

RESEARCH PAPER

## Taxonomic catalogue of the family Ochteridae with description of *Ochterus papaceki* sp. nov. from Socotra Island and Tanzania (Hemiptera: Heteroptera)

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Accepted:  
5<sup>th</sup> February 2020

Published online:  
29<sup>th</sup> February 2020

**Abstract.** The world catalogue of the family Ochteridae (Hemiptera: Heteroptera: Nepomorpha: Ochteroidea) is compiled. The fossil subfamily Propreocorinae Popov, Dolling & Whalley, 1994, recently excluded from Ochteridae by other authors, is formally raised to family rank as Propreocoridae stat. nov. The fossil genus *Meropachys* Popov, 1986 is found to be a junior homonym of *Meropachys* Burmeister, 1835 (Hemiptera: Heteroptera: Coreidae) and is replaced by a new substitute name, *Yuripachys* nom. nov., resulting in one new combination: *Yuripachys dubius* (Popov, 1986) comb. nov. *Neochterus* Mahner, 1993 (originally proposed as subgenus of *Ochterus* Latreille, 1807) is considered an unavailable name. *Ochterus papaceki* Kment & Carapezza sp. nov. is described and illustrated as a new species from the island of Socotra (Yemen) and Tanzania. Gender agreement in *Ochterus paucistriata* Baehr, 1990 is corrected to *O. paucistriatus* Baehr, 1990. The name *Ochterus perbosci* (Guérin-Méneville, 1843), an incorrect subsequent spelling of *O. perbosci* in prevailing usage, is fixed according to Article 33.3.1 of the ICZN (1999). The spelling of *Angulochterus quadrimaculatus* Yao, Zhang & Ren, 2011 is corrected according to Article 32.5.1 of ICZN (1999). The original publication of *Ochterus barberi* Schell, 1943, *O. bidentatus* Schell, 1943, *O. hungerfordi* Schell, 1943, and *O. parvus* Schell, 1943 is clarified. The name bearing types of *Ochterus barberi*, *O. bidentatus*, *O. hungerfordi*, *O. parvus*, *O. perbosci*, and *Pelagonus splendidulus* Montandon, 1898 (= *Ocyochterus vactor* (Bolívar, 1879)) are considered as lectotypes. The family Ochteridae currently includes 3 recent genera and 88 described species group taxa (84 species and 4 subspecies): *Megochterus* Jaczewski, 1934 (2 species from Australia), *Ochterus* (80 species and 4 subspecies distributed worldwide), and *Ocyochterus* Drake & Gómez-Menor, 1954 (2 species from NW South America). The fossil record of Ochteridae currently includes 4 genera and 5 species: *Angulochterus* Yao, Zhang & Ren, 2011 (1 species from Early Cretaceous of China), *Floricaudus* Yao, Ren & Shih, 2011 (1 species from Early Cretaceous of China), *Pristinochterus* Yao, Cai & Ren, 2007 (2 species from Late Jurassic to Early Cretaceous of China), and *Riegerochterus* Popov & Heiss, 2014 (1 species from Miocene Dominican amber). In addition the fossil genus *Yuripachys* (1 species from Early Cretaceous of Mongolia) is classified as Ochteridae incertae sedis, *Propreocoris* Popov, Dolling & Whalley, 1994 (1 species from Early Jurassic of England) as common ancestor of Ochteridae and Gelastocoridae in its own family Propreocoridae, and *Grimaldinia* Popov & Heiss, 2014 (1 species from Burmese Amber) and *Heterochterus* Evans, 1971 (1 species based on an isolated wing, Late Triassic of Australia) as Ochteroidea incertae sedis. The following new records are provided: *Ochterus aeneifrons surinamensis* Nieser, 1975 (Colombia), *O. caffer* (Stål, 1855) (Mozambique, Sudan), *O. feae* (Laos, Thailand), *O. marginatus marginatus* (Latreille, 1804) (China: Anhui, Shaanxi; Central African Republic; India: Rajasthan; Oman; Sudan), and *O. nicobarensis* Chandra & Jehamalar, 2012 (Myanmar). The distribution of all species is reviewed and the zoogeographic patterns and biodiversity of Ochteridae are discussed.

**Key words.** Heteroptera, Nepomorpha, Ochteroidea, Ochteridae, Propreocorinae, new species, new substitute name, catalogue, nomenclature, taxonomy, fossils, distribution

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## Introduction

Velvety shore bugs of the family Ochteridae represent a small monophyletic lineage of aquatic bugs of the infraorder Nepomorpha. Ochteridae, the toad bugs (Gelastocoridae), and two fossil families, Propreocoridae stat. nov. (POPOV et al. 1994) and Pseudonethridae (LÓPEZ RUF et al. 2005) jointly form the monophyletic Ochteroidea (MAHNER 1993; HEBSGAARD et al. 2004; YAO et al. 2011; LI et al. 2012, 2014; WANG et al. 2016; WEIRAUCH et al. 2019; YE et al. 2020). WANG et al. (2016) dated the split between Ochteridae and Gelastocoridae to the Early Jurassic based on a molecular phylogenetic analysis calibrated by fossils. This estimate is in agreement with the fossil record, which includes well preserved compressions from the Late Jurassic and the Early Cretaceous of China, which are morphologically similar to modern Ochteridae (YAO et al. 2007, 2011). The fossil Propreocoridae, considered a stem group of Ochteroidea (GRIMALDI & ENGEL 2005, YAO et al. 2011) comes from Early Jurassic of England, and a single hind wing described as *Heterochterus timmsii* Evans, 1971, tentatively assigned to Ochteroidea, was found in the Late Triassic of Queensland (Australia) (EVANS 1971, SHCHERBAKOV & POPOV 2002).

The Ochteroidea is a peculiar group of insects, being the only lineage of the secondarily aquatic Nepomorpha which returned back to a terrestrial way of life. The recent Ochteridae may be found mostly in riparian habitats, such as margins of streams or ponds, typically located on sandy and stony places with little vegetation, which are usually sunlit (although some species seem to prefer rather shaded habitats). Their cryptic coloration makes them nearly invisible when they are sitting on their preferred substrate. They can run rapidly, jump when disturbed, and they are also capable of flight (BOBB 1951, GAPUD & SAN VALENTIN 1977, MENKE 1979, BOULARD & COFFIN 1991, SCHUH & SLATER 1995, NIESER & CHEN 1999, ANDERSEN & WEIR 2004, CHEN et al. 2005, SCHUH & WEIRAUCH 2020). Recently, POLHEMUS & POLHEMUS (2016) reported *Ochterus explanatus* Polhemus & Polhemus, 2016 and *O. obscurus* Polhemus & Polhemus, 2016 from leaf litter samples collected in high elevation tropical montane and cloud forests in Central America. Despite the close phylogenetic relationship, Ochteridae and Gelastocoridae are not similar to each other. While Gelastocoridae are generally larger and more robust, equipped with raptorial fore legs, resembling small toads and often covered with mud, Ochteridae are smaller, gracile, widely oval, velvety black often with small yellowish spots (e.g., SCHUH & SLATER 1995, ANDERSEN & WEIR 2004, CHEN et al. 2005, SCHUH & WEIRAUCH 2020). Ochteridae are habitually much more similar to the leptopodomorphian family Saldidae, sharing with Ochteridae the oval body (though more ovoid in Saldidae), head with large kidney-shaped eyes, usually dark colouration of dorsum with whitish or yellowish spots, and life in the riparian habitats. Both these families are an interesting case of convergent evolution, though both can be easily distinguished by the shape of antennae, which are long and robust in Saldidae (as well as in the remaining terrestrial or semiaquatic Heteroptera) (e.g., SCHUH & SLATER 1995, SCHUH & WEIRAUCH 2020),

and very short and inconspicuous in Ochteridae. The very short antennae, usually concealed in grooves below the eyes, are an important synapomorphy for Nepomorpha, connected with their adaptation to the subaquatic way of life (e.g., RIEGER 1976, MAHNER 1993, SCHUH & SLATER 1995, ANDERSEN & WEIR 2004, HEBSGAARD et al. 2004); convergently, shortened antennae are also known in many beetle families with aquatic adults (Coleoptera: Adephaga and Polyphaga) (e.g., BEUTEL & LESCHEN 2016).

Due to the morphological homogeneity of Ochteridae, only three recent genera and 88 species group taxa are currently recognized (see below). The main diagnostic characters at the species level include the structure and striation of the frons (the so called frontal plate), shape and structure of pronotum, colouration of body dorsum, shape of the male genital capsule, and especially, the structure of the right paramere (e.g., ANDERSEN & WEIR 2004; POLHEMUS & POLHEMUS 2012, 2016). Although a world catalogue or monograph of Ochteridae has never been compiled, there are several valuable revisions, monographs or catalogues dealing with faunas of particular zoogeographical regions: Afrotropical Region (KORMILEV 1973, POLHEMUS & POLHEMUS 2008), Palaearctic Region (POLHEMUS 1995a), Oriental Region (KORMILEV 1971, NIESER & CHEN 1992, POLHEMUS & POLHEMUS 2012), Malesia (KORMILEV 1971; NIESER & CHEN 1992, 1999; CHEN et al. 2005; POLHEMUS & POLHEMUS 2012, 2015), Philippines (GAPUD & SAN VALENTIN 1977; GAPUD 1981, 1986, 2003; CHEN et al. 2005), New Guinea (KORMILEV 1971, BAEHR 1990b, CHEN et al. 2005), Australia (KORMILEV 1971; BAEHR 1989, 1990a,b; CASSIS & GROSS 1995; ANDERSEN & WEIR 2004), North America (SCHELL 1943a,b; POLHEMUS & POLHEMUS 1988a, 2016), Central America (CHAMPION 1901; SCHELL 1943a,b; HECKMAN 2011; POLHEMUS & POLHEMUS 2016), and South America (SCHELL 1943a,b; NIESER 1975; HECKMANN 2011; MOREIRA et al. 2011, 2019; CIANFERONI 2012; CORDEIRO et al. 2014; POLHEMUS & POLHEMUS 2014, 2016; BARBOSA & RODRIGUES 2015). Despite the considerable progress in Ochteridae taxonomy since 1971, there are still many species awaiting description. In order to assist in future taxonomic and phylogenetic efforts in Ochteridae, we provide here a taxonomic catalogue of all the described taxa of this family, extant as well as fossil, we review their distribution and discuss their zoogeographic patterns.

## Material and methods

The presented description of *Ochterus papaceki* Kment & Carapezza sp. nov. is based on material collected mostly in Socotra by Attilio Carapezza and by members of the Czech expeditions in 2010 and 2012. For further information on results of the Czech expeditions see e.g. HÁJEK & BEZDĚK (2012, 2014, 2017, 2019), BEZDĚK & HÁJEK (2017), KMENT et al. (2017) or BIONDI et al. (2019). For brief description of the natural conditions of Socotra see BATELKA (2012). For details on the Iranian localities sampled by the Czechoslovak-Iranian expeditions in 1970, 1973 and 1977 see HOBERLANDT (1974, 1981, 1983).

In quoting the labels of the holotype, a slash (/) is used to divide data on different rows of one label, double slash (//)

is used to divide data on different labels, authors' comments are given in square brackets [ ], and the abbreviation 'p' is used to indicate printed text. Localities of paratypes and other specimens are standardized. The names of the Socotran localities follow BEZDĚK et al. (2012).

The specimens examined are deposited in the following collections:

ACPI	Attilio Carapezza collection, Palermo, Italy;
AMNH	American Museum of Natural History, New York, USA;
AMSA	Australian Museum, Sydney, Australia;
BMKB	Brunei Museum, Kota Baru, Brunei;
BMNH	The Natural History Museum, London, United Kingdom;
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA;
CASC	California Academy of Sciences, San Francisco, California, USA;
CNUB	Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China;
CRNG	Christian Rieger collection, Nürtingen, Germany;
CZMA	Coleção Zoológica do Maranhão, Centro de Estudos Superiores de Caxias, Caxias, Maranhão, Brazil;
EHIA	Ernst Heiss collection, Innsbruck, Austria;
EIHU	Entomological Institute, Hokkaido University, Sapporo, Japan;
IEEM	Instituto Español de Entomología, Madrid, Spain;
ISNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium;
IZAS	Institute of Zoology, Academia Sinica, Beijing, China;
JDKD	Jakob Damgaard collection, Zoological Museum, Kobenhavn, Denmark;
JTPC	John T. Polhemus collection, Englewood, Colorado, USA;
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina;
MCSN	Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy;
MMBC	Moravian Museum, Brno, Czech Republic;
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain;
MNHN	Muséum National d'Histoire Naturelle, Paris, France;
MUDH	Museon, The Hague, the Netherlands;
MZFN	Museo Zoológico, Università degli Studi di Napoli Federico II (former Istituto di Zoologia, Università di Napoli), Napoli, Italy;
MZLU	Museum of Zoology, Lund University, Lund, Sweden;
NCTN	Nico Nieser collection, Tiel, the Netherlands;
NHMW	Naturhistorisches Museum in Wien, Vienna, Austria;
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden;
NMPC	National Museum, Prague, Czech Republic;
NZSI	National Zoological Collection, Zoological Survey of India, Calcutta, India;
PIN	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia;
RMNH	Naturalis Biodiversity Center (former Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands;
QMBA	Queensland Museum, Brisbane, Australia;
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA;
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany;
UM	Zoölogisch Museum der Rijksuniversiteit, Utrecht, The Netherlands;
UPLB	Museum of Natural History, University of the Philippines, Los Baños College, Laguna, Philippines;
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA;
VPGP	Victor P. Gapud collection, Department of Entomology, University of the Philippines, Los Baños College, Laguna, Philippines;
WAMA	Western Australian Museum, Perth, Australia;
ZJPC	Zdeněk Jindra collection, Prague, Czech Republic;
ZMAN	Zoologisch Museum, University of Amsterdam, Amsterdam, The Netherlands;

ZMAS	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia;
ZMPA	Zoological Institute, Polish Academy of Sciences, Warsaw, Poland;
ZMUH	Zoologisches Museum, Universität von Hamburg, Hamburg, Germany;
ZRCS	Zoological Reference Collection, Lee Kong Chian Natural History Museum (former Raffles Museum of Biodiversity Research), Singapore;
ZSMC	Zoologische Staatssammlung, München, Germany.

Measurements were taken using a Leica MZ75 stereomicroscopes provided with an ocular micrometer and subsequently standardized to absolute values. Non-coated specimens were examined by a Hitachi S-3700N environmental scanning electron microscope at the Department of Palaeontology, National Museum, Praha. Habitus photographs were taken using a Canon MP-E 65 mm macro lens attached to a Canon EOS 550D camera, light microscope photographs were taken using an Olympus BX44 microscope with an attached Canon EOS 1100D camera. The photographs were stacked from multiple layers using the Helicon Focus 5.1 Pro software.

The general morphological terminology follows mostly ANDERSEN & WEIR (2004), TSAI et al. (2011), KMENT et al. (2016, 2019) and RÉDEI (2017); male genitalia (POLHEMUS & POLHEMUS 2016), and antennomeres ZRZAVÝ (1990).

## Description of a new species

### *Ochterus papaceki* Kment & Carapezza, sp. nov.

(Figs 1–6, 9–12)

**Type locality.** Yemen, Socotra, Noged plain, lower part of Wadi Matyaf, 12°27'13.50"N 54°18'13.95"E.

**Type material.** HOLOTYPE: ♂ (Fig. 1), 'SOCOTRA 21.I.2014 / Noged – lower part / of Wadi Matyaf / leg. A. Carapezza // COLLECTIO / NATIONAL MUSEUM / Praha, Czech Republic // ♂ [p] // HOLOTYPE / OCHTERUS / PAPACEKI / sp. nov. / det. Kment & Carapezza 2020 [p, red label]' (NMPC). The holotype is card-mounted, complete, with dissected genital capsule and right paramere glued on the same piece of card. PARATYPES (16 ♂♂ 12 ♀♀ 1 L5): YEMEN: SOCOTRA: Hallah Arhar [= Halla area, Arher] (spring), 15 m, 12°33.0'N 54°27.6'E, 11.xi.2010, 2 ♂♂ 2 ♀♀, J. Bezděk lgt. (MMBC), 3 ♂♂ 1 ♀, J. Hájek lgt. (NHMW), 1 ♀, P. Hlaváč lgt. (MMBC); Halla area, Arher (12°33.0'N 54°27.6'E), freshwater spring in sand dune, 5 m a.s.l., 9.–10.vi.2012, 4 ♂♂ 4 ♀♀ 1 L5, Socotra expedition 2012: J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. (3 ♂♂ 3 ♀♀ 1 L5 NMPC, 1 ♂ 1 ♀ BMNH); Noged, lower part of wadi Matyaf, 12°27'13.50"N 54°18'13.95"E, 21.i.2014, 6 ♂♂ 3 ♀♀, A. Carapezza lgt. (5 ♂♂ 3 ♀♀ ACPI, 1 ♂ NMPC). TANZANIA: NE, 100 km SW of Tanga, Makinda env., 14.iii.2002, 1 ♂ 1 ♀, M. Snížek lgt. (ZJPC). All the paratypes bear the following label: 'PARATYPE / OCHTERUS / PAPACEKI / sp. nov. / det. Kment & Carapezza 2020 [p, red label]'.

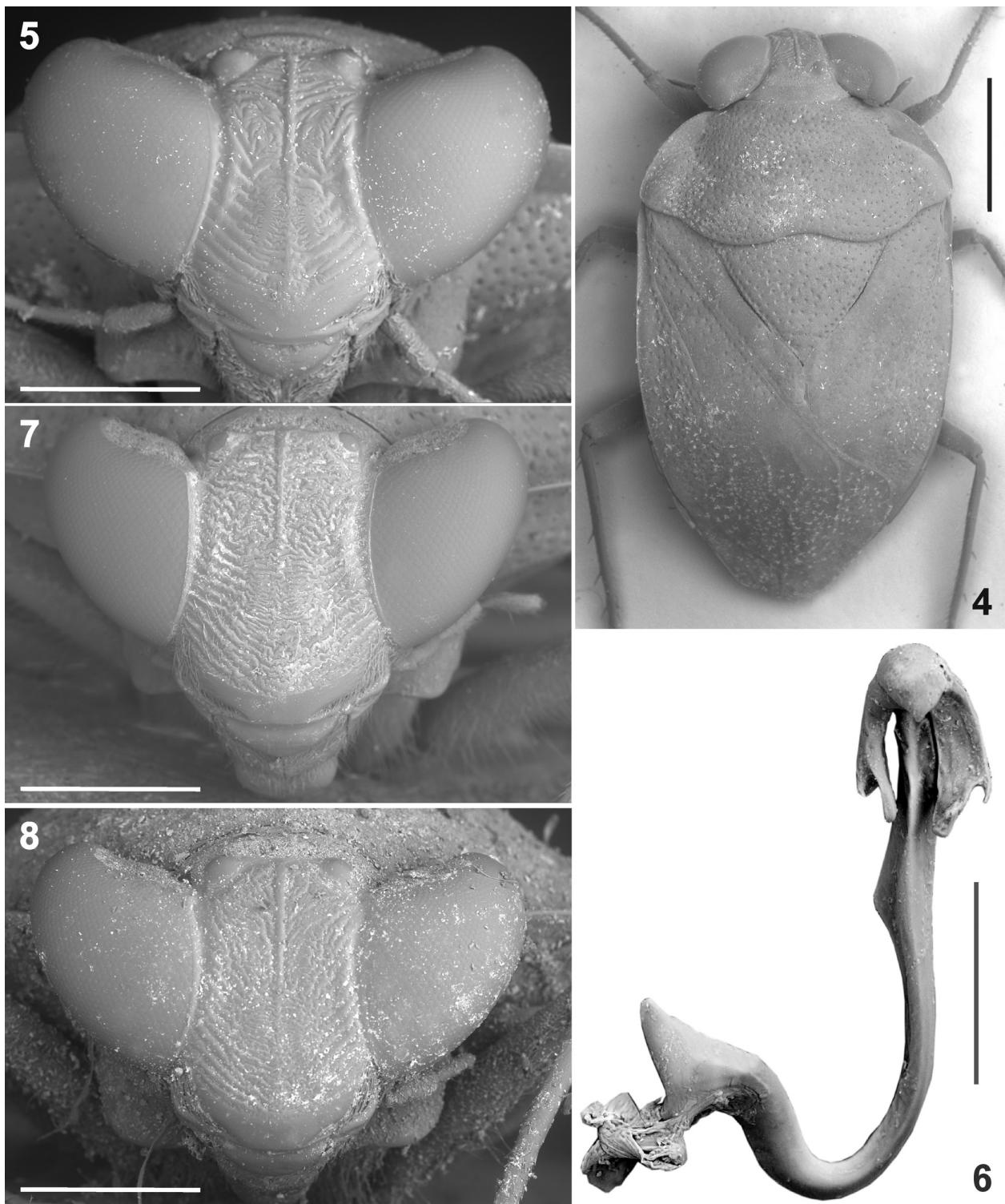
**Description. Adult. Colouration** (Fig. 1). Body dorsally very dark brown to black with following yellowish pattern: flattened lateral pronotal margins; posterior pronotal margin narrowly, with larger spots on postero-lateral angles and medially; costal margin of corium narrowly (anteriorly somewhat wider than posteriorly), connected with two round lateral spots, one ca. in middle and second in posterior half of embolium; one nebulous spot (sometimes indistinct) posteriad of R+M vein; two nebulous spots in anterodistal and posterodistal angles of corium (adjacent to membrane). Hemelytra speckled



Figs 1–3. *Ochterus papaceki* Kment & Carapezza sp. nov.  
 1 – holotype, ♂, wadi Matyaf (body length 4.80 mm);  
 2 – larva, Arher (body length 4.10 mm); 3 – aedeagus  
 (magnification 100×).

with irregular greyish-white pruinose marks (sometimes artificially disappearing due to harsh killing or mounting method). Eyes dark brown, or with silver or metallic green shimmer. Anterior margin of frontal plate, labrum, scape and pedicel yellow. Bucculae, basiflagellum and distiflagellum black. Rostrum widely black basally and apically, median part brownish to dark brown. Body ventrally black, acetabula with yellowish margins, broad

at proacetabula, narrow at meso- and metacetabula; posterolateral margin of metapleuron more or less narrowly yellowish. Hypocostal lamina yellow. Ventrites with lateral margins (all segments) and posterior margins laterally (except segment II) yellowish, more widely in posterior segments. Connexivum dorsally yellowish with blackish spots in anterolateral angles. Legs pale yellowish, with apices of femora, tibiae, and tarsal segments infuscated



Figs 4–8. 4–6 – *Ochtherus papaceki* sp. nov., ♂, Arher: 4 – body, dorsal view (magnification 27×); 5 – head, frontal view (80×); 6 – paramere, ventral view (magnification 180×). 7 – *O. marginatus* (Latreille, 1804), head, frontal view (75×) (♂, Turkey, Tunceli Prov., Ovacik env., NMPC). 8 – *O. caffer* (Stål, 1855), head, frontal view (70×) (♂, Democratic Republic of the Congo, Ituri, NMPC). Scale bars: 0.2 mm (Fig. 6), 0.5 mm (Figs 5, 7–8), 1 mm (Fig. 4).

with black; dorsal margin of metatibiae with brownish line in anterior two thirds; claws black.

**Structure.** Body of elongate shape with lateral margins parallel-sided. Dorsal surface of body bare (Fig. 4).

Head with very large eyes (Figs 4–5), smallest interocular distance 0.33 times of head width. Vertex smooth, dull, unpunctured. Frontal plate (Fig. 5) lustrous with long median carina throughout its black portion, pos-

teriorly (between ocelli and posterior margin of eyes) with distinct transverse wrinkles (forming a tree-shaped figure), medially with shallow, rather indistinct skew and transverse wrinkles, anterior portion of frontal plate with U-shaped wrinkles, the 6–7 apical ones very deep and distinct (Fig. 5). Apical yellowish portion of frontal plate smooth, without wrinkles. Anterior margin of frontal plate not produced forwards, head anteriorly rounded in lateral

view. Scape and pedicel cylindrical, much thicker than two apical segments; basiflagellum slender, cylindrical; distiflagellum narrowly spindle-shaped. Rostrum long, reaching between metacoxae.

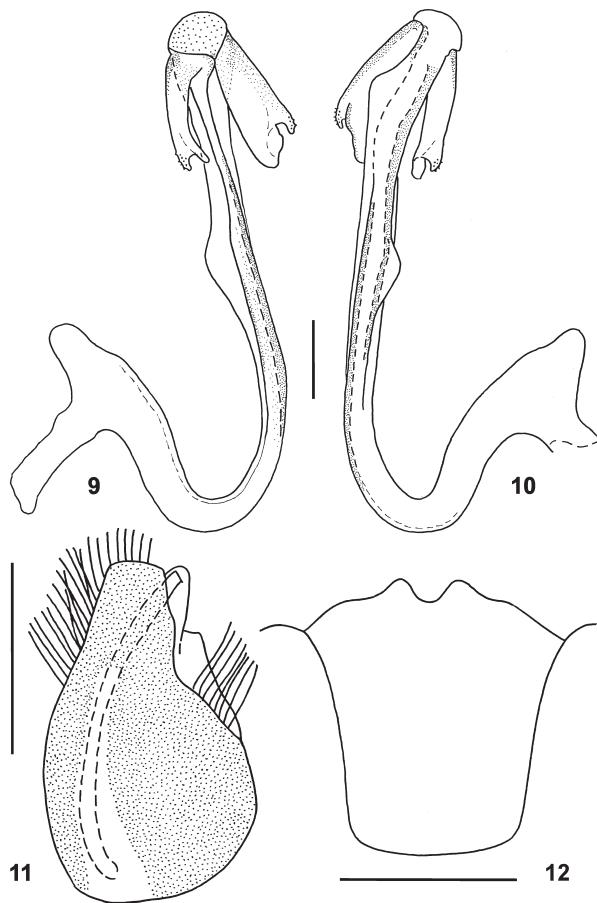
**Thorax.** Pronotum strongly transverse, width 2.3 times its median length. Lateral pronotal margins regularly rounded, only at anterolateral angles more rounded (Figs 1, 4). Yellowish flattened lateral portion of pronotum 4.3 times longer than wide (Fig. 1). Posterior margin of pronotum trisinuate. Disc of pronotum punctured, posteriorly more deeply than anteriorly (Fig. 4). Mesoscutellum triangular, convex, sparsely punctured. Hemelytron (Fig. 4) unevenly punctured: clavus with few deep punctures anteromedially, few shallow punctures posteromedially, and one row of small punctures along lateral claval margin; endocorium with scattered deep punctures in anterior half and along claval margin, rest of posterior half unpunctured; embolium with regularly dispersed deep punctures except the unpunctured costal margin; portion of corium posteriad of R+M vein with sparse shallow punctures.

**Legs.** Femora unarmed, ventral surface with long, thin, whitish setae. Pro- and mesotibiae covered with short pale spines, mesotibiae also with few longer spines. Metatibiae externally with 5 long, stout, pale brownish spines and sparse, short, fine setae, internally with one long, stout, pale brownish spines subapically, and row of long, fine, brownish setae; apical margin of metatibiae with 5 long, stout, brown spines.

**Male abdomen.** Abdominal segments VII and VIII and male genitalia asymmetrical. Apical border line of male abdomen slightly incised posteriad of genital capsule. Genital capsule ventrally slightly keeled medially, apically produced into subquadrate process (Fig. 11) beset with long to short setae on left side (shortening towards apex) and additional row of long setae subapically on right side. Right paramere (Figs 6, 9–10) with short, widely rounded, punctate cap, ventrally pointed into short tooth (Fig. 9); both appendages rather adjacent to the shaft (Figs 6, 9–10); left appendage (Figs 6, 9) more slender and slightly shorter than right one, slightly curved towards shaft; right appendage (Fig. 9) wider, slightly longer, slightly diverging laterad from shaft; both appendages apically narrowly incised, bearing microscopic granulation (best visible laterally); paramere shaft triangular in cross section, ventrally keel-like (Fig. 6), dorsally flattened, lamellate, with two rounded lateral processes, right apical one about midlength of appendages (Fig. 10) and left middle one about half-length of shaft (also visible in ventral view) (Figs 6, 9–11). Aedeagus with distal flagellum distinctly shorter than basal portion of flagellum, slender, with closely appressed phallotheca (Fig. 3).

**Female abdomen** symmetrical. Subgenital plate (sternite VII) strongly convex, its posterior margin trisinuate, with pair of shallow submedian insinuations and one deep and narrow median insinuation (Fig. 12).

**Larva** (5th instar) (Fig. 2). Body dark brown, with explanate lateral margins of pronotum, wing pads, postero-lateral areas of connexival segments and legs yellowish brown. Anterior margin of frontal plate with row of 14



Figs 9–12. *Ochterus papaceki* sp. nov. 9–11 – ♂, wadi Matyaf: 9–10 – paramere (9 – ventral view, 10 – dorsal view; magnification 20×); 11 – pygophore, ventral view. 12 – ♀, Arher, subgenital plate, ventral view. Scale bars: 0.1 mm (Figs 9–10), 0.5 mm (Figs 11–12).

short, stout spines, the posterior ones shortest and thinnest, anterior ones longest and stoutest. Anterolateral angles of pronotum narrowly rounded, prominent, lateral pronotal angles widely rounded. Wing pads reaching posterior margin of thorax. Head, thorax and abdominal tergites covered with short, adpressed to semierect whitish setae.

**Measurements (mm).** Males: Socotra (n = 10; median (minimum–maximum)). Body length: 4.61 (4.49–4.80); head width: 1.51 (1.46–1.61); pronotum width: 2.49 (2.44–2.59); maximum width of body (ca. in corium midlength): 2.49 (2.44–2.59); length of antennal segments: scape (I) – 0.10 (0.10–0.10), pedicel (II) – 0.14 (0.14–0.16), basiflagellum (III) – 0.26 (0.25–0.27), distiflagellum (IV) – 0.29 (0.23–0.29). Tanzania (n = 1). Body length: 4.71; head width: 1.57; pronotum width: 2.55; maximum width of body: 2.60; length of antennal segments: scape (I) – 0.12, pedicel (II) – 0.15, basiflagellum (III) – 0.30, distiflagellum (IV) – 0.32.

Females. Socotra (n = 9). Body length: 4.97 (4.76–5.12); head width: 1.56 (1.51–1.56); pronotum width: 2.59 (2.54–2.63); maximum width of body (ca. in corium midlength): 2.63 (2.59–2.63); length of antennal segments: I – 0.10 (0.10–0.10), II – 0.14 (0.14–0.16), III – 0.27 (0.25–0.27), IV – 0.29 (0.27–0.31). Tanzania (n = 1). Body length: 5.20; head width: 1.60; pronotum width: 2.75; maximum

width of body: 2.77; length of antennal segments: scape (I) – 0.12, pedicel (II) – 0.15, basiflagellum (III) – 0.32, distiflagellum (IV) – 0.30.

5<sup>th</sup> instar larva (n = 1). Body length: 4.10; head width: 1.56; pronotum width: 2.54; maximum width of body (across wing pads): 3.02.

**Differential diagnosis.** *Ochterus papaceki* sp. nov. resembles several other *Ochterus* species in which the costal margin of corium is yellowish, connected with two rounded yellowish lateral spots on embolium, and the dorsal surface of the body is bare (see KORMILEV 1973; POLHEMUS & POLHEMUS 2008, 2012; CHANDRA & JEHAMALAR 2012), but differs from these similar species by the unique combination of the rough striation of the frontal plate and shape of the right paramere. The apex of the head is anteriorly rounded in lateral view; the frontal plate is bearing a series of deep U-shaped wrinkles anteriorly and a tree-like figure posteriorly (Fig. 5), resembling *O. marginatus* (Latreille, 1804) (Fig. 7) and *O. nicobarensis* Chandra & Jehamalar, 2012 (CHANDRA & JEHAMALAR 2012: fig. 2), and among differently coloured species e.g. to *O. australicus* Jaczewski, 1934 (ANDERSEN & WEIR 2004: fig. 18.4.C), but all of these species have the paramere shaft simply cylindrical and the left and right appendages of different shape (see JACZEWSKI 1937; KORMILEV 1973; ANDERSEN & WEIR 2004; POLHEMUS & POLHEMUS 2008, 2012; CHANDRA & JEHAMALAR 2012). The paramere with its laterally lamellate shaft (Figs 6, 9–11) resembles that of *O. caffer* (Stål, 1855), but its lamella and appendages have different shapes, the appendages being distinctly divergent from the shaft (see JACZEWSKI 1934: figs 11–13, KORMILEV 1973: figs 7–8); that species differs also in regard to the regularly and shallowly wrinkled frontal plate (Fig. 8). *Ochterus papaceki* and *O. caffer* also differ from *O. marginatus* by the shape of the lateral pronotal margin, which is less rounded laterally, with more rounded and therefore more prominent anterolateral pronotal angles in the first two species, while in *O. marginatus* it is strongly and regularly rounded without apparent anterolateral pronotal angles. The enigmatic *O. strigicollis* Horváth, 1913, described from Israel, differs clearly from the new species by the shape and structure of the pronotum as figured by HORVÁTH (1913: fig. 2, mislabelled as *O. marginatus*). *Ochterus africanus* Jaczewski, 1938, known only from the female holotype (Figs 14–16), differs markedly from the new species by the frontal plate being lamellate anteriorly, and protruding forwards (see JACZEWSKI 1938: figs 1–2).

**Etymology.** We dedicate this species to our dear colleague, professor Miroslav Papáček (1953–2019), an eminent specialist in the morphology, taxonomy, bionomics and ecology of aquatic and semiaquatic bugs (see DITRICH et al. 2020). Mirek was my (P. Kment) first tutor and supervisor in Heteroptera during my master studies and I will always remain indebted to him for all of his advice and kind help.

**Habitat.** At Arher the species was collected by hand or by suction sampler from wet places with short-grazed grasses on sand, surrounding a small brook situated among sand dunes and groups of *Tamarix nilotica* (Ehrenb.) Bunge about 50 m from sea coast (P. Kment,



Fig. 13. Socotra, Halla Arher, habitat of *Ochterus papaceki* sp. nov.

pers. observ.; see Fig. 13). In Wadi Matyaf the species was collected by hand on the wet sandy banks of the estuarine area of the river, about 800 m far from sea coast (A. Carapezza, pers. observ.). Both localities belong to the coastal zone of Socotra (0–200 m a.s.l., see BROWN & MIES 2012).

#### Key to *Ochterus* species of Afrotropical Region

(Modified from KORMILEV (1973) and POLHEMUS & POLHEMUS (2008))

- 1 Frontal plate apically produced, forming sharp lamella (best seen in lateral view) (Figs 15–17; JACZEWSKI 1938: figs 1–2). Central African Republic. .... *O. africanus* Jaczewski, 1934
- Frontal plate apically not produced, bluntly rounded in lateral view. .... 2
- 2 Body covered with more or less erect stiff bristles, venter covered with dense, inclined, and long hairs (KORMILEV 1973: figs 9–10). Striation of the frontal plate sharp, particularly on the upper half of the plate. Right paramere with its shaft lamellate (KORMILEV 1973: fig. 11). Angola. .... *O. piliferus* Kormilev, 1973
- Body bare, without more or less erect stiff bristles. ... 3
- 3 Hemelytra usually with three irregular or semicircular yellowish spots along costal margin of corium (sometimes overlain with pruinose spots). Europe, Africa or Asia. .... 4
- Hemelytra without yellowish spots along costal margin of corium, but with irregular pruinose spots (sometimes weakly formed). Seychelles or Mascarene Islands. .... 7

- 4 Shaft of right paramere essentially cylindrical ..... 5  
 - Shaft of right paramere flattened, lamellate laterally. ....  
       ..... 6
- 5 Striation of the frontal plate sharp, particularly on the upper half of the plate (Fig. 7). Right paramere figured e.g. in JACZEWSKI (1934: figs 6–10), KORMILEV (1973: figs 2–3) and POLHEMUS & POLHEMUS (2012: figs 5–7). S Europe, Africa, Asia. ....  
       ..... *O. marginatus marginatus* Latreille, 1804
- Striation of the frontal plate fine, particularly on the upper half of the plate (KORMILEV 1973: fig. 4). Right paramere figured in KORMILEV (1973: fig. 5). Tropical Africa. .... *O. minor* Kormilev, 1973
- 6 Striation of the frontal plate sharp, particularly on the upper half of the plate with distinct tree-shaped figure (Fig. 5). Lateral appendages of right paramere adjacent to the shaft, shaped as on Figs 6, 9–10. Socotra, Tanzania. .... *O. papaceki* Kment & Carapezza sp nov.
- Striation of the frontal plate fine, particularly on the upper half of the plate (Fig. 8). Lateral appendages of right paramere distinctly divergent from the shaft, shaped as figured in JACZEWSKI (1934: figs 11–13) and KORMILEV (1973: fig. 5). Tropical Africa and Madagascar. .... *O. caffer* Stål, 1855
- 7 Posterior part of endocorium with obvious punctures. Right paramere figured in POLHEMUS & POLHEMUS (2008: figs 2–4). Mauritius. ....  
       ..... *O. stysi* D. A. Polhemus & J. T. Polhemus, 2008
- Posterior part of endocorium without, or with very weak punctures. Right paramere figured in POLHEMUS (1992a: fig. 3) and POLHEMUS & POLHEMUS (2013: figs 47–48). Seychelles. ....  
       ..... *O. seychellensis* D. A. Polhemus, 1992

## Taxonomic catalogue of modern species of the family Ochteridae

### Superfamily OCHTEROIDEA Kirkaldy, 1906 [1815]

Ochteridæ Kirkaldy, 1906a: 149 (according to principle of coordination).

Ochteroideæ: REUTER (1910): 60 (as superfamily).

Gelastocooroidea: POPOV (1971): 98 (as superfamily)

Ochteroidea: ŠTYS & JANSSON (1988): 7, 22 (clarification of nomenclature).

### Family OCHTERIDAE Kirkaldy, 1906 [1815]

Pelagonida Leach, 1815: 123 (diagnosis). Type genus: *Pelagonus* Latreille, 1809 [= *Ochterus* Latreille, 1807].

Pelegonidae (incorrect subsequent spelling): PUTON (1869): 38 (list).

Pelagonidae: DOHRN (1859): 52 (list).

Pelogniidae (incorrect subsequent spelling): CHINA & MILLER (1955): 267 (nomenclature).

Ochteridæ Kirkaldy, 1906: 149 (new substitute name for Pelagonidae). Type genus: *Ochterus* Latreille, 1807.

Ochteridae: CHINA & MILLER (1959): 16 (nomenclature); POLHEMUS & POLHEMUS (1988a): 542 (nomenclature); ŠTYS & JANSSON (1988): 7, 22 (nomenclature).

**Note.** Ochteridae is an unnecessary new substitute name for Pelagonidae, but having gained general acceptance it takes the date of the replaced name and is deemed to be

its senior synonym (ICZN 1985: Art. 40b, Recommend. 40A) (POLHEMUS & POLHEMUS 1988a: 542; ŠTYS & JANSSON 1988: 7).

### Genus *Megochterus* Jaczewski, 1934

*Megochterus* Jaczewski, 1934: 610–612 (description, differential diagnosis). Type species: *Pelagonus nasutus* Montandon, 1898 by original designation.

*Megochterus*: JACZEWSKI (1935): 482 (key to genera and species); SCHELL (1943a): 30 (key to genera); KORMILEV (1971): 443 (diagnosis); ŠTYS & JANSSON (1988): 7 (catalogue); BAEHR (1989): 112 (key to genera); BAEHR (1990a): 198–202 (key to species, revision); CASSIS & GROSS (1995): 259 (catalogue); ANDERSEN & WEIR (2004): 264–265, 335 (key to genera, diagnosis, checklist); CHEN et al. (2005): 78 (key to genera); YAO et al. (2007): 828, 830 (key to genera, differential table); YAO et al. (2011): 590, 597–598 (key to genera, phylogeny); MELO (2015): 344 (key to genera, diagnosis).

### *Megochterus nasutus* (Montandon, 1898)

*Pelagonus nasutus* Montandon, 1898: 72–73 (original description, differential diagnosis). LECTOTYPE: ♀ (designated by BAEHR 1990a: 198), ‘Australia’ (MNHN).

*Megochterus nasutus*: JACZEWSKI (1934): 610–613 (redescription, illustrations); JACZEWSKI (1935): 482 (key to species); KORMILEV (1971): 434, 443–444 (partim, specimens from Queensland; redescription, illustrations); BAEHR (1990a): 198–201 (key to species, redescription, illustrations, lectotype designation); CASSIS & GROSS (1995): 259 (catalogue); ANDERSEN & WEIR (2004): 264–265, 335 (key to species, illustrations, checklist); CHEN et al. (2005): 80 (illustration); POPOV & HEISS (2014a): 188 (illustration).

**Distribution. Australian Region:** Australia: New South Wales (BAEHR 1990a), Queensland (KORMILEV 1971; BAEHR 1989, 1990a; ANDERSEN & WEIR 2004), South Australia (ANDERSEN & WEIR 2004), Tasmania (BAEHR 1990a, ANDERSEN & WEIR 2004).

### *Megochterus occidentalis* Baehr, 1990

*Megochterus nasutus*: KORMILEV (1971): 444 (partim, specimen from Kelmscott, Western Australia).

*Megochterus occidentalis* Baehr, 1990a: 198–202 (key to species, description, illustrations). HOLOTYPE: ♂, Australia: Western Australia: ‘3 km N.E. Broke Inlet, E. of Walpole’ (WAMA).

*Megochterus occidentalis*: CASSIS & GROSS (1995): 259 (catalogue); ANDERSEN & WEIR (2004): 264–265, 335 (key to species, illustrations, checklist).

**Distribution. Australian Region:** Australia: Western Australia (BAEHR 1990a, ANDERSEN & WEIR 2004).

### Genus *Ochterus* Latreille, 1807

*Ochterus* Latreille, 1807: 142–143 (original description). Type species: *Acanthia marginata* Latreille, 1804 [= *Ochterus marginatus*], by monotypy.

*Ochtherus* Agassiz, 1847: 254. Unjustified emendation, junior objective synonym of *Ochterus* Latreille, 1807.

*Ochtherus* (incorrect subsequent spelling): BERGROTH (1890a): lxvi (nomenclature).

*Ochthera* (incorrect subsequent spelling): BERGROTH (1890a): lxvi (nomenclature).

*Octherus* (incorrect subsequent spelling): BERGROTH (1890b): cxix (nomenclature).

*Ochtherus* (incorrect subsequent spelling): BERGROTH (1890b): cxix (nomenclature).

*Ochtherus*: KOLENATI (1857): 453–454 (redescription); KIRKALDY (1906): 149 (catalogue); KIRKALDY & TORRE BUENO (1909): 179 (catalogue); OSCHANIN (1912): 89 (catalogue); BARBER (1913): 213–215 (key

to species, taxonomy); VAN DUZEE (1917): 475–476 (catalogue); BLATCHLEY (1926): 1020–1022 (key to species, review); JACZEWSKI (1934): 601–610 (diagnosis, revision); JACZEWSKI (1935): 482 (key to genera and species); WU (1935): 557 (catalogue); SCHELL (1943a): 30–36 (key to genera, revision); SCHELL (1943b): 37–47 (revision); CHAPMAN (1958): 119–120 (key to species); KORMILEV (1971): 433–443 (revision); NIESER (1975): 26 (key to genera and species); MENKE (1979): 124–125 (catalogue); FROESCHNER (1981): 61 (key to genera); ŠTYS & JANSSON (1988): 8 (catalogue, nomenclature); BAEHR (1989): 112–125 (key to species); BAEHR (1990b): 450–476 (diagnosis, key to species, revision); CASSIS & GROSS (1995): 259–262 (catalogue); POLHEMUS (1995a): 25 (catalogue); ANDERSEN & WEIR (2004): 264, 266–271, 335–336 (key to genera, diagnosis, checklist); CHEN et al. (2005): 78, 423 (key to genera, checklist); EPLER (2006): 1.15, 12.1–12.4 (key to species); YAO et al. (2007): 828, 830 (key to genera, differential table); MAZZUCCONI et al. (2009a): 212–213 (key to genera, illustration); HECKMAN (2011): 457–463 (key to genera and species); YAO et al. (2011): 590, 597–598 (key to genera, phylogeny); POLHEMUS & POLHEMUS (2014): 164 (key to genera); BARBOSA & RODRIGUES (2015): 163, 166, 174, 176, 182 (key to genera, illustrations); LLANO & GUTIÉRREZ (2015): 378 (distribution, illustrations); MELO (2015): 344 (key to genera, diagnosis); MOREIRA et al. (2019): 179, 182, 188, 190 (key to genera, illustrations).

*Pelagonus* Latreille, 1809: 384 (new substitute name). Junior objective synonym; unnecessary new substitute name for *Ochterus* Latreille, 1809, proposed because of presumed homonymy with *Ochthera* Latreille, [1802] (Diptera).

*Pélogone* (vernacularization): LATREILLE (1825): 423.

*Pelagonus* (incorrect subsequent spelling): LAPORTE (1832): 6, 13 (diagnosis); PUTON (1869): 38 (list); PUTON (1880): 209 (diagnosis).

*Pelagonus*: LE PELETIER & SERVILLE (1825): 33 (redescription); DUFOUR (1833): 192–193 (comparative notes); BURMEISTER (1835): 202–204 (key to genera, redescription); BRULLÉ (1836): 276–277 (differential diagnosis); BLANCHARD (1840): 93–94 (redescription); AMYOT & SERVILLE (1843): 407–409 (redescription); HERRICH-SCHÄFFER (1849): 18, 23–24 (key, redescription); FIEBER (1851): 14–15 (redescription); FIEBER (1861): 103 (redescription, catalogue); STAL (1866): 170 (redescription); CHAMPION (1901): 344–346 (key to species, revision); DISTANT (1906): 13–14 (catalogue, redescription); OSHANIN (1909): 955 (catalogue).

*Neochterus* Mahner, 1993: 92, 191 (as subgenus of *Ochterus*). Type species: *Ochterus manni* Hungerford, 1927, original designation. Unavailable name.

*Neochterus*: POLHEMUS (1995a): 25 (listed as valid); CIANFERONI (2012): 62 (listed as valid); BARBOSA & RODRIGUES (2015): 174 (listed as valid).

**Note.** MAHNER (1993) established this presumably paraphyletic taxon to accommodate American species of *Ochterus*. However, this taxon was defined merely as opposite to *Palaeochterus* Mahner, defined by its apomorphic structure of the right paramere, and its geographic distribution, without providing a single morphological character, which renders *Neochterus* Mahner an unavailable name according to Articles 13.1 (ICZN 1999) (P. Štys, in litt., as well as our opinion).

*Palaeochterus* Mahner, 1993: 92, 191 (as subgenus of *Ochterus*). Type species: *Acanthia marginata* Latreille, 1804, original designation. Junior objective synonym of *Ochterus* Latreille, 1807, recognized by ANDERSEN (1995: 161) and POLHEMUS (1995a: 25).

**Note.** MAHNER (1993) established this taxon for Old World species of *Ochterus*, which he considered a monophyletic taxon based on the characteristic right paramere with rounded capitulum and two subapical appendages. *Palaeochterus* Mahner is thus an available name according to Articles 13.1 and 13.3 (ICZN 1999), but its author ignored the principle of coordination and created thus a junior objective synonym of *Ochterus*, as both taxa share the same type species, *Acanthia marginata* Latreille, 1804 (ICZN 1999: Art. 43.1).

**Note.** LLANO & GUTIÉRREZ (2015) provided records and habitus photographs of two unidentified *Ochterus* species from Colombia.

### *Ochterus acutangulus* (Champion, 1901)

*Pelagonus acutangulus* Champion, 1901: 345–346, Pl. XX: fig. 11 (key, original description, illustration). HOLOTYPE: ♀, Guatemala: ‘Rio Naranjo’ (BMNH).

*Ochterus acutangulus*: KIRKALDY & TORRE BUENO (1909): 179 (catalogue); BARBER (1913): 214 (key to species); SCHELL (1943b): 38–39 (original description repeated); ?DRAKE (1952): 73–74 (checklist, comparative note, illustration); ALAYO (1971): 4–5 (key to species); ALAYO (1974): 34–35 (key to species); HECKMAN (2011): 459–460 (key to species, illustration); POLHEMUS & POLHEMUS (2016), 17–20 (key to species, redescription, illustrations).

**Distribution.** *Neotropical Region: Central America:* Belize (POLHEMUS & POLHEMUS 2016); Guatemala (CHAMPION 1901, KIRKALDY & TORRE BUENO 1909, DRAKE 1952, POLHEMUS & POLHEMUS 2016); Mexico (DRAKE 1952): Chiapas (POLHEMUS & POLHEMUS 2016).

**Notes.** Comparative notes and record of *O. acutangulus* from Mexico: Tejupilco by SCHELL (1943b) actually refers to *O. schellae* (see DRAKE 1952), also her records from Mexico: Veracruz and Panama: Porto Bello (SCHELL 1943b) seem doubtful and require revision. DRAKE (1952: 74) provided an illustration of a female from Cuba. The distribution in Cuba was accepted by ALAYO (1971, 1974). However, there is no other record from Cuba (MUÑOZ RIVIAUX et al. 2010a,b; NARANJO et al. 2010), and its presence on the island is considered doubtful by POLHEMUS & POLHEMUS (2016).

### *Ochterus aeneifrons aeneifrons* (Champion, 1901)

*Pelagonus marginatus* (misidentification, partim): UHLER (1893): 706 (list, ‘two forms’); UHLER (1894): 222 (variability).

*Pelagonus aeneifrons* Champion, 1901: 344–**345**–346, Pl. XX: figs 12, 13, 13a (key, original description, variability, illustrations). SYNTYPES: 24 spec. (♂♂ ♀♀), Mexico: Tabasco: ‘Teapa’; Guatemala: ‘San Gerónimo, Guatemala city’; Panama: ‘Tolé, Peña Blanca, San Feliz’; Grenada; St. Vincent (BMNH).

*Ochterus aeneifrons*: KIRKALDY & TORRE BUENO (1909): 179 (catalogue).

*Ochterus aenifrons* (incorrect subsequent spelling): BARBER (1913): 213 (key to species).

*Ochterus aenifrons* (incorrect subsequent spelling): SCHELL (1943a): 32, 35 (key to species, illustration); SCHELL (1943b): 43–44 (original description repeated, differential diagnosis); DRAKE (1952): 74 (checklist).

*Ochterus aeneifrons*: FROESCHNER (1981): 61 (catalogue); FROESCHNER (1999): 148 (catalogue); HECKMAN (2011): 462 (key to species); CIANFERONI (2012): 67 (key to species for Ecuador).

*Ochterus aeneifrons aeneifrons*: NIESER & ALKINS KOO (1991): 14 (key); POLHEMUS & POLHEMUS (2012): 17, 20–24 (key to species, redescription, illustrations).

*Ochterus barberi* (misidentification): SCHELL (1943b): 42 (paratypes from Orizaba, Mexico) (see POLHEMUS & POLHEMUS 2016).

**Distribution.** *Neotropical Region: Central America:*

Belize (POLHEMUS & POLHEMUS 2016); Costa Rica (SCHELL 1943b, POLHEMUS & POLHEMUS 2016); El Salvador (POLHEMUS & POLHEMUS 2016); Guatemala (CHAMPION 1901, KIRKALDY & TORRE BUENO 1909, SCHELL 1943b, POLHEMUS & POLHEMUS 2016); Honduras (SCHELL 1943b); Mexico (KIRKALDY & TORRE BUENO 1909, SCHELL 1943b, DRAKE 1952); Chiapas (POLHEMUS & POLHEMUS 2016), Colima (POLHEMUS & POLHEMUS 2016), Guerrero (POLHEMUS & POLHEMUS 2016), Jalisco (POLHEMUS & POLHEMUS 2016), Mexico (POLHEMUS & POLHEMUS 2016), Nayarit (POLHEMUS & POLHEMUS 2016), Nuevo León (POLHEMUS & POLHEMUS

2016), Oaxaca (POLHEMUS & POLHEMUS 2016), Puebla (POLHEMUS & POLHEMUS 2016), Queretaro (POLHEMUS & POLHEMUS 2016), San Luis Potosí (POLHEMUS & POLHEMUS 2016), Tabasco (CHAMPION 1901), Tamaulipas (POLHEMUS & POLHEMUS 2016), Veracruz (POLHEMUS & POLHEMUS 2016); Nicaragua (POLHEMUS & POLHEMUS 2016); Panama (CHAMPION 1901, KIRKALDY & TORRE BUENO 1909, SCHELL 1943b, FROESCHNER 1999, POLHEMUS & POLHEMUS 2016). *Caribbean Islands*: Grenada (UHLER 1894, as *P. marginatus*; CHAMPION 1901; KIRKALDY & TORRE BUENO 1909); St. Vincent (UHLER 1893, as *P. marginatus*; CHAMPION 1901; KIRKALDY & TORRE BUENO 1909); Trinidad and Tobago (KIRKALDY & TORRE BUENO 1909, SCHELL 1943b, NIESER & ALKINS KOO 1991, POLHEMUS & POLHEMUS 2016). *South America*: Colombia (SCHELL 1943b, DRAKE 1952, POLHEMUS & POLHEMUS 2016); Ecuador (SCHELL 1943b; FROESCHNER 1981; NIESER & CHEN 1992, as *O. aeneifrons*).

**Note.** The subspecies identity of the specimens recorded from Ecuador only as *O. aeneifrons* by NIESER & CHEN (1992) requires confirmation.

#### *Ochterus aeneifrons surinamensis* Nieser, 1975

(Fig. 14)

*Ochterus aeneifrons surinamensis* Nieser, 1975: 26–27–28, 31, Pl. 2b (key to species, description, illustrations). HOLOTYPE: ♂, Suriname: Carolinakreek, upstream of bridge (UM → ZMAN → RMNH).

*Ochterus aeneifrons surinamensis*: HECKMAN (2011): 458, 462 (diagnosis, illustration); MOREIRA et al. (2011): 58 (checklist Brazil); CORDEIRO et al. (2014): 67 (key to species for Brazil, illustration); BARBOSA & RODRIGUES (2015): 182 (illustrations).



Fig. 14. *Ochterus aeneifrons surinamensis* Nieser, 1975, female, Colombia: Rio Frio, 4.51 mm.

**Material examined.** COLOMBIA: CUNDINAMARCA: Rio Frio, 15.iii.1925, 2 ♀♀ (Fig. 14), C. J. Drake det. as *O. aeneifrons*, P. Kment revid. (NMPC).

**Distribution.** *Neotropical Region*: South America: Brazil: Amazonas (PEREIRA & MELO 2007, MOREIRA et al. 2011, CORDEIRO et al. 2014), Minas Gerais (PELLI et al. 2006, MOREIRA et al. 2011, CORDEIRO et al. 2014); Colombia (**new record**), Suriname (NIESER 1975); Venezuela (DRAKE 1952, as *O. aeneifrons*; POLHEMUS & POLHEMUS 2016).

**Note.** The holotype of the species was originally deposited in Zoölogisch Museum der Rijksuniversiteit, Utrecht. Later, its insect collection was transferred to ZMAN, which was later merged with RMNH. However, N. Nieser recently failed to find the holotype in RMNH (N. Nieser, pers. comm.).

#### *Ochterus africanus* Jaczewski, 1938

(Figs 15–17)

*Ochterus africanus* Jaczewski, 1938: 186–187 (description, differential diagnosis, illustrations). HOLOTYPE (Figs 14–16): 1 ♀, Central African Republic: ‘Französisch Kongo, Fort Crampel’ (ZMUH).

*Ochterus africanus*: KORMILEV (1973): 2 (list, *incertae sedis*).

**Distribution.** *Afrotropical Region*: Central African Republic (JACZEWSKI 1938).

**Note.** The photographs of the holotype of *O. africanus* (Figs 15–17) are presented here for the first time.

#### *Ochterus alticola* Baehr, 1990

*Ochterus alticola* Baehr, 1990b: 451, 453, 455–459, 461, 473 (key to species, description, illustrations). HOLOTYPE: ♂, Papua New Guinea: ‘Mafula, 4000 ft. [= 1219 m a.s.l.]’ (BMNH).

*Ochterus alticola*: CHEN et al. (2005): 413 (checklist).

**Distribution.** *Australian Region*: Papua New Guinea (BAEHR 1990b).

#### *Ochterus americanus* (Uhler, 1876)

*Pelagonus americanus* Uhler, 1876: 335–336 (original description).

SYNTYPES: USA: ‘Texas, Illinois, Eastern Massachusetts, Pennsylvania’ (USNM).

*Pelagonus americatus* (incorrect subsequent spelling): SNOW (1906): 180 (distribution).

*Ochterus americanus*: TORRE BUENO (1906): 50 (list); KIRKALDY & TORRE BUENO (1909): 179 (catalogue); BARBER (1913): 213 (key to species); VAN DUZEE (1917): 476 (catalogue); HUNGERFORD (1919): 51, 53–54, pl. III: fig. 9 (key to species, original description repeated); BLATCHLEY (1926): 1020–1021 (key to species, redescription, illustration); SCHELL (1943a): 32, 35 (key to species, illustration); SCHELL (1943b): 42–43 (original description repeated, differential diagnosis); DRAKE (1952): 74 (checklist); CHAPMAN (1958): 119 (key to species); WILSON (1958): 154 (key to species); BOBB (1974): 17, 20 (key to species); BENNETT & COOK (1981): 35 (diagnosis, illustrations); POLHEMUS & POLHEMUS (1988a): 542 (catalogue); EPLER (2006): 12.3–12.4 (key to species, illustrations); HECKMAN (2011): 461 (key to species, illustration); HOFFMAN (2012): 58–59 (illustration, distribution); POLHEMUS & POLHEMUS (2016): 16, 24–26 (key to species, diagnosis, illustrations).

*Ochterus americanum* (incorrect subsequent spelling): BARBER (1913): 215.

**Distribution.** *Nearctic Region*: Canada: Ontario (MAW et al. 2000); USA: ? Arizona (SNOW 1906, KIRKALDY & TORRE BUENO 1909, BLATCHLEY 1926, POLHEMUS & POLHEMUS 1988a), Florida (BARBER 1914, BLATCHLEY 1926, ? CHAPMAN 1958, POLHEMUS & POLHEMUS 2016), Georgia (POLHEMUS &



Figs 15–17. *Ochterus africanus* Jaczewski, 1938, female, holotype: 15 – habitus in dorsal view; 16 – head, frontal view; 17 – head, lateral view. Scale bars: 15 – 1 mm, 16–17 – 0.5 mm. Photographs by V. Hartung.

POLHEMUS 2016), Illinois (UHLER 1876; KIRKALDY & TORRE BUENO 1909; BLATCHLEY 1926; SCHELL 1943b; DRAKE 1952; POLHEMUS & POLHEMUS 1988a, 2016; TINERELLA et al. 2009), Iowa (DRAKE 1952), Kansas (HUNGERFORD & BEAMER 1925; BLATCHLEY 1926; POLHEMUS & POLHEMUS 1988a, 2016), Louisiana (POLHEMUS & POLHEMUS 1988a, 2016), Maryland (KIRKALDY & TORRE BUENO 1909; DRAKE 1952; POLHEMUS & POLHEMUS 1988a, 2016), Massachusetts (UHLER 1876, KIRKALDY & TORRE BUENO 1909; BLATCHLEY 1926, JOHNSON 1930, DRAKE 1952; POLHEMUS & POLHEMUS 1988a), Minnesota (POLHEMUS & POLHEMUS 2016), Mississippi (SCHELL 1943b, DRAKE 1952, WILSON 1958; POLHEMUS & POLHEMUS 1988a), Missouri (POLHEMUS & POLHEMUS 1988a, 2016; EPLER 2006), Nebraska (KIRKALDY & TORRE BUENO 1909; BLATCHLEY 1926; SCHELL 1943b; DRAKE 1952; POLHEMUS & POLHEMUS 1988a, 2016), New Jersey (SMITH 1890; TORRE BUENO 1905, 1908; KIRKALDY & TORRE BUENO 1909; BLATCHLEY 1926; CHAPMAN 1959; POLHEMUS & POLHEMUS 1988a, 2016), New York (TORRE BUENO 1905, 1908; KIRKALDY & TORRE BUENO 1909; BLATCHLEY 1926; LEONARD 1928; SCHELL 1943b; POLHEMUS & POLHEMUS 1988a), North Carolina (TORRE BUENO & BRIMLEY 1907; KIRKALDY & TORRE BUENO 1909; POLHEMUS & POLHEMUS 1988a, 2016), South Carolina (EPLER 2006), Pennsylvania (UHLER 1876, WIRTNER 1904, KIRKALDY &

TORRE BUENO 1909, POLHEMUS & POLHEMUS 1988a), Texas (UHLER 1876, KIRKALDY & TORRE BUENO 1909, BLATCHLEY 1926, POLHEMUS & POLHEMUS 1988a), Virginia (POLHEMUS & POLHEMUS 1988a, HOFFMAN 2012).

**Notes.** According to T. Henry (pers. comm.), the USNM collection contains four of what appear to be syntypes of *P. americanus* Uhler: 1 ♀ and one broken specimen (abdomen missing) from ‘Mass.’; 1 ♂ from ‘N. Ill.’; and 1 ♀ from ‘Dedham, Mass, Apr. 30, 65, nr water,’ as mentioned in the original description.

UHLER (1876) included also a specimen from Cuba, writing that: ‘has the spots of the costal margin of the hemelytra almost obsolete; but it agrees with the United States from in all other respects’. It was listed from Cuba also by BLATCHLEY (1926) and HECKMAN (2011), but DRAKE (1952) and later Cuban authors (ALAYO 1971, 1974; MUÑOZ RIVIAUX et al. 2010a,b; NARANJO et al. 2010) did not confirm its presence in that island.

According to POLHEMUS & POLHEMUS (1988a) records from Florida by Drake and from South Carolina (ROBACK 1958) require confirmation; the Florida specimens determined by Drake as *O. americanus* and reexamined by POLHEMUS & POLHEMUS (1988a) were actually *O. banksi*. The South Carolina distribution was confirmed by EPLER (2006).

### *Ochterus atridermis* Baehr, 1989

*Ochterus atridermis* Baehr, 1989: 114, 116, 118, 122–123 (key to species, description, illustrations). HOLOTYPE: ♂, Australia: Queensland: ‘Beerway [= Beerwah], S. E. Qld.’ (QMBA).

*Ochterus atridermis*: BAEHR (1990b): 18, 453–454, 456, 459, 461, 467 (key to species, redescription, illustrations).

*Ochterus atridermis*: CASSIS & GROSS (1995): 260 (catalogue); ANDERSEN & WEIR (2004): 268, 335 (key to species, checklist).

**Distribution. Australian Region:** Australia: Northern Territory (BAEHR 1989, ANDERSEN & WEIR 2004), Queensland (BAEHR 1989, ANDERSEN & WEIR 2004).

### *Ochterus australicus* Jaczewski, 1934

*Ochterus marginatus* (misidentification): DISTANT (1920): 164 (specimen from Gondé, see JACZEWSKI 1934: 609).

*Ochterus australicus* Jaczewski, 1934: 607–610 (description, differential diagnosis, illustration) (partim, see Note). LECTOTYPE: ♂ (designated by BAEHR 1990b: 452), New Caledonia (BMNH).

*Ochterus australicus* (partim): KORMILEV (1971): 434, 439–442 (partim; redescription based on specimens from Queensland: North Stradbroke Island, illustrations).

*Ochterus australicus*: JACZEWSKI (1935): 482 (key to species); BAEHR (1989): 113, 114–116, 118 (key to species, redescription, illustrations); BAEHR (1990b): 452–456, 459, 461 (key to species, redescription, illustrations, lectotype designation); CASSIS & GROSS (1995): 260 (catalogue); ANDERSEN & WEIR (2004): 267–270, 335 (key to species, illustrations, checklist); CHEN et al. (2005): 413 (checklist); DAMGAARD & ZETTEL (2014): 227, 236 (checklist).

**Material examined. AUSTRALIA: NEW SOUTH WALES:** Bellinger River N.P., Darkwood Rd., W of Darkwood Bridge, 30°26.80'S 152°37.12'E, 95 m a.s.l., 27.xi.2014, 2 ♂♂, D. Rédei & Q. Xie lgt., D. Rédei 2016 det., P. Kment revid. (NMPC).



Fig. 18. *Ochterus bacchusi* Baehr, 1990, male, Australia: New South Wales: Ku-ring-gai Chase NP, 4.31 mm.

**Distribution. Australian Region:** Australia: New South Wales (KORMILEV 1971, ANDERSEN & WEIR 2004), Northern Territory (BAEHR 1990b), Queensland (KORMILEV 1971; BAEHR 1989, 1990b; ANDERSEN & WEIR 2004), South Australia (KORMILEV 1971, BAEHR 1989, ANDERSEN & WEIR 2004), Tasmania (MANCINI 1939a, BAEHR 1990b, ANDERSEN & WEIR 2004), Victoria (BAEHR 1990b, ANDERSEN & WEIR 2004), Western Australia (KORMILEV 1971, ANDERSEN & WEIR 2004); New Caledonia (DISTANT 1920, as *O. marginatus*; JACZEWSKI 1934; KORMILEV 1971; BAEHR 1990b; ANDERSEN & WEIR 2004); Papua New Guinea (MANCINI 1939a, BAEHR 1990b); Vanuatu (as New Hebrides) (JACZEWSKI 1934; BAEHR 1989, 1990b; ANDERSEN & WEIR 2004); Solomon Islands (ANDERSEN & WEIR 2004): Choiseul (KORMILEV 1971), Guadalcanal (KORMILEV 1971, BAEHR 1990b), San Cristobal (KORMILEV 1971).

**Note.** All the syntypes of *O. australicus* from Australia (JACZEWSKI 1934) belong to *O. eurythorax* (see BAEHR 1990b). Several of KORMILEV's (1971) records from Victoria, southeastern Queensland, the Cape York Peninsula, Indonesia (Papua, West Papua), Papua New Guinea, and all records from Tasmania actually refer to other species (BAEHR 1989).

### *Ochterus bacchusi* Baehr, 1990

(Fig. 18)

*Ochterus bacchusi* Baehr, 1990b: 452–454, 456–459, 461, 465 (key to species, description, illustrations). HOLOTYPE: ♂, Australia: New South Wales: ‘Wentworth Falls, Blue Mts.’ (BMNH).

*Ochterus bacchusi*: CASSIS & GROSS (1995): 260–261 (catalogue); ANDERSEN & WEIR (2004): 267–268, 270, 335 (key to species, illustrations, checklist).

**Material examined. AUSTRALIA: NEW SOUTH WALES:** Ku-ring-gai Chase National Park, near McCarrs Creek, 22.x.1993, 17 ♂♂ 15 ♀♀, P. Štys lgt., P. Kment det. (13 ♂♂ 11 ♀♀ MMBC, 3 ♂♂ 3 ♀♀ NMPC, 1 ♂ 1 ♀ ZJPC).

**Distribution. Australian Region:** Australia: New South Wales (BAEHR 1990b, ANDERSEN & WEIR 2004).

### *Ochterus baehri baehri* Rieger, 1977

*Ochterus baehri* Rieger, 1977: 215–216 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Australia: Queensland: ‘Stewart River, Cope [= Cape] York Peninsula, North Queensland’ (CRNG).

*Ochterus baehri baehri*: BAEHR (1989): 114, 116, 118–119 (key to species, redescription, illustrations); BAEHR (1990b): 451, 453, 455–456, 472 (key to species, illustrations); CASSIS & GROSS (1995): 261 (catalogue); ANDERSEN & WEIR (2004): 268, 335 (key to species, checklist).

**Distribution. Australian Region:** Australia: Queensland (RIEGER 1977; BAEHR 1989, 1990b; ANDERSEN & WEIR 2004).

**Note.** The type depository was cited as ZSMC in error by ANDERSEN & WEIR (2004) (Ch. Rieger, pers. comm.).

### *Ochterus baehri riegeri* Baehr, 1989

*Ochterus baehri riegeri* Baehr, 1989: 114, 116, 118–119–121 (key to species, description, illustrations). HOLOTYPE: ♂, Australia: Northern Territory: ‘Humpty Doo, NT’ (QMBA).

*Ochterus baehri riegeri*: BAEHR (1990b): 451, 459, 461, 472 (key to species, illustrations); CASSIS & GROSS (1995): 261 (catalogue); ANDERSEN & WEIR (2004): 268, 270, 335 (key to species, illustrations, checklist).

**Distribution. Australian Region:** Australia: Northern Territory (BAEHR 1989, 1990b; ANDERSEN & WEIR 2004).

***Ochterus baltazarae* Gapud & San Valentín, 1977**

*Ochterus baltazarae* Gapud & San Valentín, 1977: 272, 278–283, 285–286, 288–289, 296–298 (key to species, description, illustrations, variation; partim, except paratypes of Zambales form). HOLOTYPE: ♂, Philippines: Luzon: ‘Quezon National Park, Atimonan, Quezon’ (UPLB).

*Ochterus baltazarae*: GAPUD (1986): 32, 36–38 (key to species, redescription, illustration); GAPUD (2003): 103, 107 (taxonomy, checklist); CHEN et al. (2005): 413 (checklist).

**Distribution.** *Oriental Region:* Philippines: Luzon (GAPUD & SAN VALENTÍN 1977).

**Note.** Specimens of ‘Zambales form’ belong actually to *O. luzonicus* Gapud, 2003 (GAPUD 2003).

***Ochterus banksi* Barber, 1913**

*Ochterus banksi* Barber, 1913: 213–214–215 (key to species, original description, illustration). SYNTYPES: 3 ♂♂ 1 ♀, USA: Virginia: ‘at Glencarlyn’ (coll. N. Banks → AMNH).

*Ochterus banksi*: VAN DUZEE (1917): 476 (catalogue); HUNGERFORD (1919): 51–53 (key to species, original description repeated); BLATCHLEY (1926): 1020–1021 (key to species, redescription); SCHELL (1943a): 32, 35 (key to species, illustration); DRAKE (1943b): 45 (original description repeated, differential diagnosis); BOBB (1951): 93–100 (redescription, description of egg and larval instars I–V, biology, ecology); DRAKE (1952): 74 (checklist); CHAPMAN (1958): 119–120 (key to species); WILSON (1958): 154 (key to species); BOBB (1971): 17–20 (key to species, redescription, larval instars, illustrations); POLHEMUS & POLHEMUS (1988a): 542 (catalogue); EPLER (2006): 12.1–12.4 (key to species, variability, illustrations); HOFFMAN (2012): 59 (illustration, distribution); POLHEMUS & POLHEMUS (2016): 11, 13, 17, 26–30 (key to species, redescription, illustrations, new synonymy).

*Ochterus banksii* (incorrect subsequent spelling): HECKMAN (2011): 463 (key to species, illustration).

*Ochterus flaviclavus* Barber, 1913: 213, 215 (key to species, original description). HOLOTYPE: ♂, USA: Florida: ‘Ormond’ (coll. Barber → USNM). Junior subjective synonym, suggested by EPLER (2006: 12.4), confirmed by POLHEMUS & POLHEMUS (2016: 26).

*Ochterus flaviclavus*: VAN DUZEE (1917): 476 (catalogue); HUNGERFORD (1919): 51–52 (key to species, original description repeated); BLATCHLEY (1926): 1020, 1022 (key to species, redescription); SCHELL (1943a): 32, 35 (key to species, illustration); SCHELL (1943b): 40–41 (original description repeated, differential diagnosis); DRAKE (1952): 74 (checklist); CHAPMAN (1958): 119–120 (key to species); POLHEMUS & POLHEMUS (1988a): 542 (catalogue); EPLER (2006): 12.3–12.4 (key to species, taxonomy, illustrations); HECKMAN (2011): 460 (key to species, illustration).

**Material examined.** USA: ILLINOIS: Union Co., Pine Hills 3, 10.viii.1984, J. E. McPherson, R. J. Packauskas & T. E. Vogt lgt., Z. Jindra det., P. Kment revid. (ZJPC). NEW YORK: White Plains, 15.xii.[19]17, 1 ♂, JRTB Collr [= J. R. Torre Bueno lgt.], C. J. Drake det. (NMPC).

**Distribution.** *Nearctic Region:* USA: Connecticut (POLHEMUS & POLHEMUS 2016), Florida (DRAKE 1913, 1914; BLATCHLEY 1926, both as *O. flaviclavus*; SCHELL 1943b; DRAKE 1952; CHAPMAN 1958; POLHEMUS & POLHEMUS 1988a, 2016; EPLER 2006), Illinois (TINERELLA et al. 2009), Indiana (BLATCHLEY 1926; POLHEMUS & POLHEMUS 1988a), Kansas (POLHEMUS & POLHEMUS 1988, as *O. flaviclavus*; 2016), Louisiana (POLHEMUS & POLHEMUS 1988a, as *O. flaviclavus*; 2016), Maryland (POLHEMUS & POLHEMUS 2016), Massachusetts (DRAKE 1952, POLHEMUS & POLHEMUS 1988a), Michigan (POLHEMUS & POLHEMUS 2016), Mississippi (DRAKE 1952; WILSON 1958; POLHEMUS & POLHEMUS 1988a, 2016); New Jersey (SCHELL 1943b; DRAKE 1952, POLHEMUS & POLHEMUS 1988a), New York (BLATCHLEY 1926, LEONARD 1928, SCHELL

1943b, DRAKE 1952, POLHEMUS & POLHEMUS 1988a), Ohio (POLHEMUS & POLHEMUS 2016), Pennsylvania (POLHEMUS & POLHEMUS 2016), South Carolina (BOBB 1951, POLHEMUS & POLHEMUS 1988a), Texas (POLHEMUS & POLHEMUS 1988a, 2016; POLHEMUS 1997; EPLER 2006), Virginia (BARBER 1913; BLATCHLEY 1926; SCHELL 1943b; DRAKE 1952; BOBB 1951, 1974; POLHEMUS & POLHEMUS 1988a, 2016; HOFFMAN 2012), West Virginia (POLHEMUS & POLHEMUS 2016).

**Note.** BARBER (1913) described the species based on a single male from the collection of Mrs. Annie Trumbull Slosson. Later, SCHELL (1943b) mentioned that the holotype was deposited in Barber’s collection. Currently it is deposited in USNM (T. Henry, pers. comm.).

***Ochterus barberi* Schell, 1943**

*Ochterus barberi* Schell, 1943a: 32, 35 (key to species, illustration). LECTOTYPE (designated by SCHELL 1943b: 42, as holotype): ♂, USA: Arizona: ‘Colorado Canyon’ [= Grand Canyon of Colorado River] (USNM).

*Ochterus barberi*: SCHELL (1943b): 41–42 (original description, differential diagnosis); DRAKE (1952): 74 (checklist); MENKE (1979): 125 (distribution, illustration); POLHEMUS & POLHEMUS (1988a): 542 (catalogue); POLHEMUS (1992b): 442 (note on type labels); HECKMAN (2011): 287, 463 (key to species, illustration); POLHEMUS & POLHEMUS (2016): 17, 30–33 (key to species, redescription, illustrations).

**Distribution.** *Nearctic Region:* USA: Arizona (SCHELL 1943b; DRAKE 1952; POLHEMUS 1973; POLHEMUS & POLHEMUS 1976, 1988a, 2016; STEVENS & POLHEMUS 2008), California (MENKE 1979; POLHEMUS & POLHEMUS 1988a, 2016), Colorado (POLHEMUS & POLHEMUS 2016), New Mexico (DRAKE 1952; POLHEMUS 1973; POLHEMUS & POLHEMUS 1988a, 2016); Mexico: Sonora (POLHEMUS & POLHEMUS 1988a, 2016).

**Note.** SCHELL (1943b) also listed paratypes [actually paralectotypes] from Orizaba, in the Mexican state of Veracruz, but these specimens have proven on closer examination to represent females of *O. aeneifrons* (POLHEMUS & POLHEMUS 2016).

The revision of American *Ochterus* including the description of *O. barberi* was published divided in two parts, first published in January 1943 (SCHELL 1943a) and second in April 1943 (SCHELL 1943b). The species was first introduced in the key, which is sufficient to make it available (ICZN 1999: Art. 13.1.1), without any mention of type specimens (SCHELL 1943a: 32), while the original description including the holotype designation appeared in the second part (SCHELL 1943b: 41). As a holotype is defined as ‘the single specimen upon which a new nominal species-group taxon is based in the original publication’ (ICZN 1999: Art. 73.1), in this case, the subsequently designated ‘holotype’ must be considered the lectotype according to ICZN (1999: Art. 74.5).

***Ochterus barrosoi* Gapud, 1981**

*Ochterus barrosoi* Gapud, 1981: 305–307–309 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Philippines: Leyte: ‘Calbiga-a River, Mt Pangasugan’ (UPLB).

*Ochterus barrosoi*: GAPUD (1981): 107 (checklist); CHEN et al. (2005): 413 (checklist).

**Distribution.** *Oriental Region:* Philippines: Leyte (GAPUD 1981).

### *Ochterus bidentatus* Schell, 1943

*Ochterus bidentatus* Schell, 1943a: 32, 35 (key to species, illustration).

LECTOTYPE (designated by SCHELL 1943b: 44, as holotype): ♂, Peru: ‘Vic. San Pedro’ (SEMC).

*Ochterus bidentatus* SCHELL (1943b): 44 (original description, differential diagnosis); DRAKE (1952): 74 (checklist); HECKMAN (2011): 462–463 (key to species, illustration).

**Distribution.** *Neotropical Region:* South America: Peru (SCHELL 1943b, DRAKE 1952, NIESER & CHEN 1992).

**Note.** The revision of American *Ochterus* including the description of *O. bidentatus* was published divided in two parts, the first published in January 1943 (SCHELL 1943a) and the second in April 1943 (SCHELL 1943b). The species was first introduced in the key, which is sufficient to make it available (ICZN 1999: Art. 13.1.1), without any mention of type specimens (SCHELL 1943a: 32), while the original description including the holotype designation appeared in the second part (SCHELL 1943b: 44). As a holotype is defined as ‘the single specimen upon which a new nominal species-group taxon is based in the original publication’ (ICZN 1999: Art. 73.1), in this case, the subsequently designated ‘holotype’ must be considered the lectotype according to ICZN (1999: Art. 74.5).

### *Ochterus brachysoma* Rieger, 1977

*Ochterus brachysoma* Rieger, 1977: 214–215 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Australia: Queensland: ‘Stewart River, Cope [=Cape] York Peninsula, North Queensland’ (CRNG).

*Ochterus brachysoma*: BAEHR (1989): 114, 116, 118, 121–122 (key to species, redescription, illustrations); BAEHR (1990b): 450, 453, 455, 456, 459, 461, 472–473 (key to species, redescription, illustrations); CASSIS & GROSS (1995): 261 (catalogue); ANDERSEN & WEIR (2004): 267, 270, 335 (key to species, illustrations, checklist).

**Distribution.** *Australian Region:* Australia: Queensland (RIEGER 1977; BAEHR 1989, 1990b; ANDERSEN & WEIR 2004).

### *Ochterus breviculus* Nieser & Chen, 1992

*Ochterus breviculus* Nieser & Chen, 1992: 9–11 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, China: Tibet: ‘Beibeng, 850 m’ (IZAS).

*Ochterus breviculus*: POLHEMUS (1995a): 25 (catalogue); XIE & LIU (2013): 6 (checklist).

**Distribution.** *Oriental/Palaearctic Region:* China: Yunnan (NIESER & CHEN 1992, XIE & LIU 2013), Xizang (= Tibet) (NIESER & CHEN 1992, XIE & LIU 2013).

### *Ochterus bruneiensis* Zettel & Lane, 2010

*Ochterus bruneiensis* Zettel & Lane, 2010: 98–101 (description, illustrations). HOLOTYPE: ♂, Brunei: Brunei-Muara District, Sungai Akar, waterfall area near main road, 47 m a.s.l., N 04°56'45" E 114°59'13" (BMKB).

**Distribution.** *Oriental Region:* Brunei (ZETTEL & LANE 2010).

### *Ochterus brunneus* Hungerford, 1927

*Ochterus brunneus* Hungerford, 1927: 188–189 (description, differential diagnosis). SYNTYPES: 2 ♂♂, Bolivia: ‘Huachi Rio Beni’ (USNM).

*Ochterus brunneus*: SCHELL (1943a): 32, 35 (key to species, illustration); SCHELL (1943b): 41 (original description repeated, differential diagnosis); DRAKE (1952): 74 (checklist); HECKMAN (2011): 461 (key to species, illustration).

**Distribution.** *Neotropical Region:* South America: Bolivia (HUNGERFORD 1927, DRAKE 1952).

### *Ochterus caffer* (Stål, 1855)

(Figs 8, 19)

*Pelogonus caffer* Stål, 1855: 46 (original description). SYNTYPE(s): South Africa: Natal (NHRS).

*Pelogonus marginatus* (partim): STÅL (1866): 170–171 (redescription, catalogue); STÅL (1876): 137 (catalogue).

*Ochterus marginatus caffer*: JACZEWSKI (1934): 606–607 (differential diagnosis, illustrations); JACZEWSKI (1935): 483 (key to species); POISSON (1948): 169 (distribution); POISSON (1949): 48 (distribution); POISSON (1954): 363 (distribution); BERTRAND (1962): 882 (distribution); POISSON (1968a): 401 (distribution); POISSON (1968b): 34 (distribution); POISSON & SALLIER DUPIN (1969): 19 (distribution).

*Ochterus caffer*: MANCINI (1939a): 124–125 (raised to species status, variability, illustrations); KORMILEV (1973): 2–3, 5–6, 8 (redescription, illustrations), POLHEMUS & POLHEMUS (2008): 286 (key to species for Indian Ocean).

**Material examined.** ?: Environs du Tsad [= environs of Lake Chad], 1937, 5 ♂♂ 1 ♀, Škulina lgt., P. Kment det. (NMPC). **BENIN:** SE, Cove, Zou river, 16.iv.2000, 2 ♂♂, J. Halada lgt., P. Kment det. (ZJPC). **CAMEROON:** NW, Tubah sbdiv., Big Babanki, N of Bamenda, 2100 m a.s.l., xii.2009, 1 ♂, R. Sehnal lgt., P. Kment det. (ZJPC). **DEMOCRATIC REPUBLIC OF THE CONGO:** ITURI: Congo b., Ituri, 1937, 1 ♂, Škulina lgt., P. Kment det. (NMPC). **CENTRAL AFRICAN REPUBLIC:** ca. 60 km W Bouar, 5°45'N 15°13'E, 660 m a.s.l., 23.iii.2010, 1 ♂, J. Halada lgt., P. Kment det. (MMBC); 60 km W Bouar, 5°42'N 16°00'E, 860 m a.s.l., 30.iii.2010, 1 ♂, J. Halada lgt., P. Kment det. (MMBC). **IVORY COAST:** Bouaké, 22.–23.iv.1964, 1 ♂, R. H. Cobben lgt., P. Kment det. (ACPI). **MADAGASCAR:** CE, 1 km E of Andreba, village, 2 km E of Alaotra lake, 30.x.2003, 2 ♂♂ 1 ♀, P. Baňař lgt., P. Kment det.



Fig. 19. *Ochterus caffer* (Stål, 1855), female, Sudan: Ed Damazin, 5.20 mm.

(1 ♂ 1 ♀ MMBC, 1 ♂ NMPC); NE, Ankarafansika N.P., 22.–24.iv.2011, ca. 100 m a.s.l., sweeping close to main entrance, 1 ♂, P. Baňák lgt., P. Kment det. (MMBC). **MOZAMBIQUE:** CW, 30 km NE Guro, 17°14'S 33°27'E, 620 m a.s.l., 11.xii.2005, 1 ♂ 1 ♀, J. Halada lgt., P. Kment det. (MMBC). **SOUTH SUDAN: UPPER NILE:** near Malakal, 5.–20.i.1963, 1 ♂ 1 ♀, R. E. Linnavuori lgt., P. Kment det. (ACPI). **SUDAN: BLUE NILE:** Blue Nile Prov., Ed Damazin [= Ad-Damazin], 2.xii.1967, 1 ♂ 5 ♀♀ (Fig. 19), P. Štys lgt. (1169), P. Kment det. (1 ♂ 4 ♀♀ MMBC, 1 ♀ NMPC). **SENNAR:** Blue Nile prov., Dinder Game Reserve, Galegu, 28.ii.1967, 4 ♂♂ 4 ♀♀, P. Štys lgt. (653), P. Kment det. (3 ♂♂ 3 ♀♀ MMBC, 1 ♂ 1 ♀ NMPC); same locality, 4.iii.1967, 4 ♂♂ 6 ♀♀, P. Štys lgt. (686), P. Štys det. as *O. marginatus caffer*, P. Kment revid. (3 ♂♂ 5 ♀♀ MMBC, 1 ♂ 1 ♀ NMPC).

**Distribution. Afro-tropical Region:** Benin (KORMILEV 1973); Burkina Faso (LINNAUORI 1981); Cameroon (POISSON 1948); Cape Verde Islands: Santiago Island (MANCINI 1939a); Central African Republic (LINNAUORI 1981); Chad (LINNAUORI 1981); Democratic Republic of the Congo (POISSON 1949, 1968b; POISSON & SALLIER DUPIN 1969); Ethiopia (DE CARLINI 1895, MANCINI 1956); Gambia (NIESER & CHEN 1992); Guinea (POISSON 1954, BERTRAND 1962); Ivory Coast (POISSON 1968a); Kenya (JACZEWSKI 1934); Madagascar (POLHEMUS & POLHEMUS 2008); Mozambique (**new record**); Nigeria (JACZEWSKI 1934, LINNAUORI 1981); Republic of the Congo (BERTRAND 1962); São Tomé and Príncipe: Príncipe Island (MANCINI 1939a); Senegal (NIESER & CHEN 1992); Sierra Leone (JACZEWSKI 1934); Somalia (MANCINI 1939a,b; LINNAUORI 1982); South Africa (STÅL 1855, JACZEWSKI 1934, KORMILEV 1973); South Sudan (LINNAUORI 1971, 1980); Sudan (**new record**); Tanzania (JACZEWSKI 1934).

### *Ochterus cheesmannaiae* Baehr, 1990

*Ochterus cheesmannaiae* Baehr, 1990b: 450, 453, 455–459, 461, **473–474** (key to species, description, illustrations). HOLOTYPE: ♂, Indonesia: West Papua: ‘N. Dutch New Guinea: Waigeu, Camp Nok., 2500 ft [= 762 m a.s.l.]’ (BMNH).

*Ochterus cheesmannaiae*: CHEN et al. (2005): 413 (checklist).

**Distribution. Australian Region:** Indonesia: West Papua: Waigeo Island (BAEHR 1990b, CHEN et al. 2005)

### *Ochterus chiapensis*

#### D. A. Polhemus & J. T. Polhemus, 2016

*Ochterus chiapensis* D. A. Polhemus & J. T. Polhemus, 2016: 14, 17, 33–36 (key to species, description, illustrations). HOLOTYPE: ♂, Mexico: ‘Chiapas, seeping roadside rock faces near Ixhuatan [2.5 mi. S of Ixhuatan, vic. 17°16'04"N, 93°01'26"W, elev. ~640 m]’ (JTPC → USNM).

**Distribution. Neotropical Region: Central America:** Mexico: Chiapas (POLHEMUS & POLHEMUS 2016).

### *Ochterus costaricensis*

#### D. A. Polhemus & J. T. Polhemus, 2016

*Ochterus costaricensis* D. A. Polhemus & J. T. Polhemus, 2016: 17, **36–39** (key to species, description, illustrations). HOLOTYPE: ♂, Costa Rica: ‘Puntarenas, roadside waterfall 15 mi. N of Palmar Norte [8°58'14"N, 83°18'15"W, elev. 70 m]’ (JTPC → USNM).

**Distribution. Neotropical Region: Central America:** Costa Rica (POLHEMUS & POLHEMUS 2016); El Salvador (POLHEMUS & POLHEMUS 2016); Panama (POLHEMUS & POLHEMUS 2016).

### *Ochterus dufouri* (Montrouzier, 1864)

*Pelagonus Dufouri* Montrouzier, 1864: 241 (original description). LECTOTYPE (designated by BAEHR 1990b: 456): ♂, New Caledonia: ‘N. Calédonie, Kanala’ (ISNB).

*Pelagonus Dufouri*: STÅL (1876): 137 (catalogue).

*Pelagonus Dufouri* (incorrect subsequent spelling): SCHOUTEDEN (1907): 117 (types).

*Ochterus dufouri*: JACZEWSKI (1934): 609–610 (repeating original description, differential diagnosis); KORMILEV (1971): 442–443 (repeating original description); BAEHR (1990b): 451, 453–454, 456–459, 461 (key to species, redescription, illustrations, lectotype designation); DAMGAARD & ZETTEL (2014): 237 (checklist).

**Distribution. Australian Region:** New Caledonia (MONTROUZIER 1864, BAEHR 1990b).

### *Ochterus erythorax* Baehr, 1989

*Ochterus marginatus* (misidentification): HALE (1925): 14–15 (distribution, partim) (see JACZEWSKI 1934: 607, as *O. australicus*).

*Ochterus australicus* (misidentification): JACZEWSKI (1934): 607–610 (partim, few syntypes from Australia) (see BAEHR 1990: 452).

*Ochterus australicus* (misidentification): KORMILEV (1971): 434: Fig. 12, 439–440, 442: Fig. 22 (redescription) (see BAEHR 1989: 115, 1990: 452).

*Ochterus erythorax* Baehr, 1989: 114, 116–118 (key to species, description, illustrations). HOLOTYPE: ♂, Australia: Queensland: ‘Dunwich, Stradbroke Isl., S. E. Qld’ (QMBA).

*Ochterus erythorax*: BAEHR (1990b): 452–454, 456, 459, 461–462, 464 (key to species, redescription, illustrations); CASSIS & GROSS (1995): 261 (catalogue); ANDERSEN & WEIR (2004): 267–268, 335 (key to species, illustration, checklist).

**Distribution. Australian Region:** Australia: Australian Capital Territory (BAEHR 1990b, ANDERSEN & WEIR 2004), New South Wales (JACZEWSKI 1934, as *O. australicus*; BAEHR 1990b; ANDERSEN & WEIR 2004), Queensland (JACZEWSKI 1934, as *O. australicus*; BAEHR 1989, 1990b; ANDERSEN & WEIR 2004), South Australia (BAEHR 1989, ANDERSEN & WEIR 2004), Tasmania (BAEHR 1989, 1990b; ANDERSEN & WEIR 2004), Victoria (BAEHR 1989, 1990b; ANDERSEN & WEIR 2004). **Note.** Records from Papua New Guinea (BAEHR 1989) refer presumably to another species (see BAEHR 1990b).

### *Ochterus explanatus*

#### D. A. Polhemus & J. T. Polhemus, 2016

*Ochterus explanatus* D. A. Polhemus & J. T. Polhemus, 2016: 11, 16, **39–41** (key to species, description, illustrations). HOLOTYPE: ♀, Mexico: Durango: ‘Durango [incorrectly indicated as Sonora], 7 mi. W of Los Bancos [vic. 23°38'54"N, 105°47'56"W, elev. ~2320 m]’ (JTPC → USNM).

**Distribution. Neotropical Region: Central America:** Mexico: Durango (POLHEMUS & POLHEMUS 2016), Oaxaca (POLHEMUS & POLHEMUS 2016).

### *Ochterus feae* Mancini, 1939

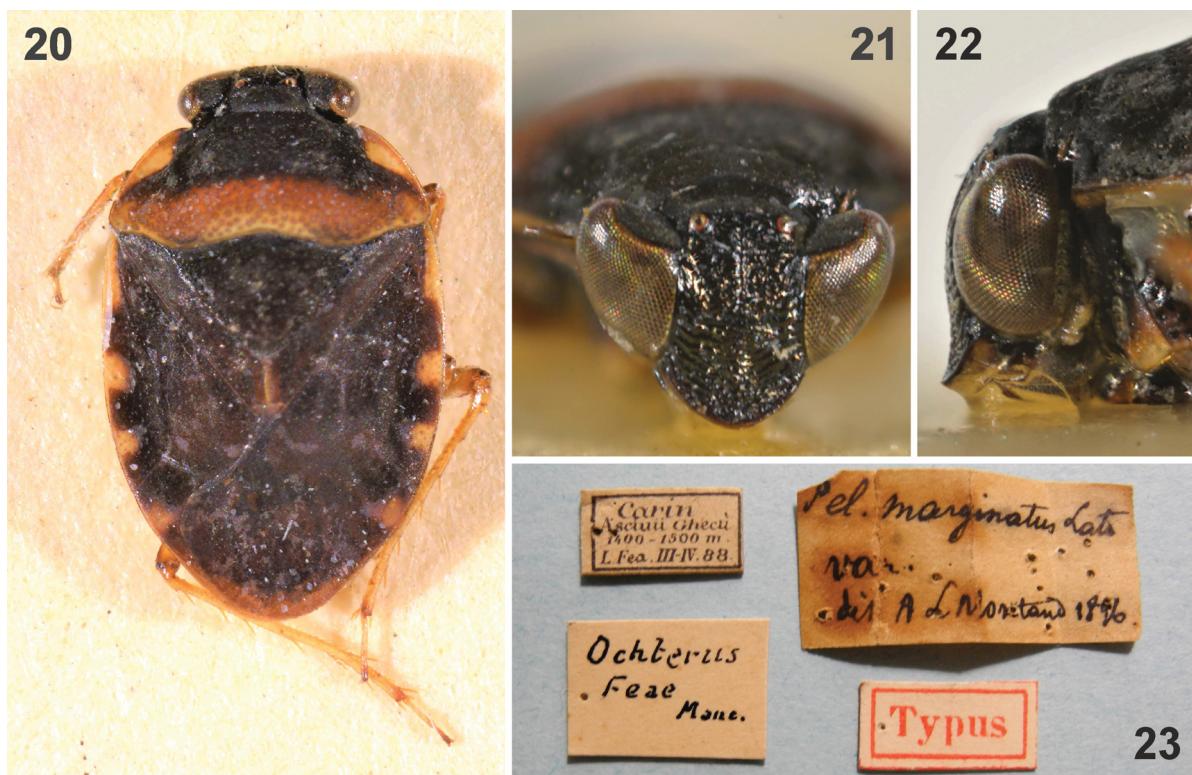
(Figs 20–23)

*Pelagonus marginatus* (misidentification): MONTANDON (1897): 365 (variability, distribution); DISTANT (1906): 14 (illustration of the specimen from MONTANDON 1897).

*Ochterus Feae* Mancini, 1939a: **125–126** (description, differential diagnosis, illustrations). HOLOTYPE: ♀ (Figs 20–23), Myanmar: ‘Carin: Asciuii Ghecu’ (MCSN).

*Ochterus feae*: KORMILEV (1971): 443 (list).

**Material examined. LAOS:** LUANG PRABANG: Louang Phrabang prov., Ban Song Cha (5 km W), 20°33'–34'N 102°14'E, ca. 1200 m a.s.l., 24.iv.–16.v.1999, 6 ♂♂, V. Kubáň lgt. (4 ♂♂ MMBC, 2 ♂♂ NMPC). **OU DOMXAY:** Oudomxai (17 km NEE), 20°46'N 102°09'E, ca. 1100 m



Figs 20–23. *Ochterus feae* Mancini, 1939, female, holotype: 20 – habitus in dorsal view; 21 – head, frontal view; 22 – head, lateral view; 23 – type labels. Photographs by R. Poggi.

a.s.l., 1.–9.v.2002, 1 ♂ 1 ♀, V. Kubán lgt. (MMBC). **MYANMAR:** CHIN: Chin hills, NW of Falam, 400–500 m a.s.l., v.–vi.2016, 12 ♂♂ 6 ♀♀, A. Carapezza det. (ACPI). **THAILAND:** CHIANG MAI: San Pakia village, 19.19°N 98.50°E, 1400 m a.s.l., 1 ♂ 3 ♀♀, 1.–15.v.1998, V. Kubán lgt. (1 ♂ 2 ♀♀ MMBC, 1 ♀ NMPC). MAE HONG SON: Ban Huai Po, 1600–2000 m a.s.l., 1 ♂, J. Horák lgt. (NMPC). TAK: Umphang, 16°04'N 98°53'E, 500 m a.s.l., 26.iv.–6.v.[19]91, 1 ♀, D. Král lgt. (NMPC). All P. Kment det.

**Distribution. Oriental Region:** Laos (new record); Myanmar (MONTANDON 1897, DISTANT 1906, as *P. marginatus*; MANCINI 1939a); Thailand (new record).

**Note.** This species was described based on a female holotype and has never been recorded again. It is related to *O. marginatus*, from which it differs mainly by the anterior margin of the head being distinctly reflexed (see KORMILEV 1971). The photographs of the holotype of *O. feae* (Figs 20–23) are presented here for the first time.

#### *Ochterus foersteri* Kormilev & De Carlo, 1952

*Ochterus foersteri* Kormilev & De Carlo, 1952: 155–159. HOLOTYPE: ♂, Paraguay: ‘Caaguazú, Paso Yobai’ (MACN).

*Ochterus foersteri*: KORMILEV & DECARLO (2017): 204 (catalogue); BACHMANN (1999): 207 (types); HECKMAN (2011): 461 (key to species).

**Distribution. Neotropical Region:** Argentina: Misiones (MELO 2015; BACHMANN & MAZZUCCONI 1995, 2017; BACHMANN 1998); Paraguay (KORMILEV & DE CARLO 1952, BACHMANN & MAZZUCCONI 2017).

#### *Ochterus grandiusculus* Nieser & Chen, 1992

*Ochterus grandiusculus* Nieser & Chen, 1992: 11–12 (description, differential diagnosis, illustration). HOLOTYPE: ♂, Indonesia: Sulawesi: ‘Sulawesi Tenggara, road Kolaka-Kendari Km 20’ (MUDH).

*Ochterus grandiusculus*: NIESER & CHEN (1999): 89–90 (key, illustration); CHEN et al. (2005): 413 (checklist).

**Distribution. Australian Region:** Indonesia: Sulawesi (NIESER & CHEN 1992).

#### *Ochterus gressitti* Kormilev, 1971

*Ochterus gressitti* Kormilev, 1971: 434, 438–439 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Papua New Guinea: Morobe Province: ‘NE New Guinea, Wampit V. near Gurakor village, near Wau, 550 m’ (BPBM).

*Ochterus gressitti*: GAPUD (1981): 303–305, 307 (diagnosis, illustrations); BAEHR (1990b): 451, 453, 455–459, 461, 471 (key to species, redescription, illustrations); CHEN et al. (2005): 413 (checklist).

**Distribution. Australian Region:** Indonesia: Papua (KORMILEV 1971), West Papua (KORMILEV 1971); Papua New Guinea (KORMILEV 1971, GAPUD 1981, BAEHR 1990b), incl. New Britain (KORMILEV 1972).

#### *Ochterus homorfos* Nieser & Chen, 1999

*Ochterus homorfos* Nieser & Chen, 1999: 90–91–92, 123 (key, description, illustrations). HOLOTYPE: ♂, Indonesia: Sulawesi Utara, Gunung Ambang NSG (NHMW).

*Ochterus homorfos*: CHEN et al. (2005): 413 (checklist).

**Distribution. Australian Region:** Indonesia: Sulawesi (NIESER & CHEN 1999).

#### *Ochterus hungerfordi* Schell, 1943

*Ochterus americanus* (partim, misidentification): UHLER (1876): 336 (specimen from Cuba).

*Ochterus hungerfordi* Schell, 1943a: 32, 35 (key to species, illustration). LECTOTYPE (designated by SCHELL 1943b: 37, as holotype): ♂, Cuba: ‘Mantanzas, Mumuri Valley’ (SEMC).

*Ochterus hungerfordi*: SCHELL (1943b): 37 (original description, differential diagnosis); DRAKE (1952): 74 (checklist); ALAYO (1971): 4–5 (key to species); ALAYO (1974): 34–35 (key to species); HECKMAN (2011): 459 (key to species, illustration).

**Material examined.** CUBA: Sierra Maestra, x.[19]28, 1 ♀, Dr. Rambosek lgt., L. Hoberlandt det., P. Kment revid. (NMPC).

**Distribution.** *Neotropical Region:* Caribbean Islands: Cuba (SCHELL 1943b; DRAKE 1952; ALAYO 1971, 1974; MUÑOZ RIVIAUX et al. 2010a,b; NARANJO et al. 2010).

**Note.** The revision of American *Ochterus* including the description of *O. hungerfordi* was published divided in two parts, the first published in January 1943 (SCHELL 1943a) and the second in April 1943 (SCHELL 1943b). The species was first introduced in the key, which is sufficient to make it available (ICZN 1999: Art. 13.1.1), without any mention of type specimens (SCHELL 1943a: 32), while the original description including the holotype designation appeared in the second part (SCHELL 1943b: 37). As a holotype is defined as ‘the single specimen upon which a new nominal species-group taxon is based in the original publication’ (ICZN 1999: Art. 73.1), in this case, the subsequently designated ‘holotype’ must be considered the lectotype according to ICZN (1999: Art. 74.5).

#### *Ochterus jaczewskii* Kormilev, 1971

*Ochterus jaczewskii* Kormilev, 1971: 434, 439 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Indonesia: West Papua: ‘NW New Guinea, Vogelkop, Irai R., N of Lake Anggi Giji, 1850 m’ (BPBM).

*Ochterus jaczewski* (incorrect subsequent spelling): GAPUD (1981): 302–303, 305, 307 (diagnosis, illustrations).

*Ochterus jaczewskii*: BAEHR (1990b): 452–454, 456–459, 461, 466–467 (key to species, redescription, illustrations); CHEN et al. (2005): 413 (checklist).

**Distribution.** *Australian Region:* Indonesia: Papua (POLHEMUS & POLHEMUS 1998), West Papua (KORMILEV 1971, BAEHR 1990b); Papua New Guinea, incl. Normanby Island (KORMILEV 1971, 1972; GAPUD 1981).

#### *Ochterus kokodae* Baehr, 1990

*Ochterus kokodae* Baehr, 1990b: 452–454, 456–459, 461, 465–466 (key to species, description, illustrations). HOLOTYPE: ♂, Papua New Guinea: ‘Papua, Kokoda, 1200 ft. [= 366 m a.s.l.]’ (BMNH).

*Ochterus kokodae*: CHEN et al. (2005): 413 (checklist).

**Distribution.** *Australian Region:* Papua New Guinea (BAEHR 1990b, CHEN et al. 2005).

#### *Ochterus latior* Baehr, 1990

*Ochterus latior* Baehr, 1990b: 451, 453, 455–458, 474–475 (key to species, description, illustrations). HOLOTYPE: ♀, Papua New Guinea: ‘Madang Distr., Finisterre Mts., Momo C., 5550 ft. [= 1692 m a.s.l.]’ (BMNH).

*Ochterus latior*: CHEN et al. (2005): 413 (checklist).

**Distribution.** *Australian Region:* Papua New Guinea (BAEHR 1990b, CHEN et al. 2005).

#### *Ochterus louisiana* Baehr, 1990

*Ochterus louisiana* Baehr, 1990b: 451, 453, 455–459, 461, 470–471 (key to species, description, illustrations). HOLOTYPE: ♂, Papua New Guinea: Rossel Island: ‘SE: Louisiada Archipelago, Yela I., Wo Po River, 400 m’ (BMNH).

*Ochterus louisiana*: CHEN et al. (2005): 413 (checklist).

**Distribution.** *Australian Region:* Papua New Guinea: Louisiada Archipelago (BAEHR 1990b, CHEN et al. 2005).

#### *Ochterus luzonicus* Gapud, 2003

*Ochterus baltazarae* (partim, paratypes of Zambales form): GAPUD & SAN VALENTIN (1977): 280, 282–283, 296–298 (diagnosis, illustrations).

*Ochterus luzonicus* Gapud, 2003: 100–103, 107. HOLOTYPE: ♂, Philippines: Luzon: ‘La Union: Bacnotan, Don Mariano Marcos Memorial State University’ (VPGP).

*Ochterus luzonicus*: CHEN et al. (2005): 413 (checklist).

**Distribution.** *Oriental Region:* Philippines: Luzon (GAPUD 2003).

#### *Ochterus magnificus*

Gapud & San Valentin, 1977

*Ochterus magnificus* Gapud & San Valentin, 1977: 272, 282–283–289, 294, 296–298 (key to species, description, illustrations). HOLOTYPE: ♂, Philippines: Luzon: ‘National Botanic Garden, Real, Quezon’ (UPLB).

*Ochterus magnificus*: GAPUD (1986): 32, 38–40 (key to species, redescription, illustration); GAPUD (2003): 107 (checklist); CHEN et al. (2005): 413 (checklist).

**Distribution.** *Oriental Region:* Philippines: Luzon (GAPUD & SAN VALENTIN 1977).

#### *Ochterus magnus* Gapud & San Valentin, 1977

*Ochterus magnus* Gapud & San Valentin, 1977: 272, 282, 285–287–291, 296–298 (key to species, description, illustrations). HOLOTYPE: ♂, Philippines: Luzon: ‘Humayao Creek, Pajo, Alfonso, Cavite’ (UPLB).

*Ochterus magnus*: GAPUD (1986): 32, 40–42 (key to species, redescription, illustration); GAPUD (2003): 107 (checklist); CHEN et al. (2005): 413 (checklist).

**Distribution.** *Oriental Region:* Philippines: Luzon (GAPUD & SAN VALENTIN 1977, GAPUD 1981).

#### *Ochterus manni* Hungerford, 1927

*Ochterus manni* Hungerford, 1927: 189 (description, differential diagnosis). HOLOTYPE: ♂, Bolivia: ‘Huachi Rio Beni’ (USNM).

*Ochterus manni*: SCHELL (1943a): 32, 35 (key to species, illustration); SCHELL (1943b): 46 (original description repeated, differential diagnosis); DRAKE (1952): 74 (checklist); HECKMAN (2011): 463 (key to species, illustration); CIANFERONI (2012): 67 (key to species); HERRERA MADRIGAL (2015): 256 (illustrations); POLHEMUS & POLHEMUS (2016): 12, 15–16, 41–44 (key to species, redescription, illustrations).

**Material examined.** PANAMA: DARIÉN: Cerro Chucantí Reserve, base camp, 8°47.3'N 78°27.1'W, 800–1000 m a.s.l., lower montane forest, at light, 27.–30.viii.2017, 2 ♀♀, M. Fikáček, J. Hájek, M. Seidel & L. Sekerka lgt., P. Kment det. (NMPC).

**Distribution.** *Neotropical Region:* Central America: Costa Rica (SCHELL 1943b, HERRERA MADRIGAL 2015, POLHEMUS & POLHEMUS 2016), Panama (POLHEMUS & POLHEMUS 2016); Bolivia (HUNGERFORD 1927, DRAKE 1952, POLHEMUS & POLHEMUS 2016). South America: Brazil: Pará (POLHEMUS & POLHEMUS 2016), Ecuador (CIANFERONI 2012, POLHEMUS & POLHEMUS 2016), Peru (SCHELL 1943b, POLHEMUS & POLHEMUS 2016).

**Note.** According to POLHEMUS & POLHEMUS (2016), *O. unidentatus* Nieser & Chen, 1992 described from Ecuador may be synonym of this species.

#### *Ochterus marginatus* marginatus (Latreille, 1804)

(Fig. 7)

*Acanthia marginata* Latreille, 1804: 242–243 (original description).

SYNTYPE(S): France: Bordeaux (depository unknown, cf. POLHEMUS 1995a: 25).

*Ochterus marginatus*: LATREILLE (1807): 143 (new combination).

*Pelagonus marginatus* Latreille, 1809: 384 (new combination).

*Pelagonus marginatus*: LE PELETIER & SERVILLE (1825): 33 (redescription); DUFOUR (1833): 192–196, Pl. V: fig. 58 (diagnosis, distribution, illustration); BURMEISTER (1835): 203–204 (diagnosis, distribution); BRULLÉ (1836): 277–278 (redescription, distribution); BLANCHARD (1840): 93–94 (redescription, catalogue); AMYOT & SERVILLE (1843): 409 (diagnosis, distribution); HERRICH-SCHÄFFER (1849): 18, 23–24, Pl. CCXC: fig. 892 (diagnosis, catalogue, illustration); FIEBER (1861): 103 (catalogue); COSTA (1862): 331 (redescription); REUTER (1888): 721–722 (catalogue); OSANIN (1909): 955–956 (catalogue); SINGH-PRUTHI (1925): 184, Pl. XVIII: fig. 130 (male genitalia, illustrations). *Pelagonus marginatus* (partim): STÅL (1866): 170–171 (redescription, catalogue); STÅL (1876): 137 (catalogue); DISTANT (1906): 14 (redescription).

*Pelagonus marginatus*: PUTON (1869): 38 (list); PUTON (1880): 209 (redescription, distribution).

*Ochterus marginatus*: HOFFMANN (1933): 249–250 (catalogue); JACZEWSKI (1935): 482 (key to species); WU (1935): 557 (catalogue); KORMILEV (1971): 433–436 (redescription, illustrations, variation); KORMILEV (1973): 2–4, 8 (diagnosis, variability, illustrations); RIEGER (1976): 109–188 (head and prothorax morphology, illustrations); RIEGER (1977): 213–214 (differential diagnosis, illustration); TAMANINI (1979): 18, 45, 51 (key, redescription, illustrations); NIESER (1982): 11, 46 (illustration, distribution); BOULARD & COFFIN (1991): 58–67 (adult and larval morphology, biology); NIESER & CHEN (1992): 9 (illustration of paramere); NIESER et al. (1994): 4, 20–21, 44 (key, illustrations); CHEN (1999): 9–10 (diagnosis, illustrations); NIESER & CHEN (1999): 90–91 (key, illustration); CHEN et al. (2005): 78–79, 81, 413 (illustrations, bionomics, checklist); KANYUKOVA (2006): 46–47 (redescription, illustrations); POLHEMUS & POLHEMUS (2008): 286 (key to species); LINNAUORI et al. (2011): 76 (photo); POLHEMUS & POLHEMUS (2012): 345 (key to species); POLHEMUS & POLHEMUS (2015): 207, 209–210 (key to species, illustrations); POPOV & HEISS (2014a): 187–188 (illustrations).

*Ochterus marginatus marginatus*: JACZEWSKI (1934): 601–605 (redescription, variability, illustrations); JACZEWSKI (1935): 483 (key to species); POISSON (1957): 24–25 (redescription, illustrations); HOFFMANN (1941): 67–69 (catalogue); POLHEMUS (1995a): 25 (catalogue); POLHEMUS & POLHEMUS (2012): 345–347 (diagnosis, variability, illustrations); AUKEMA et al. (2013): 8 (catalogue); XIE & LIU (2013): 6–7 (checklist); THIRUMALAI (2017): 15–16, 69 (catalogue); HAYASHI & MIYAMOTO (2018): 259, 261 (identification, illustration).

*Pelagonus indicus* Guérin-Méneville, 1843: 113 (original description, differential diagnosis). SYNTYPE(s): India: ‘le plateau des Neelgherries, dans le Coromandel’ [= Nilgiri Hills] (MZFN, see POLHEMUS 1995a: 25). Junior subjective synonym by MONTANDON (1910: 1).

*Pelagonus indicus*: STÅL (1876): 137 (catalogue).

*Pelagonus armeniacus* Kolenati, 1857: 454–455. SYNTYPES: 6 (♂♀), Azerbaijan: Karabagh: ‘in littore lacuum alpestrium [= at coast of alpine lakes] Balloch-ghöll, Sullü-ghöll, Schamlogh-ghöll, Kaepes-ghöll in provincia Karabagh’ (ZMAS, probably additional syntypes in NHMW, see POLHEMUS 1995a: 25). Junior subjective synonym by KIRITSHENKO (1918: 172).

*Pelagonus armeniacus*: STÅL (1876): 137 (catalogue).

*Pelagonus flavomarginatus* Scott, 1874: 446–447 (original description). HOLOTYPE: ?sex, Japan (BMNH). Junior subjective synonym by JACZEWSKI (1934: 598, 605).

*Pelagonus flavo-marginatus* (incorrect subsequent spelling): STÅL (1876): 137 (catalogue).

*Pelagonus flavomarginatus*: MATSUMURA (1915): 103 (catalogue).

*Ochterus marginatus flavomarginatus*: MIYAMOTO (1961): 230–231, 257, pl. 42: figs 235–237 (morphology of alimentary organs, illustrations); MIYAMOTO & LEE (1966): 398 (catalogue, distribution); TOMOKUNI (1981): 111 (distribution).

*Ochterus flavomarginatus*: HAYASHI (1995): 20 (distribution, habitat).

*Salda rutherfordi* Distant, 1915: 506 (original description). HOLOTYPE: ?sex, Sri Lanka: ‘Peradeniya’ (BMNH). Junior subjective synonym; suspected synonymy suggested by W. E. China in JACZEWSKI (1934: 598) (see also POLHEMUS 1979: 112).

*Pelagonus formosanus* Matsumura, 1915: 103–104 (differential diagnosis). SYNTYPES: 2 ♂♂ 1 ♀, Taiwan: ‘Kagi’ [= Chiayi] and ‘Koshun’ [= Hengchun] (EIHU). Junior subjective synonymy by ESAKI (1926:

184); upgraded to subspecies by MIYAMOTO (1960: 78), synonymy confirmed by KORMILEV (1971: 433).

*Ochterus formosanus*: TAKAHASHI (1921): 119–125 (biology); TAKAHASHI (1923): 67–68 (biology).

*Ochterus thienemannii* (misidentification): NIESER & CHEN (1992): 12 (corrected by NIESER & CHEN 1999).

**Material examined.** **Palaearctic Region: Europe.** **BULGARIA:** K’rdzhali env., Arda river, 23.viii.1948, 4 ♂♂ 1 ♀, M. Josifov det. (NMPC); Momchilgrad, Djebel, 24.vi.1961, 6 ♂♂ 3 ♀♀, L. Hoberlandt & Slouková lgt., P. Kment det. (NMPC). **FRANCE:** Dép. du Var, [18]99, 1 ♀, no collector, L. Hoberlandt det. (NMPC); Dept. Var, Le Lavandou, 1930, 1 ♂, J. Obenberger lgt., P. Kment det. (NMPC); Mandelieu, Esleret [?], viii., 1 ♀, Bordeaux lgt., J. Roubal det., P. Kment revid. (MMBC). **GREECE: EAST MACEDONIA AND THRACE:** Drama, Paranestion, 15.v.1937, 1 ♂, Bartoň lgt., P. Kment det. (NMPC). **ITALY: SICILY:** Balestrate (PA), 7.vii.1972, 1 larva, 22.xi.1972, 1 larva, A. Carapezza lgt. & det. (ACPI); Madonie, Petralia Sottana, 1000 m a.s.l., 9.vi.1972, 1 ♀, A. Carapezza lgt. & det. (ACPI); Mezzouso (PA), 22.v.1977, 1 ♂, A. Carapezza lgt. & det. (ACPI). Palermo Prov., Scillato env., Torrente Fichera, ca. 180 m a.s.l., 28.iv.2014, 1 ♂, J. Hájek & K. Kalíková lgt., P. Kment det. (NMPC). **North Africa: ALGERIA:** Ghardimaou, 19.–26.iv.[19]27, 2 ♀♀, Mařan lgt., P. Kment det. (NMPC). **Asia: AFGHANISTAN: LAGHMAN:** Nen-grahar prov., Laghman (30), 860 m a.s.l., 20.iii.1966, 1 ♂, Povolný & Tenora lgt., P. Kment det. (MMBC). **Nuristan:** Bashgult [= Landai Sin valley], 1100 m a.s.l., 14.vii.1952, J. Klapperich lgt., P. Kment det. (NMPC). **CHINA: ANHUI:** Dabieshan Mts., 65 km SW of Huoshan, 1400 m a.s.l., 23.vi.1998, 1 ♂ 1 ♀, L. Bocák lgt., P. Kment det. (ZJPC). **BEIJING:** Pearl Lake [= Zhenzhu Lake], 70 km W of Beijing, 16.–18.vi.2000, 1 ♂, Z. Jindra lgt., P. Kment det. (ZJPC). **FUJIAN:** Kuatun, 9.vii.1946, 1 ♀, Tschung Sen lgt., P. Kment det. (NMPC). **SHAANXI:** Qing Ling Shan Mts., road Baoji–Taibai village, ca. 35 km S of Baoji, 18.vii.1998, 1 ♀, Z. Jindra lgt., P. Kment det. (ZJPC). **YUNNAN:** Cheli env., 700 m a.s.l., 30.iv.1957, 1 L5, D. Panfilov lgt. (NMPC); Lunan env., Stone Forest, 29.vii.1995, 1 ♂, Z. Jindra lgt., P. Kment det. (ZJPC); 50 km SW of Mojiang, 1100 m a.s.l., 2.iv.1955, Kryzhanovskiy lgt., P. Kment det. (NMPC); Xiaomengyang, 810 m a.s.l., 26.iii.1957, 2 ♂♂ 1 ♀, S.-Y. Wang lgt., P. Kment det. (NMPC); Xiaomengyang, 850 m a.s.l., 29.iii.1957, 2 ♂♂ 1 ♀, L.-C. Zang lgt., P. Kment det. (NMPC); Tengchong, S margin of the city, 24°59.4'N 98°28.9'E, 1650 m a.s.l., [Ch12], individually collected under stones, on soil surface, on plants and shrubs, in pool with clay bottom, margin of mixed forest above the rice fields, 1 ♀, J. Hájek & J. Růžička lgt., P. Kment det. (NMPC); Gengma, 5.v.1955, 1 ♀, T.-R. Huang lgt., P. Kment det. (NMPC); 30 km SW of Jinping, Měnglā, 400 m a.s.l., 3.v.1956, 1 ♀, K.-R. Huang lgt., P. Kment det. (NMPC); Jingdong, 1200 m a.s.l., 21.iii.1957, 1 ♂, A. Monchadskiy lgt., P. Kment det. (NMPC). **IRAN:** Iran, no more details, 6.ix.1961, 28 ♂♂ 18 ♀♀, J. Klapperich lgt., P. Kment det. (NMPC). **ALBORZ:** Kandavan – pass, S slope, 2700–2900 m a.s.l., (36°10'N 51°15'E, Loc. No. 395), 4.–9.vii.1977, 1 ♀, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC); Karaj, 1200 m a.s.l., 23.vi.1960, 3 ♂♂, J. Klapperich lgt., P. Kment det. (NMPC); Karaj, 3 km N of Dam, 1650 m a.s.l. (35°48'N 50°59'E, Loc. No. 85), 10.viii.1970, 2 ♂♂, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC). **ARDABIL:** 5 km NW Kolur, ‘Shahrud’ river valley, 37°26.1'N 48°41.2'E, 1670 m a.s.l., 4.–5.vi.2006, 1 ♀, J. Hájek & P. Chvojka lgt., P. Kment det. (NMPC). **FARS:** 5 km E of Furk, on the road Hajiabad–Darab, 900 m a.s.l. (28°18'N 55°16'E, Loc. No. 217), 28.v.1973, 1 ♀, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC); Aliabad, 75 km NW Jahrom (29°30'N 52°35'E; Loc. No. 53), 10.vii.1970, 1 ♂ 1 L, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC); Dasht-e Arzhan, 50 km W of Shiraz, Shur river (29°39'N 51°58'E, Loc. No. 44), 5.vii.1970, 2 ♂♂ 2 L, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC); Tang-e Chogan-e Olia, ruins of Bis-hapur, 1000 m a.s.l. (29°47'N 51°36'E, Loc. No. 233), 10.vi.1973, 4 ♂♂ 1 L, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC). **GILAN:** Racht [= Rasht], 7.v.1965, 1 ♂ 1 ♀, Safavi lgt., P. Kment det. (NMPC). **HORMOZGAN:** 20 km SE of Minab (27°05'N 57°14'E, Loc. No. 204), 21.v.1973, 1 ♀, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC); Bashagerd [mts.], Senderk, 11.v.1977, 1 ♀, Safavi & Pazuki lgt., P. Kment det. (NMPC); Faryab, Rud-e Rudan river, 350 m a.s.l. (27°28'N 57°07'E, Loc. No. 201), 17.–18.v.1973, 1 ♀, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC); Teleng, 40 km SE of Minab (26°53'N 57°16'E, Loc. No. 205), 21.v.1973,

1 ♂ 2 ♀ 2 L, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC). **KERMAN:** 33 km W Sabzvaran [=Jiroft] (28°44'N 57°28'E, Locality No. 189), 1100 m a.s.l., 6.–7.v.1973, 1 ♀, Exp. Nat. Mus. Praha, P. Kment det. (NMPC); Deh Bakri (29°03'N 57°56'E, Locality No. 186), 1700–1750 m a.s.l., 30.iv.–3.v.1973, 1 ♂ 1 ♀ 1 spec., Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC). **QAZVIN:** Hasan Sabbagh Castle, 36°27.0'N 50°34.9'E, 2075 m a.s.l., streamlet valley, 13.v.2008, 1 ♀, J. Hájek & P. Chvojka lgt., P. Kment det. (NMPC). **SISTAN AND BALUCHISTAN:** 16 km SE of Tangé-Sarhé, 61 km NNW Nikshahr, 900 m a.s.l. (26°29'N 60°02'E, Loc. No. 154), 10.iv.1973, 3 ♀♀, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC); Taftan [Mts.], Tamandan Valley (28°36'N 61°02'E, Locality No. 167), 2100 m a.s.l., 20.iv.1973, 1 ♀, Exp. Nat. Mus. Praha lgt., P. Kment det. (NMPC). **TEHRAN:** Elburgsgeb. [=Elburz Mts.], Laschkarak Tal [=Lashgarak valley], 1800 m a.s.l., vii.–x.1961, 1 ♂ 3 ♀♀, J. Klapperich lgt., P. Kment det. (NMPC). **ZANJAN:** 7 km E Sa'id Abad, 36°23.3'N 48°11.7'E, 1635 m a.s.l., 11.–12.v.2008, steppe stream, at light, 1 ♀, J. Hájek & P. Chvojka lgt., P. Kment det. (NMPC). **OMAN:** NE, 17 km W of Sur, 15.iii.2015, 1 ♂ 1 ♀, M. Snížek lgt., P. Kment det. (ZJPC). **TURKEY:** ADIYAMAN: Burmapinar env., bank of river in canyon above Septimus Severus bridge, 37°55'57" 38°36'31", 704 m a.s.l., 3.vii.2011, 2 ♂♂ 1 L1 L2, P. Kment lgt. & det. (NMPC). ANTALYA: Köprülü canyon, Beşkonak, 80 km NE of Antalya, 7.ix.1992, 3 ♂♂ 1 L, Z. Jindra lgt., P. Kment det. (ZJPC). TUNCELİ: Ovacık env., bank of Munzur river downstreams the village before entering Munzur Vadisi Milli Parkı, 4.vii.2011, 7 ♂♂ 4 ♀♀ 1 L, P. Kment lgt. (6 ♂♂ 4 ♀♀ NMPC, 1 ♂ 1 L JDKD). **Afrotropical Region:** ANGOLA: Angola (No. 10238.12), 1 ♀, P. Kment det. (NMPC). LUNDA NORTE: Luachimo (Ang. No. 915.6), 11.vii.1948, 1 ♂ 1 ♀, A. B. Machado lgt., P. Kment det. (NMPC); Luachimo (M) (Ang. No. 3967.2), 6.vi.1959, 1 ♂ 2 ♀♀, Mus. do Dundo, P. Kment det. (NMPC); Luachimo, Route Turismo, M. H. B (Ang. No. 20175), 28.vi.1957, 1 ♀, Mus. do Dundo, P. Kment det. (NMPC). LUNDA SUL: Alto Chicapa, Camutongola river, Luhembe (M) (Ang. No. 4174.7), 1 ♂, 22.vi.1954, Mus. do Dundo, P. Kment det. (NMPC); Alto Chicapa, Camutongola river, Luhembe (M) (Ang. No. 4166.10, 4168.7, 4181), 11 ♂♂ 11 ♀♀, 24.vi.1954, Mus. do Dundo, P. Kment det. (NMPC); Alto Chicapa, Tehissango / Cuango Muquè (Ang. No. 4308.14), 1 ♀, 16.vii.1954, Mus. do Dundo, P. Kment det. (NMPC); Alto Cuilo (M), Cavuemba (Ang. No. 4082.24), 31.v.1954, 3 ♀♀, Mus. do Dundo, P. Kment det. (NMPC). **CENTRALAFRICAN REPUBLIC:** 90 km NNE Bangui, 5°03'N 18°47'E, 380 m a.s.l., 14.iii.2010, 1 ♂, J. Halada lgt., P. Kment det. (MMBC). **DEMOCRATIC REPUBLIC OF THE CONGO:** KASAI OCCIDENTAL: Tshikapa (Ang. No. 880.4), vi.–vii.1948, 2 ♂♂ 1 ♀, A. B. Machado lgt., P. Kment det. (NMPC). **NIGERIA:** TARABA: Gashaka Gumti NP, 30 km SE Serti env., 7°21'N 11°32'E, ca. 450 m a.s.l., 24.iv.–8.v.2011, 1 ♂ 1 ♀, J. Halada lgt., P. Kment det. (ZJPC). **SUDAN:** SENNAR: Blue Nile prov., Dinder Game Reserve, Galegu, 4.iii.1967, 1 ♂ 2 ♀♀, P. Štys lgt. (686), P. Kment det. (MMBC). **Oriental Region: INDIA:** MAHARASHTRA: 10 km E from Savantvadi, 22.v.2006, 2 ♂♂, Z. Kejval lgt., P. Kment det. (MMBC); 15 km E of Savantvadi, 15°55'N 75°53'E, 40 m a.s.l., riverside, 22.v.2006, 1 ♂, Z. Kejval lgt., P. Kment det. (MMBC); 40 km W of Pune, Mulshi env., 30.ix.–2.x.2005, 1 ♀, J. Bezděk lgt., P. Kment det. (NMPC); Western Ghats Mts., Panchgani, Wai env., 3.–5.vi.2008, 2 ♂♂ 1 ♀, Z. Kejval lgt., P. Kment det. (MMBC). **PUDUCHERRY:** Karaikal, Kurumbagaram, 23.iii.1947, 48 ♂♂ 25 ♀♀, Nathan lgt., L. Hoberlandt det., P. Kment revid. (43 ♂♂ 24 ♀♀ NMPC, 5 ♂♂ 1 ♀ MMBC). **RAJASTHAN:** 20 km N of Dausa, Golakabas env., Sarsadevi, 27°05.46'N 78°17.18'E [sic!], 380 m a.s.l., 19.xi.2002, P. Šípek lgt., P. Kment det. (NMPC); 20 km N of Dausa, Naranimate env., 27°05.46'N 78°17.18'E [sic!], 400 m a.s.l., light trap, 7.–8.xi.2002, 1 ♀, P. Šípek lgt., P. Kment det. (NMPC); 50 km W of Agra, Bharatpur env., 27°12.42'N 77°30.48'E, 220 m a.s.l., 31.viii.–5.ix.2002, 1 ♀ 1 L5, P. Šípek & M. Fikáček lgt., P. Kment det. (NMPC). **TAMIL NADU:** Madras occ., Tiruchirappalli, 16.v.1970, 1 ♀, J. Hloušek lgt., P. Kment det. (MMBC). **LAOS: VIENTIANE:** Phou Khao Khouay NBCA, ca. 50 km N Vientiane (lake env.), 18°23.2'N 102°45.5'E, 745 m a.s.l., 18.v.2010, 1 ♂, J. Hájek lgt., P. Kment det. (NMPC); Vang-Veng, 18°55'23"N 102°26'53", 300 m a.s.l., 10.–15.v. & 1.–6.vii.2001, 1 ♂, J. Kolibáč lgt., P. Kment det. (MMBC). **MALAYSIA: SABAH:** Mt. Kinabalu env., 28.v.1999, M. Snížek lgt., P. Kment det. (ZJPC); Sapulut env., 1.–6.vi.2001, 1 ♀, J. Stolarczyk lgt., P. Kment det. (ZJPC); W, Crocker Range E, W of Apin Apin, v.1999, 1 ♂, M. Snížek lgt., P. Kment det. (ZJPC).

**SARAWAK:** Kapit distr., Rumah Ugap env., Sut river valley, 3.–9.iii.1994, 2 ♀♀, P. Bilek lgt., P. Kment det. (ZJPC); Kapit distr., Sebong, Baleh river, 6.–21.iii.1994, 2 ♂♂, S. Bílý lgt., P. Kment det. (NMPC). **PAKISTAN:** PUNJAB: Rawalpindi env., Basal, Kalachitta Range, 4.–7.i.1956, 1 ♂, Chr. Lindemann lgt., L. Hoberlandt det., P. Kment revid. (NMPC). **SRI LANKA: CENTRAL PROVINCE:** Sigirya near Dambulla, Pidurangala archeological areal, 7°58.18'N 80°45.60'E, 24.ii., 5 ♂♂ 2 ♀♀ (4 ♂♂ 1 ♀ ZJPC, 1 ♂ 1 ♀ NMPC). **RATNAPURA:** Panamure env., 11.xii.1995, 1 ♀, S. Bečvář lgt., P. Kment det. (MMBC). **SOUTHERN PROVINCE:** Tissamaharama env., 90 km NE of Matara, 14.iii.1994, 1 ♂ 1 ♀, Z. Kejval lgt., P. Kment det. (ZJPC). **THAILAND:** CHIANG MAI: Doi Suthep Mt., 1.v.1996, 1 ♂, S. Bílý lgt., P. Kment det. (NMPC). SATUN: Thale Ban, 6°45'N 100°09'E, 200 m a.s.l., 8.–13.iv.1997, 1 ♀, J. Kolibáč lgt., P. Kment det. (MMBC).

**Distribution.** **Palaearctic Region: Europe:** Bulgaria (JOSIFOV 1954, 1960, 1963; GÖLLNER-SCHEIDING & ARNOLD 1988; STOIANOVA & SIMOV 2016); France (LATREILLE 1804, 1807; DUFOUR 1833; BURMEISTER 1835; BRULLÉ 1836; AMYOT & SERVILLE 1843; PUTON 1880; POISSON 1925, 1957; DE SEabra 1926, JACZEWSKI 1934; RIEGER 1976, 1977; ELDER 2017); Gibraltar (MAYR 1868, HOFFMANN 1941); Greece (JOSIFOV 1959, ZIMMERMANN 1982, POLHEMUS & POLHEMUS 2012); Italy, incl. Sicily (COSTA 1862, MANCINI 1952, SERVADEI 1967, TAMANINI 1981, CIANFERONI & TERZANI 2013); North Macedonia (PROTIĆ 1998); Portugal (DE SEabra 1926, NIESER & MONTES 1984, BAENA & VÁZQUEZ 1986, HEBSGAARD et al. 2004); Russia (Daghestan) (KANYUKOVA 1997, 2006); Spain (DUFOUR 1833; BURMEISTER 1835, DE SEabra 1926, LINDBERG 1929, BAENA RUIZ & FERRERAS ROMERO 1982, NIESER & MONTES 1984, BAENA & VÁZQUEZ 1986, GARCÍA ROJAS et al. 1987, NIESER & CHEN 1992, PAGOLA-CARTE & RIBES 2007, GÜNTHER & GÜNTHER 2019); Turkey: European Part (FENT et al. 2011, FENT & DURSUN 2018). **North Africa:** Algeria (SIENKIEWICZ 1964, ECKERLEIN & WAGNER 1965); Egypt (PRISENER & ALFIERI 1953, LINNAVUORI 1964); Morocco (LINDBERG 1929, VIDAL 1937, AGUESSE et al. 1982, GHEIT 1995, L'MOHDI et al. 2008); Tunisia (LINDBERG 1922, CARAPEZZA 1997, SLIMANI et al. 2015). **Asia:** Afghanistan (CHINA & MILLER 1950); Armenia (AKRAMOVSKAYA 1959, KANYUKOVA 2006); Azerbaijan, incl. Nakhichevan Republic (KOLENATI 1857; HORVÁTH 1899; KIRITSHENKO 1918, 1938; KANYUKOVA 2006); China: Anhui (new record), Beijing (NIESER & CHEN 1992, CHEN 1999, XIE & LIU 2013), Fujian (KORMILEV 1971, NIESER & CHEN 1992, CHEN 1999, HUA 2000, XIE & LIU 2013), Guangdong (HOFFMANN 1933, 1941; NIESER & CHEN 1992; CHEN 1999; HUA 2000; CHEN et al. 2001; XIE & LIU 2013), Guizhou (NIESER & CHEN 1992, CHEN 1999, XIE & LIU 2013), Hainan (HOFFMANN 1933, 1941; NIESER & CHEN 1992; CHEN 1999; XIE & LIU 2013), Hebei (LIU & BU 2009), Henan (SHEN et al. 2014, CAI et al. 2016), Hong Kong (HOFFMANN 1941, KORMILEV 1971), Hubei (NIESER & CHEN 1992, CHEN 1999, XIE & LIU 2013), Hunan (NIESER & CHEN 1992, CHEN 1999, XIE & LIU 2013), Inner Mongolia (NIESER & CHEN 1992, CHEN 1999, XIE & LIU 2013), Jiangsu (NIESER & CHEN 1992, CHEN 1999, XIE & LIU 2013), Jiangxi (ZHANG 1994, HUA 2000, LI et al. 2008), Shanxi (MIYAMOTO 1960, as *O. m. flavomarginatus*), Shaanxi (new record), Sichuan (NIESER & CHEN 1992, CHEN 1999, HUA 2000, XIE & LIU 2013), Tianjin (NIESER & CHEN 1992, CHEN 1999), Xizang (=Tibet) (HUA 2000), Yunnan (CHENG et al. 2006), Zhejiang (KORMILEV 1971, NIESER & CHEN 1992,

CHEN 1999, XIE & LIU 2013); Cyprus (LINDBERG 1948, GEORGHIOU 1977, POLHEMUS & POLHEMUS 2012); Georgia (KIRITSHENKO 1918, KANYUKOVA 2006); Iran (LINNAUORI & HOSSEINI 2000, GHAHARI et al. 2013); Israel (POLHEMUS & POLHEMUS 2012); Japan (SCOTT 1874, as *P. flavomarginatus*); Hokkaido (HAYASHI 1995, as *P. flavomarginatus*; HAYASHI et al. 2016; HAYASHI & MIYAMOTO 2018), Honshu (MATSUMURA 1905, 1915, as *P. flavomarginatus*; HIURA 1967, as *O. m. flavomarginatus*; KORMILEV 1971; TOMOKUNI 1981, as *O. m. flavomarginatus*; HAYASHI et al. 2016; HAYASHI & MIYAMOTO 2018), Kyushu (MATSUMURA 1905, 1915, as *P. flavomarginatus*; JACZEWSKI 1934; KORMILEV 1971; HIURA 1967, as *O. m. flavomarginatus*; TAKENO 1998; HAYASHI et al. 2016; HAYASHI & MIYAMOTO 2018), Ryukyu Islands (MIYAMOTO 1964, HAYASHI et al. 2016; HAYASHI & MIYAMOTO 2018), Shikoku (HIURA 1967, as *O. m. flavomarginatus*; YANO et al. 2012; HAYASHI et al. 2016; HAYASHI & MIYAMOTO 2018), Tanegashima Islands (HAYASHI & MIYAMOTO 2018); Jordan (KATBEH et al. 2000); Korea (MIYAMOTO & LEE 1966, JOSIFOV & KERZHNER 1972, LEE & KWON 1991, LEE et al. 1993, LEE et al. 2013); Lebanon (LINDBERG 1922); Oman (**new record**); Russia: Far East: Kunashir Island (KERZHNER 1978, KERZHNER & MARUSIK 1997, KERZHNER et al. 2004, KANYUKOVA 2006, KANYUKOVA & MARUSIK 2006, VINOKUROV et al. 2010); Saudi Arabia (BROWN 1951, LINNAUORI 1986); Syria (FIEBER 1861, POISSON 1934, NIESER & MOUBAYED 1985); Taiwan (MATSUMURA 1915, as *P. formosanus*; BERGROTH 1914; ESAKI 1926; JACZEWSKI 1934, KORMILEV 1971, XIE & LIU 2013); Turkmenistan (KIRITSHENKO 1957, KANYUKOVA 2006); Turkey (Asian part) (LINDBERG 1922, HOBERLANDT 1952, FENT et al. 2011, MATOCQ et al. 2014, ÖZGEN et al. 2017, ÇERÇİ et al. 2018, DURSUN & FENT 2018, FENT & DURSUN 2018); United Arab Emirates (LINNAUORI et al. 2011). **Afrotropical Region:** Angola (KORMILEV 1973); Botswana (KRÜGER & DECKERT 2016); Burkina Faso (LINNAUORI 1981); Cameroon (KORMILEV 1973); Cape Verde Islands (LINDBERG 1959); Central African Republic (**new record**), Democratic Republic of the Congo (KORMILEV 1973); Ethiopia (JACZEWSKI 1934, BROWN 1951); Gambia (NIESER & CHEN 1992); Guinea-Bissau (MANCINI 1939a); Ivory Coast (LINNAUORI 1981); ? Kenya (MONTANDON 1914); Mozambique (POISSON 1934); ? Namibia (HESSE 1925); Nigeria (KORMILEV 1973, LINNAUORI 1981); ? Senegal (SIENKIEWICZ 1964); South Sudan (LINNAUORI 1980); Sudan (**new record**); Tanzania (NIESER & CHEN 1992, POLHEMUS & POLHEMUS 2012); ? Uganda (MONTANDON 1914); Yemen (BROWN 1951, LINNAUORI 1989). **Oriental Region:** India (DISTANT 1906): Assam (THIRUMALAI 2007, POLHEMUS & POLHEMUS 2012), Bihar (MAXWELL-LEFROY 1909, DISTANT 1910, KATIYAR 1953, THIRUMALAI 2007), Kerala (DISTANT 1910, THIRUMALAI 2007), Madhya Pradesh (THIRUMALAI 2007, THIRUMALAI et al. 2007), Maharashtra (PAIVA 1919b; JACZEWSKI 1934; THIRUMALAI & SHARMA 2002, 2012), Manipur (BAL & BASU 2004, THIRUMALAI 2007), Meghalaya (PAIVA 1919a, BAL & BASU 1998, THIRUMALAI 2007), Mizoram (BAL & BASU 2007), Orissa (DISTANT 1910, GHOSH et al. 1989, THIRUMALAI 2007), Puducherry: Karaikal (KORMILEV 1971, THIRUMALAI 2007), Rajasthan (new record),

Tamil Nadu (KATIYAR 1953; SIENKIEWICZ 1964; THIRUMALAI 1989, 1999, 2001, 2007; POLHEMUS & POLHEMUS 2012), Tripura (BAL & BASU 2000), Uttar Pradesh (DISTANT 1910, THIRUMALAI 2007), West Bengal (DISTANT 1910, THIRUMALAI 2007, POLHEMUS & POLHEMUS 2012); Indonesia: Bali (SCHOUTEDEN 1933, POLHEMUS & POLHEMUS 2012), Java (JACZEWSKI 1935, KORMILEV 1971), Sumatra (JACZEWSKI 1934, MANCINI 1939a); Laos (KORMILEV 1971); Malaysia: Peninsular part (KORMILEV 1971, KOVAC & YANG 1989, POLHEMUS & POLHEMUS 2012), Sabah (KORMILEV 1971; NIESER & CHEN 1992, 1999), Sarawak (KORMILEV 1971); Myanmar (DISTANT 1910, JACZEWSKI 1934); Nepal (DISTANT 1910); Pakistan (HAMID & HAMID 1973); Singapore (POLHEMUS & POLHEMUS 2012); Sri Lanka (DISTANT 1910, as *P. marginatus*, 1915, as *S. rutherfordi*; JACZEWSKI 1934; POLHEMUS 1979; POLHEMUS & POLHEMUS 2012); Thailand (KORMILEV 1971, POLHEMUS & POLHEMUS 2012); Vietnam (DISTANT 1906, JACZEWSKI 1934, as Cochinchine; KORMILEV 1971, POLHEMUS & POLHEMUS 2012). **Australasian Region:** Indonesia: Sulawesi (NIESER & CHEN 1999).

**Notes.** POLHEMUS (1995a) listed *O. marginatus* from Bosnia and Herzegovina and Croatia, however, there are no such records in the relevant literature (cf. JOSIFOV 1986, PROTIC 1998, KMENET & BERAN 2011) and taking into account its confinement to the southernmost regions of Balkan Peninsula (JOSIFOV 1986, STOIANOV & SIMOV 2016) they are probably based on misinterpretation of records from former Yugoslavia. The records of *O. marginatus* from Australia (KIRKALDY 1908, based on a larva; HALE 1925), Tasmania, New Guinea and New Caledonia (MONTANDON 1897) belong to other species. The record from New Caledonia (DISTANT 1920) belong to *O. australicus* (JACZEWSKI 1934). The records of *O. marginatus* from Kenya, Uganda (MONTANDON 1914), Namibia (HESSE 1925) or Senegal (SIENKIEWICZ 1964) requires confirmation. The records from Myanmar by MONTANDON (1897) and DISTANT (1906) refer to *O. feae*.

POLHEMUS & POLHEMUS (2012) discussed variability of Oriental populations of *O marginatus*, finding the male genitalia of specimens from Malaysia and Singapore structurally similar to those from India and the west Palaearctic Region. The populations from Bali are smaller and have also slightly different shapes of the superior appendage on the right paramere and the process of the male pygophore. They wrote that these more eastern populations may be assignable to the subspecies *O. marginatus insularis* from Philippines, but an analysis of further material from throughout the Malay Archipelago region will be necessary to properly determine the subspecific designations that should be applied to these insular forms (POLHEMUS & POLHEMUS 2012). According to N. Nieser and P.-p. Chen, *O. marginatus* in its present sense represents rather a complex of several species (CHEN et al. 2005). In this paper we identify *O. m. marginatus* as a polymorphic species in the sense of JACZEWSKI (1934), KORMILEV (1973) and POLHEMUS & POLHEMUS (2012). However, we observed considerable differences in the shape of the parameral cap and the parameral appendages among the populations, e.g. when comparing specimens from tropical Africa, Mediterranean and south India, and agree with the above-mentioned opinion of CHEN et al. (2005).

***Ochterus marginatus insularis***  
**Rieger, 1977**

*Ochterus marginatus insularis* Rieger, 1977: 213–214 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Philippines: Mindanao: ‘Süd [= South] Mindanao, Port Banga’ (ZSMC).

*Ochterus marginatus* (partim): KORMILEV (1971): 435–436 (partim, distribution); GAPUD & SAN VALENTIN (1977): 271, 273–276, 281, 285–286, 288–289, 294, 296–298 (key to species, redescription, illustrations, variation); GAPUD (1981): 301–302 (taxonomy); GAPUD (1986): 32–34 (key to species, redescription, illustration); NIESER & CHEN (1999): 91 (partim, distribution); CHEN et al. (2005): 413 (checklist); POLHEMUS & POLHEMUS (2012): 345 (partim, distribution).

*Ochterus marginatus insularis*: GAPUD (2003): 107 (checklist); POLHEMUS & POLHEMUS (2012): 345, 347 (variability).

**Distribution.** *Oriental Region:* Philippines: Cebu (GAPUD 2003), Leyte (GAPUD 1981), Luzon (KORMILEV 1971, RIEGER 1977, GAPUD & SAN VALENTIN 1977, YANO et al. 1981, NIESER & CHEN 1999, POLHEMUS & POLHEMUS 2012), Mindanao (RIEGER 1977, GAPUD 1981, NIESER & CHEN 1999, POLHEMUS & POLHEMUS 2012), Mindoro (KORMILEV 1971, GAPUD & SAN VALENTIN 1977), Palawan (KORMILEV 1971, GAPUD 2003), Romblon (GAPUD 1981).

**Note.** According to GAPUD (1981), out of the twelve individuals he examined, all except one agreed with the diagnosis of *O. marginatus insularis* by RIEGER (1977). He considered difficult to assess whether these characters are sufficient for a subspecies delimitation. According to POLHEMUS & POLHEMUS (2012), the population of *O. marginatus* from Bali may also belong to this subspecies (see Notes under *O. marginatus marginatus*).

***Ochterus mexicanus***

**D. A. Polhemus & J. T. Polhemus, 2016**

*Ochterus mexicanus* D. A. Polhemus & J. T. Polhemus, 2016: 17, 44–47 (key to species, description, illustrations). HOLOTYPE: ♂, Mexico: ‘Sinaloa, Rio Quelite at El Quelite [23°32'11"N, 106°28'46"W, elev. 25 m]’ (JTPC → USNM).

**Distribution.** *Neotropical Region: Central America:* Mexico: Colima (POLHEMUS & POLHEMUS 2016), Guerrero (POLHEMUS & POLHEMUS 2016), Jalisco (POLHEMUS & POLHEMUS 2016), Morelos (POLHEMUS & POLHEMUS 2016), Oaxaca (POLHEMUS & POLHEMUS 2016), Puebla (POLHEMUS & POLHEMUS 2016), Sinaloa (POLHEMUS & POLHEMUS 2016).

***Ochterus minor***  
**Kormilev, 1973**

*Ochterus minor* Kormilev, 1973: 2–4–5, 8 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Democratic Republic of the Congo: ‘CONGO, Matadi’ (CASC).

**Material examined.** ANGOLA: Bié: Catabola, 17.–27.xi.2012, FIT [= flight interception trap], 1 ♂, T. Lackner lgt. MMBC). CUNENE: Chuttes de Ruacana [= Ruacana Falls], (Ang. No. 1903.3), 6.x.[19]49, 1 ♂, A. B. Machado lgt. (NMPC). All. P. Kment det.

**Distribution.** *Afrotropical Region:* Angola (KORMILEV 1973); Burkina Faso (LINNAUORI 1981); Benin (LINNAUORI 1981); Chad (LINNAUORI 1981); Democratic Republic of the Congo (KORMILEV 1973); Ivory Coast (LINNAUORI 1981); Nigeria (KORMILEV 1973, LINNAUORI 1981).

***Ochterus monteithorum* Baehr, 1990**

*Ochterus monteithorum* Baehr, 1990b: 451, 453, 454, 456–459, 461, 468 (key to species, description, illustration). HOLOTYPE: ♂, Australia: Queensland: ‘Leo creek Road, McIwraith Range, 30 km NE. of Coen, 500 m’ (QMBA).

*Ochterus monteithorum*: CASSIS & GROSS (1995): 260 (catalogue); ANDERSEN & WEIR (2004): 267–268, 270, 335 (key to species, illustrations, checklist).

**Distribution.** *Australian Region:* Australia: Queensland (BAEHR 1990b, ANDERSEN & WEIR 2004).

***Ochterus nicobarensis* Chandra & Jehamalar, 2012**

*Ochterus nicobarensis* Chandra & Jehamalar, 2012: 24–26 (description, illustrations). HOLOTYPE: ♂, India: Nicobar Islands: ‘Nicobar District, Great Nicobar Biosphere Reserve, Campbell Bay, Govind Nagar, Ring Road, attracted to light near a pond 0.5 km away from sea, 40 ft. [12 m a.s.l.], 7°00.075'N 93°54.594'E’ (NZSI).

**Material examined.** MYANMAR: Burma, Rangoon Distr., Hlegu – Goygon, v.1997, 1 ♂ 1 ♀, M. Klich lgt., P. Kment det. (ZJPC).

**Distribution.** *Oriental Region:* India: Nicobar Islands (CHANDRA & JEHAMALAR 2012); Myanmar (**new record**).

***Ochterus nigrinus* Baehr, 1990**

*Ochterus nigrinus* Baehr, 1990b: 451, 453–454, 456–459, 461, 464–465 (key to species, description, illustrations). HOLOTYPE: ♂, Solomon Islands: ‘Guadalcanal, Monitor Creek, Umasami R.’ (BMNH).

*Ochterus nigrinus*: CHEN et al. (2005): 413 (checklist).

**Distribution.** *Australian Region:* Solomon Islands: Guadalcanal (BAEHR 1990b)

***Ochterus noualhieri* Baehr, 1990**

*Ochterus noualhieri* Baehr, 1990c: 91–93 (key to species, description, illustrations). HOLOTYPE: ♂, Indonesia: Java: ‘Java Occ., Volc. Géde’ (MNHN).

*Ochterus noualhieri*: NIESER & CHEN (1999): 90–91 (key, illustrations); CHEN et al. (2005): 413 (checklist); POLHEMUS & POLHEMUS (2012): 345, 352, 354–356 (key to species, diagnosis, illustration); POLHEMUS & POLHEMUS (2015): 208–209, 212 (key to species, illustrations).

**Distribution.** *Oriental Region:* Indonesia: ? Bali (NIESER & CHEN 1999, female only), Java (BAEHR 1990c). *Australian Region:* Indonesia: Sulawesi (NIESER & CHEN 1999, POLHEMUS & POLHEMUS 2012).

***Ochterus obscurus***

**D. A. Polhemus & J. T. Polhemus, 2016**

*Ochterus obscurus* D. A. Polhemus & J. T. Polhemus, 2016: 15–16, 48–50 (key to species, description, illustrations). HOLOTYPE: ♂, Panama: ‘Chiriquí, 5.6 km N of Boquete, La Culebra Trail, 1800 m’ (USNM).

**Distribution.** *Neotropical Region: Central America:* Costa Rica (POLHEMUS & POLHEMUS 2016); Panama (POLHEMUS & POLHEMUS 2016).

***Ochterus occidentalis* Baehr, 1990**

*Ochterus occidentalis* Baehr, 1990b: 452–454, 456–460–462 (key to species, description, illustrations). HOLOTYPE: ♂, Australia: Western Australia: ‘Margaret River’ (BMNH).

*Ochterus occidentalis*: CASSIS & GROSS (1995): 261 (catalogue); ANDERSEN & WEIR (2004): 268, 270, 335–336 (key to species, illustrations, checklist).

**Distribution. Australian Region:** Australia: Western Australia (BAEHR 1990b, ANDERSEN & WEIR 2004).

***Ochterus ovatus***

**D. A. Polhemus & J. T. Polhemus, 2016**

*Ochterus ovatus* D. A. Polhemus & J. T. Polhemus, 2016: 17, 50–53 (key to species, description, illustrations). HOLOTYPE: ♂, Mexico: ‘Chiapas, Soyaló, Rio Blanco, on road to Villahermosa ~14 mi. N of Hwy. 190, small swift mountain river with backwater pools [vic. 16°53'27"N, 92°55'30"W, elev. ~1200 m]’ (JTPC → USNM).

**Distribution. Neotropical Region:** Central America: Mexico: Chiapas (POLHEMUS & POLHEMUS 2016).

***Ochterus panamensis***

**D. A. Polhemus & J. T. Polhemus, 2016**

*Ochterus panamensis* D. A. Polhemus & J. T. Polhemus, 2016: 13, 18, 53–55 (key to species, description, illustrations). HOLOTYPE: ♂, Panama: ‘Panama, small stream in limestone bed at Serranía de Majé, 3 km S of Ipete, 100 m [vic. 8°57'37"N, 78°31'17"W]’ (JTPC → USNM).

**Distribution. Neotropical Region:** Central America: Panama (POLHEMUS & POLHEMUS 2016).

***Ochterus papaceki* Kment & Carapezza sp. nov.**

*Ochterus papaceki* Kment & Carapezza, sp. nov. (original description, illustrations). HOLOTYPE: ♂, Yemen: Socotra Island: ‘Noged plain, lower part of Wadi Matyaf, 12°27'13.50"N 54°18'13.95"E’ (NMPC).

**Distribution. Afrotropical Region:** Tanzania; Yemen: Socotra (this paper).



Fig. 24. *Ochterus parvus* Schell, 1943, female, Ecuador: Napo: San Pablo de Ushpayacu env., 3.73 mm.

***Ochterus papuasicus* Kormilev, 1972**

*Ochterus papuasicus* Kormilev, 1972: 585–586 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Papua New Guinea: ‘SE (PA-PUA): Rouna, 300–500 m’ (BPPBM).

*Ochterus papuasicus*: CHEN et al. (2005): 413 (checklist).

**Distribution. Australian Region:** Papua New Guinea (KORMILEV 1972).

***Ochterus pardalos* Nieser & Chen, 1999**

*Ochterus pardalos* Nieser & Chen, 1999: 90, 93–94, 123 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Philippines: Mindanao: ‘Lake Sebu area, trickle of water fed by seepage from ‘Cold River’’ (NCTN).

*Ochterus pardalos*: GAPUD (2003): 107 (checklist); CHEN et al. (2005): 413 (checklist).

**Distribution. Oriental Region:** Philippines: Mindanao (NIESER & CHEN 1999, GAPUD 2003).

***Ochterus parvus* Schell, 1943**

(Fig. 24)

*Ochterus parvus* Schell, 1943a: 32, 35 (key to species, illustration).

LECTOTYPE (designated by SCHELL 1943b: 40, as holotype): ♂, Ecuador: ‘Mera’ (SEMC).

*Ochterus parvus*: SCHELL (1943b): 39–40 (original description, differential diagnosis); DRAKE (1952): 74 (checklist); FROESCHNER (1981): 61 (catalogue); HECKMAN (2011): 460 (key to species, illustration); CIANFERONI (2012): 67 (key to species).

**Material examined. ECUADOR:** NAPO: 7.5 km SE of Archidona, San Pablo de Ushpayacu env., 0°56'52"S 77°45'01"W, 540 m a.s.l., 23.xi.2006, 1 ♀ (Fig. 24), M. Fikáček lgt., P. Kment det. (NMPC).

**Distribution. Neotropical Region:** South America: Ecuador (SCHELL 1943b, DRAKE 1952, CIANFERONI 2012).

**Note.** The revision of American *Ochterus* including the description of *O. parvus* was published divided in two parts, the first published in January 1943 (SCHELL 1943a) and the second in April 1943 (SCHELL 1943b). The species was first introduced in the key, which is sufficient to make it available (ICZN 1999: Art. 13.1.1), without any mention of type specimens (SCHELL 1943a: 32), while the original description including the holotype designation appeared in the second part (SCHELL 1943b: 39). As a holotype is defined as ‘the single specimen upon which a new nominal species-group taxon is based in the original publication’ (ICZN 1999: Art. 73.1), in this case, the subsequently designated ‘holotype’ must be considered the lectotype according to ICZN (1999: Art. 74.5).

***Ochterus paucistriatus* Baehr, 1990**

*Ochterus paucistriata* Baehr, 1990b: 450, 453, 454, 456–459, 461, 468–469 (key to species, description, illustrations). HOLOTYPE: ♂, Indonesia: Papua: ‘Dutch New Guinea: Cyclops Mts., Mt. Lina, 3500 ft. [= 1067 m a.s.l.]’ (BMNH).

*Ochterus paucistriata*: CHEN et al. (2005): 413 (checklist).

**Distribution. Australian Region:** Indonesia: Papua (BAEHR 1990b, CHEN et al. 2005)

**Note.** BAEHR (1990b) established the species name as *O. paucistriata*, citing it 11 times throughout the paper, but without providing any explanation of its etymology. CHEN et al. (2005) also accepted *O. paucistriata* as the correct original spelling. However, the species name is a compo-

sed Latin adjective *paucistriatus* (-a, -um) and the generic name *Ochterus* is masculine. Therefore, we correct here the gender agreement of the name to *O. paucistriatus* (see ICBN 1999: Art. 31.2, 34.2).

### *Ochterus perbosci* (Guérin-Méneville, 1843)

*Pelagonus Perbosci* Guérin-Méneville, 1843: 113–114 (original description, differential diagnosis). LECTOTYPE (designated by CHAMPION 1901: 345, as type): ♂, Mexico: Campeche: ‘dans la baie Campèche’ [= in the Campeche bay] (coll. Sallé → BMNH).

*Pelagonus Perbosci*: FIEBER (1851): 15 (checklist); DOHRN (1859): 52 (list); STÅL (1876): 137 (catalogue).

*Pelagonus perbosci*: CHAMPION (1901): 344–345, Pl. XX: fig. 11 (key, diagnosis, illustration).

*Ochterus perbosci*(i): TORRE BUENO (1906): 50 (list).

*Ochterus perbosci*: KIRKALDY & TORRE BUENO (1909): 179 (catalogue).

*Pelagonus Perbosci*: MONTANDON (1910): 1 (note).

*Ochterus perbosci*: BARBER (1913): 213 (key to species); VAN DUZEE (1923): 167 (distribution); SCHELL (1943a): 32–33, 35 (key to species, original description repeated, differential diagnosis, illustration); DRAKE (1952): 75 (checklist); COBBEN (1960): 54 (distribution); NIESER (1975): 26, 28–29, 31, Pl. 2a (key to species, diagnosis, illustrations); POLHEMUS (1976): 226, 242 (listed); FROESCHNER (1981): 61 (catalogue); POLHEMUS & POLHEMUS (1988a): 543 (catalogue); NIESER & ALKINS KOO (1991): 13–14 (key); NIESER & CHEN (1992): 8 (distribution); NIESER & MELO (1997): 12, 50 (distribution); FROESCHNER (1999): 148 (catalogue); BASS (2003): 66 (distribution); VIANNA & MELO (2003): 126–127 (distribution); MELO & NIESER (2004): 44 (distribution); SOUZA et al. (2006): 808 (distribution); PEREIRA & MELO (2007): 645 (distribution); HECKMAN (2011): 458 (key to species, illustration); MOREIRA et al. (2011): 58 (checklist, Brazil); CIANFERONI (2012): 67 (key to species); BROŽEK (2013): 342, 343, 345, 372 (morphology); CORDEIRO et al. (2014): 496 (key to species, illustrations); BARBOSA & RODRIGUES (2015): 163 (listed); BROŽEK (2015): 6, 14, 21–24 (morphology); LLANO & GUTIÉRREZ (2015): 377 (list); POLHEMUS & POLHEMUS (2016): 13, 15–16, 55–58 (key to species, redescription, illustrations).

*Pelagonus marginatus* (misidentification, partim): UHLER (1893): 706 (list, ‘two forms’); UHLER (1894): 222 (variability).

**Material examined.** MEXICO: BAJA CALIFORNIA SUR: [El] Triunfo, 8.vii.1914, 1 ♂, G. H. Harris lgt., C. J. Drake det. (NMPC). SAN LUIS POTOSÍ: Valles, 17.vii.1950, 2 ♂♂ 1 ♀, Drake & Hottes lgt., C. J. Drake det. (NMPC). TAMAULIPAS: Tampico, 16.vii.1950, 1 ♂, Drake & Hottes lgt., C. J. Drake det. (NMPC).

**Distribution.** *Nearctic Region:* North America: USA: Arizona (DRAKE 1952, POLHEMUS & POLHEMUS 1988a), Texas (SCHELL 1943a; DRAKE 1952; POLHEMUS & POLHEMUS 1988a, 2016), Utah (POLHEMUS & POLHEMUS 2016). *Neotropical Region:* Central America: Belize (POLHEMUS & POLHEMUS 2016); Costa Rica (SCHELL 1943a); Guatemala (SCHELL 1943a, POLHEMUS & POLHEMUS 2016); Honduras (POLHEMUS & POLHEMUS 2016); Mexico (KIRKALDY & TORRE BUENO 1909, SCHELL 1943a, DRAKE 1952, POLHEMUS & POLHEMUS 1988a): Baja California Sur (POLHEMUS & POLHEMUS 2016), Campeche (CHAMPION 1901, MONTANDON 1910, POLHEMUS & POLHEMUS 2016), Chiapas (POLHEMUS & POLHEMUS 2016), Guanajuato (POLHEMUS & POLHEMUS 2016), Guerrero (POLHEMUS & POLHEMUS 2016), Jalisco (POLHEMUS & POLHEMUS 2016), Mexico (POLHEMUS & POLHEMUS 2016), Morelos (POLHEMUS & POLHEMUS 2016), Nayarit (POLHEMUS & POLHEMUS 2016), Oaxaca (POLHEMUS & POLHEMUS 2016), Pueblo (POLHEMUS & POLHEMUS 2016), San Luis Potosí (new record), Sinaloa (CHAMPION 1901, POLHEMUS & POLHEMUS 2016), Tamaulipas (POLHEMUS & POLHEMUS 2016), Veracruz (CHAMPION 1901, POLHEMUS & POLHEMUS 2016); Nicaragua

(POLHEMUS & POLHEMUS 2016); Panama (POLHEMUS & POLHEMUS 2016). Caribbean Islands: Curaçao (COBBEN 1960); Grenada (UHLER 1894, as *P. marginatus*, partim; CHAMPION 1901, KIRKALDY & TORRE BUENO 1909, SCHELL 1943a, POLHEMUS & POLHEMUS 2016); St. Vincent (UHLER 1893, as *P. marginatus*, partim; CHAMPION 1901, KIRKALDY & TORRE BUENO 1909, SCHELL 1943a, POLHEMUS & POLHEMUS 2016); Trinidad and Tobago (NIESER & ALKINS KOO 1991, NIESER & CHEN 1992, BASS 2003). South America: Brazil: Amazonas (PEREIRA & MELO 2007, MOREIRA et al. 2011, CORDEIRO et al. 2014), Minas Gerais (NIESER & MELO 1997, VIANNA & MELO 2003, MELO & NIESER 2004, SOUZA et al. 2006, MOREIRA et al. 2011, CORDEIRO et al. 2014); Colombia (DRAKE 1952); Ecuador (SCHELL 1943a, NIESER & CHEN 1992, CIANFERONI 2012); Paraguay (SCHELL 1943a); Peru (SCHELL 1943a, DRAKE 1952); Suriname (NIESER 1975); Venezuela (POLHEMUS & POLHEMUS 2016).

**Notes.** GUÉRIN-MÉNEVILLE (1843) dedicated the species to its collector, M. Perbos, using the latinized form of his name (*Perboscius*, stem *perbosci-*) to form the name as *O. perbosci*, which is the correct original spelling of the name. The name was cited as *O. perbosci* at least five times (for references see above) until KIRKALDY & TORRE BUENO (1909), with a single exception of CHAMPION (1901). CHAMPION (1901), MONTANDON (1910), and all subsequent authors (for 27 additional references see above) used the incorrect subsequent spelling of the name, *O. perbosci* (see ICBN 1999: Art. 32.1–3, 33.3, 33.4). In this case the Article 33.3.1 (ICBN 1999) applies in favour of *O. perbosci*: ‘when an incorrect subsequent spelling is in prevailing usage and is attributed to the publication of the original spelling, the subsequent spelling and attribution are to be preserved and the spelling is deemed to be a correct original spelling.’ We recognize *O. perbosci* as being in prevailing usage and therefore the correct original spelling in the sense of ICBN (1999).

GUÉRIN-MÉNEVILLE (1843) described the species based on unknown number of specimens and without information on their depository. CHAMPION (1901) wrote that: ‘The type of this insect was obtained by us from the Sallé collection’. CIANFERONI (2012) specified the sex of the specimen, incorrectly labelled as holotype, as male. Using the term ‘the type’ for the syntype he used for definition of the taxon, CHAMPION (1901) fulfilled the requirements of the Article 74.5 (ICBN 1999) and his action constitutes a valid lectotype designation.

It was also recorded from Cuba by CHAMPION (1901) and KIRKALDY & TORRE BUENO (1909) by error (see NARANJO et al. 2010, POLHEMUS & POLHEMUS 2016).

### *Ochterus philippinensis* Kormilev, 1971

*Ochterus philippinensis* Kormilev, 1971: 434, 436–437 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Philippines: Mindoro: ‘San Jose’ (CASC).

*Ochterus philippinensis*: GAPUD & SAN VALENTIN (1977): 272, 281, 291–292 (key to species, redescription, illustration); GAPUD (1981): 303–304, 307 (diagnosis, illustrations); GAPUD (2003): 107 (checklist); CHEN et al. (2005): 413 (checklist).

**Distribution.** *Oriental Region:* Philippines: Mindoro (KORMILEV 1971, GAPUD & SAN VALENTIN 1977, GAPUD 1981).

### *Ochterus piliferus* Kormilev, 1973

*Ochterus piliferus* Kormilev, 1973: 2, 6–8 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Angola: ‘Vila Luso, Moxico’ (CASC).

**Distribution. Afrotropical Region:** Angola (KORMILEV 1973).

### *Ochterus polhemusi* Gapud, 1981

*Ochterus brunneus* Gapud & San Valentin, 1977: 272, 276–278, 281, 285–286, 288, 296–298 (key to species, description, illustrations). HOLOTYPE: ♂, Philippines: Luzon: ‘Molawin Creek, Mt. Makiling, Laguna’ (UPLB). Junior homonym of *Ochterus brunneus* Hungerford, 1927.

*Ochterus brunneus*: GAPUD (1986): 32, 34–36 (key to species, redescription, illustration).

*Ochterus polhemusi* Gapud, 1981: 300–301 (nomenclature). New substitute name for *Ochterus brunneus* Gapud & San Valentin, 1977.

*Ochterus polhemusi*: GAPUD (2003): 107 (checklist); CHEN et al. (2005): 413 (checklist).

**Distribution. Oriental Region:** Philippines: Cebu (GAPUD 2003), Laguna (GAPUD & SAN VALENTIN 1977, GAPUD 1981), Leyte (GAPUD 1981), Mindanao (GAPUD 1981), Mindoro (GAPUD & SAN VALENTIN 1977), Negros (GAPUD 2003).

### *Ochterus pseudomarginatus*

**D. A. Polhemus & J. T. Polhemus, 2012**

*Ochterus pseudomarginatus* D. A. Polhemus & J. T. Polhemus, 2012: 345–346, 349–351, 355 (key to species, description, illustrations). HOLOTYPE: ♂, Malaysia: Johor: ‘Endau Rompin, Sungai Pantai Burung, off Sungai Endau’ (BPBM).

*Ochterus pseudomarginatus*: POLHEMUS & POLHEMUS (2015): 208–209, 211 (key to species, illustrations).

**Distribution. Oriental Region:** Indonesia: Sumatra (POLHEMUS & POLHEMUS 2012); Malaysia: Peninsular part (POLHEMUS & POLHEMUS 2012); Singapore (POLHEMUS & POLHEMUS 2012).

### *Ochterus pseudorotundus*

**D. A. Polhemus & J. T. Polhemus, 2016**

*Ochterus pseudorotundus* D. A. Polhemus & J. T. Polhemus, 2016: 13, 18, 58–61 (key to species, description, illustrations). HOLOTYPE: ♂, Mexico: ‘Tamaulipas, Bocatoma, 7 km SSE of Gomez Farias [vic. 23°01'04"N, 99°07'28"W, elev. 135 m]’ (JTPC → USNM).

**Distribution. Neotropical Region: Central America:** Mexico: Nuevo León (POLHEMUS & POLHEMUS 2016), San Luis Potosí (POLHEMUS & POLHEMUS 2016), Tamaulipas (POLHEMUS & POLHEMUS 2016), Veracruz (POLHEMUS & POLHEMUS 2016).

### *Ochterus rotundus*

**J. T. Polhemus & M. S. Polhemus, 1976**

*Ochterus viridifrons* (misidentification): SCHELL (1943b): 38 (specimens from Grand Canyon); DRAKE (1952): 75 (record from Arizona) (see POLHEMUS & POLHEMUS 1976: 223).

*Ochterus rotundus* J. T. Polhemus & M. S. Polhemus, 1976: 223–225 (original description, illustrations). HOLOTYPE: ♂, Mexico: Durango: ‘W Los Bancos, km 175, on top of divide’ (JTPC → USNM).

*Ochterus rotundus*: POLHEMUS & POLHEMUS (1988a): 542 (catalogue); POLHEMUS & POLHEMUS (2016): 13, 18, 61–64 (key to species, redescription, illustrations, type depository).

**Distribution. Nearctic Region:** USA: Arizona (SCHELL 1943, as *O. viridifrons*; POLHEMUS & POLHEMUS 1976, 1988a, 2016; STEVENS & POLHEMUS 2008); Mexico: Durango (POLHEMUS & POLHEMUS 1976, 2016), Jalisco (POLHEMUS & POLHEMUS 1976, 2016), Michoacan (POLHEMUS & POLHEMUS 1976, 2016), Nayarit (POLHEMUS & POLHEMUS 1976, 2016), Sinaloa (POLHEMUS & POLHEMUS 1976, 2016), Sonora (POLHEMUS & POLHEMUS 1976, 2016).

**Note.** Two series of female specimens from Jalisco (Mis maloya) and Nayarit (Compostela), identified tentatively as *O. rotundus* by POLHEMUS & POLHEMUS (1976) probably belong to *O. schellae* (see POLHEMUS & POLHEMUS 2016).

### *Ochterus santosi* Cordeiro & Moreira, 2014

*Ochterus santosi* Cordeiro & Moreira, 2014 in CORDEIRO et al. (2014): 494–496 (key to species, description, illustrations). HOLOTYPE: ♂, Brazil: Piauí: ‘Piauí-Piracurua, Parque Nacional de Sete Cidades, Olho d’água dos milagres, 4°05'32"S 41°40'48"W, 180 m a.s.l.’ (CZMA).

**Distribution. Neotropical Region: South America:** Brazil: Piauí (CORDEIRO et al. 2014).

### *Ochterus schellae* Drake, 1952

*Ochterus acutangulus* (misidentification): SCHELL (1943a): 32, 35 (key to species, illustration); SCHELL (1943b): 38–39 (differential diagnosis) (see DRAKE 1952, POLHEMUS & POLHEMUS 2016).

*Ochterus schellae* Drake, 1952: 73, 75 (description). HOLOTYPE: ♂, Mexico: Mexico: Tejupilco, alt. 1340 m (coll. Drake → USNM).

*Ochterus schellae*: DRAKE (1952): 75 (checklist); POLHEMUS & POLHEMUS (2016): 13, 18, 64–66 (key to species, redescription, illustrations).

*Ochterus rotundus* (misidentification): POLHEMUS & POLHEMUS (1976): 223 (two series of female specimens from Jalisco (Mis maloya) and Nayarit (Compostela), tentatively identified as *O. schellae* by POLHEMUS & POLHEMUS 2016).

**Distribution. Neotropical Region: Central America:** Guatemala (POLHEMUS & POLHEMUS 2016); El Salvador (POLHEMUS & POLHEMUS 2016, females only); Mexico (DRAKE 1952): ? Jalisco (POLHEMUS & POLHEMUS 2016, females only), Mexico (DRAKE 1952, POLHEMUS & POLHEMUS 2016), ? Nayarit (POLHEMUS & POLHEMUS 2016, females only), Sinaloa (POLHEMUS & POLHEMUS 2016, females only).

### *Ochterus secundus secundus* Kormilev, 1971

*Ochterus secundus* Kormilev, 1971: 434, 441–442 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Australia: New South Wales: ‘N. S. W., N. Cronnelly [= Cronulla]’ (AMSA).

*Ochterus secundus*: BAEHR (1989): 113, 116, 118, 123–124 (key to species, redescription, illustrations).

*Ochterus secundus secundus*: BAEHR (1990b): 450, 461, 475 (key to species, diagnosis, illustration, new status); CASSIS & GROSS (1995): 262 (catalogue); ANDERSEN & WEIR (2004): 266–267, 270, 336 (key to species, illustrations, checklist).

**Distribution. Australian Region:** Australia: Australian Capital Territory (BAEHR 1990b, ANDERSEN & WEIR 2004), New South Wales (KORMILEV 1971, BAEHR 1989, ANDERSEN & WEIR 2004), Queensland (KORMILEV 1971, BAEHR 1989, 1990b; ANDERSEN & WEIR 2004), South Australia (BAEHR 1989, ANDERSEN & WEIR 2004), Victoria (KORMILEV 1971; BAEHR 1989, 1990b; ANDERSEN & WEIR 2004), Western Australia (BAEHR 1989, ANDERSEN & WEIR 2004).

***Ochterus secundus pseudosecundus* Bachr, 1989**

*Ochterus pseudosecundus* Baehr, 1989: 113, 114, 116, 118, 124–125 (key to species, description, illustrations). HOLOTYPE: ♂, Australia: Western Australia: ‘Gascoyne River, 15 km N. of Carnarvon, W.A.’ (QMBA).

*Ochterus secundus pseudosecundus*: BAEHR (1990b): 450, 453, 455, 60, 461, 476 (key to species, diagnosis, illustration, new status); CASSIS & GROSS (1995): 260 (catalogue); ANDERSEN & WEIR (2004): 266–267, 270, 336 (key to species, illustrations, checklist).

**Distribution. Australian Region:** Australia: Western Australia (BAEHR 1989, 1990b; ANDERSEN & WEIR 2004).

***Ochterus seychellensis* D. A. Polhemus, 1992**

*Ochterus seychellensis* D. A. Polhemus, 1992a: 418–422 (description, illustrations). HOLOTYPE: ♂, Seychelles: Mahé: ‘Mahe, seeping rock faces along Foret Noire road near Congo Rouge trailhead, 390 m’ (USNM).

*Ochterus seychellensis*: POLHEMUS & POLHEMUS (2008): 284, 286 (illustration, key to species); POLHEMUS & POLHEMUS (2013): 94–95 (diagnosis, illustrations).

**Distribution. Afro-tropical Region:** Seychelles: Mahé (POLHEMUS 1992a, POLHEMUS & POLHEMUS 2013).

***Ochterus sheardi*****D. A. Polhemus & J. T. Polhemus, 2016**

*Ochterus sheardi* D. A. Polhemus & J. T. Polhemus, 2016: 17, 66–69 (key to species, description, illustrations). HOLOTYPE: ♂, Costa Rica: ‘Alajuela, La Fortuna, Querado Burio’ (JTPC → USNM).

**Distribution. Neotropical Region: Central America:** Costa Rica (POLHEMUS & POLHEMUS 2016).

***Ochterus signatus*****D. A. Polhemus & J. T. Polhemus, 2012**

*Ochterus signatus* D. A. Polhemus & J. T. Polhemus, 2012: 345–347–349, 355 (key to species for Singapore, Malay Peninsula, Sumatra and Java; description, illustrations). HOLOTYPE: ♂, Vietnam: Lam Dong Province: ‘tributary stream to main river at Suoi Vang hydro, 1430 m, 11°59'26"N, 108°22'06"E’ (BPBM).

*Ochterus signatus*: POLHEMUS & POLHEMUS (2015): 208–209, 211 (key to species, illustrations).

**Distribution. Oriental Region:** Malaysia: Peninsular part (POLHEMUS & POLHEMUS 2012), Vietnam (POLHEMUS & POLHEMUS 2012).

***Ochterus singaporensis*****D. A. Polhemus & J. T. Polhemus, 2012**

*Ochterus singaporensis* D. A. Polhemus & J. T. Polhemus, 2012: 345–346, 351–353, 355 (key to species, description, illustrations). HOLOTYPE: ♂, Singapore: ‘MacRitchie Catchment Reservoir, NS 123B #G (stream towards reservoir)’ (ZRCRS).

*Ochterus singaporensis*: POLHEMUS & POLHEMUS (2015): 207, 209–210 (key to species, illustrations).

**Distribution. Oriental Region:** Singapore (POLHEMUS & POLHEMUS 2012).

***Ochterus smaragdinus*****D. A. Polhemus & J. T. Polhemus, 2016**

*Ochterus smaragdinus* D. A. Polhemus & J. T. Polhemus, 2016: 18, 69–71 (key to species, description, illustrations). HOLOTYPE: ♂, Mexico: Chiapas: ‘swift mountain river, 7 mi. N of Santa Fe [vic. 17°25'56"N, 93°02'05"W, elev. ~150 m]’ (JTPC → USNM).

**Distribution. Neotropical Region: Central America:** Mexico: Chiapas (POLHEMUS & POLHEMUS 2016), Veracruz (POLHEMUS & POLHEMUS 2016).

***Ochterus strigicollis* Horváth, 1913**

*Ochterus strigicollis* Horváth, 1913: 478–479, Fig. 2 (mislabelled as *O. marginatus*) (description, differential diagnosis, illustration). HOLOTYPE: ♀, Israel: ‘Wad-es Semakh’ (NZSI).

*Ochterus strigicollis*: POLHEMUS (1995a): 26 (catalogue).

**Distribution. Palaearctic Region:** Israel (HORVÁTH 1913, LINNAUORI 1960).

***Ochterus stysi*****D. A. Polhemus & J. T. Polhemus, 2008**

*Ochterus stysi* D. A. Polhemus & J. T. Polhemus, 2008: 282–286 (description, illustrations, key to species for Indian Ocean). HOLOTYPE: ♂, Mauritius: Black River District: ‘stream 1.2 km. S. of Chamarel, 200 m’ (BPBM).

**Distribution. Afro-tropical Region:** Mauritius (POLHEMUS & POLHEMUS 2008).

***Ochterus surigaoensis* Gapud, 1995**

*Ochterus surigaoensis* Gapud, 1995: 42–43 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Philippines: Mindanao: ‘Men-dozana Falls, Bislig, Surigao del Sur’ (UPLB).

*Ochterus surigaoensis*: GAPUD (2003): 107 (checklist); CHEN et al. (2005): 413 (checklist).

**Distribution. Oriental Region:** Philippines: Mindanao (GAPUD 1995).

***Ochterus tenebrosus* Nieser, 1975**

*Ochterus tenebrosus* Nieser, 1975: 26, 29–31, Pl. 2c (key to species, description, illustration). HOLOTYPE: ♂, Suriname: ‘Marowijne, road Albinga-Moengo’ (RMNH).

*Ochterus tenebrosus*: HECKMAN (2011): 462 (key to species, illustration); MOREIRA et al. (2011): 58 (checklist, Brazil); CORDEIRO et al. (2014): 67 (key to species, illustration).

**Distribution. Neotropical Region: South America:** Brazil: Amazonas (PEREIRA & MELO 2007, MOREIRA et al. 2011, CORDEIRO et al. 2014); Suriname (NIESER 1975).

***Ochterus thienemanni* Jaczewski, 1935**

*Ochterus thienemanni* Jaczewski, 1935: 480–482 (description, key to species, illustrations). HOLOTYPE: ♂, Indonesia: Sumatra: ‘Mittel-sumatra, See von Singkarak, am Wasserfall von Panjingahan, Höhe 362 m’ [= Central Sumatra, Singkarak lake, Panjingahan waterfall, 362 m a.s.l.] (?ZMPA).

*Ochterus thienemanni*: NIESER & CHEN (1999): 90–91 (key to species, illustration); CHEN et al. (2005): 413 (checklist); POLHEMUS & POLHEMUS (2012): 345, 352–355 (key to species, diagnosis, illustrations); POLHEMUS & POLHEMUS (2015): 208–209, 212 (key to species, illustrations).

**Distribution. Oriental Region:** Indonesia: Bali (JACZEWSKI 1935, POLHEMUS & POLHEMUS 2012), Java (JACZEWSKI 1935, POLHEMUS & POLHEMUS 2012), Sumatra (JACZEWSKI 1935, POLHEMUS & POLHEMUS 2012).

**Note.** The holotype was originally deposited in ZMPA, Warsaw, but it might have been lost during World War II when a large part of Jaczewski’s collection was destroyed (see JACZEWSKI 1949: 107–108, POLHEMUS & POLHEMUS

2012: 354). Our attempt to contact ZMPA to investigate the whereabouts of the holotype has remained unanswered.

Previous records from New Guinea (KORMILEV 1971, BAEHR 1990c, CHEN et al. 2005) represent misidentifications (POLHEMUS & POLHEMUS 2012). The tentative identification of females from Sulawesi by NIESER & CHEN (1992) was later corrected to *O. marginatus* by NIESER & CHEN (1999); the species was listed from Sulawesi by CHEN et al. (2005) in error.

#### *Ochterus* sp. not *thienemanni* Jacewski, 1935

*Ochterus thienemanni* (misidentification): KORMILEV (1971): 437–438 (description, differential diagnosis, illustration); BAEHR (1990b): 451, 453–454, 456–458, 461, 469–470 (key to species, redescription, illustrations); POLHEMUS & POLHEMUS (2012): 354 (clarification of the misidentification).

**Distribution. Australian Region:** Papua New Guinea (KORMILEV 1971, BAEHR 1990b).

#### *Ochterus trichotos* Nieser & Chen, 1999

*Ochterus trichotos* Nieser & Chen, 1999: 90–92–93, 123 (key, description, illustrations). HOLOTYPE: ♂, Indonesia: Sulawesi: ‘Sulawesi Selatan, Malino-Manipi, 700 m’ (NHMW).

*Ochterus trichotos*: CHEN et al. (2005): 413 (checklist).

**Distribution. Australian Region:** Indonesia: Sulawesi (NIESER & CHEN 1999).

#### *Ochterus unidentatus* Nieser & Chen, 1992

*Ochterus unidentatus* Nieser & Chen 1992: 7–8 (description, differential diagnosis, illustration). HOLOTYPE: ♂, Ecuador, ‘Pichin, Tinalandia’ (MZLU).

*Ochterus unidentatus*: CIANFERONI (2012): 63–64, 67 (key to species for Ecuador, variability, illustrations).

**Material examined. ECUADOR:** NAPO: 2.7 km SW of Diaz de Pineda, 0°19'10"S 77°45'33"W, 1560 m a.s.l., bank of the stony stream, sandy and clay bottom with algae with thin layer of the water, exposed, 1.xii.2006, 1 ♂, M. Fikáček & J. Skuhrovec lgt., P. Kment det. (NMPC). PASTAZA: Puyo env., 11.–15.xii.2000, E-38, 1 ♀, V. Mařík lgt., P. Kment det. (NMPC).

**Distribution. Neotropical Region:** South America: Colombia (MANZANO et al. 1995, PADILLA-GIL 2015); Ecuador (CIANFERONI 2012).

**Note.** According to POLHEMUS & POLHEMUS (2016: 44) this species may be a junior synonym of *O. manni*.

#### *Ochterus viridifrons* (Champion, 1901)

*Pelagonus viridifrons* Champion, 1901: 345–346, Pl. XX: fig. 14 (key, original description, illustration). SYNTYPES: ♂, Guatemala: ‘Rio Naranjo’ (BMNH); ♀, Guatemala: ‘San Gerónimo’ (BMNH).

*Ochterus viridifrons*: KIRKALDY & TORRE BUENO (1909): 179 (catalogue); BARBER (1913): 214 (key to species); SCHELL (1943a): 32, 35 (key to species, illustration); SCHELL (1943b): 37–38 (original description repeated, differential diagnosis); DRAKE (1952): 75 (checklist); FROESCHNER (1999): 148 (catalogue); HECKMAN (2011): 459 (key to species, illustration); CIANFERONI (2012): 67 (key to species); HERRERA MADRIGAL (2015): 256 (illustration); POLHEMUS & POLHEMUS (2016): 10, 15, 18, 71–73 (key to species, redescription, illustrations).

**Distribution. Neotropical Region:** Central America: Costa Rica (SCHELL 1943b, HERRERA MADRIGAL 2015, POLHEMUS & POLHEMUS 2016); Guatemala (CHAMPION 1910, KIRKALDY & TORRE BUENO 1909, POLHEMUS & POLHEMUS 2016); Honduras (POLHEMUS & POLHEMUS 2016); Mexico (DRAKE

1952); Chiapas (POLHEMUS & POLHEMUS 2016), Durango (NIESER & CHEN 1992), Guerrero (POLHEMUS & POLHEMUS 2016), Oaxaca (POLHEMUS & POLHEMUS 2016); Panama (SCHELL 1943b, FROESCHNER 1999, POLHEMUS & POLHEMUS 2016). South America: Ecuador (CIANFERONI 2012).

**Note.** A specimen from Grand Canyon, Arizona, mentioned by SCHELL (1943b: 38) and DRAKE (1952) belongs to *O. rotundus* (see POLHEMUS & POLHEMUS 1976: 224).

#### *Ochterus xustos* Nieser & Chen, 1992

*Ochterus xustos* Nieser & Chen, 1992: 12–13 (description, differential diagnosis, illustration). HOLOTYPE: ♂, Malaysia: Sabah: ‘Jesselton, Sensuran road, mile 25, 4000 ft [= 1219 m a.s.l.]’ (RMNH).

*Ochterus xustos*: NIESER & CHEN (1999): 90–91 (key, illustration); CHEN et al. (2005): 413 (checklist).

**Distribution. Oriental Region:** Malaysia: Sabah (NIESER & CHEN 1992).

#### *Ochterus zetteli* Gapud, 2003

*Ochterus zetteli* Gapud, 2003: 103–107 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, Philippines: Palawan: ‘Busuanga Island, W. Borac’ (UPLB).

*Ochterus zetteli*: CHEN et al. (2005): 413 (checklist).

**Distribution. Oriental Region:** Philippines: Palawan: Busuanga Island (GAPUD 2003).

#### *Ochterus* sp. near *zetteli* Gapud, 2003

*Ochterus* sp. (2 ♀♀ from Philippines: Palawan: Cabayugan River): GAPUD (2003): 106–107 (diagnosis).

**Distribution. Oriental Region:** Philippines: Palawan (GAPUD 2003).

**Note.** According to GAPUD (2003), this species is highly likely to be new, though closely related to *O. zetteli*. A male specimen is required in order to determine its species status.

#### Genus *Ocyochterus* Drake & Gómez-Menor, 1954

*Ocyochterus* Drake & Gómez-Menor, 1954: 157–158 (original description). Type species: *Pelagonus victor* Bolívar, 1879, by original designation.

*Ocyochterus*: NIESER (1975): 26 (key to genera and species); FROESCHNER (1981): 61 (key to genera); ŠTYS & JANSSON (1988): 8 (catalogue); YAO et al. (2007): 828, 830 (key to genera, differential table); MAZZUCONI et al. (2009a): 213 (key to genera); HECKMAN (2011): 457 (key to genera); YAO et al. (2011): 590, 597–598 (key to genera, phylogeny); POLHEMUS & POLHEMUS (2014): 164–170 (key to genera and species, revision); BARBOSA & RODRIGUES (2015): 174, 176 (key to genera, illustrations); MELO (2015): 344 (key to genera, diagnosis); MOREIRA et al. (2019): 179, 183, 188, 190 (key to genera, illustrations).

**Note.** HERRERA MADRIGAL (2015) published what was indicated to be the first record of this genus from Colombia, but he was preceded by POLHEMUS & POHEMUS (2014).

#### *Ocyochterus irmae*

D. A. Polhemus & J. T. Polhemus, 2014

*Ocyochterus irmae* D. A. Polhemus & J. T. Polhemus, 2014: 164–170 (key to species, description, illustrations). HOLOTYPE: ♂, Colombia: ‘Valle de Cauca, Farallones de Cali National Park, seeping bedrock faces along upper Rio Ponce, near El Topacio, 1550 m, [vic. 3°19'47"N 76°38'13"W]’ (USNM).

**Distribution.** *Neotropical Region:* South America: Colombia (POLHEMUS & POLHEMUS 2014); Ecuador (POLHEMUS & POLHEMUS 2014).

### *Ocyochterus vitor* (Bolívar, 1879)

*Pelagonus vitor* Bolívar 1879: 144 (original description). HOLOTYPE: ♂,

Ecuador: ‘Pichincha’ (IEEM → MNCN).

*Pelagonus vitor:* CHAMPION (1901): 344 (list).

*Pelagonus Vitor:* CAMPOS (1925): 5 (catalogue).

*Ochterus vitor:* TORRE BUENO (1906): 50 (list); KIRKALDY & TORRE BUENO (1909): 179 (catalogue); SCHELL (1943a): 33 (as *incertae sedis*); SCHELL (1943b): 46 (original description repeated).

*Ochterus vitors* (incorrect subsequent spelling): DRAKE (1952): 75 (checklist).

*Ocyochterus vitor:* DRAKE & GÓMEZ-MENOR (1954): 158–159, pl. X: Fig. 1 (new combination, illustrations); FROESCHNER (1981): 61 (catalogue); HECKMAN (2011): 457 (illustrations); CIANFERONI (2012): 67 (key to species for Ecuador); POLHEMUS & POLHEMUS (2014): 164, 168, 170 (key to species, diagnosis, illustrations); HERRERA MADRIGAL (2015): 256 (illustration); POPOV & HEISS (2014a): 187–188 (illustrations).

*Pelagonus splendidulus* Montandon, 1898: 73–75 (original description, differential diagnosis). LECTOTYPE (designated by DRAKE & GÓMEZ-MENOR 1954: 158, as type): ♂, Ecuador: ‘Nanegal’ (MNHN). Junior subjective synonym by DRAKE & GÓMEZ-MENOR (1954: 158).

*Pelagonus splendidulus:* CHAMPION (1901): 344 (list); CAMPOS (1925): 5 (catalogue).

*Ochterus splendidulus:* TORRE BUENO (1906): 50 (list); KIRKALDY & TORRE BUENO (1909): 179 (catalogue); SCHELL (1943a): 32–36 (key to species, translation of original description, differential diagnosis, illustration).

*Ochterus spendilulus* (incorrect subsequent spelling): DRAKE (1952): 75 (checklist).

**Distribution.** *Neotropical Region:* South America: Colombia (HERRERA MADRIGAL 2015); Ecuador (BOLÍVAR 1879, MONTANDON 1898, KIRKALDY & TORRE BUENO 1909, DRAKE 1952, POLHEMUS & POLHEMUS 2014).

**Note.** MONTANDON (1898) described *Pelagonus splendidulus* based on an unknown number of specimens. DRAKE & GÓMEZ-MENOR (1954) wrote: ‘type, male, in Museum d’Histoire Naturelle, Paris, and a female also labeled type (should be allotype) in British Museum of Natural History, London’. Using the term ‘type’ for one of the syntypes they used for definition of the taxon, DRAKE & GÓMEZ-MENOR (1954) fulfilled the requirements of the Article 74.5 (ICZN 1999) and their action constitutes a valid lectotype designation.

### Fossil record

#### Family OCHTERIDAE Kirkaldy, 1906 [1815]

##### Genus †*Angulochterus* Yao, Zhang & Ren, 2011

*Angulochterus* Yao, Zhang & Ren, 2011 in YAO et al. (2011): 590, 595–598 (key to genera, original description, phylogeny). Type species: *Angulochterus quadrimaculatus* Yao, Ren & Shih, 2011, by original designation.

##### †*Angulochterus quadrimaculatus* Yao, Zhang & Ren, 2011

*Angulochterus quadrimaculatus* Yao, Zhang & Ren, 2011 in YAO et al. (2011): 595–598 (incorrect original spelling) (original description, illustrations). HOLOTYPE: ♂, CNU-HELB2006644pc (part and counterpart) (CNUB). Type locality and horizon: China: ‘Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.’

*Angulochterus quatlimaculatus* (incorrect original spelling): YAO et al. (2011): 590 (cladogram).

*Angulochterus quadrimaculatus:* SCHUH & WEIRAUCH (2020): 150–151 (list).

**Distribution.** China: Liaoning (Yixian Formation: Early Cretaceous) (YAO et al. 2011).

**Note.** The species name occurs in two different original spellings throughout the text, *A. quadrimaculatus* seven times throughout the text, *A. quatlimaculatus* (lapsus calami) twice in the cladogram on page 590. According to their etymology, the ‘species name is combination of the Latin *quatri-* (four) [lapsus calami for *quadri-*] and *maculatus* (marking)’. We correct here the spelling of the name as *A. quadrimaculatus* according to the Article 32.5.1 (ICZN 1999).

##### Genus †*Floricaudus* Yao, Ren & Shih, 2011

*Floricaudus* Yao, Ren & Shih, 2011 in YAO et al. (2011): 590, 593–594, 597–598 (key to genera, original description, phylogeny). Type species: *Floricaudus multilocellus* Yao, Ren & Shih, 2011, by original designation.

##### †*Floricaudus multilocellus* Yao, Ren & Shih, 2011

*Pristinochterus zhangi* (misidentification): YAO et al. (2007): 832: fig. 18, 833: fig. 22 (illustration of specimen CNU-HE-LB2006317, see YAO et al. 2011).

*Floricaudus multilocellus* Yao, Ren & Shih, 2011 in YAO et al. (2011): 591, 593–594, 598 (original description, illustrations). HOLOTYPE: ♂, CNU-HE-LB2008006 (CNUB). Type locality and horizon: China: ‘Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.’

*Floricaudus multilocellus:* SCHUH & WEIRAUCH (2020): 150–151 (list).

**Distribution.** China: Liaoning (Yixian Formation: Early Cretaceous) (YAO et al. 2011).

##### Genus †*Pristinochterus* Yao, Cai & Ren, 2007

*Pristinochterus* Yao, Cai & Ren, 2007: 827–830 (key to genera, original description, differential table). Type species: *Pristinochterus zhangi* Yao, Cai & Ren, 2007, by original designation.

*Pristinochterus:* YAO et al. (2011): 590, 592–593, 597–598 (key to genera, revision, phylogeny).

##### †*Pristinochterus ovatus* Yao, Zhang & Ren, 2011

*Pristinochterus ovatus* Yao, Zhang & Ren, 2011 in YAO et al. (2011): 591–592–593, 598 (key to species, original description, illustrations). HOLOTYPE: ♂, CNU-HELB2009096pc (part and counterpart) (CNUB). Type locality and horizon: China: ‘Huangbanjigou, Chaomidian Village, Beipiao City and Dawangzhangzi Village, Lingyuan City, Liaoning Province, Yixian Formation, Early Cretaceous, 125 Ma.’

*Pristinochterus ovatus:* SCHUH & WEIRAUCH (2020): 152–153 (list).

**Distribution.** China: Liaoning (Yixian Formation: Early Cretaceous) (YAO et al. 2011).

**Note.** The exact locality of holotype is not mentioned in the original description.

##### †*Pristinochterus zhangi* Yao, Cai & Ren, 2007

*Pristinochterus zhangi* Yao, Cai & Ren, 2007: 828–830–832 (original description of adult and larva, illustrations). HOLOTYPE: ♀, CNU-HE-LB2006301–302 (part and counterpart) (CNUB). Type locality and horizon: China: ‘Huangbanjigou, Chaomidian Village, Beipiao City and Dawangzhangzi Village, Lingyuan City, Liaoning Province, Yixian Formation, Late Jurassic; Balihan Village, Ningcheng County, Chifeng City, Inner Mongolia Autonomous Region, China, Jiufotang Formation, Early Cretaceous.’

*Pristinochterus zhangi*: YAO et al. (2010): 142–143 (diagnosis, illustration); YAO et al. (2011): 591–592, 598 (key to species); SCHUH & WEIRAUCH (2020): 152–153 (list).

**Distribution.** China: Liaoning (Yixian Formation: Late Jurassic to Early Cretaceous) (YAO et al. 2007, 2010), Inner Mongolia (Jiufotang Formation: Early Cretaceous) (YAO et al. 2007, 2010).

**Note.** Exact locality of holotype is not mentioned in the original description.

#### Genus †*Riegerochterus* Popov & Heiss, 2014

*Riegerochterus* Popov & Heiss, 2014a: 186–187 (description, differential diagnosis). Type species: *Riegerochterus baehri* Popov & Heiss, 2014a, by original designation.

#### †*Riegerochterus baehri* Popov & Heiss, 2014

*Riegerochterus baehri* Popov & Heiss, 2014a: 187–188 (description, differential diagnosis, illustrations). HOLOTYPE: ♂, ‘in a piece of irregular shaped Dominican Amber (17 × 17 × 13 mm), Type. Kat. Nr. Do-4667-B’ (SMNS).

*Riegerochterus baehri*: SCHUH & WEIRAUCH (2020): 152–153 (list).

**Distribution.** Dominican amber (?Early to Middle Miocene) (POPOV & HEISS 2014a).

### Ochteridae incertae sedis

#### Genus †*Yuripachys* nom. nov.

*Meropachys* Popov, 1986: 78–79 (original description). Type species: *Meropachys dubius* Popov, 1986, by original designation. Junior homonym of *Meropachys* Burmeister, 1835 (Hemiptera: Coreidae). *Meropachys*: POPOV & HEISS (2014a): 186 (systematic placement).

**Note.** The generic name *Meropachys* Popov, 1986 is a junior homonym of *Meropachys* Burmeister, 1835, a valid genus of the family Coreidae (Hemiptera: Heteroptera), including two valid species from South America (PAC-KAUSKAS 2010, ANONYMUS 2019). As there is no junior synonym available as a replacement name, we propose here a new substitute name, *Yuripachys* nom. nov., to replace *Meropachys* Popov, 1986. The new name is dedicated to Yuri A. Popov (1936–2016), a great Russian specialist in heteropteran palaeontology, being composed of his given name and the Greek adjective *pachys* ( $\pi\alpha\chi\omega\varsigma$ ), meaning for example thick, large, stout, coarse, fat, or great. The gender is masculine; the grammatical stem is *Yuripache-*.

#### †*Yuripachys dubius* (Popov, 1986) comb. nov.

*Meropachys dubius* Popov, 1986: 75: fig. 45, 79, Pl. V: fig. 5 (original description, illustrations). HOLOTYPE: ♀, positive part, body dorsally without head and fore legs, ‘ПИН, № 3152/806’, ‘Myangad, 221/17’ (PIN).

*Meropachys dubius*: POPOV & HEISS (2014a): 186 (systematic placement); SCHUH & WEIRAUCH (2020): 180–181 (listed in Pachymeridiidae).

**Distribution.** West Mongolia (Gurban-Eren Formation: Early Cretaceous) (POPOV 1986).

**Note.** The species was originally placed in the Mesozoic lygaeoid family Pachymeridiidae (POPOV 1986), but according to POPOV & HEISS (2014a) it more probably belongs to Ochteridae; this change was overlooked by SCHUH & WEIRAUCH (2020).

### Family †PROPREOCORIDAE Popov, Dolling & Whalley, 1994, stat. nov.

‘Leptopodomorpha. Family nov. 2’: WHALLEY (1985): 145. Propreocorinae Popov, Dolling & Whalley, 1994: 335–336 (original description). Type genus: *Propreocoris* Popov, Dolling & Whalley, 1994. Propreocorinae: SHCHERBAKOV & POPOV (2002): 151 (systematic placement); SCHUH & WEIRAUCH (2020): 152–153 (list).

Properocorinae (incorrect subsequent spelling): SCHUH & WEIRAUCH (2020): 139 (list).

Propreocorinae (incorrect subsequent spelling): SCHUH & WEIRAUCH (2020): 140 (list).

**Note.** According to GRIMALDI & ENGEL (2005) and YAO et al. (2011) *Propreocoris* represents a common ancestor of the Ochteridae and Gelastocoridae. As long as Propreocorinae are no longer included in Ochteridae, we formally raise this taxon to family rank.

#### Genus †*Propreocoris* Popov, Dolling & Whalley, 1994

‘Gen. et sp. nov. 2A’: WHALLEY (1985): 144: fig. 41, 145 (diagnosis, illustration).

*Propreocoris* Popov, Dolling & Whalley, 1994: 317, 333, 336–337 (original description). Type species: *Propreocoris maculatus* Popov, Dolling & Whalley, 1994, by original designation.

*Propreocoris*: GRIMALDI & ENGEL (2005): 320–321 (systematic placement); YAO et al. (2007): 828, 830 (key to genera, differential table); YAO et al. (2011): 591–592 (systematic placement).

#### †*Propreocoris maculatus* Popov, Dolling & Whalley, 1994

‘Gen. et sp. nov. 2A’: WHALLEY (1985): 144: fig. 41, 145 (diagnosis, illustration).

*Propreocoris maculatus* Popov, Dolling & Whalley, 1994: 317, 333, 336 (original description, illustrations). HOLOTYPE: ?sex (part and counterpart), In.59152, United Kingdom: England: ‘The Woodstone, Black Ven, Charmouth, Dorset; Lower Lias’ (BMNH: coll. Jackson).

*Propreocoris maculatus*: SCHUH & WEIRAUCH (2020): 139, 152–153 (list).

**Distribution.** United Kingdom: England: Dorset (Charmouth fauna: Early Jurassic (Lower Lias)) (POPOV et al. 1994).

**Note.** The fossil is represented by a poorly preserved partial body, lacking legs and head.

### Ochteroidea incertae sedis

#### Genus †*Grimaldinia* Popov & Heiss, 2014

*Grimaldinia* Popov & Heiss, 2014b: 445–448 (original description). Type species: *Grimaldinia pronotalis* Popov & Heiss, 2014b, by original designation.

*Grimaldinia*: SCHUH & WEIRAUCH (2020): 139, 152–153 (revised systematic placement).

**Note.** POPOV & HEISS (2014b) described the genus *Grimaldinia* in family Leptopodidae, subfamily Leptosaldinae. SCHUH & WEIRAUCH (2020) concluded that the fossil belongs to Ochteroidea based on the short antennae that are held at rest and inserted under the eyes and the anastomosing veins forming numerous membrane cells, characters not present in any known Leptopodomorpha.

#### †*Grimaldinia pronotalis* Popov & Heiss, 2014

*Grimaldinia pronotalis* Popov & Heiss, 2014b: 446–449 (original description, illustrations). HOLOTYPE: ?sex, sub-macropterous (BUB-LEP-1), Burmese Amber (EHIA).

*Grimaldinia pronotalis*: SCHUH & WEIRAUCH (2020): 139, 152–153 (revised systematic placement).

**Distribution.** Myanmar: Kachin (Burmese Amber: Mid-Cretaceous, Late Albian–Early Cenomanian, ca. 97–110 mya) (POPOV & HEISS 2014b).

### Genus †*Heterochterus* Evans, 1971

*Heterochterus* Evans, 1971: 149–150 (original description). Type species: *Heterochterus timmsii* Evans, 1971, by original designation.

*Heterochterus*: JELL (2004): 65 (redescription, illustrations).

**Note.** EVANS (1971) placed this isolated wing in Heteroptera and noted that it is closely resembling the wing of *Ochterus marginatus*. This fossil has not been mentioned by any of the previous papers focused on fossil Ochteridae (cf. POPOV et al. 2004; YAO et al. 2007, 2011; POPOV & HEISS 2014a), except SHCHERBAKOV & POPOV (2002: 150) who listed it as ‘possible Ochteroidea’.

### †*Heterochterus timmsii* Evans, 1971

*Heterochterus timmsii* Evans, 1971: 149–150 (original description, illustration). HOLOTYPE: ?sex, wing, Australia: Queensland: ‘Mt Crosby, coll. B. V. Timms, presented by Department of Entomology, University of Queensland, Q.M. F6473’ (QMBA).

*Heterochterus timmsii*: JELL (2004): 65 (redescription, illustrations).

**Distribution.** Australia: Queensland (Ipswich Coal Measures: Late Triassic) (EVANS 1971, JELL 2004).

## Discussion

The first described species of velvety shore bugs was the widely distributed *Acanthia marginata* Latreille, 1804, discovered in southern France, and soon after accommodated in its own new genus, *Ochterus* Latreille, 1807,

and new family, Pelagonida Leach, 1815 (based on an unnecessary new replacement name *Pelogenous* Latreille, 1809). Additional two taxa were described by GUÉRIN-MÉNEVILLE (1843), *Pelogenous indicus* (junior synonym of *O. marginatus marginatus*) from India, and the first American species, *Pelogenous perbosci* from Mexico. Until the end of 19th century, altogether eleven species of Ochteridae were described, seven of which still remain valid. Among them were also two species which were in the future designated as types of new genera, *Ocyochterus* Drake & Gómez-Menor, 1954 (*Pelogenous victor* Bolívar, 1879) and *Megochterus* Jaczewski, 1934 (*Pelogenous nasutus* Montandon, 1898). Between 1901 and 1970, 17 additional species of Ochteridae were described, mostly from the American continent where important contributions were published by CHAMPION (1901), BARBER (1913), HUNGERFORD (1927), and especially the revision by SCHELL (1943a,b). In the Old World, only five species were described in this period (HORVÁTH 1913; JACZEWSKI 1934, 1935, 1938; MANCINI 1939). SINGH-PRUTHI (1925) first described and illustrated male genitalia including the right paramere of *Ochterus marginatus*, a character soon applied in ochterid taxonomy by HUNGERFORD (1927) and JACZEWSKI (1934). Big progress in describing new Ochteridae started in 1970s with three revisional papers by Nicolas A. Kormilev for Australian, Oriental and Afrotropical taxa (KORMILEV 1971, 1972, 1973), largely based on the structure of the right paramere. Soon followed the papers of NIESER (1975) (Suriname), POLHEMUS & POLHEMUS (1976) (SW USA), RIEGER (1977) (Australia, Philippines), and GAPUD & SAN VALENTIN (1977) (Philippines). Victor P. Gapud continued his work on the fauna of Philippines also in the following three decades (GAPUD 1981, 1995, 2003). In the same time,

Table 1. Number of species-group taxa of Ochteridae described over the time (valid recent taxa only).

Decade	Number per decade	Cumulative number	Decade	Number per decade	Cumulative number	Decade	Number per decade	Cumulative number
1800s	1	1	1900s	3	10	1970s	16	40
1840s	1	2	1910s	2	12	1980s	6	46
1850s	1	3	1920s	2	14	1990s	21	67
1860s	1	4	1930s	4	18	2000s	3	70
1870s	2	6	1940s	4	22	2010s	17	87
1890s	1	7	1950s	2	24	2020s	1	88

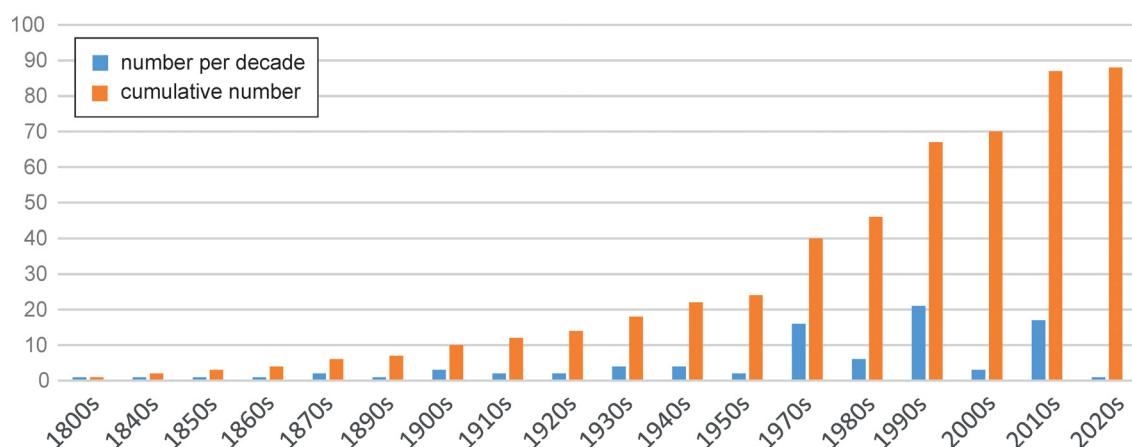


Fig. 25. Progress in describing new species-group taxa of Ochteridae (valid recent taxa only).

Table 2. Distribution of recent Ochteridae in particular zoogeographical regions. In the table Yemen is treated as part of Afrotropical Region, China: Yunnan as part of Oriental Region, and Mexico: Sonora as part of Nearctic Region. We use Wallace line as the boundary between Oriental and Australian Region, and boundary between Thailand and Malaysia as boundary between Continental Asia and Sundaland. New Guinea includes also the Bismarck Archipelago.

	<b>Afrotropical</b>	<b>African continent</b>	<b>Islands E of Africa</b>	<b>Palaearctic</b>	<b>W Palaeartic</b>	<b>E Palaeartic</b>	<b>Oriental</b>	<b>Continental Asia</b>	<b>Sundaland</b>	<b>Philippines</b>	<b>Australian</b>	<b>Neotropical</b>
<i>Megochterus nasutus</i> (Montandon, 1898)												
<i>M. occidentalis</i> Baehr, 1990											●	C America
<i>Ochterus africanus</i> Jaczewski, 1938	●	●										
<i>O. caffer</i> (Stål, 1855)	●	●	●									Caribbean
<i>O. minor</i> Kormilev, 1973	●	●	●									
<i>O. piliferus</i> Kormilev, 1973	●	●	●									
<i>O. papaceki</i> Kment & Carapezza, 2020	●	●	●									
<i>O. seychellensis</i> D.A. Polhemus, 1992	●		●									
<i>O. stysi</i> D.A. Polhemus & J.T. Polhemus, 2008	●		●									
<i>O. marginatus marginatus</i> (Latreille, 1804)	●	●		●	●	●	●	●	●	●		
<i>O. strigicollis</i> Horváth, 1913				●	●							
<i>O. breviculus</i> Nieser & Chen, 1992				●		●	●					
<i>O. feae</i> Mancini, 1939							●	●				
<i>O. nicobarensis</i> Chandra & Jehamalar, 2012							●	●				
<i>O. signatus</i> D.A. Polhemus & J.T. Polhemus, 2012							●	●	●			
<i>O. bruneiensis</i> Zettel & Lane, 2010							●		●			
<i>O. pseudomarginatus</i> D.A. Polhemus & J.T. Polhemus, 2016							●		●			
<i>O. singaporensis</i> D.A. Polhemus & J.T. Polhemus, 2016							●		●			
<i>O. thienemanni</i> Jaczewski, 1935							●		●			
<i>O. xustos</i> Nieser & Chen, 1992							●		●			
<i>O. baltazarae</i> Gapud & San Valentin, 1977							●			●		
<i>O. barrosoi</i> Gapud, 1981							●		●			
<i>O. luzonicus</i> Gapud, 2003							●		●			
<i>O. magnificus</i> Gapud & San Valentin, 1977							●		●			
<i>O. magnus</i> Gapud & San Valentin, 1977							●		●			
<i>O. marginatus insularis</i> Rieger, 1977							●		●			
<i>O. pardalos</i> Nieser & Chen, 1999							●		●			
<i>O. philippinensis</i> Kormilev, 1971							●		●			
<i>O. polhemusi</i> Gapud, 1981							●		●			
<i>O. surigaensis</i> Gapud, 1995							●		●			
<i>O. zetteli</i> Gapud, 2003							●		●			
<i>O. noualhieri</i> Baehr, 1990							●	●	●	●		
<i>O. grandiusculus</i> Nieser & Chen, 1992										●		
<i>O. homorfos</i> Nieser & Chen, 1999										●		
<i>O. trichotos</i> Nieser & Chen, 1999										●		
<i>O. alticola</i> Baehr, 1990										●		
<i>O. cheesmannae</i> Baehr, 1990										●		
<i>O. gressitti</i> Kormilev, 1971										●		
<i>O. jaczewskii</i> Kormilev, 1971										●		
<i>O. kokodae</i> Baehr, 1990										●		
<i>O. latior</i> Baehr, 1990										●		
<i>O. louisiana</i> Baehr, 1990										●		
<i>O. nigrinus</i> Baehr, 1990										●		
<i>O. papuasicus</i> Kormilev, 1972										●		
<i>O. paucistriatus</i> Baehr, 1990										●		
<i>O. australicus</i> Jaczewski, 1934										●		
<i>O. atridermis</i> Baehr, 1989										●		
<i>O. bacchus</i> Baehr, 1990										●		
<i>O. baehri baehri</i> Rieger, 1977										●		
<i>O. baehri riegeri</i> Baehr, 1989										●		
<i>O. brachysoma</i> Rieger, 1977										●		
<i>O. eurythorax</i> Baehr, 1989										●		
<i>O. monteithorum</i> Baehr, 1990										●		

Table 2. Continued.

	<b>Afrotropical</b>	African continent	Islands E of Africa	Palaearctic	W Palaearctic	E Palaearctic	<b>Oriental</b>	Continental Asia	Sundaland	Philippines	•	<b>Australian</b>	•	Wallacea (Sulawesi)	New Guinea	•	<b>Australasia</b>	•	Neotropical	C America	Caribbean	S America	Island distribution
<i>O. occidentalis</i> Baehr, 1990																							
<i>O. secundus secundus</i> Kormilev, 1971																							
<i>O. secundus pseudosecundus</i> Baehr, 1989																							
<i>O. dufourii</i> (Montrouzier, 1864)																							
<i>O. americanus</i> (Uhler, 1876)																							
<i>O. banksi</i> Barber, 1913																							
<i>O. barberi</i> Schell, 1943																							
<i>O. rotundus</i> J.T. Polhemus & M.S. Polhemus, 1976																							
<i>O. perbosci</i> (Guérin-Méneville, 1843)																							
<i>O. acutangulus</i> (Champion, 1901)																							
<i>O. chiapensis</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. costaricensis</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. explanatus</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. mexicanus</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. obscurus</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. ovatus</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. panamensis</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. pseudorotundus</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. schellae</i> Drake, 1952																							
<i>O. sheppardi</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. smaragdinus</i> D.A. Polhemus & J.T. Polhemus, 2016																							
<i>O. hungerfordi</i> Schell, 1943																							
<i>O. aeneifrons aeneifrons</i> (Champion, 1901)																							
<i>O. manni</i> Hungerford, 1927																							
<i>O. viridifrons</i> (Champion, 1901)																							
<i>O. aeneifrons surinamensis</i> Nieser, 1975																							
<i>O. bidentatus</i> Schell, 1943																							
<i>O. brunneus</i> Hungerford, 1927																							
<i>O. foersteri</i> Kormilev & De Carlo, 1952																							
<i>O. parvus</i> Schell, 1943																							
<i>O. santosi</i> Cordeiro & Moreira, 2014																							
<i>O. tenebrosus</i> Nieser, 1975																							
<i>O. unidentatus</i> Nieser & Chen, 1992																							
<i>Ocyochterus irmae</i> D.A. Polhemus & J.T. Polhemus, 2014																							
<i>O. victor</i> (Bolívar, 1879)																							
<b>Number of species in the region</b>	<b>8</b>	6	4	<b>3</b>	2	2	<b>22</b>	5	8	11	<b>29</b>	5	11	13	2	<b>5</b>	<b>28</b>	17	3	14	33		

Table 3. Stratigraphic and geographic distribution of fossil Ochteroidea.

		Late Triassic	Early Jurassic	Middle Jurassic	Late Jurassic	Early Cretaceous	Late Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	
Ochteroidea <i>incertae sedis</i>	<i>Heterochterus timmsii</i> Evans, 1971	●											Australia
Propreocoridae	<i>Propreocoris maculatus</i> Popov, Dolling & Whalley, 1994		●										England
Ochteridae <i>incertae sedis</i>	<i>Yuripachys dubius</i> (Popov, 1986)					●							Mongolia
Ochteridae	<i>Pristinochterus zhangi</i> Yao, Cai & Ren, 2007				●	●							China
Ochteridae	<i>Angulochterus quadrimaculatus</i> Yao, Zhang & Ren, 2011					●							China
Ochteridae	<i>Floricaudus multilocellus</i> Yao, Ren & Shih, 2011					●							China
Ochteridae	<i>Pristinochterus ovatus</i> Yao, Zhang & Ren, 2011					●							China
Ochteridae	<i>Riegerochterus baehri</i> Popov & Heiss, 2014											●	Dominican amber
Ochteroidea <i>incertae sedis</i>	<i>Grimaldinia pronotalis</i> Popov & Heiss, 2004						●						Burmese amber

Martin Baehr, a renowned German coleopterist specialised in Carabidae (Coleoptera), revised Ochteridae of the Australian Region in a series of four papers (BAEHR 1989, 1990a,b,c). In 1990s, Nico Nieser and Ping-ping Chen described seven additional species mostly from Malesia, but also from southern China and South America (NIESER & CHEN 1992, 1999). Finally, Dan A. Polhemus started describing new Ochteridae with *Ochterus seychellensis* in 1992 (POLHEMUS 1992a), and continued, together with his father John T. Polhemus, with series of revisional papers on *Ochterus* of Mauritius (POLHEMUS & POLHEMUS 2008), Malaysia and the Oriental part of Indonesia (2012, 2015), North and Central America (POLHEMUS & POLHEMUS 2016), as well as a revision of the genus *Ocyochterus* with the description of one new species (POLHEMUS & POLHEMUS 2014). Since 1971, 64 species of Ochteridae were described, nearly three times the number described before this date (see Table 1 and Fig. 25). The most prolific authors were D. A. and J. T. Polhemus, who described together 17 species of Ochteridae, followed by M. Baehr with 16 species and subspecies, N. Nieser with 9 species, and N. A. Kormilev and V. P. Gapud each with 8 species (cf. Table 2). The species inventory of Ochteridae is certainly far from complete, as it is documented by mentions of a probable new species of *Ochterus* from Palawan (GAPUD 2003) and several undescribed species from New Guinea (POLHEMUS & POLHEMUS 1998, 2012), and Oriental Region, as well as due to the probable polyphyly of *O. marginatus* (CHEN et al. 2005). Also our unpublished results suggest existence of additional undescribed species, especially in the Oriental Region, the Afrotropical Region and Madagascar.

The extant members of the family Ochteridae are distributed in the tropical and subtropical regions of all continents. The present lack of published records from Lesser Sunda and Maluku Islands (Indonesia) is probably due to sampling bias, as we have at hand unidentified material from Maluku, superficially resembling *O. nicobarensis* (ZJPC). Further Ochteridae inhabit temperate zones of Australia and Tasmania (ANDERSEN & WEIR 2004), East Palearctic (north to the northernmost Japanese island, Hokkaido, and to Kunashir, the southernmost island of Kuriles) (POLHEMUS 1995a, KANYUKOVA 2006, HAYASHI et al. 2016, HAYASHI & MIYAMOTO 2018) and Eastern Nearctic Region (north to Massachusetts, Michigan, Minnesota and Ontario (POLHEMUS & POLHEMUS 1988a, 2016; MAW et al. 2000). On the contrary, Ochteridae are missing in temperate Europe, continental regions of Central Asia (POLHEMUS 1995a, KANYUKOVA 2006), from the Appalachian Mountains and the Ozark Plateau in the eastern part, as well as from most of the western part of USA (POLHEMUS & POLHEMUS 1988a, 2016), from New Zealand, and from temperate and subtropical South America (the most southern species being *O. foersteri* reaching the Misiones province of Argentina – MELO 2015, BACHMANN & MAZZUCONI 2017). The zoogeographical pattern of Gelastocoridae resembles that of Ochteridae, with three exceptions: i) Gelastocoridae in South America occur further south, into central Chile; ii) in the Eastern Palearctic they extend northward only to central China and the southern Japanese islands of Kyushu

and Shikoku; and iii) they are completely absent in the Western Palearctic (except one record from coast of Sinai, Egypt) (e.g., TODD 1955, 1961; POLHEMUS & POLHEMUS 1988b; POLHEMUS 1995b; ANDERSEN & WEIR 2004; CHEN et al. 2005; KMENET & JINDRA 2008; FAÚNDEZ & ASHWORTH 2015; FAÚNDEZ & CARVAJAL 2017; NIESER et al. 2020).

Concerning the biodiversity pattern, we can recognize two distinct biodiversity centres, the Australasian Region with 29 species-group taxa and the Neotropical Region with 28 species-group taxa. Within the Neotropical Region, most of these taxa (i.e. 17) are known from Central America, while only 14 species and subspecies are known from South America (see Table 2). This situation may be influenced by the existence of the recent excellent revision of Central American fauna by POLHEMUS & POLHEMUS (2016) and future research will elucidate the precise number of species actually occurring in South America. In the Caribbean, so far only one endemic species is known (*O. hungerfordi* from Cuba) and two widely distributed species shared with the continent (*O. aeneifrons aeneifrons* and *O. perbosci*), which is in contrast with high number of island endemics occurring in Malesia and islands of the Indian Ocean. In the Australian Region, 5 species occur in Sulawesi (including the widely distributed *O. marginatus marginatus* and *O. noualhieri* shared with Sundaland), 11 species in New Guinea, Vanuatu and Solomon Islands, 13 species and subspecies in Australia, and 2 species in New Caledonia (one of them endemic). The Oriental Region seems also species rich with 22 species-group taxa, but only 5 species are so far known in its western (mostly continental) part north of the border of Malaysia; 8 species occur in Sundaland and 11 species and subspecies are confined to the Philippines. The Afrotropical Region harbours 8 species, 6 of them occurring on the continent and 4 on the adjacent islands; *O. caffer* and *O. papaceki* sp. nov. occur in both the African mainland and islands (Madagascar and Socotra, respectively), while Mauritius and Seychelles each harbour a single endemic species. The fauna of the Nearctic Region includes five species (with *O. rotundus* and *O. perbosci* confined to its southernmost regions and shared with Neotropical Region) (POLHEMUS & POLHEMUS 2016). The least species rich is fauna of the Palaearctic Region, including only three described species, the widely distributed *O. marginatus marginatus*, *O. strigicollis* endemic to Israel, and *O. breviculus* confined to the transitional zone between the Palaearctic and the Oriental Region in Yunnan and Xizang (Tibet) in southern China (NIESER & CHEN 1992, POLHEMUS 1995a). In alternative zoogeographical regionalisation, Malesia (including the Malay Peninsula, Sundaland, Philippines, Wallacea, New Guinea and Solomon Islands), would harbour 33 species and subspecies – see CHEN et al. 2005, ZETTEL & LANE 2010, POLHEMUS & POLHEMUS 2012). In contrast to the New World, we must stress the importance of island endemism for the species diversity in Old World Ochteridae – among 55 Old World species, 33 (60 %) of them are confined to islands. Interestingly, also Gelastocoridae also share a similar pattern of species richness, with centres of biodiversity in Neotropical and Australian Region; the Oriental Region

harbours only 9 species, 3 of them extending to Eastern Palaearctic, the Afrotropical Region has only 2 species, one of them marginally reaching the Western Palaearctic; 8 species-group taxa occur in Nearctic Region, though most of them are confined to its southernmost areas, Florida and along the Mexican border (e.g., TODD 1955, 1961; POLHEMUS & POLHEMUS 1988b; POLHEMUS 1995b; ANDERSEN & WEIR 2004; CHEN et al. 2005; KMENT & JINDRA 2008; FAÚNDEZ & ASHWORTH 2015; NIESER et al. 2020).

The phylogenetic relationships within Ochteridae were addressed by MAHNER (1993) and summarized as follows: (*Megochterus* + (*Ocyochterus* + (American *Ochterus* + Old World *Ochterus*))). The monophyly of the Old World *Ochterus* is well supported by the apomorphic structure of the right paramere, provided with a rounded apical cap and two subapical appendages; however, the monophyly of American *Ochterus* with a simple right paramere remains questionable, as their paraphyly towards the Old World clade (*Ochterus* s. str.) is also possible (MAHNER 1993). The first cladistic analysis of relationships among genera of Ochteridae was performed by YAO et al. (2011), who included the three recent genera and three fossil genera from Late Jurassic and Early Cretaceous of China, suggesting the following relationships: ((†*Floricaudus* + †*Pristinochterus*) + (†*Angulochterus* + (*Megochterus* + (*Ochterus* + *Ocyochterus*)))). For review of the fossil taxa assigned to Ochteridae and Ochteroidea stem group see Table 3. On the other hand, relationships among species-group taxa within the diverse *Ochterus* have never been rigorously tested. Considering the morphological homogeneity of this group, the use of molecular phylogenetic methods will be necessary.

### Acknowledgements

We thank the late Pavel Štys (Charles University, Prague, Czech Republic) for sharing his manuscript notes on the names and nomenclatural acts made by MAHNER (1993). We are further indebted to Elena Kanyukova (Far Eastern Federal University, Zoological Museum, Vladivostok, Russia) and Kazutaka Yamada (Tokushima Prefectural Museum, Tokushima, Japan) for their help in tracing references for the fauna of the former Soviet Union and Japan, respectively. Thomas J. Henry (USNM), Nico Nieser (Tiel, the Netherlands), and Christian Rieger (Nürtingen, Germany) kindly provided us with information on type depositories of particular species. We are also obliged to Viktor Hartung (ZMUH) and Roberto Poggi (MCSN) for taking photographs of the holotypes of *Ochterus africanus* and *O. feae*, respectively. Fabio Cianferoni (Natural History Museum, University of Florence, Italy), Leonidas R. Davranoglou (Department of Zoology, University of Oxford, United Kingdom), Dan A. Polhemus (Department of Natural Sciences, Bishop Museum, Honolulu, USA) and Dávid Rédei (Nankai University, Tianjin, China) kindly provided their critical comments on the manuscript. The work was financially supported by project of the Ministry of Culture of the Czech Republic (DKRVO 2019–2023/5.I.b, MK000023272) to the National Museum, Prague.

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