Both localities were included as *Eupsophus* sp. in the map of Fig. 3.

Figure 5. Examples of intrapopulation external variation in adult specimens of the type localities of two species of the *Eupsophus roseus* group **A** *Eupsophus roseus* from Valdivia **B** *Eupsophus migueli* from Mehuín. Both examples illustrate the variation in dorsal and ventral (**B**) coloration, iris color and snout shape.

Phylogenetic analyses

We obtained an alignment of 1304 nucleotide sites when the sequences of different length of both gene fragments were included (631 sites of cytb, 673 of COI), which was reduced to 998 when cutting ends with gaps (365 sites of cytb, 633 of COI). The four analyses (with or without sites with gaps, two or six partitions) recovered the two

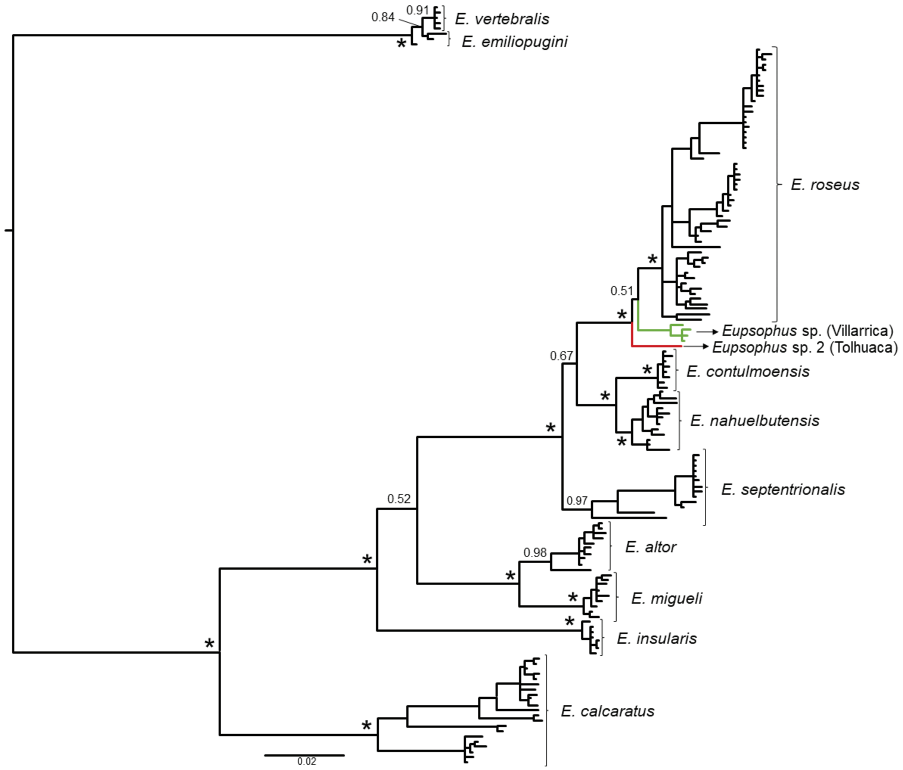


Figure 6. Consensus phylogram (50% mayority-rule) of the Bayesian analysis of the mitochondrial fragments cytochrome c oxidase subunit I and cytochrome b. For simplicity, the outgroup (Alsodes norae) is not shown. Colored branches indicate the specimens of the two putative species: Villarrica (green) and Tolhuaca (red). The values next to the nodes are the posterior probabilities (pp); asterisks represent maximum values (pp = 1). Note that all species currently recognized (Suárez-Villota et al. 2018b) are supported by high pp values (> 0.97), except for both of the vertebralis group, wich are not reciprocally monophyletic. The scale bar under the tree represents the expected substitutions per site.

species groups and all the currently recognized nominal species of the *roseus* group as well-supported clades (posterior probability, pp > 0.97), but the topology within this group is variable among analyses, including some polytomies, and only partially congruent with previous phylogenetic studies (Fig. 2). Figure 6 shows the Bayesian consensus tree (15 002 sampled trees) of the analysis of the short alignment with six partitions. An important difference with respect to prior hypotheses is the position of *E. insularis* as the sister species of the all species of the *roseus* group, except for *E. calcaratus*; though in the analysis of the short alignment with two partitions appears as the sister species of *E. migueli* + *E. altor* like in previous studies. Another difference with respect to the most recent hypothesis (Fig. 2F) is the position of *E. septentrionalis*, recovered as the sister group of *E. roseus*, *E. contulmoensis*, *E. nahuelbutensis* and Villarrica and Tolhuaca populations, which is only consistent with the results of Suárez-Villota et al. (2018a) (Fig. 2E). However, *E. septentrionalis* also formed a polytomy with *E. roseus* + Villarrica + Tolhuaca and *E. contulmoensis* + *E. nahuelbutensis* clades in both analyses with two partitions. The four analyses showed the close relationship of Villarrica and Tolhuaca populations with *E. roseus*, all of which comprise a clade with maximal support. However, the reciprocal relationship between Villarrica and Tolhuaca populations could not be resolved since in three of the four analyses both putative taxa form a tritomy with *E. roseus* (Fig. 6 shows the only analysis where this relationship is resolved, but with low support). This lack of resolution could be due to the low number of variable nucleotide sites with respect to other studies where more genes were included, but in no case the Villarrica or Tolhuaca specimens appear mixed with those of *E. roseus*. Therefore, Tolhuaca population also should be considered a candidate species under the current taxonomy.

Discussion

During the last six decades, the taxonomic and systematic research on ground frogs, beyond of species descriptions and estimations of phylogenetic relationships, has focused on solving three fundamental issues: the delimitation of the genus, its division into species groups and the estimation of its species diversity. The monophyly and distinction of *Eupsophus* with respect to its sister genus, *Alsodes*, is now well established based on morphological, chromosomal, bioacoustic, developmental and molecular phylogenetic evidence (Gallardo 1970, Lynch 1978, Nuñez 2003, Vera Candioti et al. 2011, Blotto et al. 2013). Likewise, the subdivision of the genus into two groups is supported by cumulative morphological, chromosomal, bioacoustic, genetic, immunological, and molecular phylogenetic evidence (see references in Results; reviewed in Nuñez 2003, although this author suggested that each group could represent a different genus). However, the number of species, which progressively increased from two (Lynch 1978) to a maximum of 11 (Nuñez et al. 2012a), decreased to six in the following five years (Blotto et al. 2013, Correa et al. 2017) and more recently, raised again to 11 (Suárez-Villota et al. 2018b; Fig. 1). This recent instability is due to two opposing views about the species diversity of the *roseus* group. Correa et al. (2017) used only unilocus species delimitation methods, but their proposal took into account the scarce chromosomal and bioacoustic differentiation within the group. Instead, Suárez-Villota et al. (2018b), using a bigger dataset and more sophisticated (multilocus) analyses, ratified the validity of the same nominal species recognized by 2013 and provided support for a new putative species. This last proposal implies the consolidation of the taxonomic work of the last decades and reinforces the idea that the species diversity of the genus could be underestimated (Nuñez et al. 2011, Blotto et al. 2013). Logically, this advance depends on the robustness of the previous taxonomy, but as shown in Correa et al. (2017) and here, there are enough precedents in the literature that allow to question the "traditional" taxonomy, something that was not considered by Suárez-Villota et al. (2018b). Most of these precedents were developed in Results, so below we only discuss the main problems that emerged from the comparison and critical analysis of all that information.

Diagnoses are fundamental in taxonomy, since diagnostic characters summarize the differences among closely related taxa (Winston 1999). However, we detected two general problems with the quality of diagnoses of *Eupsophus* species: the heterogeneity in the number and type of characters included and the use of very variable characters for distinguishing species of the same group. The heterogeneity can be clearly seen in Table 1 and implies that, over time, very different criteria have been applied to define which and how many characters are sufficient to diagnose the species. Indeed, only four characters have been included in four or more diagnoses (the first four characters of Table 1). Regarding character variation, Correa et al. (2017) showed, with examples from the literature and observations of live animals, that these same four characters vary intraspecifically. In fact, body coloration patterns, which are included in most diagnoses, vary even in the type series (Correa et al. 2017). These observations of the type material have been corroborated with examples of live specimens from the type localities of *E. roseus* and *E. altor* (Correa et al. 2017), and *E. roseus* and *E. migueli* (this study). These and additional examples from other populations show that variation in body coloration is widespread in the genus, but this phenomenon has rarely been recognized in the literature (Cei 1962a, 1962b, Nuñez 2003, Nuñez et al. 2012a) and its implications for the taxonomy never have been addressed. The other two external characters, iris color and snout shape (Correa et al. 2017; this study), and the shape of the xiphisternum (Díaz 1986) also vary extensively within species. Taken together, all this information weakens the evidence used to distinguish some species, particularly those whose diagnoses rest almost exclusively on these characters (e.g., *E. insularis* and *E. migueli*). These high levels of variation in diagnostic characters have deep consequences for the current taxonomy (Suárez-Villota et al. 2018b), since that proposal is based on material only from the type locality for several species and according to its proponents is concordant with the taxonomic work of the last decades.

Our review of the literature showed that, apart from external and internal morphology, morphometrics, karyotypes, and calls have been the main lines of evidence applied to the taxonomy and systematics of *Eupsophus*. Although these kinds of data have been rarely incorporated into diagnoses, they have been included in the descriptions of several species (Formas 1978a, 1989, Veloso et al. 2005, Nuñez et al. 2012a). Each of those three lines of evidence support the distinction between the two species groups, though they have limited utility to differentiate species within groups. Except in the case of the two species of the *vertebralis* group, *E. vertebralis* and *E. emiliopugini*, which are clearly differentiated by their karyotypes and to a lesser extent by their advertisement calls (Formas 1989), few species of the genus can be differentiated with these data. In fact, none of the species of the *roseus* group can be distinguished by their advertisement calls, since all the parameters used to describe them overlap extensively and the descriptions of the calls of some species differ among studies (Correa et al. 2017). The karyotypic evidence deserves an additional commentary, since it has been explicitly (Formas 1978b) or implicitly (Veloso et al. 2005) assumed that species of this genus have characteristic karyotypes. The comparison of all published karyotypes shows that this is not the case and that different karyotypes were described for the same species and locality by different authors (*E. roseus*, *E. migueli*, and *E. vertebralis*), suggesting strongly observer biases (Correa et al. 2017). Even though these differences were real, the level of intrapopulation and intraspecific variation in chromosome morphology and position of secondary constrictions would be as high as the variation at interspecific level (see Table 2), so that this type of evidence would not be useful in the taxonomy of the *roseus* group.

The review of the geographic information also revealed difficulties in establishing the spatial boundaries of the species of the genus. Recently, Correa et al. (2017) compiled records of the literature (that we expand here), showing a high degree of overlap of distribution ranges and cases of sympatry among species of the same group that had not been recognized in previous studies and reviews (e.g., Nuñez 2003, Blotto et al. 2013). These compilations of records differ from the most recent published maps (Nuñez 2003, Rabanal and Nuñez 2008, IUCN 2019), which show mainly allopatric distributions for species of the same group and do not coincide with each other for some species. These discrepancies between available maps and the points collected are closely linked to the four species (*E. migueli*, *E. contulmoensis*, *E. nahuelbutensis* and *E. altor*) described within of the distribution range of *E. roseus*, whose limits and degree of sympatry have been never precisely established. The records compiled here also show an overlap between the distribution ranges of *E. roseus* and *E. calcaratus*, which is partially supported by molecular evidence but does not coincide with the previously established limits (e.g., Nuñez 2003). The proposal of Correa et al. (2017), by expanding the taxonomic limits of *E. roseus* and *E. migueli*, resulted in a considerable reduction in the levels of overlap of the distribution ranges, but the rebuttal of Suárez-Villota et al. (2018b) implicitly meant returning to the confusing situation derived of the geographic information of the literature. Moreover, they added one more factor of uncertainty when affirming that some species (*E. migueli*, *E. altor*, *E. contulmoensis*, *E. nahuelbutensis*, *Eupsophus* sp. and *E. septentrionalis*) have "restricted distributions", which implies that the genus would have a highly fragmented distribution at present. This pattern is incompatible with the information available since there are historical records of *E. roseus* (see map of Fig. 3) and taxonomically undetermined populations (Correa et al. 2017) between the localities assigned to these species. Currently, it is not clear how these intermediate populations would fit into the taxonomic scheme of Suárez-Villota et al. (2018b). The problems to define the boundaries between species are not only limited to Chile, where the greatest diversity of species is found, but also extend to Argentina where the boundary between *E. roseus* and *E. calcaratus* is not clear.

This review summarizes six decades of taxonomy and systematic research on *Eupsophus* (partially reviewed by Correa et al. 2017), but unlike the last comprehensive review treating these topics (Nuñez 2003) the information from various sources is compared. Only this retrospective and comparative approach allowed to reveal the high degree of variation described in some morphological characters used for the descriptions and diagnoses, the lack of significant differentiation in morphometrics and advertisement calls, and the incongruences in the chromosomal evidence and geographic data (see also Correa et al. 2017). These patterns agree with the general decoupling between the morphological and phylogenetic differentiation implied for the last phylogenetic studies (Blotto et al. 2013, Correa et al. 2017, Suárez-Villota et al. 2018b), which had already been suggested by the comparative studies with allozymes and morphometry (Formas et al. 1983, Formas et al. 1991, Formas et al. 1992). Moreover, a practical issue emerged from this comparative synthesis. Since the levels of intra/interspecific morphological variation and divergence among species are high but poorly known, especially in the *roseus* group (regardless of the taxonomy adopted), field identification would be reliable only within the assumed distribution ranges and, as we have demonstrated, there has not been consensus about them. Therefore, inconsistent diagnoses, field misidentifications and misleading geographic data might be intimately linked, explaining most cases of sympatry and range overlap inferred from the compilation of localities. In turn, erroneous geographic data might influence the identification of atypical specimens, particularly in the distribution limits and unexplored zones. The problem of field misidentification is expected to persist under the most recent taxonomic arrangement (Suárez-Villota et al. 2018b) since that proposal is mainly based on material from the type localities or surroundings (except for *E. calcaratus*) and, as we pointed out above, the diagnoses of *Eupsophus* species are unreliable and their geographic boundaries are still poorly defined.

In this context, phylogenetic and species delimitation studies with DNA sequences have emerged as an independent and powerful way to reassess the taxonomy of *Eupsophus*. However, except for Correa et al. (2017), those studies (Nuñez et al. 2011, 2012a, Blotto et al. 2013, Suárez-Villota et al. 2018a, b) have progressively reinforced the previous taxonomic work, without questioning the bases that support it. In addition, they have installed the idea that diversity at the species level would be underestimated by identifying two candidate species (Villarrica and Tolhuaca populations). Apparently, these advances constitute the consolidation of decades of taxonomic research based on other types of evidence, but the critical examination of the taxonomic literature done here allows us to outline two issues that weaken this assertion. First, there is scarce morphometric, karyotypic and bioacoustic differentiation and a very high level of intrapopulation variation in some external and internal characters (e.g., shape of the head, body coloration, shape of the xiphisternum) in the *roseus* group (patterns already noted by Correa et al. 2017), which excludes them as reliable sources of characters to distinguish the species. Taken together, these types of characters, which support most of the descriptions and diagnoses of the species, suggest that the diversity of the genus at species level is not well described so it is not clear how a delimitation approach based exclusively on molecular evidence can ratify such taxonomic scheme. Second, the claim that most species of the *roseus* group have "restricted distributions" (see above) has important consequences for the biogeography and taxonomy of the genus. Historical records and intermediate undetermined populations show that this pattern of isolated species does not adequately reflect the distribution of the genus, but more importantly, some of these populations occupy intermediate phylogenetic positions between some narrow-range species of the *roseus* group, decreasing the genetic divergence among them (Correa et al. 2017). The latter implies that the populations that make up these species with restricted distributions do not represent well the overall phylogenetic diversity of the genus, so that this dimension of its diversity is not adequately reflected by the current taxonomy. Therefore, future taxonomic and systematic studies of *Eupsophus*, whether molecular or not, should take into account the incongruities between the patterns of molecular, morphological, bioacoustic and chromosomal divergence and incorporate more intermediate populations to obtain a more accurate estimate of its species diversity.

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Appendix 1. List of localities of *Eupsophus* species compiled from the literature

This list contains all localities included in Fig. 3, ordered by species, according to the current taxonomy (Suárez-Villota et al. 2018b; Fig. 1), and then by latitude, from north to south, or geographic proximity. Localities in bold indicate where more than one species of the same species group is present according to the literature (circles with two or three colors in Fig. 3) or according to the phylogenetic analysis of Correa et al. (2017) (sympatry of *E. calcaratus* and *E. roseus* in Naguilán, brown-red star of Fig. 3A–C). Under the category *Eupsophus* spp. we grouped some populations included in Correa et al. (2017) (whose taxonomic status currently is unclear), two undescribed populations included here, and two undescribed candidate species (Fig. 1).

Eupsophus septentrionalis (Fig. 3A): 1) Estación Experimental Dr. Justo Pastor León, 2) R.N. Los Ruiles, 3) Trehualemu, 4) R.N. Los Queules, 5) 3 km east R.N. Los Queules, 7) Trehuaco.

Eupsophus roseus (Fig. 3A): 8) Tomé, 9) Tumbes, 10) Concepción (Cerro Caracol), 11) Laguna Grande (San Pedro), 13) Coronel, 22) Los Lleulles, 23) **P.N. Nahuelbuta**, 24) **M.N. Contulmo**, 31) 10 km west Galvarino, 33) Rucamanque, 34) M.N. Cerro Ñielol, 35) Maquehue, 36) Santa Amelia, 37) Pumalal, 38) Lago Tinquilco, 40) Cuesta Lastarria, 43) Pocura, 45) Malalhue, 46) Lago Pellaifa, 47) San Pablo de Tregua, 48) Panguipulli, 49) Lago Paimún (Argentina), 50) Fundo San Clemente, 51) Desembocadura del Lago Riñihue, 53) Termas de Epulafquén (Argentina), 54) Huilo Huilo; (Fig.

3B): 57) **Queule**, 58) **Mehuín**, 60) Puringue, 61) **Alepúe**, 65) Huifco (torre 21), 66) Iñipulli, 67) Bosque or Fundo San Martín, 68) Fundo Santa María, 69) Máfil (Torre 41), 72) Valdivia (city), 73) Cuesta de Soto, 74) Huachocopihue, 75) Llancahue, 76) **Los Molinos**, 77) Corral, 79) Camino Viejo a La Unión, 80) Reserva Costera Valdivia, 81) **Naguilán**, 83) Chamil, 85) Paillaco (Torre 140); (Fig. 3C): 91) Pichirropulli, 92) **Cerro Mirador (Cordillera Pelada)**, 95) Los Mañíos.

Eupsophus spp. (Fig. 3A): 6) Sector Guanaco or Cerro El Guanaco, 12) Cerros de Chiguayante, 14) Santa Juana, 15) Llico, 16) Quidico, 18) Las Lianas (this study), 20) Alto Biobío, 21) Loncopangue, 25) Pemehue, 26) Pidenco (this study), 27) Tolhuaca (*Eupsophus* sp. 2 of Blotto et al. 2013), 28) Río Traiguén, 39) Villarrica (*Eupsophus* sp. of Suárez-Villota et al. 2018b), 41) Camino a P.N. Villarrica.

Eupsophus nahuelbutensis (Fig. 3A): 17) **Ramadillas**, 19) Rucapehuén, 23) **P.N. Nahuelbuta**.

Eupsophus contulmoensis (Fig. 3A): 17) **Ramadillas**, 24) **M.N. Contulmo**; also recorded at Reserva Forestal Contulmo, located 2.4 km SW, in a straight line, from M.N. Contulmo (not shown in Fig. 3).

Eupsophus insularis (Fig. 3A): 29) Isla Mocha, 30) Primer Agua (Webb and Greer 1969 reported the presence of *E. roseus* at 7 km SSE Tirúa, the almost exact location of Primer Agua, so we left only this last record because it is supported by exact geographic information and molecular evidence), 32) Camino a Villa Las Araucarias.

Eupsophus migueli (Fig. 3B): 56) Colehual Alto, 57) **Queule**, 58) **Mehuín**, 62) San José de la Mariquina, 76) **Los Molinos**.

Eupsophus altor (Fig. 3B): 61) **Alepúe**, 63) Chanchán, 64) Llenehue, 70) Parque Oncol, 71) Curiñanco.

Eupsophus calcaratus (Fig. 3A): 23) **P.N. Nahuelbuta**, 42) Lago Quillén (Argentina), 44) Lago Tromen (Argentina), 52) near Paso Carirriñe (Argentina), 55) Lago Lolog (Argentina); (Fig. 3B): 59) Mississipi, 78) Reumén (Suárez-Villota et al. 2018b included three very close localities (<2 km between them), associated with the name Reumén, but here we show only the one where the presence of *E. vertebralis* was also reported), 81) **Naguilán**, 82) Chaihuín, 84) Tres Chiflones, 86) R.N. Valdivia, 87) Lagunas Gemelas; (Fig. 3C): 88) Lago Queñi (Argentina), 89) Lago Lácar (Argentina), 90) Baños de Queñi (Argentina), 92) **Cerro Mirador (Cordillera Pelada)**, 93) Camino a P.N. Alerce Costero, 94) La Barra, 96) Namun Lahual, 97) Lago Espejo (Argentina), 98) Ruca Malén (Argentina), 99) Pucatrihue, 100) Bahía Mansa, 101) P.N. Puyehue, 102) Antillanca, 103) Huellelhue, 104) Catrihuala (Puente La Herradura), 105) Rupanco, 106) La Picada, 107) Puerto Blest (Argentina), 108) Arroyo Patiruco (Argentina), 109) Punta Huano (P.N. Vicente Pérez Rosales), 110) Río Manzano (P.N. Vicente Pérez Rosales), 111) Lago Fonck (Argentina), 112) Sarao, 113) Llico Bajo, 114) Río Blanco, 115) Río Correntoso, 116) P.N. Alerce Andino, 117) Ralún, 118) Río Rollizo, 119) Lago Martín (Argentina), 120) El Manso (Argentina), 121) Lenca, 122) Guabún (Punta Huechucucui), 123) Caulín, 124) Coquiao, 125) Chepu, 126) Puntra, 127) Lago Puelo (Argentina), 128) Los Hitos (Argentina), 129) Arroyo Melo (Argentina), 130) Metahue (Isla Butachauques), 131) Quetalco, 132) San Juan, 133) Mocopulli,

134) Abtao, 135) Castro, 136) Isla Alao, 137) Arroyo Torrecillas (Argentina), 138) near the mouth of the creek Zanjón Hondo (Argentina), 139) Lago Futalaufquén (Argentina), 140) Cucao, 141) Huillinco, 142) Terao, 143) Caleta Tenedor (Isla Talcán), 144) Pumalín, 145) El Amarillo, 146) Lago Amutui Quimei (Argentina), 147) Yaldad, 148) Futaleufú, 149) Río Chico, 150) Villa Santa Lucía, 151) Palena, 152) Isla Guafo, 153) Raúl Marín Balmaceda, 154) La Junta, 155) Lago Verde, 156) Puyuhuapi, 157) Queulat, 158) Lago Yulton, 159) Puerto Aguirre, 160) Isla Vergara, 161) Isla Chaculay, 162) Puerto Aysén, 163) Isla Rivero, 164) Fiordo Quitralco, 165) Isla Guerrero, 166) Puente Traihuanca, 167) Bahía Murta, 168) Área del Glaciar, 169) Canal de Ofqui, 170) Área de San Quintín, 171) Puerto Almirante Barroso, 172) Puerto Bertrand, 173) Tortel, 174) Laguna Caiquenes, 175) Isla Berta, 176) Isla Merino Jarpa, 177) Isla San Juan Stuven, 178) Lago Quetru, 179) Seno Huemules, 180) Bahía James, 181) Seno Edimburgo, 182) Puerto Edén, 183) Puerto Río Frío, 184) Bahía Broome.

Eupsophus vertebralis (Fig. 3D): 17) Ramadillas, 22) Los Lleulles, 24) M.N. Contulmo, 27) Tolhuaca, 57) Queule, 58) Mehuín, 63) Chanchán, 64) Llenehue, 66) Iñipulli, 67) Bosque San Martín, 185) Lingüento, 186) Pelchuquín, 187) Máfil, 70) Parque Oncol, 72) Valdivia, 73) Cuesta de Soto, 74) Huachocopihue, 75) Llancahue, 76) Los Molinos, 77) Corral, 78) Reumén, 79) Camino Viejo a La Unión, 84) Tres Chiflones, 92) Cerro Mirador (Cordillera Pelada), 94) La Barra, 96) Namun Lahual, 99) **Pucatrihue**, 100) Bahía Mansa, 103) Huellelhue, 189) Alerce 1, 104) Catrihuala (Puente La Herradura), 107) Puerto Blest (Argentina).

Eupsophus emiliopugini (Fig. 3D): 188) Raulintal, 99) **Pucatrihue**, 190) Piedras Negras, 191) Cerro Püschel, 106) La Picada, 192) Casa Pangue, 193) Frutillar, 109) Punta Huano (P.N. Vicente Pérez Rosales), 194) El Traiguén, 195) Lahuen Ñadi, 118) Río Rollizo, 121) Lenca, 196) Puelo, 197) Camino a Maullín, 122) Guabún, 198) Lechagua, 199) Ancud, 125) Chepu, 126) Puntra, 129) Arroyo Melo (Lago Puelo, Argentina), 140) Cucao, 200) Cucao SE, 141) Huillinco, 201) Tepuhueico, 202) Quellón, 147) Yaldad, 156) Puyuhuapi, 203) Puerto Cisnes, 204) Isla Kent, 205) Isla Melchor, 206) Caleta Vidal, 163) Puerto Yates (Isla Rivero).