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Terminal-instar larval systematics and biology of west European species of Ormyridae associated with insect galls (Hymenoptera, Chalcidoidea)

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Abstract

A systematic study of the genus *Ormyrus* (Chalcidoidea, Ormyridae) was conducted based on the morphology and biology of the terminal-instar larvae of ten west European species that are parasitoids of gall wasps and gallflies of the families Cynipidae, Eurytomidae and Tephritidae. The first detailed descriptions are provided of the terminal-instar larvae of these ten species using SEM images to illustrate diagnostic characters with systematic values. A key is provided for the identification of ormyrid larvae associated with galls in Europe, which is based particularly on characters of the head, mouthparts and mandibles. Although only limited informative variation in body shape was found, the setation of the head provided several characters of potential taxonomic value. The larval biology of the ten ormyrid species inhabiting different galls is also summarised. Although *Ormyrus* larvae are usually solitary idiobiont ectoparasitoids of the host larva of various gall-inhabiting insects, evidence of secondary phytophagy was observed in some species.

Keywords

Chaetotaxy, cynipid galls, cryptic species, identification keys, immature stages, mouthparts *Ormyrus*, parasitoid

Introduction

The superfamily Chalcidoidea is the second largest superfamily of parasitoid Hymenoptera (Sharkey and Fernandez 2006, New 2012, Noyes 2016) and includes 22 different extant families (Heraty et al. 2013, Noyes 2016). Within the Chalcidoidea, Ormyridae is a small family with a worldwide distribution that is composed of approximately 140 species in 3 genera. The genera *Eubeckerella* Narendran and *Ormyrulus* Bouček are monotypic, and the third is the large genus *Ormyrus*, which includes the other species (Aguiar et al. 2013, Noyes 2016). *Ormyrus* is the only genus found in the Palaearctic region (Zerova and Seryogina 2006).

The ormyrids are chalcidoids that are morphologically well characterised by their usually bright metallic colours, coarsely crenulated sculpture of the metasoma, well-developed hind coxae, short stigmal veins and two stout and curved metatibial spurs.

The family has never been catalogued or revised worldwide. References to European and Palaearctic faunas of Ormyridae are found in Erdös (1946), Bouček (1970), Nieves-Aldrey (1984), Doganlar (1984; 1991a, b) and Askew (1994). Zerova and Seryogina (2006) revised and keyed the Palaearctic species of *Ormyrus*, and subsequently, a few new species from this zoogeographic region were recently described (Lotfalizadeh et al. 2012; Zerova and Seryogina 2014a, b; Zerova et al. 2012, 2015). Hanson (1992) studied the Nearctic fauna of *Ormyrus*, and Narendran (1999) revised the Indo-Australian fauna.

The larval ormyrids are typically solitary idiobiont ectoparasitoids of various gall-forming insects. Most Holarctic species are associated with gall wasps (Hymenoptera, Cynipidae) in temperate regions, with some species linked to gall midges and gallflies (Diptera: Cecidomyiidae and Tephritidae, respectively) (Bouček 1977, Nieves-Aldrey 1984, Askew 1994, Zerova and Seryogina 2006, Noyes 2016). The galls of eurytomids (Chalcidoidea, Eurytomidae) in Spain and also those of gall-making weevils (Coleoptera, Curculionidae) in China (Askew and Blasco-Zumeta 1998, Yao and Yang 2004) are also parasitized by one *Ormyrus* species. In tropical areas, primarily in the Afrotropical and Oriental regions, some species of Ormyridae are parasitoids of the inhabitants of fig wasp galls (Chalcidoidea, Agaonidae) on *Ficus* trees (Bouček et al. 1981, Narendran 1999, van Noort 2004, Nieves-Aldrey et al. 2007, Rasplus et al. 2011). According to Simon Van Noort (pers. comm.), *Ormyrus* species are likely parasitoids or inquilines of Eurytomidae or Epichrysomallinae (Pteromalidae) that instigate fig gall formation or modify other galls.

Twenty-nine ormyrid species have been recorded in Europe, of which only seven are relatively common and widely distributed in western Europe, whereas three species, *O. salmanticus*, *O. monegricus* and *O. cupreus*, are restricted to the Iberian Peninsula. Approximately 75% of the European species of *Ormyrus* are associated with galls of Cynipidae on herbs or oak trees, with the other species linked to gall midges (Cecidomyiidae), gallflies (Tephritidae) and eurytomid galls (Eurytomidae).

Taxonomy and classification of the Ormyridae is based almost entirely on the morphological characters of the adults, with molecular data for this family remaining virtually absent (but see Hernández Nieves 2007). Given the relative uniformity of external morphological characters of the species of *Ormyrus*, biological data such as host insect species and host plant species are essential for the characterisation and identification of the species. Moreover, cryptic species have been identified in some groups of *Ormyrus* among the species associated with oak gall wasps (Hernández Nieves 2007, Graham Stone pers. comm.). However, biological data on associated plant and insect hosts are sporadic and therefore are of limited value in taxonomic approaches with Ormyridae. Phenological data, patterns of parasitism and general biological data of Ormyridae are far from complete and remain unknown for many of the European species.

Studies on the immature stages of Ormyridae are scarce or rare in the literature. Parker (1924) and Parker and Thompson (1925) are the oldest references for Ormyridae larvae. Parker (1924) contains a drawing of an ormyrid egg spiracle, whereas in Parker and Thompson (1925), ormyrids are included in a group with the Eulophidae, Elasmidae and two genera of the family Torymidae (*Megastigmus* and *Callimomus*). The group included ectoparasitic larvae with a well-defined head, thirteen body segments, an integument without pigmentation, and a barely sclerotized body with short setae or that is glabrous and four spiracles between segments II and VI. Since these classic works, only a few further papers have been published that contain information on larval morphology of the family Ormyridae. Rivosecchi (1958) provided the first detailed description of an ormyrid species, *Ormyrus hungaricus* Erdös (= *Ormyrus orientalis* Walker), which is a parasitoid of gallflies (Tephritidae) in flower heads of Asteraceae species. Later, Sellenschlo and Wall (1984) included descriptions of immature stages of Ormyridae, and Askew and Blasco-Zumeta (1998) described the larvae of *Ormyrus cupreus*. More recently, Vardal et al. (2016) provided the first data on the ovarian eggs for the family Ormyridae. However, no general study addresses the comparative morphology of the terminal larvae of *Ormyrus* species.

This study is the first comprehensive analysis of the larval morphology of the more common species of *Ormyrus* of Europe. The work is part of a wider study examining the larval morphology, biology and phylogeny of Chalcidoidea associated with gall wasps in Spain and western Europe. Studies of the larval morphology of Torymidae, Eurytomidae and Pteromalidae are completed (Gómez et al. 2008, 2011, 2013; Nieves-Aldrey et al. 2008; Gómez and Nieves-Aldrey 2012), and studies of the larval morphology of Eupelmidae and Eulophidae (Gómez and Nieves-Aldrey 2017). In this paper, we describe the terminal larvae and the biology of ten European species of Ormyridae: *Ormyrus capsalis* Askew, *O. cupreus* Askew, *O. diffinis* (Fonscolombe), *O. gratiosus* (Förster), *O. nitidulus* (Fabricius), *O. orientalis* Walker, *O. papaveris* Perris, *O. pomaceus* (Geoffroy), *O. rufimanus* Mayr and *O. wachtli* Mayr. These species are associated with insect galls on the herbaceous plants, shrubs and trees of several plant families. In this study, we aimed to contribute to the knowledge of immature stages of European ormyrid wasps in two ways. First, we identified and described larval and biological characters that are potentially useful in systematic and phylogenetic morphological work on the family Ormyridae. We used scanning electron microscopy (SEM) focused on the head capsule, mouthparts and mandibles. Second, we developed a key for the identification of terminal larvae of *Ormyrus* species associated with galls in western Europe.

Materials and methods

Selected taxa and specimens. A total of 135 larval specimens belonging to ten species of Ormyridae was examined. Host galls were collected from a range of plants at sites in Spain. Sampling data are presented in Table 1. Larvae were dissected out of the galls developing on plants from different families (Asteraceae, Fagaceae, Gnetaceae, Lamiaceae, Papaveraceae and Rosaceae). Host species were identified using keys for the Iberian Cynipidae in Nieves-Aldrey (2001) and other specific key references for non-cynipid galls (Askew 1994, Askew and Blasco-Zumeta 1998). The identification of host plants species was based on Flora Europaea (Tutin et al. 1980).

Some parasitoid species in the families Eupelmidae, Eurytomidae, Pteromalidae and Torymidae (Hym., Chalcidoidea) associated with cynipid-galls were included in the study for comparative purposes in the systematic analysis of terminal-instar larvae (Table 1; Suppl. materials 1, 2).

Sampling and rearing. Samples were collected in the spring and autumn during the last 15 years with more intensive sampling in 2002–2007. Some of the galls from each sample were dissected to obtain larvae, and the remaining galls were kept separately outdoors in the open in labelled bags or were stored in rearing cages to obtain adults for identification. Some larvae from freshly dissected galls were preserved in absolute ethanol, whereas the remainder were allowed to develop to adulthood in small gelatine capsules as described by Shorthouse (1972). Information on the host galls, galled food plants and collection sites for all ormyrid species in this study are listed in Table 1. Voucher specimens of all species are deposited in the entomology collections of the Museo Nacional de Ciencias Naturales, Madrid (Spain).

Preparation for morphological studies. Larvae were transferred directly from absolute ethanol to a SEM stub for observation using a FEI Quanta 2000^{TM} scanning electron microscope at low vacuum without prior fixation or coating, following the method described by Nieves-Aldrey et al. (2005) for Cynipoidea and Gómez et al. (2008) for torymid larvae. Four images of each species were taken: ventral view of the larva, lateral view of the larva, anterior view of the head, and close-ups of the anterior view of the mouthparts. In addition, the right/left mandible was photographed in anterior view for some species, which involved prior dissection from the larval head, separate mounting, and gold coating for normal high vacuum observation under SEM.

Terminology. General terminology used in the larval descriptions follows Vance and Smith (1933) as well as Short (1952). Our terminology is also consistent with Cutler's (1955) work on Pteromalidae larval head morphology and the referred previous studies of Gómez et al. (2008, 2011, 2013), Gómez and Nieves (2012) and Nieves-Aldrey et al. (2007) on the larvae of Torymidae, Eurytomidae and Pteromalidae. The measurements given in the descriptions were taken from samples preserved in absolute ethanol. Body length was measured as head length plus the combined length of all the remaining segments (Gómez et al. 2008). The anterodorsal protuberances (*adp*) described further below were included in the maximum body width measurement. Measurements are given as means with their range in parentheses. The ratio length/width of the body (henceforth

Table 1. Summary of the host gall, host plant and sample site data for the ormyrid species included in the study. Chalcid outgroups accounted are also annotated. Depository: JLNA, JFGS and MHN; J. L. Nieves-Aldrey collection, Museo Nacional de Ciencias Naturales, Madrid, Spain.

Species	Specimens (n)	Host	Plant species	Collection data
1. *Ormyrus capsalis*	22	*Aylax minor* (Cynipidae)	*Papaver* spp. (Papaveraceae)	Spain: Monte Pajares, Rivas-Vaciamadrid, Valdemorillo (Madrid); Cabezón-San Martín de Valveni (Valladolid) (JLNA)
2. *Ormyrus cupreus*	1	*Eurytoma gallephedrae* (Eurytomidae)	*Ephedra nebrodensis* (Gnetaceae)	Spain: Monte Pajares (Madrid) (JLNA)
3. *Ormyrus diffinis*	36	*Liposthenes kerneri* (Cynipidae)	*Nepeta hispanica* (Lamiaceae)	Spain: Casa Eulogio, Rivas Vaciamadrid (Madrid) (JLNA)
4. *Ormyrus gratiosus*	11	*Isocolus scabiosae* (Cynipidae)	*Centaurea scabiosa* (Asteraceae)	Spain: Pozo de Guadalajara (Guadalajara) (JLNA)
5. *Ormyrus nitidulus*	2	*Andricus hispanicus* (Cynipidae)	*Quercus pyrenaica* (Fagaceae)	Spain: Algatocín (Málaga); Laguna de San Marcos (Salamanca) (JLNA)
6. *Ormyrus orientalis*	1	Unidentified Tephritidae (Diptera)	*Microlonchus salmanticus* (Asteraceae)	Spain: La Flecha (Salamanca) (JLNA)
7. *Ormyrus papaveris*	8	*Aylax papaveris* (Cynipidae)	*Papaver rhoeas/dubium* (Papaveraceae)	Spain: El Cardoso de la Sierra (Guadalajara); Rivas Vaciamadrid (Madrid) (JLNA); San Andrés (Soria) (JFG/JLNA)
8. *Ormyrus pomaceus*	1 1 1 11	*Andricus grossulariae* asex. (Cynipidae) *Trigonaspis mendesi* (Cynipidae) *Plagiotrochus fusifex* (Cynipidae) *Plagiotrochus razeti* (Cynipidae)	*Quercus faginea* (Fagaceae) *Quercus faginea* (Fagaceae) *Quercus coccifera* (Fagaceae) *Quercus ilex* (Fagaceae)	Spain: La Suara (Cádiz) (JLNA) Spain: Boadilla del Monte (Madrid) (JLNA) Spain: Arganda (Madrid) (JLNA) Spain: Villanueva del Pardillo (Madrid) (JLNA)
9. *Ormyrus rufimanus*	41	*Xestophanes potentillae* (Cynipidae)	*Potentilla reptans* (Rosaceae)	Spain: Cotos de Monterrey, Villalvilla, Villar del Olmo (Madrid); Colldejou (Tarragona) (JLNA)
10 *Ormyrus wachtli*	1	*Neaylax verbenacus*	*Salvia verbenaca* (Lamiaceae)	Spain: Arganda (Madrid) (JLNA)
EUPELMIDAE				
11. *Eupelmus cerris*	1	*Synophrus politus* (Cynipidae)	*Quercus suber* (Fagaceae)	Spain: El Pardo (Madrid) (JLNA)
EURYTOMIDAE				
12. *Eurytoma aspila*	1	*Timaspis urospermi* (Cynipidae)	*Urospermum picroides* (Asteraceae)	Spain: Algatocín (Málaga) (JLNA)
PTEROMALIDAE				
13. *Cecidostiba geganius*	1	*Andricus quercusradicis* asex. (Cynipidae)	*Quercus pyrenaica* (Fagaceae)	Spain: Miraflores (Madrid (JLNA)
TORYMIDAE				
14. *Torymus nobilis*	1	*Andricus testaceipes* asex. (Cynipidae)	*Quercus pyrenaica* (Fagaceae)	Spain: Miraflores (Madrid (JLNA)

L/W) was measured at the 3rd abdominal segment in ventral view. We also measured the ratio of the distance between antennae (SA) to the length of the antero-medial setae of the antennal area (LAA) (henceforth SA/LAA) and also to the distance between the antero-medial setae of vertex (DAV) (henceforth SA/DAV). The relative position of antennae on the head was estimated measuring the distance between the antennae to the anterior margin of clypeus related to the one between them to the upper margin of vertex (henceforth AC/AV). The ratio length/width of the first tooth of the mandible (henceforth L/W 1T) was calculated with the length of the tooth measured from the base to apex and the width measured at its base. The quantitative value of measurements is shown in Table 2. General terminology used is shown on figures 1 and 2.

Systematic analysis: Coding of morphological characters. Ormyrid nomenclature followed Noyes (2016). Descriptions of the taxa were based primarily on preserved material, but with additional observations from living larvae. To standardise the comparative morphological study, the morphological variation for all the *Ormyrus* larvae was coded in an observation matrix of character states, which included coding of 28 characters related to external morphology based on SEM images. The list of characters and character states are provided in Suppl. material 1, with the subsequent matrix provided in Suppl. material 2.

Results

Ormyridae Förster, 1856

General larval morphology of *Ormyrus*

The appearance of terminal-instar larvae of *Ormyrus* is hymenopteriform (Clausen 1940) and most features are shared with other chalcidoid larvae, especially Eurytomidae, as described below. The body setae are short or almost absent on the abdominal segments, but range from short to moderately long on the thorax and head. As in eurytomids, 5–7 pairs of setae are present on the head capsule (Gómez et al. 2011, 2013). Both larvae of Eurytomidae and Ormyridae (Chalcidoidea) are superficially similar, and share the same pattern of setae over the head and body, but the mandibles clearly distinguish these two families: they are bidentate and partially visible externally in Eurytomidae, as opposed to simple single-toothed and not visible externally in Ormyridae.

The labrum of Eurytomidae and Ormyridae is also similar in being divided into a medial and two lateral lobes; however, while the medial part of the labrum of *Eurytoma* is usually divided into five lobes, the medial lobe in *Ormyrus* is usually undivided or superficially divided into three lobes.

Body segmentation (Fig. 1A, B)**.** As for other hymenopteriform chalcid larvae, the body consists of the head plus 13 post-cephalic segments. Three segments form the thorax (THS1–THS3) and the remaining ten segments constitute the abdomen including the anal segment (ABS1–ABS9, ANS).

Table 2. Morphological measurements and ratios of studied specimens meaning as follows: body maximun length/width (L/W); head maximun length/width (HW/HL); distance between antennae/length of the antero-medial setae of the antennal area (LAA/SA); distance between antennae/distance between the antero-medial setae of vertex (DAV/SA); distance between the antennae to the anterior margin of clypeus/distance between the antennae to the upper margin of vertex (AC/AV); maximum length/width of the mandible tooth (L/W 1T).

Species	L/W	HW/HL	LAA/SA	DAV/SA	AC/AV	L/W 1T
Ormyrus capsalis	1.82	1.16	0.52	0.68	0.82	1.42
Ormyrus cupreus	1.93	1.10	0.22	1.08	1.33	–
Ormyrus diffinis	1.87	1.15	0.50	0.83	1.27	1.61
Ormyrus gratiosus	1.74	1.09	0.32	0.84	0.89	1.50
Ormyrus nitidulus	2.01	1.10	0.04	0.93	0.77	1.64
Ormyrus orientalis	1.74	0.89	0.41	0.76	1.22	–
Ormyrus papaveris	2.00	0.89	0.10	0.77	2.00	1.64
Ormyrus pomaceus ex *Plagiotrochus*	2.01	0.86	0.04	0.92	1.33	–
Ormyrus pomaceus ex *Trigonaspis*	1.94	0.83	0.24	0.81	1.07	1.39
Ormyrus rufimanus	2.01	1.00	0.20	0.93	1.10	1.80
Ormyrus wachtli	2.09	0.86	0.02	0.56	1.44	–

General morphology in ventral view (Fig. 1A)**.** Body fusiform, relatively short and wide but slightly broader at ABS2-ABS3 level. Anal segment looks wider than long. Body integument whitish, with a pattern of short setae regularly placed in rows.

General morphology in lateral view (Fig. 1B)**.** Body ventrally bent, with ventral margin of abdominal segments convex; between THS3 and ABS4 anterodorsal protuberances generally present (*adp*). Body segments divided in lateral view into three areas: pleural (P), including the spiracles (*epc*), ventral (V) and dorsal (D), over which body setae are located in three rows respectively, being abdominal setae shorter than the half of the width of an abdominal segment measured at *epc* level.

Spiracles (Fig. 1B)**.** The tracheal system is composed externally of nine pairs of lateral spiracles (*epc*) opening from segment THS2 to ABS7.

Head (Fig. 2A)**.** Head usually trapezoid-shaped, broader than high. Upper margin of vertex regularly rounded, with its medial area convex. Antennal area (*anr*) inconspicuous with the basal region or antennal foramina (*af*) indistinct; antennae (*an*) short but always visible on frons (*fr*), situated in the midway between clypeus (*cl*) and vertex area (*vr*). Head with 5–7 pairs of conspicuous setae always present: (i) pair of antero-medial setae on the antennal region (*am*); (ii) pair of antero-medial setae on vertex (*vam*); (iii) pair of genal setae (*gns*) on genae (*gr*); (iv) pair of clypeal setae (*cs*) on clypeus (*cl*); (v) pair of lateral clypeal setae (*lcs*) situated in lower frontal area (both iv and v with the same length); and (vi) pair of hypostomal setae. Moreover in one studied species (see *Ormyrus wachtli* later) there is a pair of extra supraclypeal setae. The clypeus (*cl*) constitutes always a more or less rectangular region with a straight ventral margin situated anterodorsally to the underlip complex (*Mpu*) and a pair of more or less extended lateral flaps on the sides of labrum (*lfsl*). The labrum (*lb*) is divided into

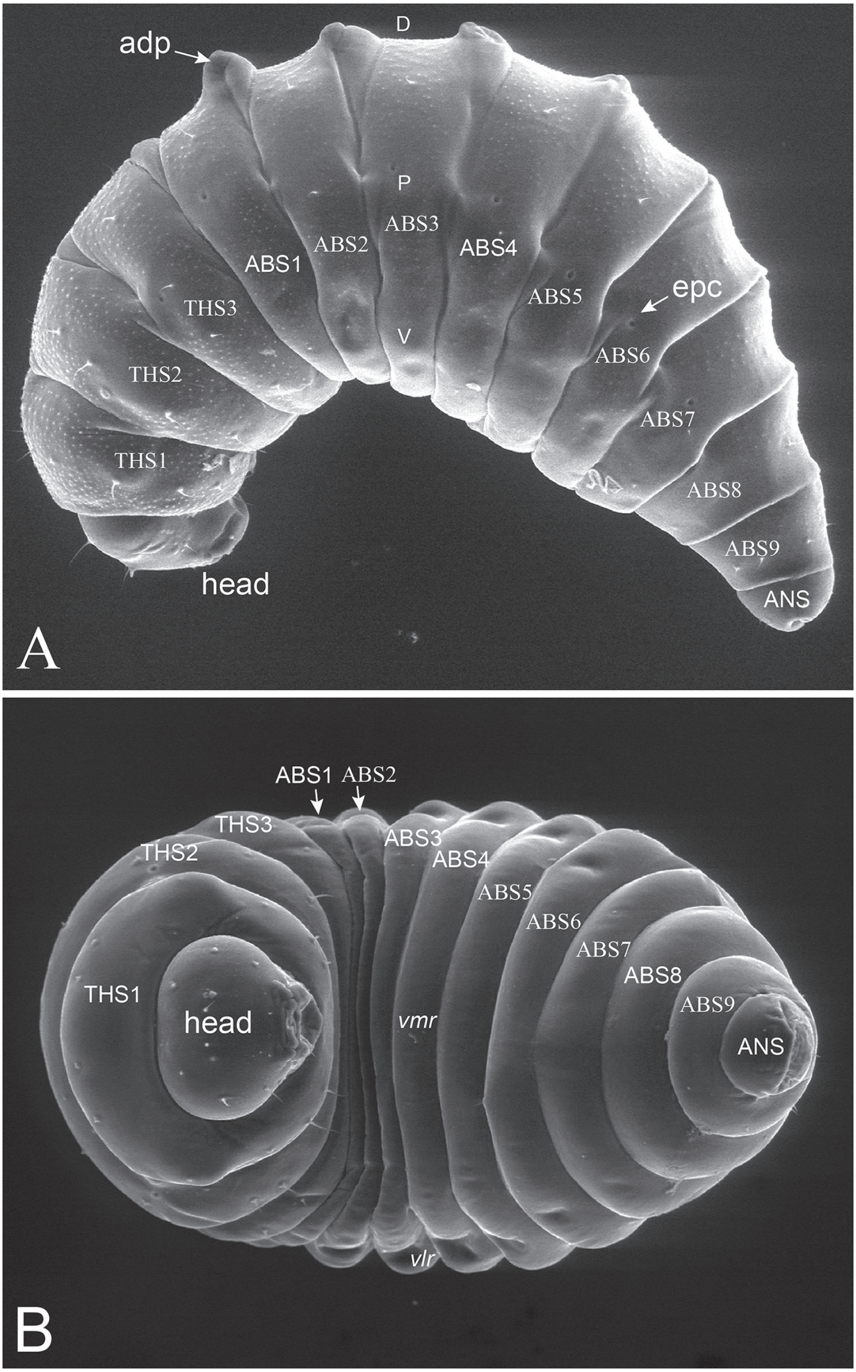

Figure 1. General morphology of body. **A** Lateral view of *Ormyrus cupreus* **B** ventral view of *Ormyrus diffinis*. Letters refer to the terminology used for general description (see text): *ABS1-ABS9*, abdominal segments; *adp*, anterodorsal protuberances; *ANS*, anal segment; *THS1-THS3*, thoracic segments; *D*, dorsal; *P*, pleural; *V*, ventral; *vlr*, ventrolateral region; *vmr*, ventromedial region.

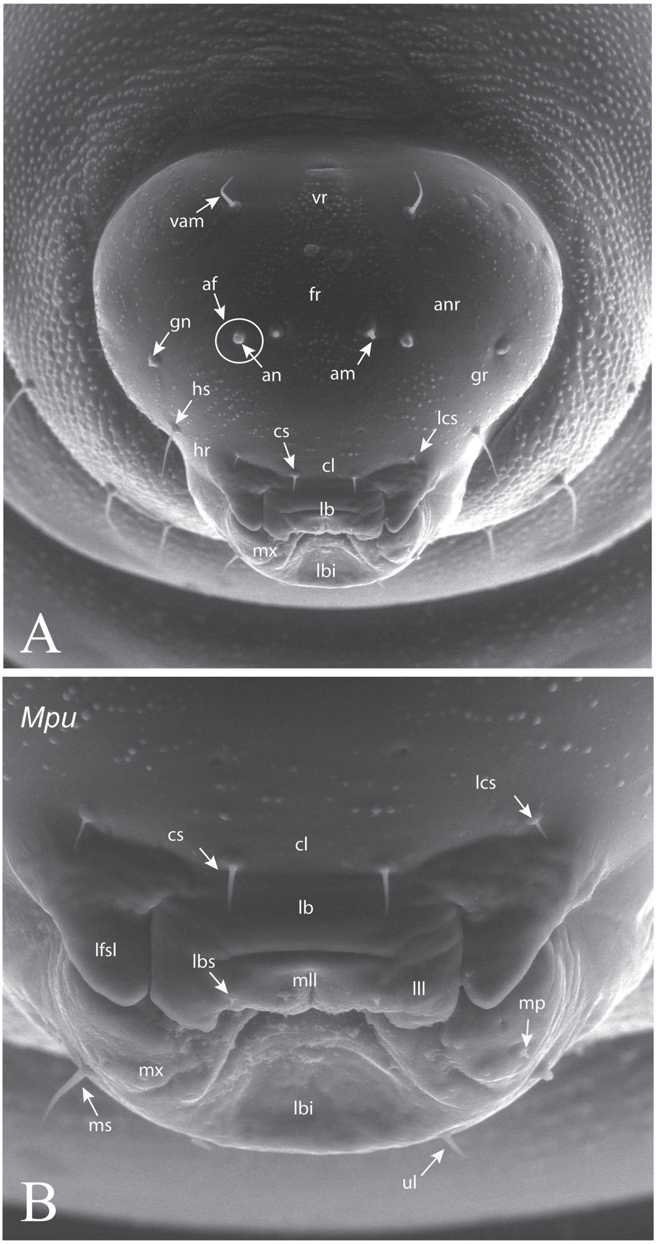

Figure 2. *Ormyrus nitidulus*. **A** Anterior view of head illustrating terminology used for general description (see text). Abbreviations: *af*, antennal foramina; *am*, antero-medial setae on the antennal region; *an*, antenna; *anr*, antennal area; *cl*, clypeus; *cs*, clypeal seate; *fr*, frons; *gn*, genal setae; *gr*, genal region; *hr*, hypostomal region; *hs*, hypostomal setae; *lb*, labrum; *lcs*, lateral clypeal setae; *vam*, antero-medial setae of vertex; *vr*, vertex region **B** Anterior view of mouthparts. Abbreviations: clypeus (*cl*); clypeal setae (*cs*); labrum (*lb*); lateral flaps of sides of labrum (*lfsl*); lateral lobe of labrum (*lll*); lateral clypeal setae (*lcs*); labral setae (*lbs*); medial lobe of labrum (*mll*). The under-lip complex (*Mpu*) is formed by labium (*lbi*) and maxillae (*mx*); maxillary palps (*mp*); *Mpu* setae: maxillary setae (*ms*) and antero-medial labial setae (*ul*).

two lateral lobes (*lll*) and a medial and undivided piece (*mll*), which is wider than lateral ones. The labrum bears a pair of labral setae (*lbs*) situated in its terminal margin.

Mouth parts (Figs 2A, B)**.** Comprise the mandibles (see below) and the underlip complex (*Mpu*), which is formed by the hypopharynx (hardly discernible), the triangle-shaped maxillae (*mx*) and the labium (*lbi*). In ormyrid terminal instar larvae the labium and maxillae are clearly separated being the last discernible. The maxillary palps (*mp*) are also conspicuous and visible. Below the maxillae ventrally is the labium, usually concave and collapsed. The maxillae and labium bear two pairs of short setae, often visible: a pair of antero-medial labial setae (*ul*) and a pair of maxillary setae (*ms*) on one of the two maxillary palps.

Mandibles (Figs 9, 10, 11)**.** *Ormyrus* larvae mandibles are simple, generally covered by labrum and only externally visible in part. Both are usually symmetrical and single-toothed, which is usually sharp and slightly curved on the apex.

Taxonomy. Descriptions of the taxa were based primarily on preserved material but with additional observations from living larvae. The diagnosis of the genus *Ormyrus* was based entirely on SEM observations and partly on previous work by Rivosecchi (1958), Sellenschlo and Wall (1984) and Askew and Blasco-Zumeta (1998). All larval descriptions and the key are new. Ormyrid nomenclature followed Noyes (2016). The key provided identifies the larvae of the ten species studied in this paper, which represented the core or most common *Ormyrus* species associated with different gall species in Europe and on the Iberian Peninsula. Some additional characters are annotated in the corresponding figures included in the key, according to the coded morphological characters listed in Suppl. material 1.

Key to the terminal-instar larvae of the commonest *Ormyrus* species associated with European gall communities.

1 Body and head integument with predominant blister-like sculpture (Figs 7B, 7:1); anteromedial setae of antennal area very short, generally < 0.3 as the distance between antennae (Fig. 7E, 15:1) **2**

– Body and head integument for the most part smooth; blister-like sculpture only on the genal area (Fig. 7D, 9:1); anteromedial setae of antennal area long, 0.3-0.7 the distance between antennae (Fig. 7D, 15:2) **5**

2 Supraclypeal setae present (Fig. 8E, 17:1); anteromedial setae of antennal area situated clearly above antennae (Fig. 8E) ....***Ormyrus wachtli***

– Supraclypeal setae absent (Figs 7C, 7F); anteromedial setae of antennal area usually situated at the same level or slightly above antennae (Figs 7B, 7D; 14:0), if clearly above (Figs 7A, 7D) then supraclypeal setae absent. **3**

3 Thoracic setae long, at least as long as the length of a thoracic segment (Figs 3B, 7B) .... ***Ormyrus cupreus***

– Thoracic setae short; shorter than the length of a thoracic segment (Figs 3E, 7E) **4**

4 Large size larvae; length reaching 3 mm (Figs 3E, 5E); blister-like sculpture mostly along head being weak on body segments (Figs 3E, 5E).... ***Ormyrus nitidulus***

– Smaller size larvae, which length rarely exceed 2 mm (Figs 4C, 6B); body segments conspicuously blister-like sculpted (Figs 4C, 6B, 8C)............ ***Ormyrus pomaceus***

5 Upper margin of vertex rounded continuous; convex at the medial area (Fig. 7F, 10:2)... ***Ormyrus orientalis***

– Upper margin of vertex slightly interrupted, the medial area of vertex appearing concave or depressed (Fig. 7C, 10:0)... **6**

6 Anteromedial setae of the antennal area situated at the same level or slightly above antennae (Fig. 7C); lateral lobes of labrum conspicuous and not fused with the medial piece (Fig. 9C, 22:2).. **7**

– Anteromedial setae of the antennal area situated clearly above antennae (Fig. 7A, 14:1); lateral lobes of labrum inconspicuous, almost fused with the medial piece (Fig. 9A, 22:1) **8**

7 Body short and wide, not abruptly tapering towards anal segment from the middle of the body (Fig. 3C); integument of thoracic segments smooth (Fig. 7C); posterior margin of medial piece of labrum convex (Fig. 9C) ....***Ormyrus diffinis***

– Body elongated and narrow, abruptly tapering towards the anal segment from the middle segments (Fig. 4D); integument of thoracic segments blister-like (Fig. 8D, 7:1); posterior margin of medial piece of labrum straight (Fig. 10B) .... ***Ormyrus rufimanus***

8 Body elongated and narrow, abruptly tapering towards the anal segment from the middle of the body (Fig. 4A); anteromedial setae of antennal area short, < 0.3 the distance between antennae (Fig. 8A, 15:1)........... ***Ormyrus papaveris***

– Body shorter and wide, not abruptly tapering towards anal segment from the middle (Figs 3A, 3D); anteromedial setae of antennal area longer; 0.5 the distance between antennae (Fig. 7D) **9**

9 Lateral clypeal setae situated slightly above clypeal setae; distance between lateral clypeal setae and clypeal setae, twice the distance separating clypeal setae (Fig. 9D) .... ***Ormyrus gratiosus***

– Lateral clypeal setae situated at the same level of clypeal setae (Fig. 9A, 18:0); distance between lateral clypeal setae and clypeal setae, the same as the distance separating clypeal setae (Fig. 9A) .... ***Ormyrus capsalis***

Descriptions of terminal larvae and biology of *Ormyrus* species

Ormyrus capsalis Askew, 1994

Material examined. ex gall *Aylax minor* Hartig on *Papaver spp.*, Spain, Guadalajara: Valdenoches, 31.VII.01, J. L. Nieves leg (n = 1); Madrid: Monte Pajares, 7.IX.03, J. L. Nieves leg (n = 11); Madrid: Rivas-Vaciamadrid, 14.V.03, J. L. Nieves leg (n = 1);

Madrid: Valdemorillo, 13.VI.04, J. L. Nieves leg (n = 2); Valladolid: Cabezón-San Martín de Valveni, 22.VI.02, J. L. Nieves leg (n = 7).

Description. n = 22; Body length: 1.68 ± 0.33 mm (min-max: 1.13-2.20 mm), width: 0.92 ± 0.16 mm (min-max: 0.67-1.20 mm). Body fusiform, relatively short and wide, slightly wider at the level of ABS2-ABS3, but not tapering abruptly towards ANS (Figs 3A, 5A) (Table 2); *adp* present from the second thoracic to fifth abdominal segment, not protruding beyond the dorsal margin of body in lateral view (Fig. 5A); integument of the body smooth; thoracic setae longer than abdominal setae but shorter than length of a thoracic segment Head 1.14 broader than long (Fig. 7A); vertex concave; distance among *vam* longer than SA; *am* situated clearly above the antennae (Table 2). On clypeus *lcs* as long as *cs* (Fig. 9A), being both situated at the same level; *lll* not clearly differentiated and almost merged with medial labrum lobe; posterior margin of labrum straight. Mandibles one-toothed with apex of tooth clearly sharp (Table 2).

Biology. This species is a common parasitoid in poppy galls of *Aylax minor* Hartig, 1840 (Hym., Cynipidae) (Fig. 12A and B). The species has also been reared from galls of *Aylax papaveris* and *Barbotinia oraniensis* on the heads of *Papaver* ssp. (Askew et al. 2006). The parasitoid behaviour of *Ormyrus capsalis* is very similar to the related species *Ormyrus papaveris*, an idiobiont ectoparasitoid of cynipid larvae (Askew et al. 2006) (Fig. 12C).

Notably, in some cases, we observed terminal-instar larvae of *Ormyrus* inside cells of *Aylax minor*, which apparently were not consumed (Fig. 12D).

Ormyrus cupreus Askew, 1998

Material examined. ex gall *Eurytoma gallephedrae* Askew on *Ephedra nebrodensis*, Spain, Madrid: Monte Pajares, 24.I.04, J. L. Nieves leg (n=1).

Description. n = 1; Body length: 1.5 mm, width: 0.61 mm. Body fusiform, broader at the level of abdominal segments ABS2-ABS3 and tapering posteriorly towards ANS; ANS broader than long (Figs 3B, 5B) (Table 2); *adp* present from second thoracic to fifth abdominal segment, protruding conspicuously beyond the dorsal margin of body in lateral view, but only at the level of abdominal area (Fig. 5B); thoracic and abdominal segments with blister-like sculpture; thoracic setae relatively long, as long as the length of a thoracic segment. Head 1.1 broader than high (Fig. 7B); blister-like sculpture extended over the head; vertex concave in the middle; distance among *vam* as distance SA; *am* situated clearly above the antennae (Table 2). The *lcs* situated above *cs*; *cs* separated from *lcs* 2.5 as distance between *cs* (Fig. 9B). Lateral lobes of labrum almost fused with the medial lobe; posterior margin of medial piece of medial lobe straight. Maxilary palps indistinct. Mandibles unidentated with apex of tooth acute (Table 2).

Biology. The larva of *O. cupreus* was described as a specific parasitoid of galls induced by *Eurytoma gallephedrae* Askew (Chalcidoidea, Eurytomidae) on *Ephedra* *nebrodensis* stems (Fig. 12E). Additionally, from this host, we also reared larvae and adults of *O. cupreus* from galls on subterranean runners of *Ephedra nebrodensis* (Fig. 12F), most likely induced by *Eurytoma flaveola* (Zerova 1796), which is a species recorded inducing galls on *Ephedra* roots in Asia (Zerova 1995). Askew and Blasco-Zumeta (1998) performed detailed observations on the biology of this species and found *O. cupreus* is a primary, solitary idiobiont ectoparasitoid of the larva of *E. gallephedrae*, also attacking the adult *Eurytoma* at times or as a hyperparasitoid attacking larvae of the eupelmids *Brasema* and *Eupelmus.* These authors also reported cannibalistic behaviour. Because the remains of an adult *Eurytoma* were found jointly with a larva of *O. cupreus,* we confirmed the observations of Askew (Fig. 12G and H).

Ormyrus diffinis **(Fonscolombe, 1832)**

Material examined. ex gall *Liposthenes kerneri* (Wachtl) on *Nepeta hispanica* Spain, Madrid: Casa Eulogio, 01.VI.03, J. L. Nieves leg (n = 8); Madrid: Rivas-Vaciamadrid, 01.VI.03, J. L. Nieves leg (n = 5); Madrid: Rivas-Vaciamadrid, 13.VI.03, J. L. Nieves leg (n = 1); Madrid: Rivas-Vaciamadrid, 17.V.03, J. L. Nieves leg (n = 22)

Description. n = 36; Body length: 1.56 ± 0.34 mm (min-max: 1.00-2.40 mm), width: 0.83 ± 0.12 mm (min-max: 0.60-1.00 mm). Body fusiform, not tapering abruptly towards anal segment (Figs 3C, 5C) (Table 2); *adp* present from second thoracic to fifth abdominal segment protruding beyond the dorsal margin of body in lateral view (Fig. 5C); integument smooth; thoracic setae relatively long, abdominal setae shorter. Head 1.12 times wider than high (Fig. 7C); integument of genal area with blister-like sculpture; *vam* more separated than distance SA; *am* situated slightly above antennae (Table 2).

On clypeus *lcs* situated at the same level of *cs*; lateral lobes of labrum strongly remarked and incompletely fused with the medial lobe; posterior margin of medial piece of labrum convex (Fig. 9C); mandible unidentate with the apex slightly visible under *lb*; tooth acute (Fig. 11B).

Biology. The species is a common parasitoid reared from cynipid galls of *Liposthenes kerneri* (Wachtl) on fruits of *Nepeta* ssp. (Lamiaceae; Fig. 12I) (Askew et al. 2006). Full-growth larva of *O. diffinis* occupied the entire primary cell of a parasitized gall after the host larvae was devoured (Fig. 12J and K). We observed that larvae of *O. diffinis* inside galls apparently entered prolonged periods of diapause, without causing normal pupation and adult emergence after the winter diapause period. Moreover, live terminal-instar larvae of *O. diffinis* were found in galls dissected two years after collection. The data indicate that *O. diffinis* is an idiobiont ectoparasitoid with a univoltine life cycle that is synchronized with the emergence and growth of their host galls on species of *Nepeta*. The insects emerge in the second year when the new galls are available again on the host plant. This species has also been reared from galls of *Neaylax salviae* and *N. nemorosae* on different species of *Salvia* (Lamiaceae) and from those of *Rhodus cyprius* on *Salvia triloba* (Lamiaceae) (Askew et al. 2006).

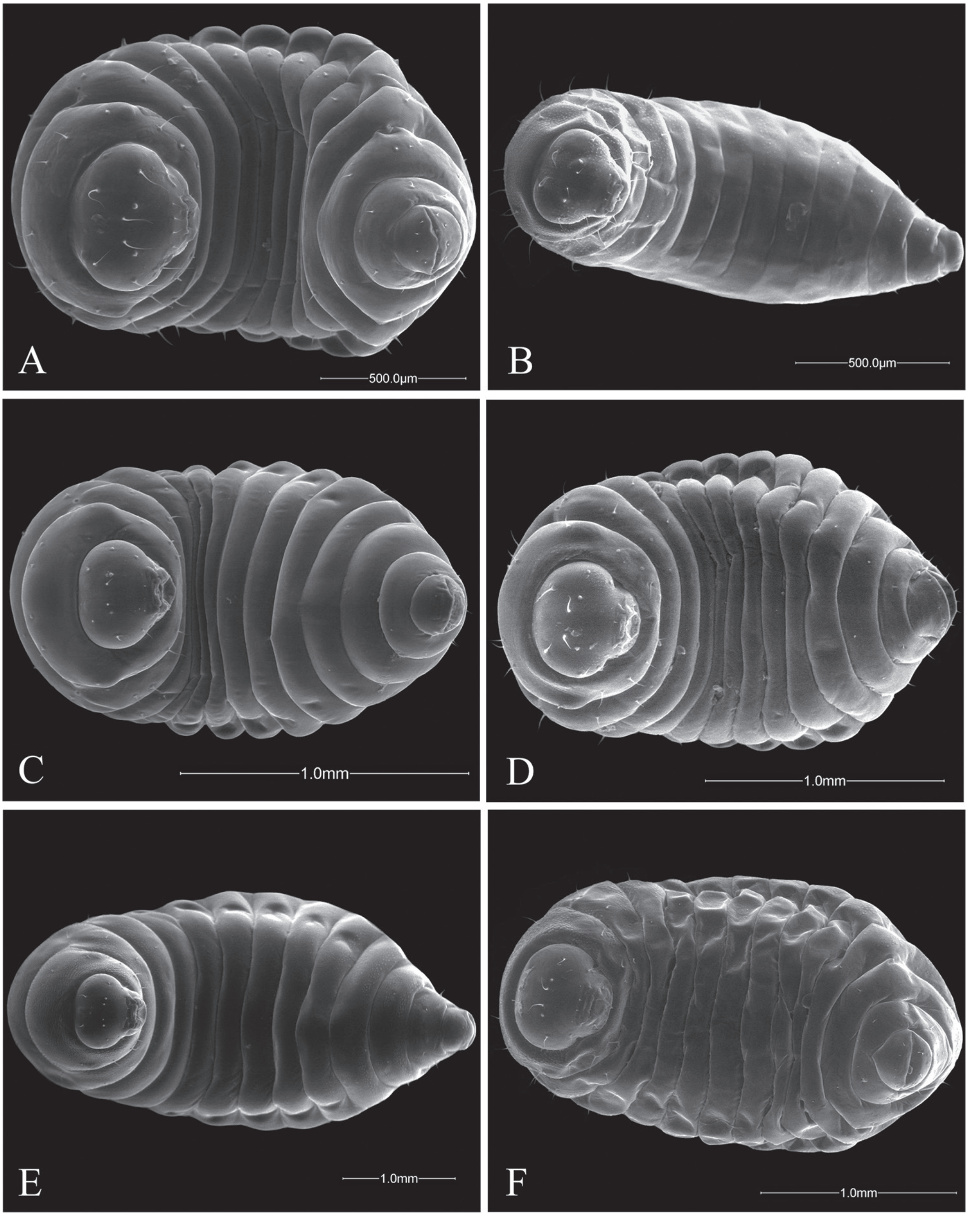

Figure 3. Ventral views of *Ormyrus* terminal-instar larvae. **A** *Ormyrus capsalis* **B** *O. cupreus* **C** *O. diffinis* **D** *O. gratiosus* **E** *O. nitidulus* **F** *O. orientalis*.

Ormyrus gratiosus (Förster, 1860)

Material examined. ex gall *Isocolus scabiosae* (Giraud) on *Centaurea scabiosa*, Spain, Guadalajara: Pozo de Guadalajara, 31.VII.02, J. L. Nieves leg (n = 4); Pozo de Guadalajara, 03.X.04, J. L. Nieves leg (n = 7).

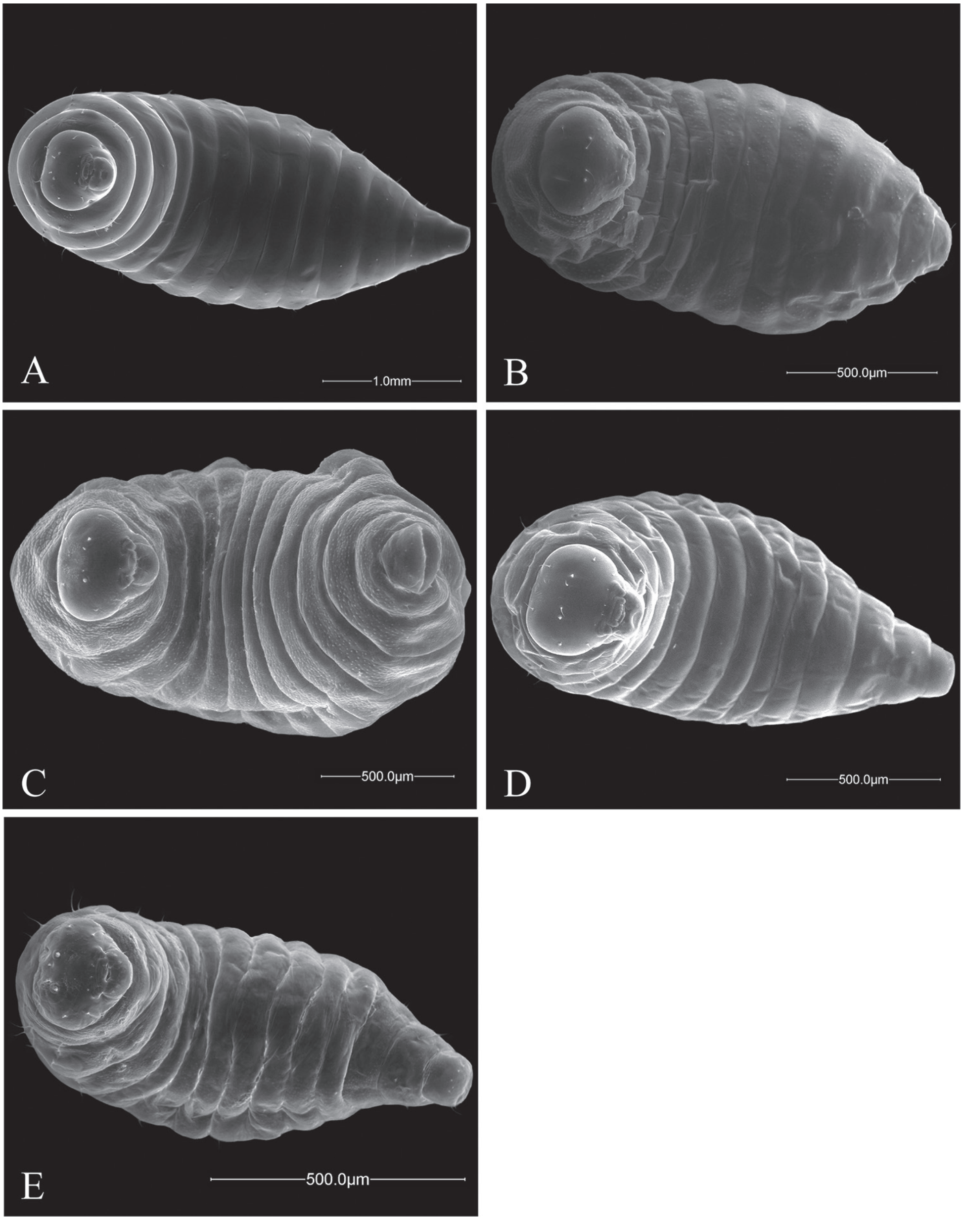

Figure 4. Ventral views of *Ormyrus* terminal-instar larvae. **A** *Ormyrus papaveris* **B** *O. pomaceus* ex *Trigonaspis mendesi* (Cynipidae) **C** *O. pomaceus* ex *Plagiotrochus razeti* (Cynipidae) **D** *O. rufimanus* **E** *O. wachtli*.

Description. n = 11; Body length: 2.22 ± 0.63 mm (min-max: 1.40-3.60 mm), width: 1.28 ± 0.31 mm (min-max: 0.67-1.87 mm). The species differs from *O. capsalis* in the following characters: head 1.1 times as wide as high; genal area, vertex and first thoracic segment with blister-like sculpture; antennae mid-situated in anterior view of

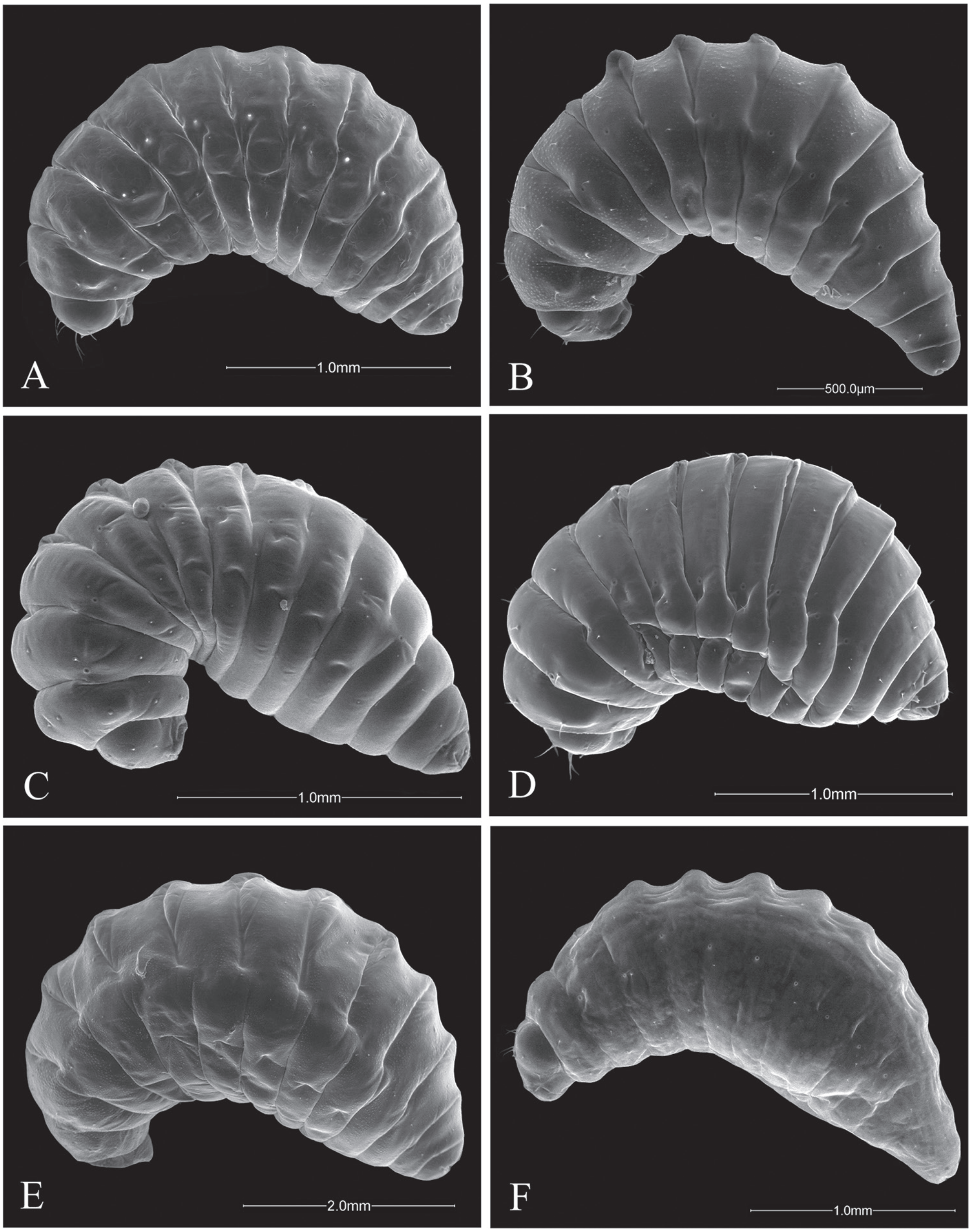

Figure 5. Lateral views of *Ormyrus* terminal-instar larvae. **A** *Ormyrus capsalis* **B** *O. cupreus* **C** *O. diffinis* **D** *O. gratiosus* **E** *O. nitidulus* **F** *O. papaveris*.

the head; antennal setae 0.35 as long as distance between antennae; *lcs* situated above *lc* (Figs 3D, 5D, 7D; Table 2).

Biology. Larvae of *O. gratiosus* are oligophagous idiobiont ectoparasitoids of species of *Isocolus* that induce galls on flower heads of *Centaurea* and *Serratula* species

(Asteraceae) (Askew et al. 2006). Additionally, the species has been reared from the galls of *Diastrophus mayri* on *Potentilla argentea* (Rosaceae). Our examined material was from dissected galled achenes of the flower heads of *Centaurea scabiosa* in Spain (Fig. 13A, B, and C).

Ormyrus nitidulus (Fabricius, 1804)

Material examined. ex gall *Andricus hispanicus* on *Quercus canariensis*, Spain, Málaga: Algatocín, 19.VIII.02, J. L. Nieves leg (n = 1); ex gall *Andricus hispanicus* on *Quercus faginea*, Spain, Salamanca: Laguna de San Marcos, 26.VIII.03, J. L. Nieves leg (n = 1)

Description. n = 2; Body length: 4.28 ± 0.87 mm (min-max: 3.67-4.90 mm), width: 2.13 ± 0.18 mm (min-max: 2.00-2.25 mm).

The larva of this species is the largest among all the European species. Is quite similar in most diagnostic characters to the larvae of the related species *O. pomaceus*, being differentiated by its large size and the blister like sculpture much less conspicuous. Other diagnostic characters are as follows: body short and wide, not tapering towards the anal segment. Setae of thoracic segments shorter than ½ length of a thoracic segment; ratio AC/AV 0.77, the shortest among all the studied species (Table 2); anteromedial seatae of antennal area short, 0.3 as long as distance among antennae; *lcs* separated from *cs* 0.7 times the distance between *cs*; maxillary palps conspicuous (Figs 3E, 5E, 7E; Table 2).

Biology. The species *O. nitidulus* is a member, with the closely allied *O. pomaceus,* of the parasitoid community associated with oak gall wasps (Hymenoptera, Cynipini). The two species were reared from more than 50 different species of cynipids associated with *Quercus* species in the west Palaearctic (Askew et al. 2013); however, *O. nitidulus* is not as common and is less polyphagous than *O. pomaceus*. In contrast to the closely related species *O. pomaceus, O. nitidulus* prefers to attack the large galls of asexual generations of heteroecic species of *Andricus*. On the Iberian Peninsula, *O. nitidulus* was reared primarily from galls of *Andricus hispanicus* (Fig. 13D, E, and F) and the asexual generation of *Andricus grossulariae*. Our observations of dissected galls showed the larva of *O. nitidulus* was a primary ectoparasitoid of the galling inducer. In the host galls of *Andricus hispanicus*, the larvae always occupied the host central larval chamber, not the secondary cells occupied by inquilines.

Ormyrus orientalis Walker, 1871

Material examined. ex gall of an undetermined Tephritidae (Diptera) on *Microlonchus salmanticus*, Spain, Salamanca: La Flecha (23/X/02), J. L. Nieves leg (n = 1).

Description. n = 1; Body length: 2.35 mm, width: 1.35 mm

Body fusiform, short and wide, slightly wider at the level of ABS2-ABS3, but not tapering abruptly towards ANS (Fig. 3F) (Table 2); body segments with conspicuous

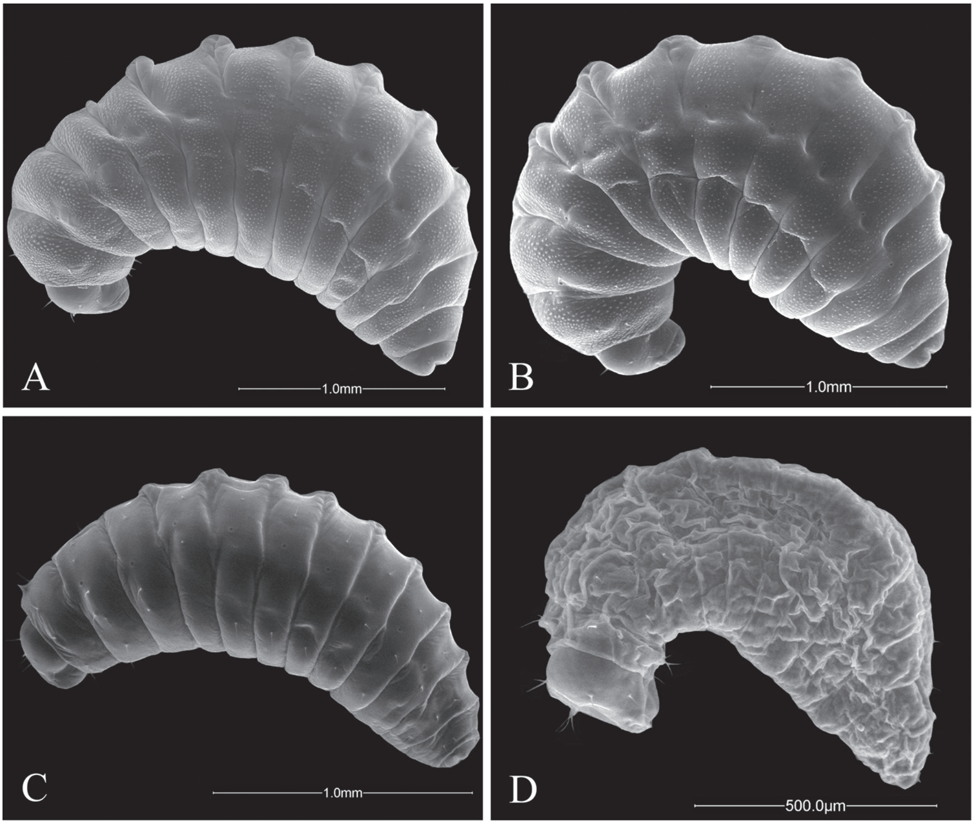

Figure 6. Lateral views of *Ormyrus* terminal-instar larvae. **A** *O. pomaceus* ex *Trigonaspis mendesi* (Cynipidae) **B** *O. pomaceus* ex *Plagiotrochus razeti* (Cynipidae) **C** *O. rufimanus* **D** *O. wachtli*.

blister-like sculpture; thoracic setae relatively long, clearly shorter than abdominal setae. Head 1.14 as wide as high (Fig. 7F); face integument smooth; medial area of vertex regularly convex; antennae situated at mid distance among vertex and ventral margin of clypeus; ratio AC/AV 1.22; *am* situated at the same level of antennae; antennal setae 0.4 as long as distance among antennae (Table 2).

On clypeus *lcs* situated at the same level of *cs,* both equal in length (Fig. 9F); lateral lobes of labrum inconspicuous and almost fused with the medial lobe; posterior margin of the medial piece of labrum straight; mandibles unidentated with the apex of tooth acute (Table 2).

Biology. In contrast to most European species of *Ormyrus*, the larvae of *O. orientalis* attack dipteran galls induced by tephritids (Diptera, Tephritidae) in the heads of different species of Asteraceae. On the Iberian Peninsula, tephritid galls containing *O. orientalis* were found on *Microlonchus salmanticus* (Asteraceae) (Fig. 13I), and the species was also reared from galls of *Myopites limbardae* Schiner (Tephritidae) on *Inula viscosa* (Asteraceae) (Fig. 13G and H). Based on our unpublished data from Malaise

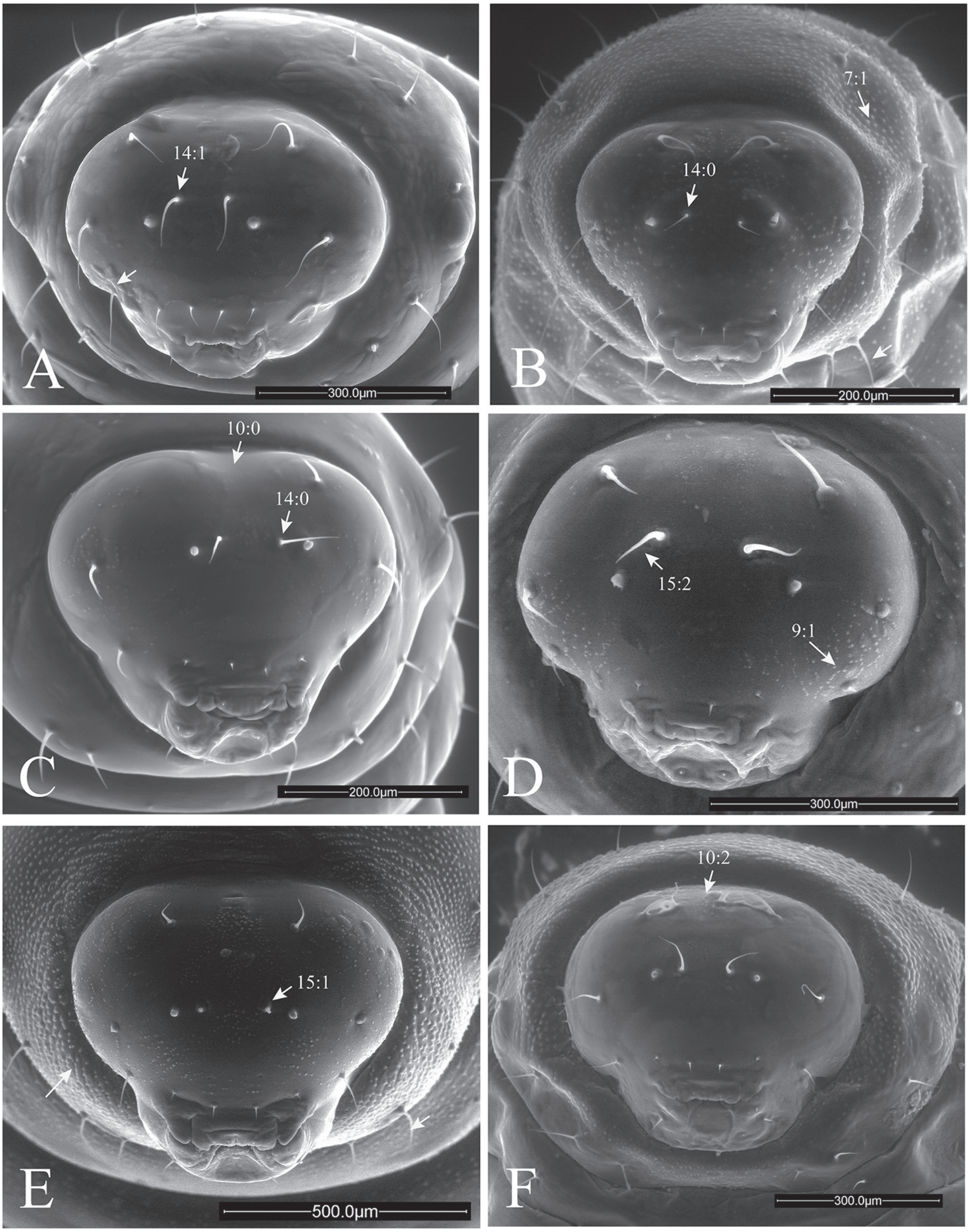

Figure 7. Anterior views of head of *Ormyrus* terminal-instar larvae. **A** *Ormyrus capsalis* **B** *O. cupreus* **C** *O. diffinis* **D** *O. gratiosus* **E** *O. nitidulus* **F** *O. orientalis*. Character states for outstanding features are arrowed.

traps and sweep net samples, *O. orientalis* was one of the most abundant ormyrid species in many habitats on the Iberian Peninsula; consequently, the list of hosts could be wider than that reported in the literature and in the data of the authors.

Ormyrus papaveris Perris, 1840

Material examined. ex gall *Aylax papaveris* on *Papaver spp.*, Spain, Guadalajara: El Cardoso de la Sierra, 30.VI.02, J. L. Nieves leg. (n = 4); Soria: San Andrés, 14.VII.05, J. L. Nieves & J. F. Gómez leg. (n = 1); ex gall *Barbotinia oraniensis* on *Papaver spp.*, Spain, Madrid: Rivas-Vaciamadrid, 25.V.02, J. L. Nieves leg. (n = 2); Madrid: Rivas-Vaciamadrid, 13.VI.04, J. L. Nieves leg. (n = 1).

Description. n = 8; Body length: 1.88 ± 0.24 mm (min-max: 1.53-2.13 mm), width: 0.94 ± 0.19 mm (min-max: 0.67-1.20 mm). This species is similar to *Ormyrus capsalis* from which may be distinguished in the body fusiform, slightly wider at the level of body segments ABS2-ABS3, tapering towards the ANS (Figs 4A, 5F) and the anteromedial setae of antennal area being relatively short, <0.3 the distance among antennae. Other descriptive diagnostic characters as follows: thoracic setae short; head 1.07 times wider than high (Fig. 8A); face integument smooth; antennae situated at mid position in the face; *am* short and situated above antennae (Table 2). On clypeus *lcs* situated at the same level of *cs,* both equal in length but short and inconspicuous (Fig. 9G); lateral lobes of labrum conspicuous and clearly separated from the medial lobe; mandibles with a single tooth with acute apex (Fig. 11E).

Biology. The larvae of *O. papaveris* are common ectoparasitoids in poppy galls of different Aylacini (Cynipidae) species, primarily *Aylax papaveris* and *Barbotinia oraniensis* (Figs 13J and K; 14A), and attack the host in the early stages of development (Askew et al. 2006). We observed the remains of the host larva on the body of a mature ormyrid larva (Fig. 14C). The host larval chamber of *Barbotinia oraniensis* was normally spherical and regular (Fig. 14B); however, when *O. papaveris* attacked the host, the chamber was shorter and irregular (Fig. 14C). The larva of *O. papaveris* moved inside the host gall larval cell touching the gall chamber walls with their mandibles, which suggested that during the terminal larval stage, *O. papaveris* might exhibit a similar phytophagous behaviour to that of *Eurytoma* species inhabiting galls (Askew and Blasco Zumeta 1998, La Salle 2005). In the galls of *Aylax papaveris*, the host larval cells were regularly ellipsoidal and were coated with a thin scum, whereas the cells attacked by ormyrid larvae were larger, more irregular and lacked the thin scum. Because we observed “in vivo” in dissected galls, the phytophagous behaviour of the *Ormyrus* larvae during their final larval stage caused the change in gall morphology.

Ormyrus pomaceus (Geoffroy, 1785)

Material examined. ex gall *Andricus grossulariae* asex. on *Quercus faginea*, Spain, Cádiz: La Suara-Jérez, 16.X.04, J. L. Nieves leg. (n = 1); ex gall *Plagiotrochus fusifex* on *Quercus coccifera*, Spain, Madrid: Arganda, 01.VI.03, J. L. Nieves leg. (n = 1); ex gall *Plagiotrochus razeti* on *Quercus ilex*, Spain, Madrid: Villanueva del Pardillo, 07/X/02, J. L. Nieves leg. (n = 11). ex gall *Trigonaspis mendesi* on *Quercus faginea*, Spain, Madrid: Boadilla del Monte, 23/IX/02, J. L. Nieves leg. (n = 1).

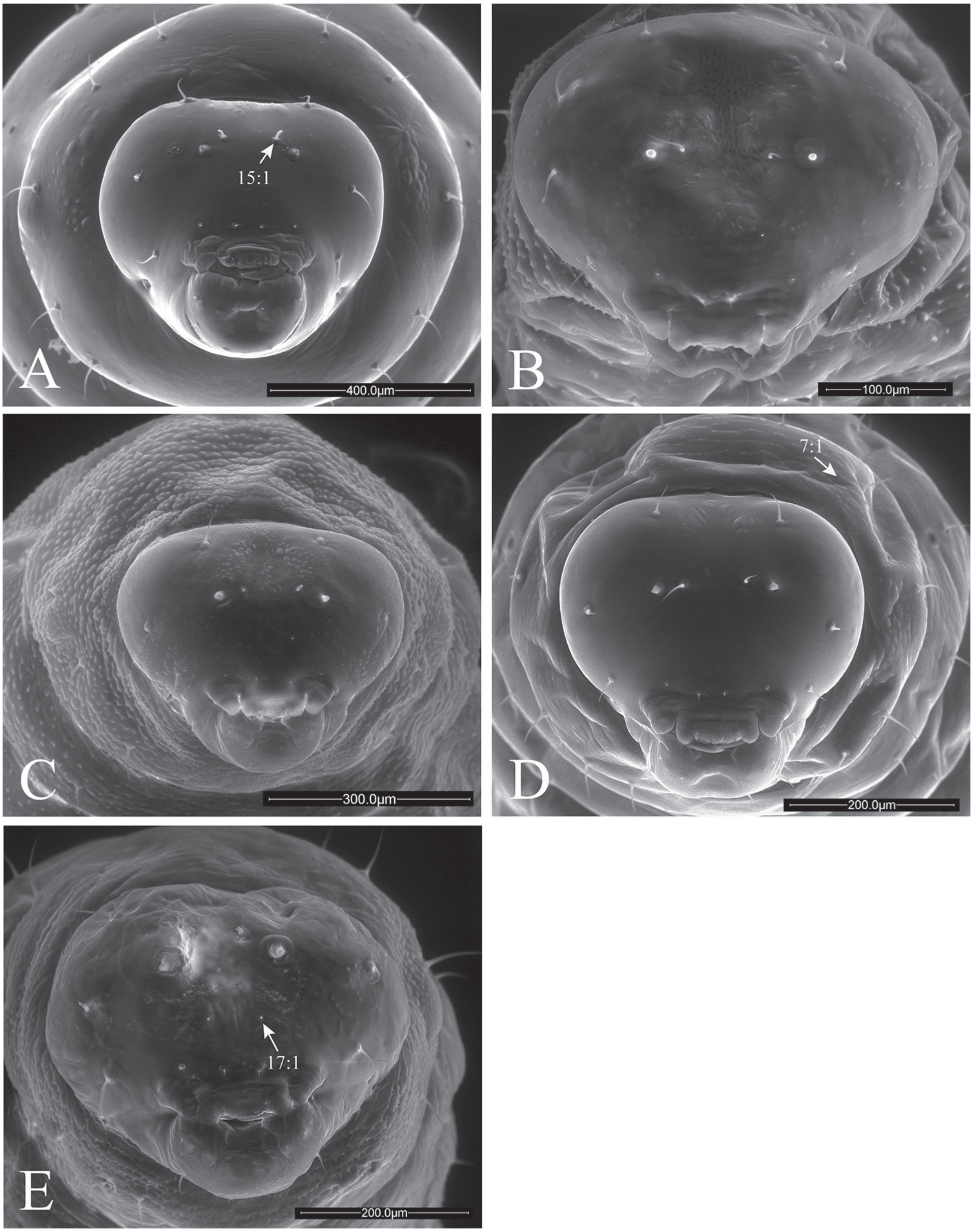

Figure 8. Anterior views of head of *Ormyrus* terminal-instar larvae. **A** *Ormyrus papaveris* **B** *O. pomaceus* ex *Trigonaspis mendesi* (Cynipidae) **C** *O. pomaceus* ex *Plagiotrochus razeti* (Cynipidae) **D** *O. rufimanus* **E** *O. wachtli*. Character states for outstanding features are pointed.

Description. Ex gall *Andricus grossulariae* asex., on *Quercus faginea,* n = 1; Body length: 2.73 mm, width: 1.67 mm; ex gall *Plagiotrochus fusifex* on *Quercus coccifera,* n = 1; Body length: 1.13 mm, width: 0.53 mm; ex gall *Plagiotrochus razeti* on *Quercus*

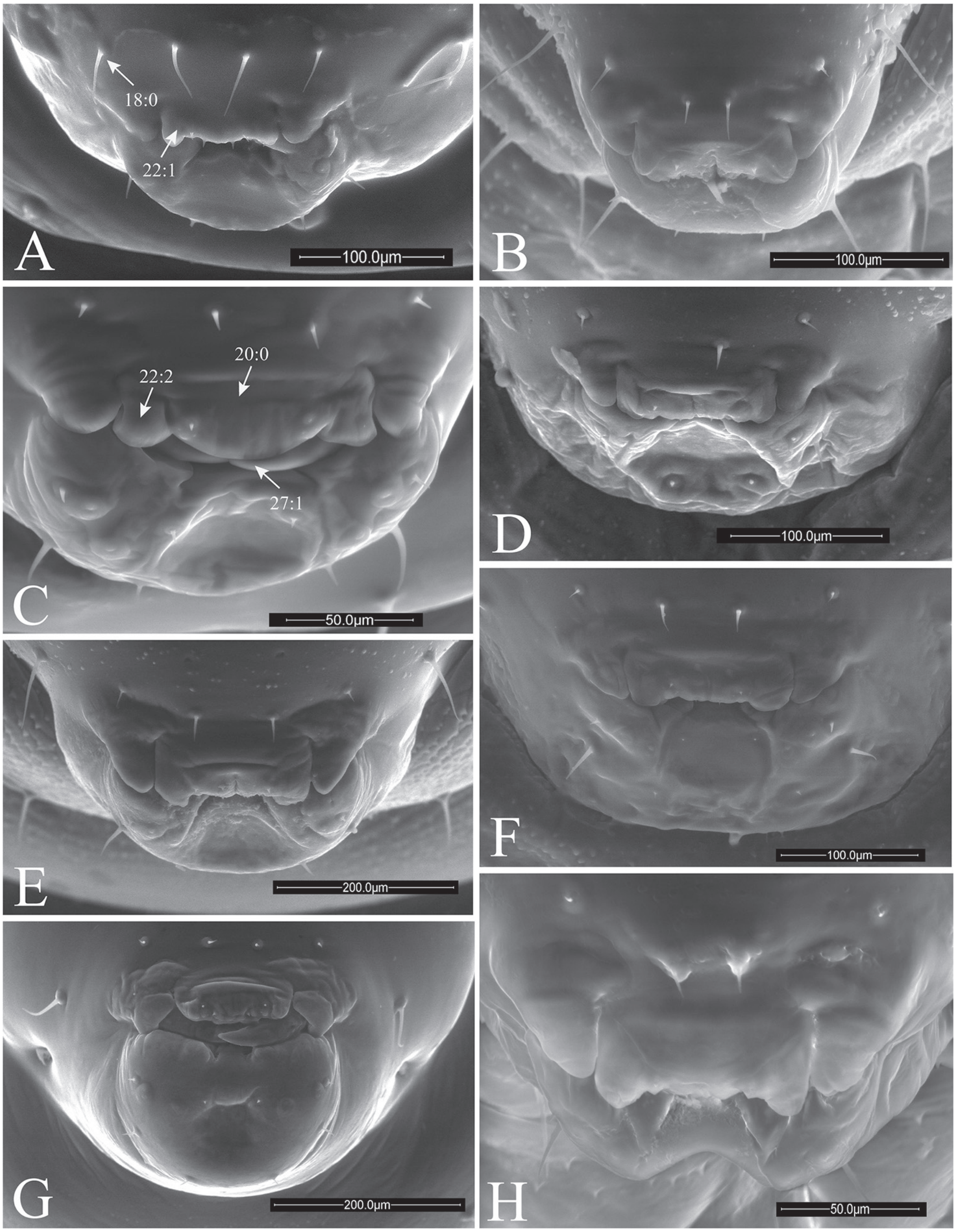

Figure 9. Anterior views of mouthparts of *Ormyrus* terminal-instar larvae. **A** *Ormyrus capsalis* **B** *O. cupreus* **C** *O. diffinis* **D** *O. gratiosus* **E** *O. nitidulus* **F** *O. orientalis* **G** *Ormyrus papaveris* **H** *O. pomaceus* ex *Trigonaspis mendesi* (Cynipidae). Character states for outstanding features are arrowed.

ilex, n = 11; Body length: 2.21 ± 0.46 mm (min-max: 1.80–3.40 mm), width: 1.10 ± 0.10 mm (min-max: 0.93–1.27 mm); ex gall *Trigonaspis mendesi* on *Quercus faginea*, n = 1; Body length: 1.55 mm, width: 0.80 mm.

The morphology of the terminal larva of this species is very similar to that of the *Ormyrus nitidulus* larva. The larvae of *O. pomaceus* from galls of *Andricus* and *Trigonaspis* species were distinguished from those of *O. nitidulus* by the following characters: integument of thoracic and abdominal segments with conspicuous blister-like sculpture; distance among vertex setae longer than the distance between antennae; *am* 0.47 as long as the distance between antennae; *lcs* situated above the level of *cs*, being separated from *cs* by 1.2-fold the distance between *cs*; and maxillary palps not visible (Table 2).

For the *O. pomaceus* larvae that inhabited *Plagiotrochus* galls (Figs 4C, 6B, 8C, and 10A), the differences between *O. pomaceus* ex *Andricus* and ex other host genera, such as *Trigonaspis* (Figs 4B, 6A, 8B, and 9H), were the following: *am* shorter in length than the separation between antennae (Table 2) and maxillary palps conspicuous.

Biology. *Ormyrus pomaceus* is a polyphagous ectoparasitoid that attacks more than 56 different cynipid galls on *Quercus* trees (Figs 14F and I; 15D and E) (Askew et al. 2013). Nevertheless, results from ongoing unpublished molecular studies clearly indicate that *O. pomaceus* includes a complex of sibling or cryptic species that are segregated according to cynipid hosts, host plant species and ecological preferences (Hernandez Nieves et al. unpublished, Stone pers. comm.). On the Iberian Peninsula, among the most regular host species of *O. pomaceus*, we found the asexual generations of *Andricus grossulariae* (Fig. 14D and E) and *A. pictus* (Fig. 14G and H), *Trigonaspis mendesi* (Fig. 14J and K) and *T. brunneicornis* (Figs 14L and 15A) on *Quercus pyrenaica* and *Q. faginea* and the galls of asexual species of *Plagiotrochus* on *Q. ilex* and *Q. coccifera* (Fig. 15B and C).

Ormyrus rufimanus Mayr, 1904.

Material examined. ex gall *Xestophanes potentillae* on *Potentilla reptans*, Spain, Madrid: Cotos de Monterrey, 24.VI.03, J. L. Nieves leg (n = 2); Madrid: Villalvilla, 26.VIII.05, J. L. Nieves leg (n = 9); Madrid: Villar del Olmo, 03.X.04, J. L. Nieves leg (n = 23); Tarragona: Colldejou, 14.VIII.03, J. L. Nieves leg (n = 7).

Description. n = 41; Body length: 1.69 ± 0.39 mm (min-max: 1.13–2.53 mm), width: 0.84 ± 0.22 mm (min-max: 0.47-1.27). Body fusiform, abdominal segments tapering abruptly towards ANS (Figs 4D, 6C); *adp* strongly remarked; integument of abdominal segments smooth but with blister-like sculpture extended in part of thoracic segments; setae on thoracic segment long, not longer than length of a thoracic segment, shorter on abdominal region. Head 1.03 as wide as high (Fig. 8D); integument on the face smooth; vertex concave; *an* situated at mid position in the face; vertex setae equally separated than the distance between antennae; *am* situated at the same level of *an*; *am* short, 0.22 times as long as the separation between antennae (Table 2). On clypeus *lcs* situated at the same level of *cs*, both equal in length (Fig. 10B); lateral lobes of labrum slightly differentiated and almost fused with the medial lobe; posterior margin of medial lobe of labrum straight; mandibles unidentated; tooth apex acute (Table 2).

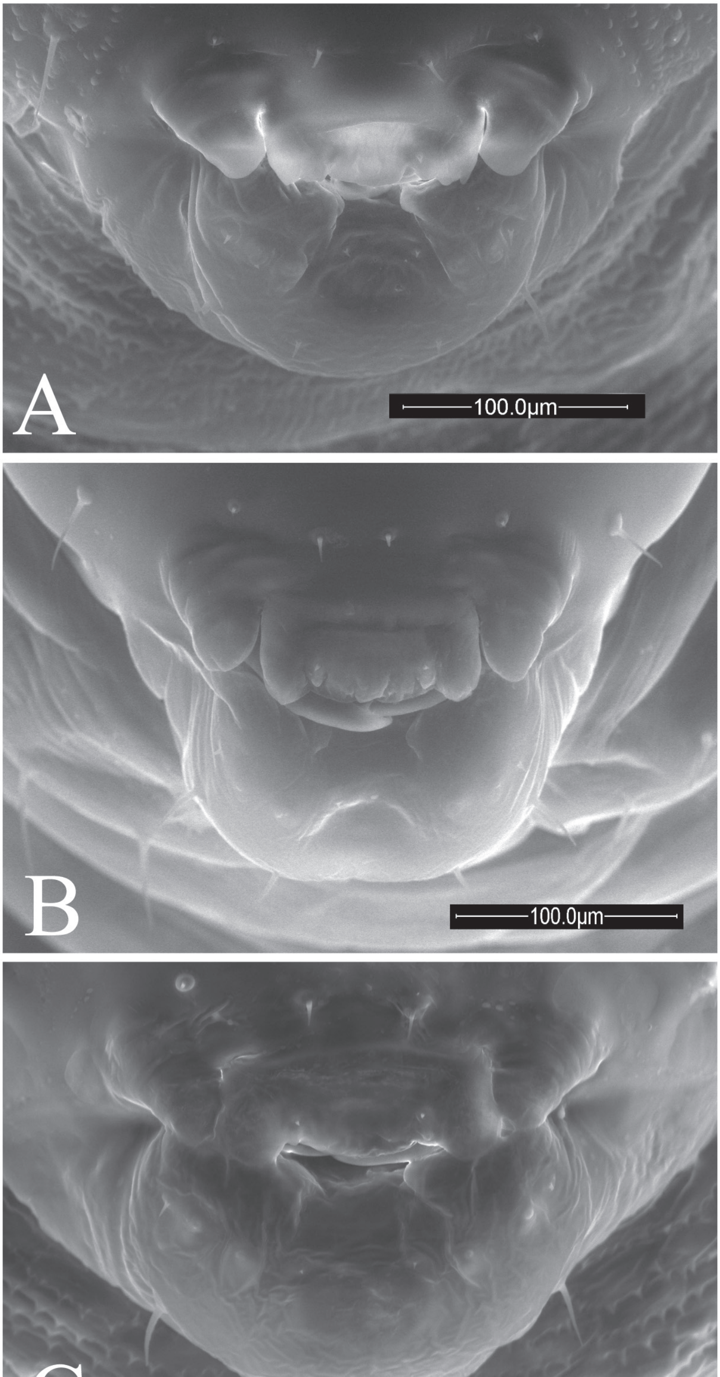

Figure 10. Anterior views of mouthparts of *Ormyrus* terminal-instar larvae. **A** *O. pomaceus* ex *Plagiotrochus razeti* (Cynipidae) **B** *O. rufimanus* **C** *O. wachtli*.

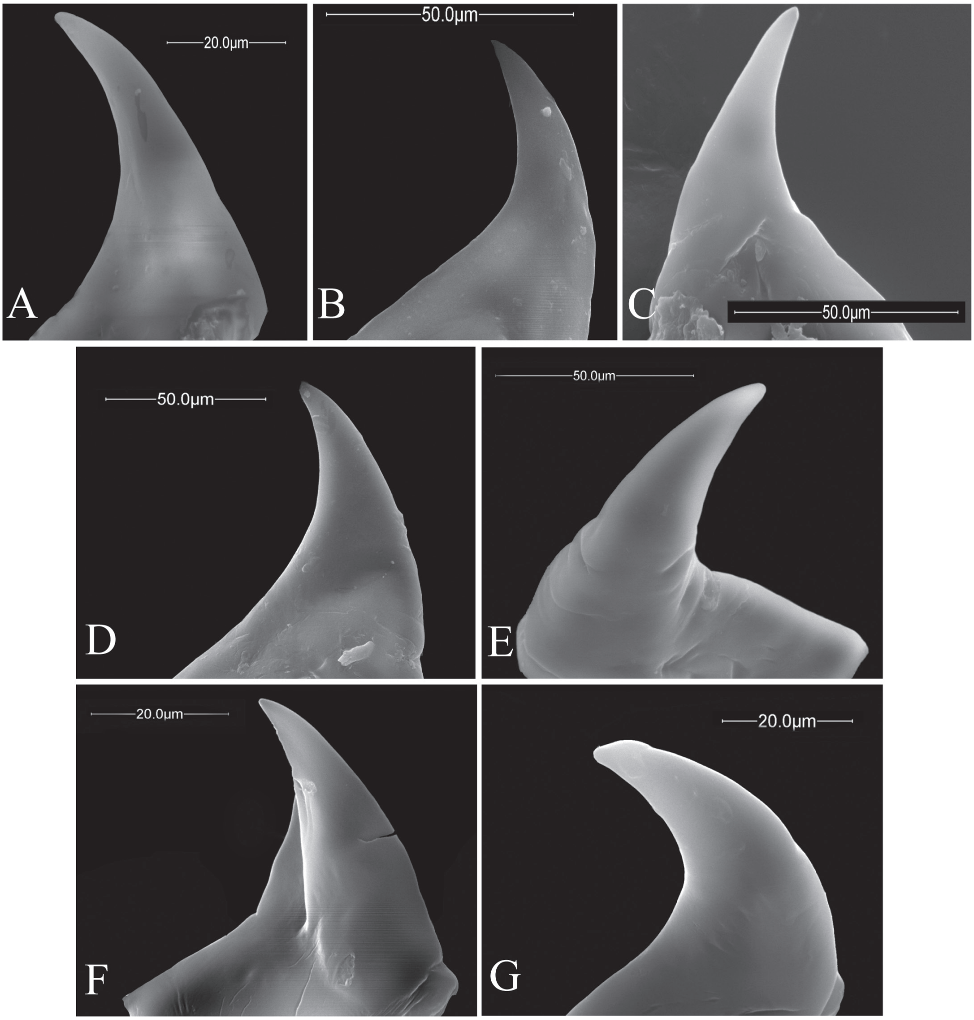

Figure 11. Anterior views of the right/left mandibles of *Ormyrus* terminal-instar larvae. **A** *Ormyrus capsalis* **B** *O. diffinis* **C** *O. gratiosus* **D** *O. nitidulus* **E** *O. papaveris* **F** *O. pomaceus* ex *Trigonaspis mendesi* (Cynipidae) **G** *O. rufimanus*.

Biology. This species is extremely host-specific and is exclusively associated with galls on the runners and roots of *Potentilla reptans* (Rosaceae) induced by *Xestophanes potentillae* (Retzius) (Fig. 15H and I) (Askew et al. 2006). On the Iberian Peninsula, two forms of the galls were found. One form was on stems or runners close to or beneath the soil surface that consisted of round swellings (Fig. 15G), and the others formed on subterranean rhizomes (Fig. 15F).

In the first stages, the larva of *O. rufimanus* and the paralyzed host larva co-occurred; in later stages, the remains of the host larva appeared on the ventral surface of the *O. rufimanus* larva. In dissected galls, the larvae of *O. rufimanus* were extracted from irregularly shaped larval gall cells, which indicated that vegetal material was consumed at the terminal larval stage, as observed with other *Ormyrus* species such as *O. papaveris*. Based on additional observations, we found larvae of *Eupelmus vesicularis* (Chalcidoidea, Eupelmidae) were hyperparasitoids of *O. rufimanus* pupae.

Ormyrus wachtli Mayr, 1904.

Material examined. ex gall *Neaylax verbenacus* on *Salvia verbenaca*, Spain, Madrid: Dehesa de Arganda, 09.VI.02 J. L. Nieves leg (n = 1).

Description. n = 1; Body length: 1.67 mm, width: 0.80 mm. The larva of this species is similar to the larva of *O. diffinis*, from which may be distinguissed as follows: body fusiform, wider at the level of segments ABS2-ABS3, tapering progresively towards ANS; anal segment wider tan length; *adp* absent; integument of the abdominal and thoracic segments blister-like. Head 1.18 as wide as high (Fig. 8E) with blister-like sculpture extended on all the head; antennae situated at mid position in the face; *ams* situated clearly above the antennae; lateral lobes of labrum almost fused with the medial lobe; ventral margin of medial lobe of labrum straight (Fig. 10C).

Biology. The larva of *O. wachtli* is a solitary ectoparasitoid of larvae of cynipids, inducing galls on fruits of *Salvia* (Lamiaceae). Along the Iberian Peninsula and in southern Europe, the species is associated with galls of *Neaylax salviae* (Giraud) on *Salvia lavandulifolia* (Fig. 15L) and *Neaylax verbenacus* (Nieves-Aldrey) on *Salvia verbenaca* (Fig. 15J and K) (Nieves-Aldrey 2001, Nieves-Aldrey and Askew 2002, Askew et al. 2006). The species has a bivoltine life cycle.

Discussion

As discussed in published studies on other families of Chalcidoidea (Gómez et al. 2008, 2011, 2013; Gómez and Nieves-Aldrey 2012, 2017; Nieves-Aldrey et al. 2008), the larval characters have potential value in systematic and phylogenetic studies of the group. Moreover, the taxonomy and identification of Chalcidoidea associated with gall-inducing insects is more robust when data on larval morphology of the species are available. In this work, for the first time, the primary morphological traits of larvae of *Ormyrus* species and their potential value in the systematics of the family Ormyridae of the Chalcidoidea is discussed.

Terminal-instar larval morphology and *Ormyrus* taxonomy

The larvae of Ormyridae have a combination of traits that differentiate this family from other related chalcidoid families with a similar lifestyle as parasitoids of gall-inducer insects. Compared with larvae of Torymidae or Pteromalidae (Gómez et al. 2008; Gómez and Nieves-Aldrey 2012), the body setae are relatively short, the abdominal segments are particularly inconspicuous, and the labrum is normally divided into three lobes, with two laterals and one larger, central.

Nevertheless, larvae of Ormyridae resemble those of Eurytomidae in the relative length of body setae, with the thoracic setae relatively longer than those of the abdominal segments (Gómez et al. 2011, 2013). However, the larvae of Ormyridae have a single-toothed mandible, whereas the larval mandibles of eurytomids are bidentate. Additionally, the labrum of Ormyridae larvae is typically undivided or only has three lobes, whereas that of Eurytomidae larvae is usually divided into five lobes. For many characters, the larva of Ormyridae also resembles the larva of Torymidae and Eupelmidae (Gómez et al. 2008; Nieves-Aldrey et al. 2008; Gómez and Nieves-Aldrey 2017), although some conspicuous traits permit easy differentiation. First, the ormyrid larvae differ from torymids because of the much shorter abdominal body setae and the lower number of cephalic setae. Second, the larvae of Eupelmidae are easily distinguished from those of Ormyridae by the ventral margin of the clypeus, which is regularly serrate in eupelmid larvae and entire in ormyrid larvae. Finally, Ormyridae are easily distinguished from other chalcidoid parasitoids of galls, such as Pteromalidae and Eulophidae because the terminal-instar larvae of these two families are essentially glabrous (Gómez and Nieves-Aldrey 2012, 2017).

Species differentiation and relationships related to terminal-instar larval characters

Based on unpublished results of combined morphological and molecular data, three primary clades defined the phylogenetic relationships of European species of *Ormyrus*, which were mostly congruent with host gall and plant data (Hernández Nieves 2007, Hernández Nieves et al. unpublished). The first clade was composed of the *Ormyrus* species that are parasitoids of oak gall wasps (tribe Cynipini), with one species, *O. rufimanus*, associated with cynipid galls on *Xestophanes* (Rosaceae) (tribe Diastrophini). The second clade was composed of *Ormyrus* species that attack cynipid gall wasps on herbs tribes Aulacideini, Aylacini and Phanacidini (Ronquist et al. 2015). The third clade contained the two *Ormyrus* species, *O. cupreus* and *O. orientalis*, that attack non-cynipid hosts.

The presence or absence of a blister-like sculpture was one larval feature that was moderately congruent with this division. Although the terminal-instar larvae of the *Ormyrus* species that are parasitoids of herb gall wasps did not present the blister-like sculpture, the sculpturing was found in the species associated with oak gall wasps (Cynipini) and in *O. cupreus*, the species associated with eurytomid galls. However, *O. wachtli* and *O. rufimanus* were exceptions, although the blister-like sculpture was found on the thorax of *O. rufimanus*. For *O. wachtli*, the conspicuous blister-like sculpture is one of the distinctive diagnostic characters, in combination with a pair of supraclypeal setae, which is absent in the other species.

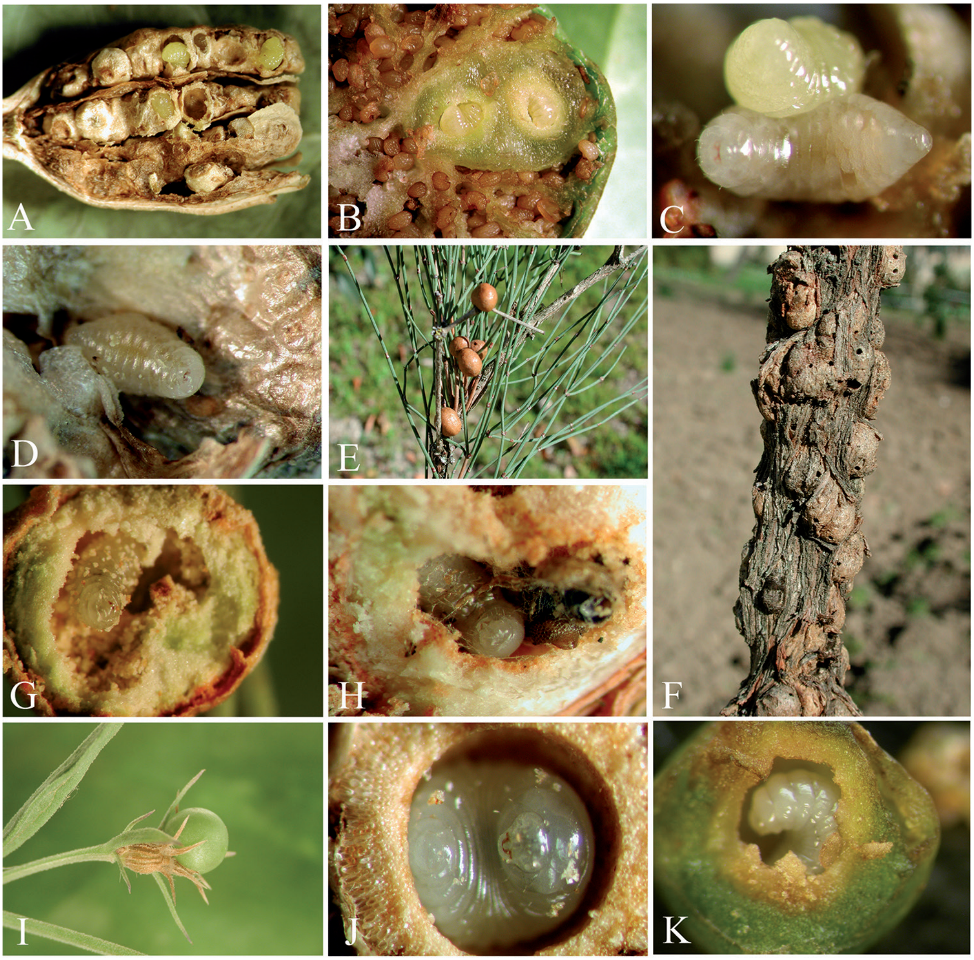

Figure 12. A Galls of *Aylax minor* on *Papaver* spp. **B** detail of cells of *Aylax minor* on *Papaver* spp. **C** larvae of *Ormyrus capsalis* on of non-parasitized larvae of *A. minor* **D** Detail of solitarious larvae of *O. capsalis* inside gall cell of *A. minor* **E** galls of *Eurytoma gallephedrae* on *Ephedra nebrodensis* **F** galls of *Eurytoma flaveola* on *Ephedra nebrodensis* **G** larvae of *Ormyrus cupreus* inside the gall cell **H** larvae of *Ormyrus cupreus* inside the gall cell with debris of adult specimen of the same species **I** gall of *Liposthenes kerneri* on *Nepeta hispanica* **J** ventral view of larvae of *O. diffinis* inside the gall cell **K** lateral view of larvae of *O. diffinis* inside the gall cell.

Identification of the larvae of *Ormyrus* species is usually relatively easy based on their host and plant specificity. Nevertheless, for polyphagous species, such as the complex of *O. pomaceus* and *O. nitidulus* associated with cynipid galls on *Quercus* and those species that share hosts, the identification is more difficult. In many cases, the relative size of the larvae of the two species is a useful diagnostic tool because the larvae of *O. nitidulus* always exceeded 3 millimetres in size and the blister-like sculpture was not as conspicuous as with *O. pomaceus*. The preference of *O. nitidulus* for occupying the

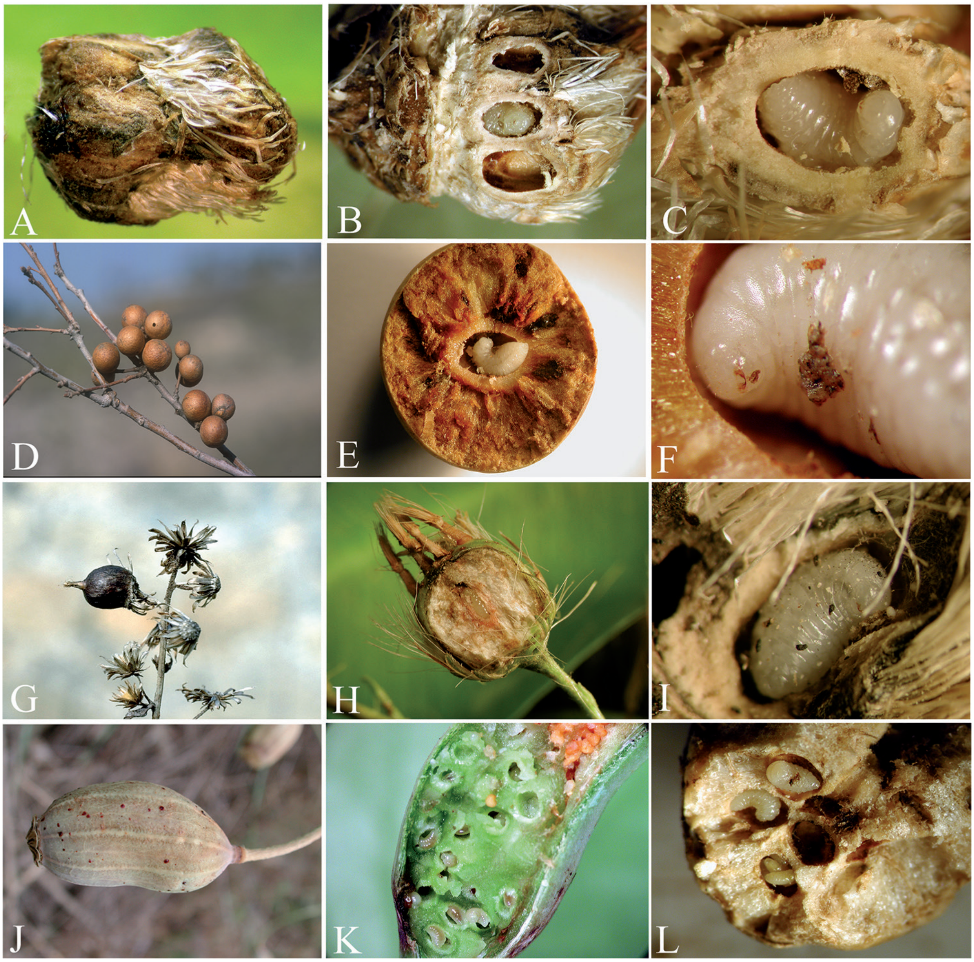

Figure 13. Fully (**A**) and dissected (**B**) galls of *Isocolus scabiosae* in achenes of heads of *Centaurea scabiosa*. **C**. detail of larvae of *Ormyrus gratiosus* inside cells of *I. scabiosae* gall **D** galls of *Andricus hispanicus* on *Quercus pyrenaica* **E** cross-section of gall of *Andricus hispanicus* with larvae of *Ormyrus nitidulus* within gall cell **F** detail of head and thorax in anterior view of larvae of *Ormyrus nitidulus* within gall cell of *A. hispanicus* **G** gall of *Myopites limbardae* on *Inula viscosa* **H** cross-section of gall of *Myopites limbardae* on *Inula viscosa* **I** detail of larva of *Ormyrus orientalis* within gall cell of Tephritidae on *Microlonchus salmanticus* **J** galls of *Aylax papaveris* on poppy heads **K** cross-section of poppy head shown cells of galls of *A. papaveris* **L** larvae of *Ormyrus papaveris* with debris of dead host within gall cells of *A. papaveris*.

central cell of the gall, as a primary parasitoid of their hosts, was another useful trait to separate these two species. By contrast, the larvae of *O. pomaceus* may parasitize inducer and lethal inquilines, both from the genus *Synergus*, which occupy secondary larval chambers inside the galls.

The morphological characters described in this work on the systematics of terminal-instar larvae of Ormyridae were constant across species within the genus *Ormyrus*.

The differences among species were not marked, although some small differences in morphological traits allowed the separation of some species or groups of species. We consider the data presented in this study to be a preliminary contribution to increasing information on the immature stages of one of the less studied families of Chalcidoidea. Therefore, the study must be expanded to include larvae of species from other zoogeographical regions and larvae of those species with biological traits different from that of the European species, such as the species associated with fig wasps on *Ficus* in tropical areas.

Biological traits

Ormyridae are cosmopolitan inhabitants of different ecosystems worldwide, although the highest diversity is reported in Holarctic and Australasian regions, with only a few species cited from other zoogeographic regions such as Afrotropical and Neotropical, but these few species are likely a function of a lack of revisions of these faunas (Noyes 2016).

With reference to the diversity of the genus *Ormyrus* in the Palaearctic region, the 34 species recorded cover a wide range of insect host species, all of which are associated with different types of galls (Hernández Nieves 2007, Lotfalizadeh et al. 2012), primarily Cynipidae (Hymenoptera) (Hanson 1992) but also Tephritidae and Cecidomyiidae and Agromyzidae/Lonchaeidae (Diptera) (Bouček 1986). The exact roles of *Ormyrus* within specific gall communities remain unknown, but all species are idiobiont ectoparasitoids or hyperparasitoids, even the few Afrotropical and Australasian species, some of which are obligate or facultative parasitoids on fig wasp communities in *Ficus* plants (van Noort et al. 2007). Moreover, many of the undescribed African *Ormyrus* species are associated with shrub galls on a variety of plant taxa (S. van Noort, pers. comm.).

Of the ten European species examined in this study, eight species formed part of the parasitoid community associated with cynipid galls, and two were associated with gall tephritids and gall eurytomids. With reference to the species associated with gall wasps, as with the related Torymidae (Gómez et al. 2008), remarkably, most are parasitoids with a narrow host range. Whereas monophagy is apparently common within the parasitoid community associated with herb gall wasps (tribes Aylacini and Aulacideini), polyphagous species are more common in parasitoid communities associated with galls on *Quercus* species (cynipid species included in the tribe Cynipini) (Askew et al. 2006, 2013).

Some of the ormyrid species that we studied were dominant in the parasitoid communities associated with their host galls. For example, *O. papaveris* was the most abundant parasitoid species in galls on poppy heads induced by *Aylax papaveris*. Similarly, *O. gratiosus* (attacking *Isocolus scabiosae*) and *O. diffinis* and *O. wachtli* (attacking galls of *Liposthenes kerneri* on *Nepeta* and *Neaylax* ssp. on *Salvia*, respectively) are the most abundant parasitoid species in those gall parasitoid communities (Askew et al. 2006, Hernández et al. unpublished). *Ormyrus wachtli* has a co-dominant relationship with *Eurytoma infracta* (Eurytomidae), which are the only known parasitoids in galls of *Neaylax verbenacus* to date and are responsible for more than 80% of gall parasitism in all geographical locations.

Ormyrus cupreus occupies a unique position within the parasitoid community of *Eurytoma gallephedrae* (Askew and Blasco-Zumeta 1998). In galls of this eurytomid species on *Ephedra nebrodensis*, the dominant species is *Brasema ephedricola* (Eupelmidae). *Ormyrus cupreus* is recorded as a hyperparasitoid of *Eupelmus* sp. within the community (Askew and Blasco-Zumeta 1998), and cannibalistic behaviour has been observed among larvae of *O. cupreus*.

According to previous molecular and morphological phylogenetic analyses (Hernández Nieves 2007), the evidence is strong that *Ormyrus pomaceus* includes a complex of cryptic or sibling species. Within this complex, we identified at least three different groups, based on morphological, molecular and biological data. The "*plagiotrochus*" group consisted of *O. pomaceus* associated with *Plagiotrochus* cynipid-galls on *Quercus* trees section *Ilex* (specifically *Q. ilex* and *Q. coccifera*) and *O. pomaceus* specimens reared from asexual galls of *Plagiotrochus razeti* (Fig. 15B), with these galls also found on runners of *Q. ilex*. The terminal-instar larva of *O. pomaceus* f. *plagiotrochus* is a solitary parasitoid that usually occupied the cynipid gall chamber, which was seldom deformed secondarily (Fig. 15D and E). We also found larvae of *O. pomaceus* in galls of *Plagiotrochus fusifex* on *Q. coccifera* (Fig. 15C).

The "*trigonaspis*" group was composed of *O. pomaceus* "*sensu lato*" specimens that attacked small leaf galls induced by species of *Trigonaspis*, a genus which is circumscribed primarily on the Iberian Peninsula and is represented by at least three endemic species: *Trigonaspis mendesi*, *T. brunneicornis* and *T. baeticus* (Nieves-Aldrey 2001). Individuals of *O. pomaceus* in this group were relatively abundant in galls of *Trigonaspis mendesi* (Fig. 14J and K) on *Quercus faginea* and *T. brunneicornis* on *Q. pyrenaica* (Figs 14L and 15A).

The "*pomaceus*" *sensu stricto* group was composed of the core individuals of *O. pomaceus* reared from the other cynipid-galls on several species of *Quercus,* with approximately 84 different cynipid host gall species recorded (Askew et al. 2013), excluding the species of *Plagiotrochus* and *Trigonaspis* (Fig. 14D, E, F, G, H, and I).

The larvae of *O. pomaceus sensu stricto* were located in dissected galls of asexual generations of *A. pictus* (Fig. 14G, H, and I) and *A. grossulariae* (Fig. 14D, E, and F), and the larvae are either parasitoids of the cynipid larvae or the gall maker or the lethal inquiline of the genus *Synergus*.

The community of ormyrid parasitoids of cynipid galls is usually composed of solitary ectoparasitoids. Notably, in this work, we reported some cases of secondary phytophagy in several ormyrid species. For example, the larvae of *O. papaveris* were observed moving inside the gall cell and touching the walls with their mandibles, which was similar to the behaviour of *O. rufimanus*; as a result, the gall cells became larger and deformed. Larval phytophagy has been described for some species of Eurytomidae (Crosby 1909; Bugbee 1941; Zerova, 1981, 1993; Bouček 1988; Henneicke et al. 1992; Dawah and Rothfritz 1996; Askew and Blasco-Zumeta 1998; La Salle 2005; Gómez et al. 2011, 2013), but this behaviour had not been previously recorded in the Ormyridae.

Figure 14. A cross-section of poppy head with galls of *Barbotinia oraniensis* **B** larvae of *Ormyrus papaveris* within gall of *B. oraniensis* **C** larvae of *Ormyrus papaveris* with debris of dead host within gall cells of *B. oraniensis* **D** gall of *Andricus grossulariae* (asexual) on *Quercus pyrenaica* **E** cross-section of gall *Andricus grossulariae* (asexual) **F** larvae of *Ormyrus pomaceus* ex gall of *A. grossulariae* **G** gall of *Andricus pictus* on *Q. pyrenaica* **H** cross-section of gall *Andricus pictus* **I** larvae of *Ormyrus pomaceus* ex gall of *A. pictus* **J** galls of *Trigonaspis mendesi* on *Q. faginea* **K** larvae of *O. pomaceus* within galls of *Trigonaspis mendesi* on *Q. faginea* **L** galls of *Trigonaspis brunneicornis* on *Q. faginea*.

Conclusions

The external morphology of final instar ormyrid larvae has been documented and the potential use of the characters in the taxonomy and systematics of this poorly studied Chalcidoidea group explored. Our data will assist in the reliable identification of the species of this chalcidoid family during studies of cynipid gall communities and food

Figure 15. A larvae of *O. pomaceus* and *Trigonaspis brunneicornis* within gall cells **B** gall of *Plagiotrochus razeti* (asexual) on *Quercus* **C** galls of *Plagiotrochus quercusilicis* on *Quercus* **D** larvae of *Ormyrus pomaceus* within cells of galls of *P. razeti* **E** detail of larva of *Ormyrus pomaceus* within cell of gall of *P. razeti* **F** galls of *Xestophanes potentillae* on subterranean rhizome of *Potentilla reptans* **G** galls of *X. potentillae* on air runners of *P. reptans* **H** larvae of *O. rufimanus* on larvae of *X. potentillae* within gall cell **I** larvae of *O rufimanus* with debris of dead host within gall cells of *X. potentillae*. **J** galls of *Neaylax verbenacus* on *Salvia verbenaca* **K** larvae of *O. wachtli* on larvae of *N. verbenacus* within gall cell **L** pupae of *O. wachtli* within gall of *Neaylax salviae*.

webs in which the accurate identifications of species are of great importance. However, much further work is required, including investigations of a wider selection of ormyrid species and descriptions of the other immature stages, in addition to more detailed observations of their parasitic behaviour.

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Supplementary material 1

Characters of *Ormyrus* larvae used for systematic study

Authors: Jose F. Gómez, María Hernández Nieves, Severiano F. Gayubo, Jose Luis Nieves-Aldrey

Data type: species data

Explanation note: Characters are listed by body region, for the body, head and under lip complex, which for the latter is subdivided between labrum, maxillae and mandibles.

Supplementary material 2

Character states of *Ormyrus* larvae included in the systematic study

Authors: Jose F. Gómez, María Hernández Nieves, Severiano F. Gayubo, Jose Luis Nieves-Aldrey

Data type: species data

Explanation note: Observed character states of characters listed in Appendix 1. Explanation of symbols: monomorphic states 0–3; not applicable (*); unknown (?). Characters are unordered.

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Baetis (*Baetis*) *cypronyx* sp. n., a new species of the *Baetis alpinus* species-group (Insecta, Ephemeroptera, Baetidae) from Cyprus, with annotated checklist of Baetidae in the Mediterranean islands

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Abstract

A detailed description of the larvae of *Baetis* (*Baetis*) *cypronyx* **sp. n.**, a representative of the *Baetis alpinus* species-group within the mayfly family Baetidae, is provided, including a differential diagnosis with regard to closely related species of the group, especially *Baetis melanonyx* (Pictet, 1843) and *B. baroukianus* Thomas & Dia, 1984. The new species is mainly distinguished by mouthparts (i.e. the shape and setation of labrum, maxillary and labial palps, details of paraglossae and mandibular incisors), setation of legs and abdominal terga, and length of paracercus. All available data on the biology of this putative endemic species of Cyprus are summarized. Annotated distributional data of the 33 species of Baetidae so far recorded from the Mediterranean islands are given, including new records and also including first data from Malta.

Keywords

Baetinae, *Baetis alpinus* species-group, checklist, distribution, endemism, Mediterranean islands

Introduction

The first contribution to the Baetidae of Cyprus (Soldán and Godunko 2008) included the description of two new species from Cyprus and neighbouring island of Rhodos in Greece. *Baetis mirkae* Soldán & Godunko, 2008 of the *Baetis lutheri* species-group was found on both islands, and later considered as East Mediterranean (Pontomediterranean) species (Bauernfeind and Soldán 2012: 124). *B. irenkae* Soldán & Godunko, 2008 of the *Baetis buceratus* species-group is so far only known from three Cypriote localities and probably is endemic to Cyprus (Soldán and Godunko 2008: 95, Bauernfeind and Soldán 2012: 167). Two of these localities are in Limassol District (Kryos River at Kalidonia waterfalls and Diplos River at Chantara waterfalls) and were sampled during an extensive survey of aquatic invertebrates in May–June of 2004 (Soldán and Godunko 2008). Both localities revealed a relatively high diversity of benthic insects, namely high abundances of the mayfly genera *Epeorus* (*Ironopsis*), *Electrogena*, and *Baetis* (*Baetis* s. str., *Nigrobaetis* Novikova & Kluge, 1987). One species belonging to the *Baetis alpinus* species-group is described below as *Baetis* (*Baetis*) *cypronyx* sp. n.

The *Baetis alpinus* species-group was established by Müller-Liebenau (1969: 46) [i.e. *alpinus*-Gruppe] for three species, namely *B.* (*B.*) *alpinus* (Pictet, 1843) B *(B.) melanonyx* (Pictet, 1843) and *B.* (*B.*) *nubecularis* Eaton, 1898. This species-group with Holarctic distribution includes 12 Western Palaearctic species from Europe, Mediterranean, Minor Asia, and North Africa. According to Müller-Liebenau (1969), Jacob (2003), Soldán and Godunko (2009), and Bauernfeind and Soldán (2012), the distinguishing characters for this species-group can be summarized as follows:

Larvae: (**i**) body flattened ventrally, with shortened abdomen; (**ii**) segments of antennal flagellum each shortened in the distal two thirds of the antenna; (**iii**) labrum usually with more than 6–7 (up to 22) long, submarginal setae; (**iv**) outer mandibular incisor group roughly triangular and often fused; (**v**) segment 2 of maxillary palp with one or more (sometimes numerous) stout setae on conical protuberance; (**vi**) pronotum with conspicuous dark pattern; (**vii**) sternal protuberances on meso- and metathorax more or less developed, pointed or rounded apically; (**viii**) outer margin of femora with medium or long bristles, acutely pointed or obtuse apically, arranged in 1–3 rows centrally and proximally; (**ix**) tarsal claws with a pair of fine subapical setae; (**x**) abdominal terga generally light, with marked dark spots centrally; (**xi**) posterior margins of abdominal terga with a row of triangular, more or less pointed spines; (**xii**) surface of abdominal terga usually without distinct corrugations, and usually covered with numerous, tongue-shaped, triangular or spatulate scales and their sockets; (**xiii**) paracercus more or less reduced (occasionally strongly reduced).

Imagines: (**xiv**) hind wings with three longitudinal veins, cross veins present or absent; (**xv**) abdominal terga relatively dark and translucent; (**xvi**) basal segment of forceps roughly cylindrical or subcylindrical, with inner, more or less expanded, conspicuous apicomedial projection, often forming a distinct rim; (**xvii**) forceps segment 2 subcylindrical, more or less constricted near base; (**xviii**) forceps segment 3 variable, egg-shaped or subcylindrical, nearly 2–3 times longer than wide.

Apart from the description of the new species, additional objectives of this contribution are to discuss its differential diagnosis and its difference to other representatives of the *B. alpinus* species-group, to summarise available data on the biology and distribution of the new species, and to present an annotated checklist of the Baetidae in the Mediterranean islands.

Material and methods

Material

Most specimens of the new species were collected in the Kryos River at Kalidonian Waterfalls; additional material was collected in Diplos River at Chantara Waterfalls (for numbers of specimens, their proper localities, and deposition see below). Holotype and 45 paratypes of the new species are housed in the Institute of Entomology, BC CAS (České Budějovice, Czech Republic), 22 paratypes in the collection of State Museum of Natural History NASU (Lviv, Ukraine), and 22 paratypes are stored in the Staatliches Museum für Naturkunde (Stuttgart, Germany). Additional paratypes are deposited in the collection of CNR-IRSA Water Research Institute (Brugherio, Italy).

Morphological study

The specimens were preserved in 70–80% ethanol. Eight paratypes were mounted on slides with Euparal liquid. Drawings were made using a Zeiss Axioplan microscope with a camera lucida. Photographs of larvae were taken using a Leica Z16 APO macroscope and processed with Leica Application Suite™ Version 3.1.8 to obtain combined photographs with enlarged depth of field. Photographs were subsequently enhanced with Adobe Photoshop™ CS3.

Specimens used for SEM were dissected and dehydrated through a stepwise immersion in ethanol and then dried by critical point drying (Leica EM CPD300). The mounted material was coated with a 5 nm Au/Pd layer (Leica EM ACE200) and subsequently examined and photographed with a Zeiss EVO LS 15 scanning electron microscope. SEMs were subsequently enhanced with Adobe Photoshop™ CS3.

Terminology

Terminology and corresponding acronyms recently proposed for the representatives of the subgenus *Rhodobaetis* Jacob, 2003 by Godunko et al. (2015) are used to describe body setation (e.g. to characterise types of stout setae and scales). Further acronyms e.g. *FT* (for designation of flat-tipped sensillum), *B* (for sensillum basiconicum) and *Hr* (for hair-like setae) used here have been proposed earlier by Gaino and Rebora (1996, 2003). Additionally, a new type of tongue-shaped scales (*SC-tg*; 7.5–11.0 µm in length) is described and depicted. Morphological characters to distinguish *Baetis* (*Baetis*) *cypronyx* sp. n. from other representatives of *B. alpinus* species-group, and especially from closely related *B. melanonyx* are given according to Müller-Liebenau (1969), Thomas et al. (1983), Thomas and Dia (1984), Peru and Thomas (2001), Jacob (2003), Kluge and Novikova (2011), Bauernfeind and Soldán (2012) and Sroka et al. (2012). All discriminating characters are summarized in Table 1.

Taxonomy

Baetis (*Baetis*) *cypronyx* sp. n.

http://zoobank.org/0B11F59C-97F2-42F2-AFD4-A68B6E3D3DCB
Figs 1–24

Type material. ***Holotype*:** mature larva, CYPRUS, Limassol [Lemesos; Λεμεσός] District, Troodos [Τρόοδος] Mts., Kryos River [Κρύος ποταμός], Kalidonia Waterfalls, app. 1250 m a.s.l., N34 53.561 E32 52.043, 22.v.2004, leg. T. Soldán.

***Paratypes*:** 75 larvae, the same date and place as holotype; 14 larvae, CYPRUS, Limassol [Lemesos; Λεμεσός] District, Troodos [Τρόοδος] Mts., Diplos River [Διπλός ποταμός], Chantara [Xantara] Waterfalls, near Trooditissa [Μοναστήρι Τροοδίτισσας] Monastery, app. 1300 m a.s.l., N34 54.429 E32 50.303, 23.v.2004, leg. T. Soldán;

4 larvae, ibid., Paphos District [Επαρχία πάφου], Gialia River [Γιαλιά], in the forest “Pochalantra”, app. 5 km upstream from Gialia [Γιαλιά] village, app. 400–410 m a.s.l., N35 04.364 E32 33.575, 12.xi.2005, leg. A. Buffagni;

10 larvae, United Nations Buffer Zone in Cyprus, Nicosia District [Επαρχία Λευκωσίας], upstream of Kargotis River [Καρκώτη], vicinity of Kakopetriya [Κακοπετριά] village, Mitro place, app. 150–200 m a.s.l., N34 59.012 E32 54.000, 22.iii.2006, leg. A. Buffagni;

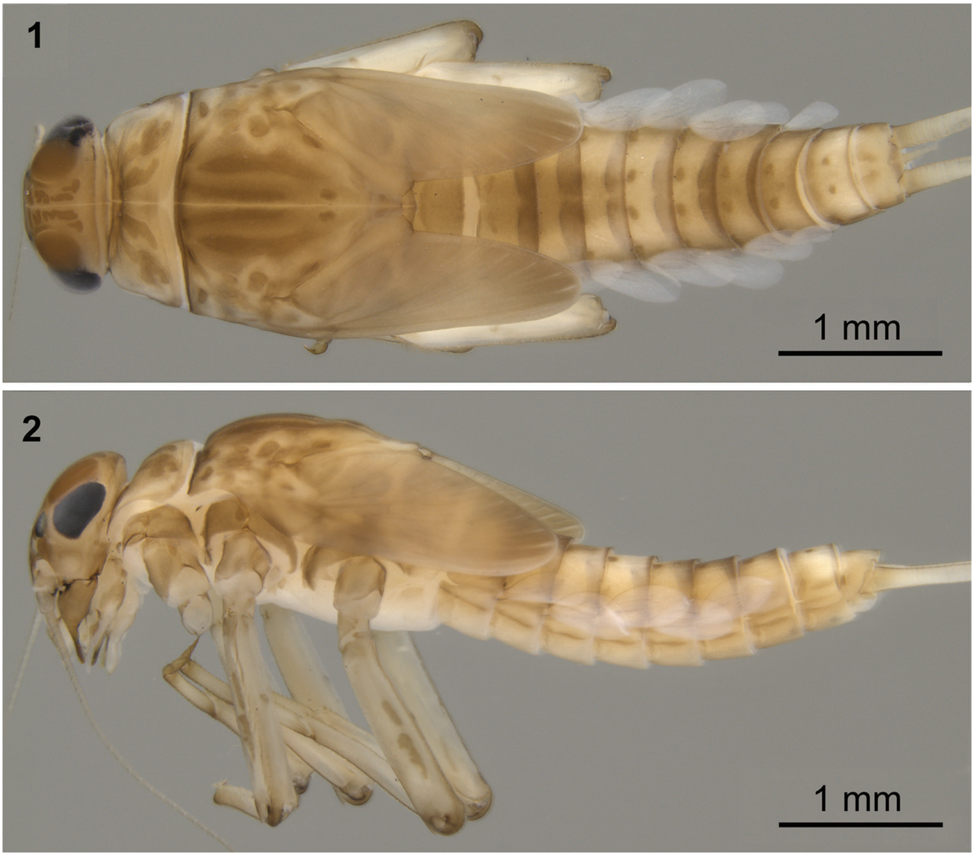
2 larvae, ibid., Agios Nikolaos Lefkas [Άγιος Νικόλαος Λεύκας] village (abandoned), app. 100–120 m a.s.l., N35 5.280 E32 53.500, 24.iii.2006, leg. A. Buffagni.

Comparative material.

Baetis baroukianus Thomas & Dia, 1984: 1 male and 1 female mature larvae, LEBANON, Chouf District, type locality of *B. baroukianus*, branch of Salam (Râs el Mâ) spring near Harêt Jandal Municipality, app. 800 m a.s.l., 25.vii.1979, leg. Dia A. (see Thomas and Dia 1984: 10).

28 larvae (10 males, 18 females), IRAN [*new record*], Elburz Mts., Gilan Province, Rudbar County, Central District, unnamed brook in Divresh village, right tributary of Siah Rud River (SE upstream of Shirkooh village), app. 285 m a.s.l., N36 53.59 E49 35.06, 13.v.2016, leg. Bojková J., Soldán T. & J. Imanpour Namin, det. Sroka P.

2 larvae (1 male, 1 female), ibid, Fuman County, Sardar-e Jangal District, unnamed brook below of Masuleh City (right tributary of Rudkhan River), app. 710 m a.s.l., N37 09.42 E49 01.17, 22.v.2016, leg. Bojková J., Soldán T. & J. Imanpour Namin, det. Sroka P.



Figures 1–2. Colour pattern of *Baetis* (*Baetis*) *cypronyx* sp. n., larva, male, paratype (material from type locality): **1** body, dorsal view **2** body, lateral view.

3 larvae (1 male, 2 females), ibid, Rudbar County, Central District, unnamed brook, left tributary of Sefīd-Rūd River, below Rostamabad City, app. 155 m a.s.l., N37 09.47 E49 00.17, 22.v.2016, leg. Bojková J., Soldán T. & J. Imanpour Namin, det. Sroka P.

Baetis melanonyx (Pictet, 1843): 30 larvae (7 larvae mounted with Liquide de Faure), Czech Republic, Ústí nad Labem district, Elbe river-basin, Divoká Orlice River, Líšnice village, 432 m a.s.l., 2.vii.1972, leg. T. Soldán (for details see Soldán 1978); 24 larvae (8 larvae mounted with Euparal), Germany: Baden-Württemberg, Boll, vor Tannegger Wasserfall, Wutach River, 623 m a.s.l., 03.vi.2008, leg. B. Frey. For other comparative material of *B. melanonyx* see Godunko (1999).

Diagnosis. *Baetis cypronyx* sp. n. differs from all other representatives of the *Baetis alpinus* species-group by the following combination of larval characters (see Table 1): (**i**) labrum of distinctly oblong shape, nearly rectangular (Fig. 6a–c), (ii) outer mandibular incisor group distinctly fused, narrow and triangular (Fig. 8); (**iii**) segment 2 of maxillary palps usually with single seta, exceptionally with two stout apical setae

Table 1. Morphological characters in *Baetis* (*Baetis*) *cypronyx* sp. n. (Figs 1–4, 5A, 5C, 6–24) B, *baroukianus* Thomas & Dia, 1984 (Figs 29–32), and *B. melanonyx* (Pictet, 1843) (Figs 5B, 5D, 25–28). Important differences in characters are marked in grey. Quotient *q* was proposed by Sroka et al. (2012), representing the degree of asymmetry of labial palps. * – based on published data and our own larval material.

No.	Character	***Baetis cypronyx* sp. n.**	***Baetis baroukianus* Thomas & Dia, 1984***	***B. melanonyx* (Pictet, 1843)***
	Head			
1.	Setation of clypeus	solitary *FT*, *B*, and *Hr* setae along with their bases	solitary *B* and *Hr* setae along with their base, *FT* setae more abundant	solitary *B* and *Hr* setae along with their base, *FT* setae more abundant
2.	Setation of frons	solitary *FT*, *B*, and *Hr* setae along with their bases	solitary *FT* and *Hr* setae, along with their bases	solitary *FT* and *Hr* setae along with their bases
3.	Setation of scape and pedicel	solitary *FT* and *Hr* setae, only *B* setae more abundant	solitary *FT* and *Hr* setae, only *B* setae more abundant	solitary *FT* and *Hr* setae, only *B* setae more abundant
	Mouthparts			
4.	Labrum: shape	distinctly oblong-shaped, nearly rectangular	distinctly oblong-shaped, nearly rectangular	rather oblong-shaped, narrowed proximally
5.	Labrum: mean width/length ratio	1.80–1.88	1.80–1.95	1.75–2.00
6.	Labrum: number of long submarginal setae	1 + 11–18	1 + 19–21 (15–18)	1 + 14–22 (14–21)
7.	Labrum: number of long marginal setae	6–9	6–8	8–12
8.	Mandibles: number of teeth of inner incisor group	3–4	2	1–2
9.	Mandibles: number of teeth on prostheca	8–10	8–10	9–10
10.	Maxillary palps: number of stout setae at the tip of distal segment	1 (occasionally 2)	1	1
11.	Paraglossae: number of regular rows of apical bristles	2	4–5	3
12.	Paraglossae: number of bristles on outer margin	5–10	6–12	8–12
13.	Paraglossae: number of setae on ventral surface	3–5	3–6	4–6
14.	Labial palps: shape of segment 3	nearly symmetrical and evenly rounded	distinctly asymmetrical and conical	nearly symmetrical and evenly rounded
15.	Labial palps: mean width/length ratio of segment 3	1.03–1.07	1.07–1.09	1.30–1.35
16.	Labial palps: number of stout setae on dorsal surface of segment 3	18–25	14–16	22–28
17.	Labial palps: degree of asymmetry [quotient *q*]	0.76–0.88	0.52–0.56	0.82–0.94
	Thorax and legs			
18.	Shape of sternal protuberances on meso- and metathorax	prominent, pointed	prominent, rounded	small, rounded
19.	Foreleg tibia/femur length ratio	1.0	0.9–1.0	0.9–1.0

20.	Hind leg tibia/femur ratio	0.9–1.0	0.9–1.0	0.8–1.0
21.	Outer margin of femora: shape of long bristles	bluntly pointed and/or obtuse apically	acutely pointed apically	acutely pointed apically
22.	Outer margin of femora: number of rows of long bristles proximally and centrally	2–3	1	1 (occasionally 2)
23.	Outer margin of femora: shape of submarginal stout setae	*STSm-bp*	*STSm-bp*	*STSe-bp*
24.	Outer margin of tibia: shape of stout setae	*STSm-p*, *STSm-bp*	*STSm-p*, *STSm-bp*	*STSe-bp*
25.	Tarsal claw: number of strong teeth	10–11	12–14	8–11
26.	Tarsal claw: number of rows of marginal teeth	1	1	1
27.	Tarsal claw: two subapical hair-like setae	present	present	present
	Abdomen			
28.	Surface of terga: scales	present, not numerous	present, not numerous	present, not numerous
29.	Surface of terga: scales sockets	present, not numerous, often absent on tergum X	present, not numerous, always present on tergum X	present, numerous, always present on tergum X
30.	Surface of terga: shape of scales	*SC-it*, *SC-tg*	*SC-it*, *SC-tg*	*SC-it*, *SC-tg*
31.	Posterior margin of terga II–VIII: shape of spines	triangular, not shortened, some bluntly pointed and some acutely pointed	triangular, shortened, some bluntly pointed and some acutely pointed	triangular, shortened, some bluntly pointed and some acutely pointed
32.	Posterior margin of terga III–VIII (IX): submarginal row of smaller spines	present	absent	absent
33.	Shape of gills I and VII	nearly symmetrical	nearly symmetrical	slightly asymmetrical
34.	Shape of gills II–V	asymmetrical	asymmetrical	asymmetrical
35.	Paraproct plate (inner margin): number of marginal spines	8–12	0–4	7–11
36.	Paraproct plate (inner margin): number of submarginal stout setae	2–8	5–8	8–12
37.	Paraproct plate (inner margin): shape of submarginal stout setae	*STSs-bp*, *STSm-bp*	*STSs-ov*, *STSm-ov*, occasional *STSs-bp* and *STSm-bp*	*STSs-ov*, *STSm-ov*, occasional *STSs-bp* and *STSm-bp*
38.	Paraproct plate (surface centrally): type of setation	tiny setae only	tiny setae only	tiny setae only
39.	Paracercus	reduced; 2–16 segments	well-developed (1/2–2/3 of cerci length) or shortened (more than 15 segments)	well developed; 1/2–2/3 of cerci length
40.	Cerci and paracercus: posterior margin of segments	row of broad triangular spines, additional uneven submarginal row of smaller spines	row of broad triangular spines	row of broad triangular spines

Figures 3–4. Colour pattern of *Baetis* (*Baetis*) *cypronyx* sp. n., larvae, male (**3**) and female (**4**), paratypes (material from type locality): **3** body, ventral view **4** body, dorsal view.

(Figs 11a–c, 19); (**vi**) paraglossae with two irregular rows of long, stout bristles apically (Fig. 9); (**v**) segment 3 of labial palps not elongated, nearly symmetrical and evenly rounded (Fig. 12a–c); (**vi**) sternal protuberances on meso- and metathorax pointed apically; (**vii**) outer margin of femora with 2–3 rows of long, apically obtuse to bluntly pointed bristles proximally and centrally (Figs 13, 20, 21); (**viii**) irregular row of small submarginal spines on abdominal terga III–VIII (IX) (Fig. 22); (**ix**) surface of abdominal terga with few scales in sockets, scales triangular to tongue-shaped, not elongated, mostly lacking on tergum X (Figs 23, 24); (**x**) paraproct plate with bluntly pointed stout setae near to inner margin (Figs 16, 17); (**xi**) paracercus strongly reduced, 2–16 segmented (Fig. 24).

Description. ***Mature larva*:** female body length: 7.5–8.0 mm, length of cerci: 9.0–11.5 mm; male body length: 6.0–8.0 mm; length of cerci: 7.0–10.0 mm; paracercus vestigial or strongly reduced.

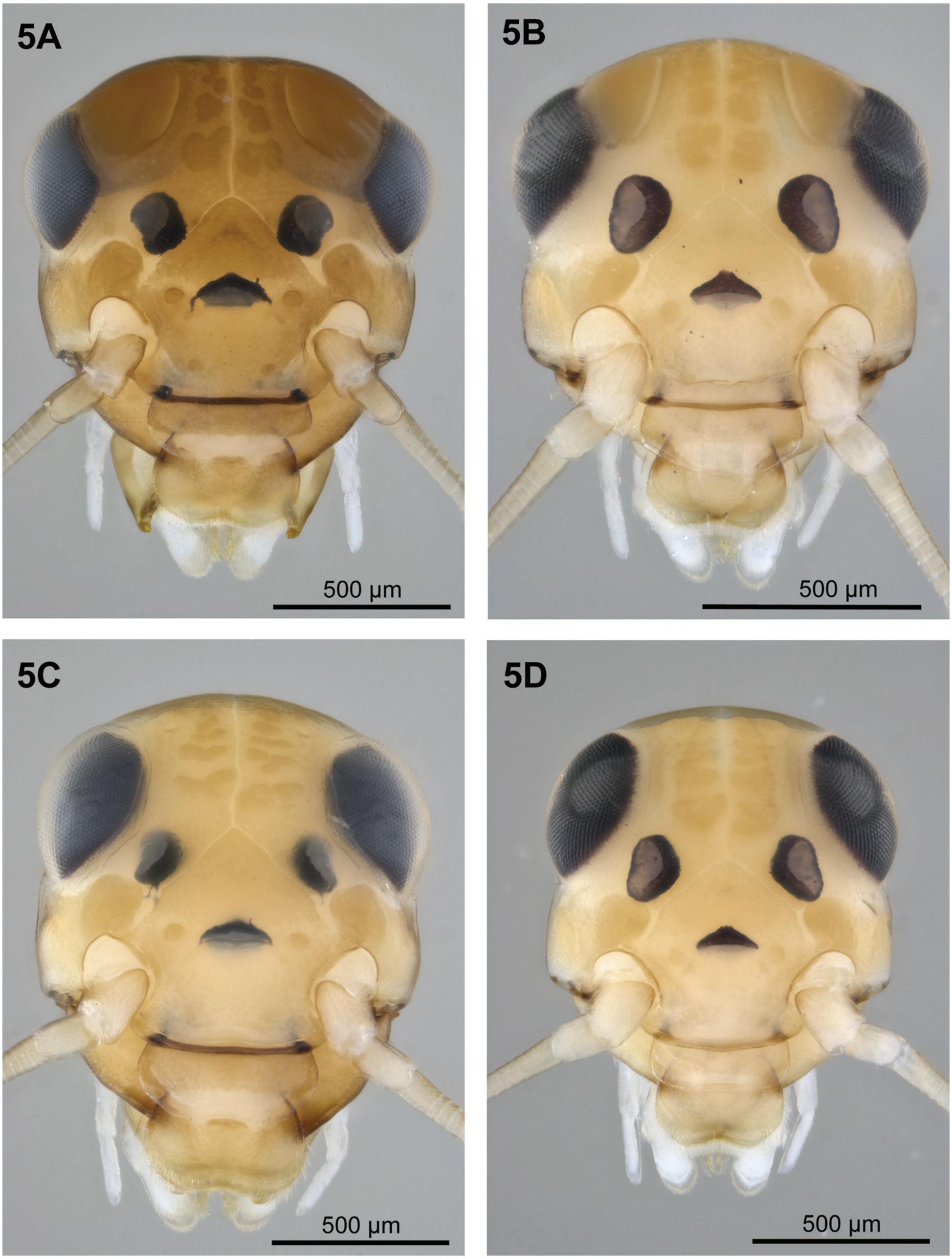
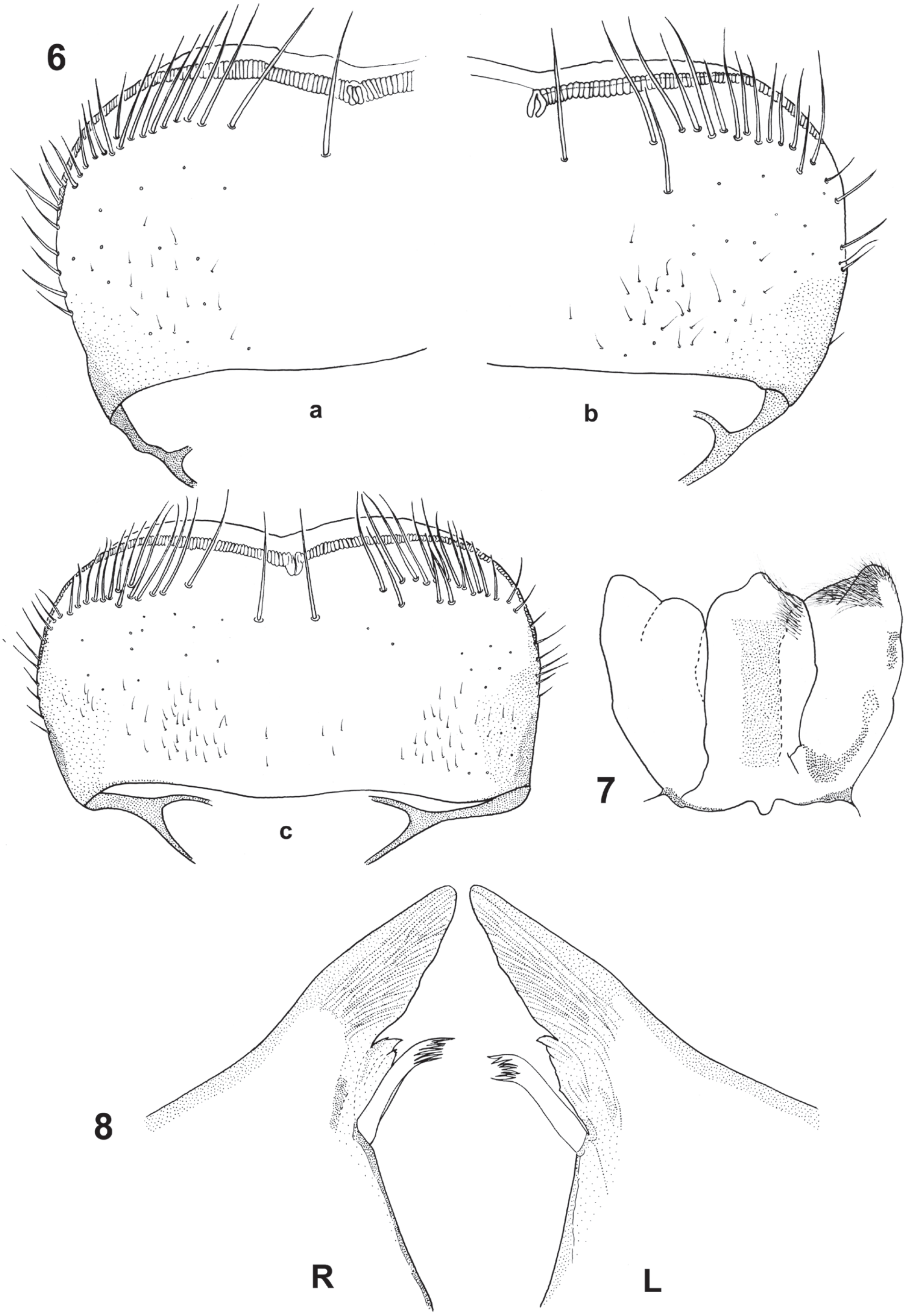
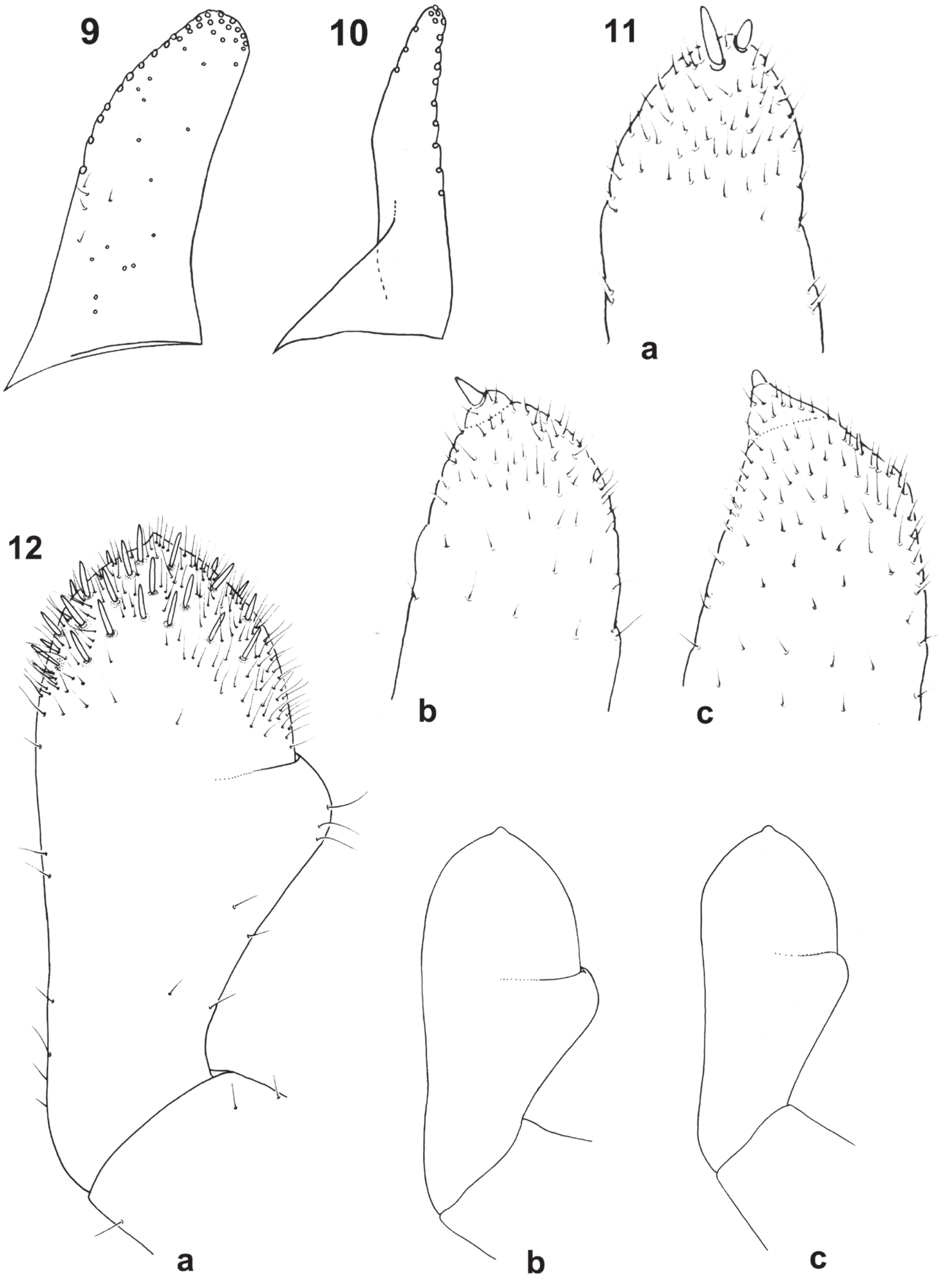


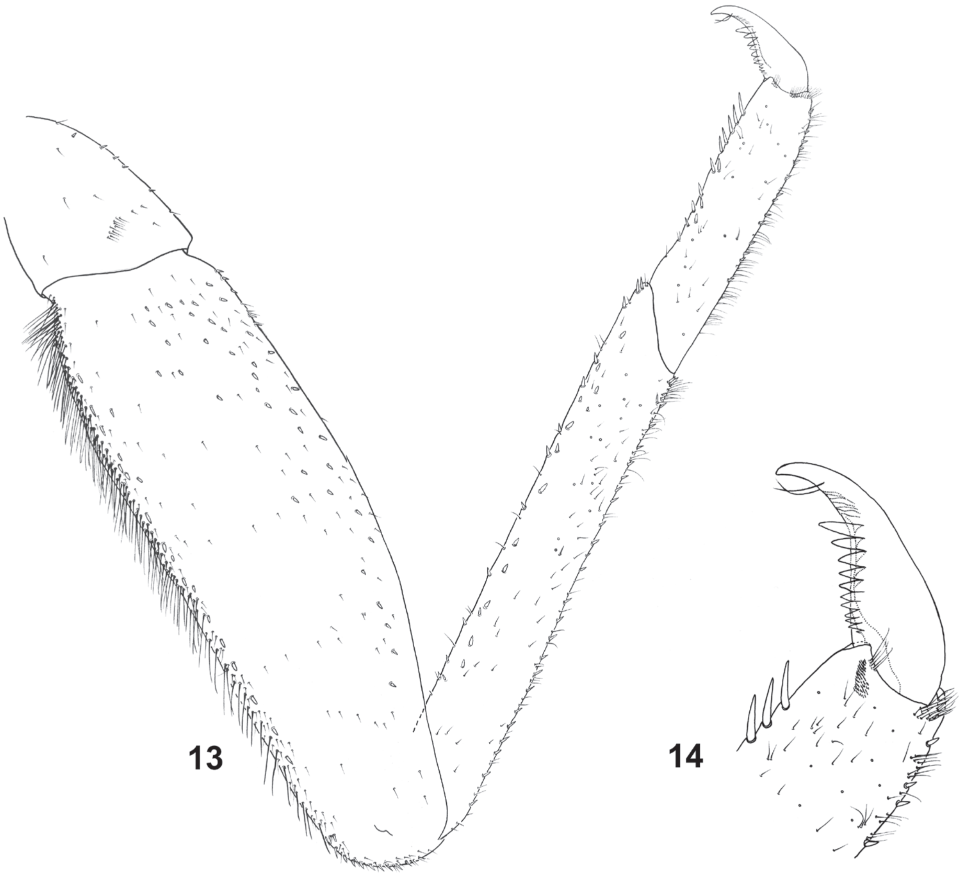
Figure 5. Colour pattern of *Baetis* (*Baetis*) *cypronyx* sp. n., larvae (**A, C** paratypes; material from Diplos River) and *Baetis* (*Baetis*) *melanonyx* (Pictet, 1843), larvae (**B, D** material from Germany): **5** head, dorsal view: **A–B** males **C–D** females.



Figures 6–8. *Baetis* (*Baetis*) *cypronyx* sp. n., larva, paratypes, details of mouthparts: **6a–c** shape of labrum, dorsal view **7** hypopharynx **8** R: right mandible (incisors and prostheca), dorsal view; L: left mandibular (incisors and prostheca), dorsal view.



Figures 9–12. *Baetis* (*Baetis*) *cypronyx* sp. n., larva, details of mouthparts: **9** paraglossa, ventral view **10** glossa; ventral view **11a–c** apical part of maxillary palp, dorsal view **12a–c** shape of third segment of labial palps, ventral view.



Figures 13–14. *Baetis* (*Baetis*) *cypronyx* sp. n., larva, paratype, hind leg: **13** general dorsal view **14** tarsal claw, dorsal view.

Cuticular coloration (Figs 1–5). Due to ten to twelve years of material storage in ethanol, the herein described colour pattern might be slightly paler compared to fresh material.

General colour yellowish brown to brown. Head light brown with paler genae; clypeus light brown; frons with several small, isolated brown spots. Antennae light brown, flagellum paler than scape and pedicel.

Pronotum yellowish brown with two pairs of oblique brownish bands; mesonotum yellowish brown to brown, with longitudinal brown bands centrally, and several spots of the same colour centrally and laterally; metanotum brown with darker smudge centrally (Figs 1, 4). Lateral sides of thorax with brown pleurites (Fig. 2). Ventral side of thorax paler than dorsal side; sterna yellowish (Fig. 3). Legs pale. Femora yellowish brown with two darker, usually isolated longitudinal spots along outer margin; tibia light brown; base and apex of tarsi brown, darker than middle part; tarsal claw brown (Figs 2, 3).

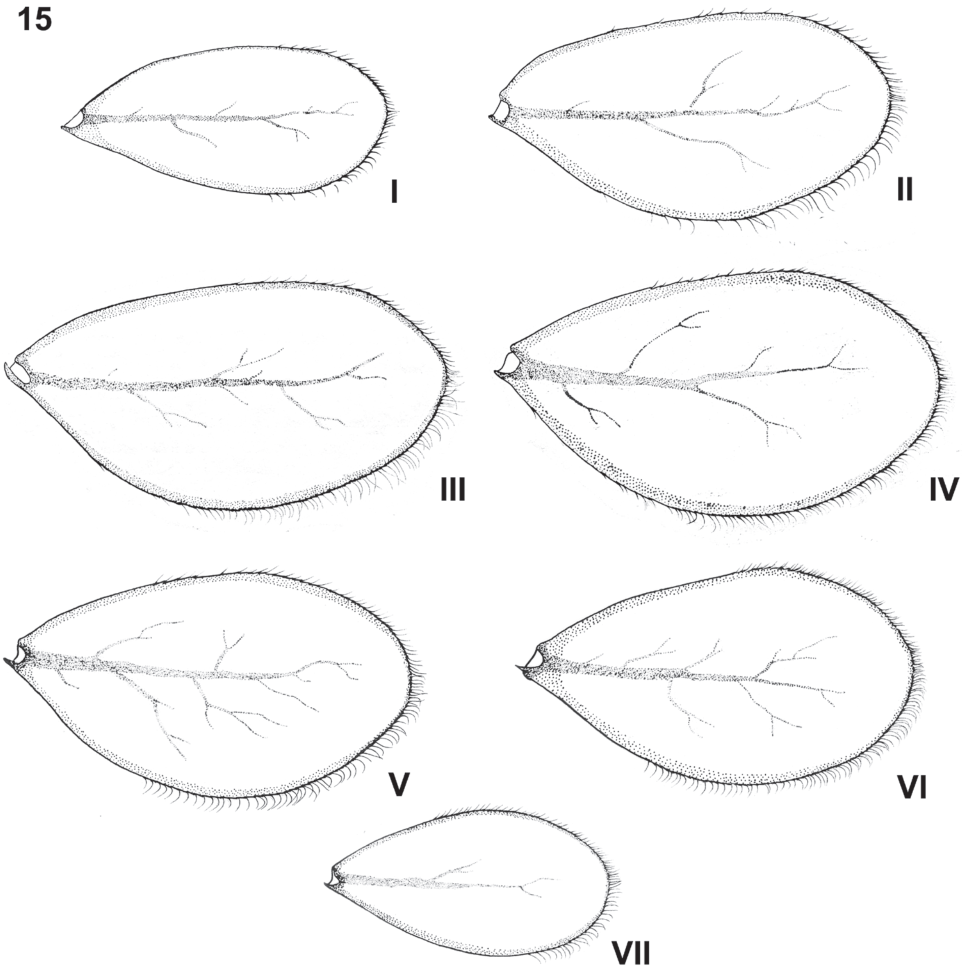
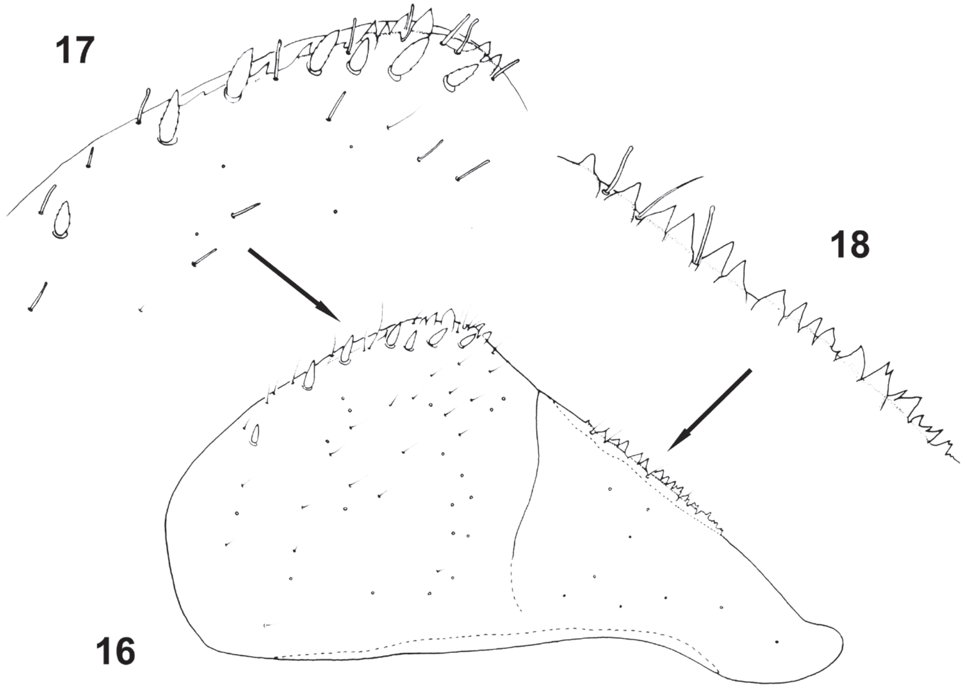


Figure 15. *Baetis* (*Baetis*) *cypronyx* sp. n., larva, paratype, gills. Roman numbers refer to the respective gill pairs.

Abdominal terga (Figs 1, 4) yellowish brown to brown; terga I–III (IV) and VI–VIII darker. Terga I–III (IV) brownish centrally, with broad pale area laterally; median brown spot on terga III and IV occasionally divided into two longitudinal spots; all terga with more or less well visible brownish band along anterior margin of segment; a pair of diffuse brownish maculae near posterior margin of terga V–VIII; a pair of brownish paramedian dots on terga II–X, terga III–VI occasionally with additional oblique streaks fused with paramedian dots and forming a diffuse brownish U-shaped pattern in anterior half of segment. Abdominal sterna with a pair of sublateral elongated spots. Cerci yellowish brown to brown, 3–5 first segments slightly darker.

Hypodermal coloration. Hypoderm without contrasting markings.



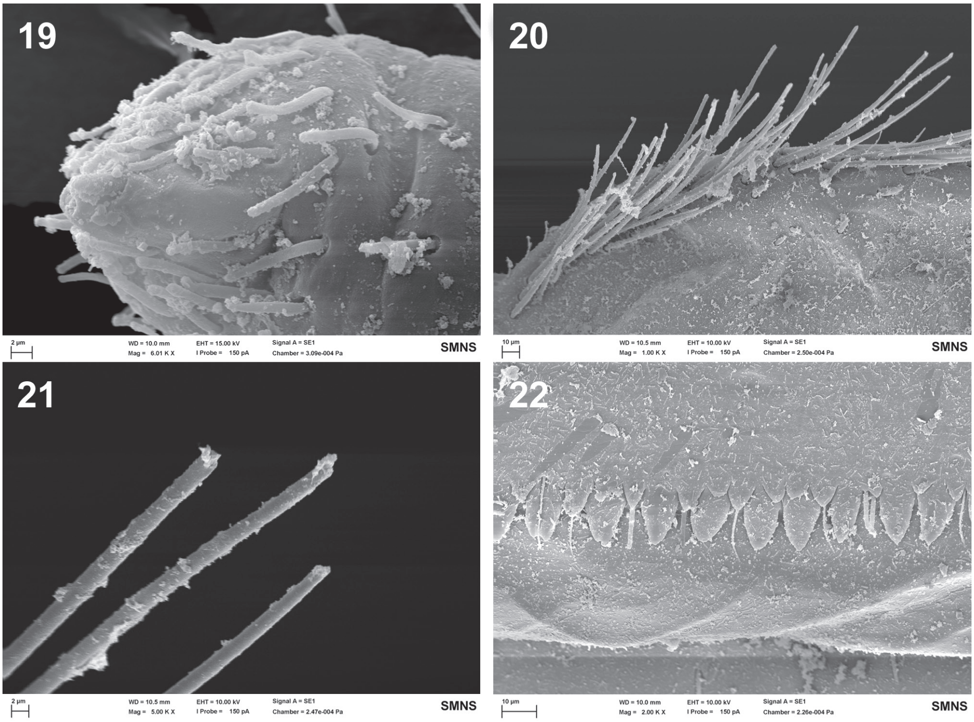
Figures 16–18. *Baetis* (*Baetis*) *cypronyx* sp. n., larva, paratype, details of paraproct: **16** paraproct, general ventral view **17** inner margin of paraproct plate, ventral view **18** spines of inner margin of cercotractor.

Head. Surface of clypeus and frons covered with solitary *FT*, *B*, and *Hr* setae. Larval turbinate eyes brown to intensively brown apically. Antennae slightly longer than 1/2 of body length. Scape and pedicel with solitary *FT* and *Hr*, and more abundant *B* setae only, without any particular cuticular ornamentation (e.g. corrugation/chagrin; see Bauernfeind and Soldán 2012), which is present in some representatives of the *B. alpinus* species-group and in the closely related *B. lutheri* and *B. pavidus* species-groups.

Mouthparts. Labrum (Figs 6a–c) distinctly wider than long, nearly rectangular, with width/length ratio 1.80–1.88; dorsal surface with 1 + 11–18 long submarginal setae, arranged in a single irregular row (occasionally 1–4 bristles form an additional weekly defined row); 6–8 smaller setae laterally on both margins; dorsal surface of labrum covered with sparsely arranged *B* and only a few *FT* setae grouped mainly posterolaterally; ventral side with 2–5 small pointed setae anterolaterally. Median incurvation of middle part of anterior margin of labrum clearly shallow and wide.

Outer mandibular incisor group narrow and triangular, distinctly fused; inner incisor group not prominent, with 3–4 small teeth (of which most distal tooth is the biggest), both groups separated by a shallow incision. Right and left prostheca of same size, nearly symmetrical, with 8–10 apical teeth (Fig. 8).

Maxillary palp two-segmented; segment 1 shorter than second segment; segment 2 asymmetrical apically, with pronounced tip (conical protuberance), and one dis-

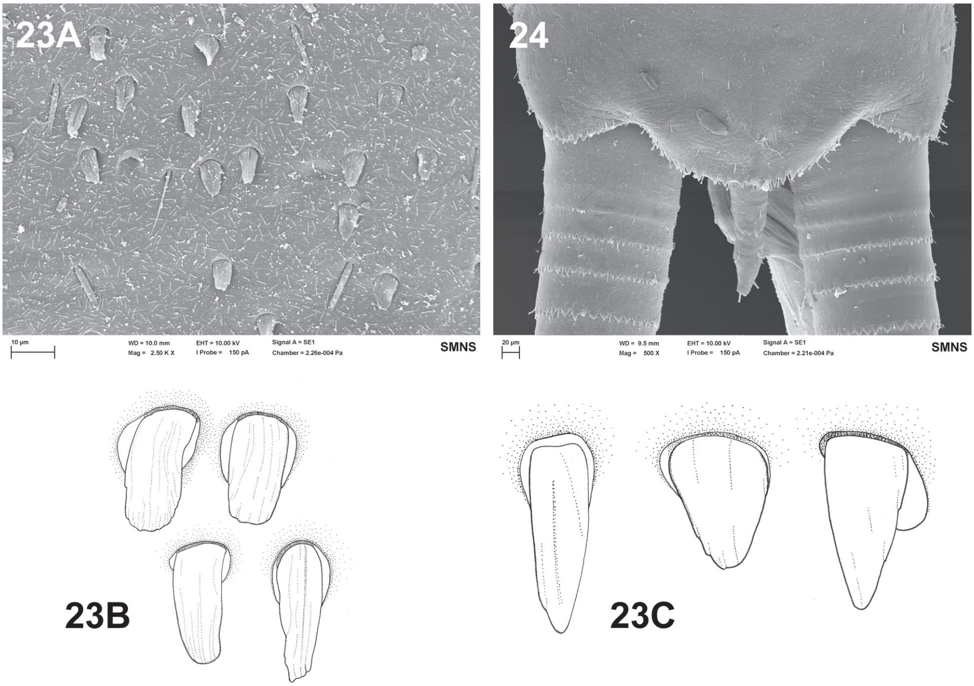


Figures 19–22. *Baetis* (*Baetis*) *cypronyx* sp. n., larva, SEM: **19** apical part of maxillary palp **20** outer margin of hind femur, proximally, dorsal view **21** apical part of long bristles of outer margin of femur, dorsal view **22** posterior margin of abdominal tergum V, dorsal view.

tinct, stout seta; one additional stout seta occasionally near apex of segment 2; surface of both segments with *B* setae [uniporous sensillum basiconicum sensu Gaino and Rebora (2003: 449, figs 19–21)] which are clearly dense on distal part of segment 2 (Figs 11a–c, 19).

Hypopharynx relatively slender, anterior side laterodistally covered with fine, elongated setae along outer margins of lingua and superlinguae, lingua with prominent central lobe, superlinguae with marked hump (Fig. 7).

Labium with relatively slender glossae, slightly shorter than paraglossae (Figs 9, 10); glossae each with 8–10 stout bristles on inner margin, and 3–5 bristles on outer margin; 5–7 pairs of long, stout bristles form two irregular rows on tip of paraglossae; additionally 5–10 long bristles along outer margin and 3–5 medium sized setae on ventral side of paraglossae. Segment 2 of labial palp 1.30–1.42 longer than segment 3, covered only with sparse *B* and *Hr* setae; segment 3 not elongated, nearly symmetrical and evenly rounded, only slightly broader than long (width/length ratio 1.03–1.07); surface of segment 3 with 18–25 slender, pointed, stout setae [long and short hairs sensu Gaino and Rebora (2003)], and long *Hr* setae; quotient *q* changes from 0.76 to 0.88 (see Sroka et al. 2012, 29, 31: fig. 2) (Fig. 12a–c).



Figures 23–24. *Baetis* (*Baetis*) *cypronyx* sp. n., larva, SEM: **23A–C** surface of tergum VII: general dorsal view (**23A**); tongue-shaped scales [*SC-tg*] (**23B**); triangular scales [*SC-it*] (**23C**) **24** tergum X, dorsal view.

Thorax. Surface of pronotum with few *FT* and *Hr* setae only. Sternal protuberances on meso- and metathorax well visible, pointed apically, yellowish brown to brown.

Outer margin of femora with 2–3 rows of long bristles with obtuse to bluntly pointed tips proximally and centrally (Figs 13, 20, 21), and one row of shorter and stouter obtuse bristles distally; central part of outer margin of femora occasionally with long bristles arranged in 1–2 rows. Long marginal bristles alternating with submarginal *STSm-bp* setae and elongated *Hr* setae. Inner margin with 2–6 *STSs-bp* setae near to proximal end. Surface of femora with *STSs-bp* and *STSs-ov* setae and tiny setae [*Hr* and more abundant *FT* setae]. Outer and inner margins of tibiae with *STSm-p* and *STSm-bp* setae and short *Hr* setae; surface of tibia with *STSs-bp* to nearly *STSs-ov* setae; a group of long *Hr* setae near distal end of outer margin of tibia. Tarsi with 6–10 middle to elongated *STS-p* setae along the inner margin, and several *STSm-p* and/or *STSm-bp* setae on outer margin; both margins of tarsi covered with tiny *Hr* setae; surface of tarsi with a few *FT* and more abundant *Hr* setae, and small *STS-bp* setae. Tarsal claws not elongated, moderately hooked; with 10–11 teeth arranged in single row and two subapical tiny *Hr* setae (Figs 13, 14).

Abdomen. Posterior margin of terga with broad triangular spines of different size, bluntly pointed or occasionally pointed apically; broader spines along posterior margin of terga III–VIII; spines alternating with 1-3 tiny *B* and a single *Hr* setae. Irregular row of smaller submarginal spines on terga III–VIII (IX) (Fig. 22). Surface of terga with few, not elongated, tongue-shaped [*SC-tg*] to triangular [*SC-it*; bluntly pointed to rounded apically] scales, and their few sockets (mainly lacking on tergum X), concentrated on central part of segment (Figs 23, 24); solitary *Hr* and more abundant *FT* setae stretched over the whole surface of terga I–X. Posterior margin and surface of sterna without spines, stout setae or scales, with *B* and *Hr* setae only.

Paraproct plate as in Figs 16–18. Inner margin of paraproct with 8–12 spines of different size along apical half, alternating with tiny setae [solitary *FT* and more abundant *B* setae], and 2–8 (mainly 4–7) submarginal *STSm-bp* setae (Figs 16, 17); a single row of relatively small and stout spines along inner margin of cercotractor (for definition of cercotractor see Kluge 2004) (Fig. 18). Surface of paraproct covered with sparse *FT*, *B* and *Hr* setae and their bases only.

Tracheal gills whitish yellow to light brown, not elongated, broadly rounded apically (Fig.15, I–VII); gills I and VII nearly symmetrical; gills II–VI asymmetrical; serrated margins of gills more or less well marked, with tiny *Hr* setae inserting in small, articulated bases; tracheation poorly visible.

Cerci as long as 1.20–1.32 of body length. Paracercus reduced to 2–16 segments (Fig. 24). Posterior margin of cercal and paracercal segments with row of broad, triangular spines, and uneven submarginal row of smaller spines. Length of paracercus of mature larvae apparently variable in different populations, as well as in specimens within each population. Paracercus in larvae from Cryos River (type locality) vestigial (evidently shorter than abdominal tergum X, consisting of approximately up to 5–7 segments, some segments at least partially fused, Fig. 1); paracercus in paratype larvae from Diplos River strongly reduced (but evidently longer than abdominal tergum X), only consisting of about 10 or more apparently separated or distinguishable segments; Fig. 4).

Male and female adults. Unknown.

Etymology. The specific epithet is a combination of the name of Cyprus, where the new species was found, and the specific epithet of the closely related species *B. melanonyx*.

Discussion

Affinities

Baetis cypronyx sp. n. can be undoubtedly attributed to the *B. alpinus* species-group as defined above based on larval body shape and presence of (**i**) numerous submarginal long setae on dorsal surface of labrum, (**ii**) triangular outer mandibular incisor group, (**iii**) 1–2 stout setae at tip of maxillary palp segment 2, (**iv**) conspicuous brownish pattern on pronotum (similar to that in *B. alpinus* (Pictet, 1843)) and well visible pair of dark spots on abdominal terga, (**v**) numerous long bristles on outer margin of femora, (**vi**) relatively large spines on posterior margin of terga, (**vii**) a pair of hair-like setae near tip of tarsal claw (see e.g. Müller-Liebenau 1969: 47; Jacob 2003: 67–68; Bauernfeind and Soldán 2012: 100–101).

The new species appears to be closely related to *B. melanonyx* known throughout Europe and to *B. baroukianus* Thomas & Dia, 1984 described from Lebanon. For the latter two species a separate subgenus *Patites* Thomas & Dia, 1999 was established based on larval and imaginal characters (Thomas and Dia 1999: 107; type species *Baetis* (*Patites*) *baroukianus* Thomas & Dia, 1984). On the other hand, Bauernfeind and Soldán (2012: 101) consider that the delimitation of taxa of *B. alpinus* species-group is rather difficult due to the high level of (probably clinal) variability combined with disjunctive area of many species. A separation of the *B. alpinus* species-group on genus or subgenus level is recently not considered to reflect phylogenetic lineages under the concept used for genera within *Baetinae* by these and other authors (e.g. Jacob 2003: 89; Bauernfeind and Soldán 2012: 101).

Baetis cypronyx sp. n., *B. baroukianus*, and *B. melanonyx* can be characterised by a distinctly fused, narrow and triangular outer mandibular incisor group; this character clearly distinguishes them from all other representatives of the *B. alpinus* species-group. Unfused teeth of outer mandibular incisors can be observed in *B. punicus* Thomas, Boumaiza & Soldán, 1983 and *B. berberus* Thomas, 1986 (Thomas et al. 1983: 108, fig. 3p; Thomas and Dia 1984: 8, fig. 4b; Peru and Thomas 2001: 77, fig. 2).

Differences between three above listed species can be observed in the arrangement of long setae on the dorsal surface of the labrum, i.e. *B. cypronyx* sp. n. with 1 + 11–18 long submarginal setae, in contrast to 1 + 14–21 long submarginal setae in *B. melanonyx*, and mainly 1 + 19–21 in *B. baroukianus* (Fig. 6a–c; Müller-Liebenau 1966: 70–78, figs 4–8; 1969: 62, fig. 27a; Thomas and Dia 1984: 8, fig. 2b). Additionally, in contrast to *B. melanonyx* with proximally narrowed labrum *B. cypronyx* sp. n. and *B. baroukianus* can also be characterized by a nearly rectangular labrum that is distinctly wider than long.

Two irregular rows of long, stout bristles can be observed on the tips of paraglossae in the new species, in contrast to 3 rows in *B. melanonyx* and 4–5 rows in *B. baroukianus* (see Table 1 and Fig. 9; Müller-Liebenau 1969: 62, fig. 27i; Thomas and Dia 1984: 8, fig. 6b).

Other differences concern the shape of labial palp segment 3, which is nearly symmetrical in *B. cypronyx* sp. n. and in *B. melanonyx* (quotient q from 0.76 to 0.94), in contrast to a markedly asymmetrical segment 3 in *B. baroukianus*, with q = 0.52–0.56 (Figs 12a–c; Thomas and Dia 1984: 9, figs 7a–c).

Thomas and Dia (1984: 7, 8, figs 1b, 1m) depicted the heads of the female larva of *B. baroukianus* and *B. melanonyx* in dorsal view, discussing the head width ratio for both species. For *B. baroukianus* was noted that its head is widest below the eyes between the genae, while in *B. melanonyx* the widest part was determined at eye level. According to Thomas and Dia (1984) the head width ratio for *B. baroukianus* / *B. melanonyx* below the eyes is 1.59 (with maximal value 1.46). However, in larvae of *B. baroukianus* from Iran that we examined, the width of head both at eye level and below eyes is nearly equal in both sexes, respectively (Figs 31, 32).

In contrast, female larvae of *B. cypronyx* sp. n. and *B. melanonyx* both have their maximal width of head at the level of eyes; the head width however is only slightly smaller at genal level below the eyes in both species (Fig. 5C, D). Similar proportions also apply for male larvae of the latter two species (Fig. 5A, B). The larval head width ratio for *B. cypronyx* sp. n. / *B. melanonyx* below the eyes at genal level is 1.05–1.15 in females, and 1.15–1.20 in males; at eye level the ratio is 1.00–1.05 in females, and 1.14–1.20 in males.

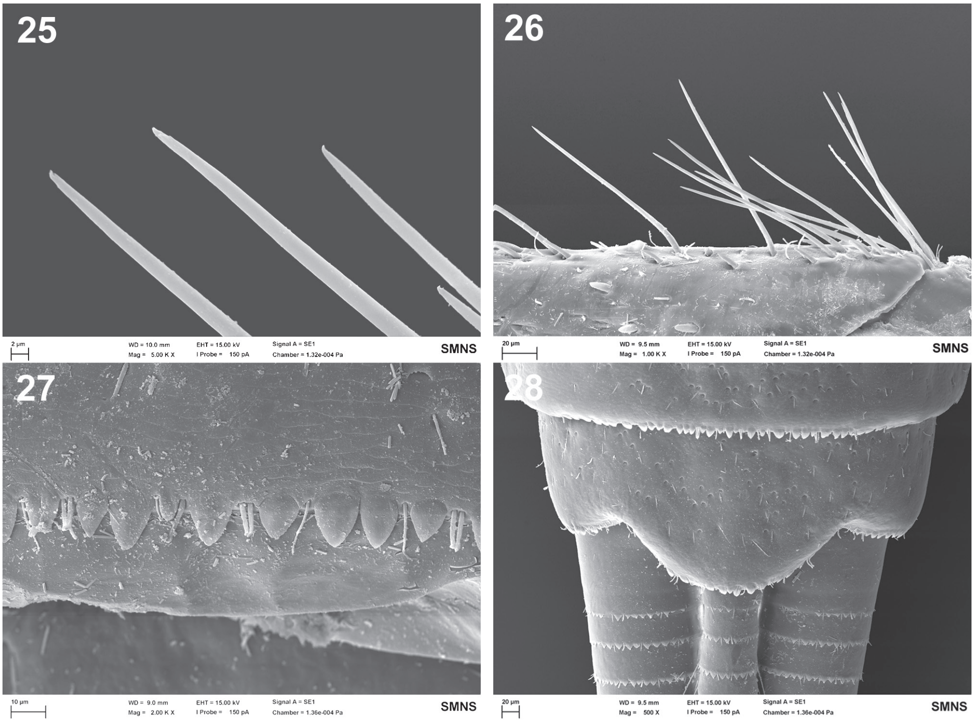
Baetis melanonyx and *B. baroukianus* markedly differ from the new species by their arrangement of setation at the outer margin of femora. There is only a single row of acutely pointed long bristles proximally and centrally, alternating with *STSe-bp* (in *B. melanonyx*) and *STSm-bp* (in *B. baroukianus*) submarginal setae, in contrast to *Baetis cypronyx* sp. n. that features 2–3 rows of bluntly pointed long bristles centrally and a group of *STSm-bp* submarginal setae (Figs 13, 20, 21). This character has been recently used for delimitation of two distinct evolutionary units of *B. alpinus* within the Central Alps (Leys et al. 2016), and much earlier for delimitation of *B. alpinus* and *B. melanonyx* (Figs 25, 26; Müller-Liebenau 1969; Godunko 1999: 26, fig. 3C).

The new species also clearly differs from *B. melanonyx* and *B. baroukianus* in the sternal protuberances near the coxae on meso- and metathorax that are pointed apically in the former species, in contrast to rounded apically protuberances in both latter species (Table 1).

Abdominal terga of *B. melanonyx* and *B. baroukianus* (including tergum X) are covered by numerous scale sockets, in contrast to only a few scales on terga of *B. cypronyx* sp. n., where scales and their sockets are missing on tergum X (see Figs 23, 24 for *B. cypronyx* sp. n.; Godunko 1999: 26, fig. 3D, and our Fig. 28 for *B. melanonyx* [the same for *B. baroukianus*]; Table 1); the shape of scales is similar in all three discussed species. The shape of marginal spines along the posterior margin of abdominal terga in all three species is generally similar, but the new species can be markedly recognized by the presence of not shortened stout spines and additional, submarginal, irregular row of smaller spines on terga III–VIII (IX) (see Fig. 22 for the new species in contrast to Fig. 27 for *B. melanonyx*); in *B. baroukianus* the single row of shortened stout spines is figured by Thomas and Dia (1984: 9, fig. 9). Marginal large spines alternating with *Hr* setae and with 1–3 setae of sensillum basiconicum type can be recognised in the new species (similarly to *B. alpinus*), in contrast to *B. melanonyx* and *B. baroukianus* showing a group of 1–5 setae.

Additional differences between the new species and the previously described *B. baroukianus* and *B. melanonyx* can be recognized in the colour pattern of abdominal terga. Thomas and Dia (1984: 10) noted similar colour patterns in *B. baroukianus*, *B. punicus*, and *B. alpinus*. Bauernfeind and Soldán (2012: 102, 106) discussed the presence of well pigmented paramedian dots and streaks or a mediolongitudinal strip on terga I (II)–IX (X) within all three species (Fig. 29). A similar pattern is described for *B. melanonyx*, but usually with terga IV, V and IX paler centrally (Müller-Liebenau 1966: 74–75, figs 6, 7; 1969: 52–53, 63–64, figs 19, 204).

Inner margin of paraproct plate of *B. cypronyx* sp. n. and *B. melanonyx* with more or less similar number of marginal spines (see Table 1), in contrast to *B. baroukianus*



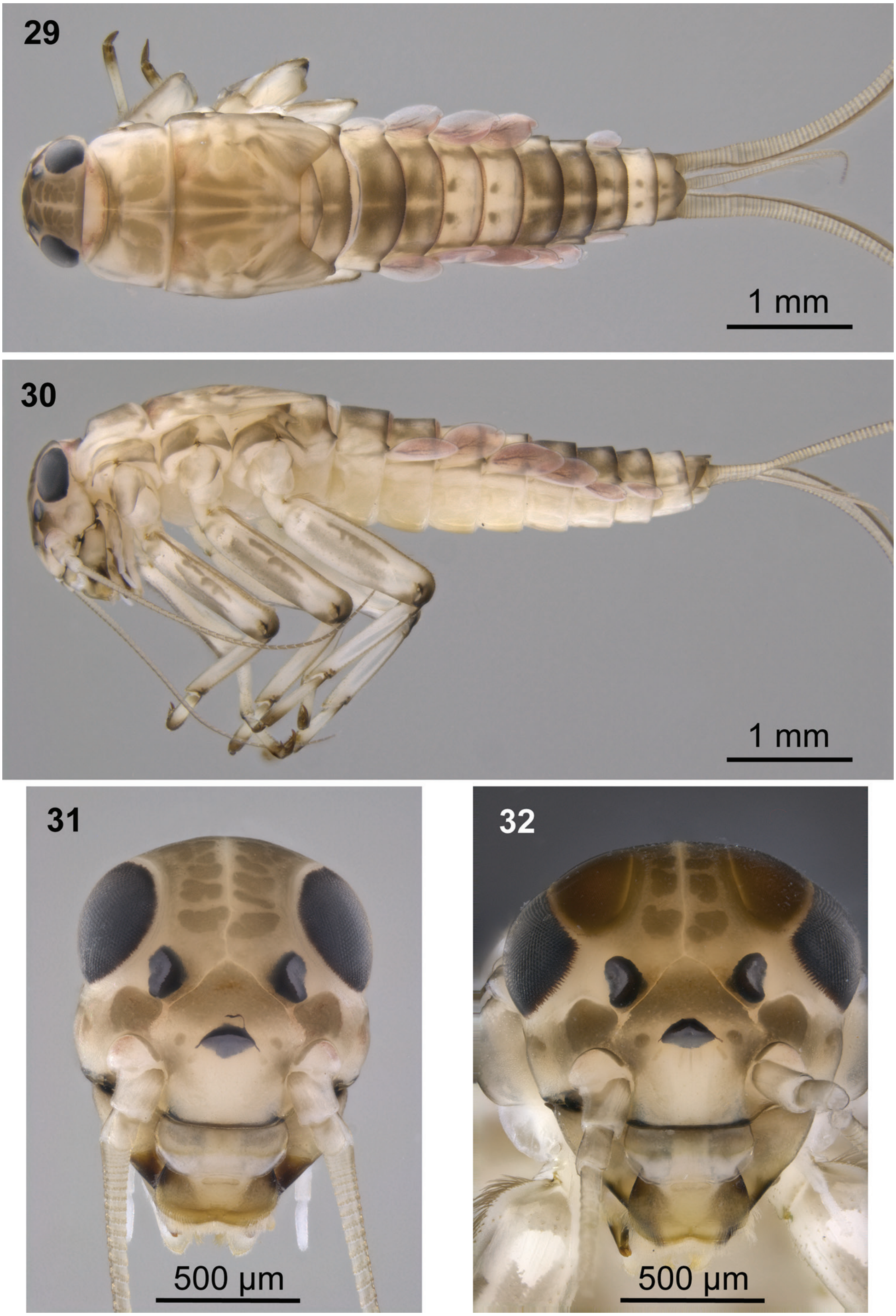
Figures 25–28. *Baetis* (*Baetis*) *melanonyx* (Pictet, 1843), Germany, larva, SEM: **25** apical part of long bristles of outer margin of femur, dorsal view **26** outer margin of hind femur, proximally, dorsal view **27** posterior margin of abdominal tergum V, dorsal view **28** tergum X, dorsal view.

with not more than four spines only. Other differences between species discussed above can be recognized in the number and shape of submarginal stout setae, i.e. 2–8 *STSs-bp* and *STSm-bp* setae in *B. cypronyx* sp. n., in contrast to 8–12 in *B. melanonyx* and up to 7 *STSs-ov* and *STSm-ov* setae in *B. baroukianus*.

Clearly visible differences between these species can be also recognized in the shape and length of paracercus, i.e. strongly reduced in *B. cypronyx* sp. n., with 2–16 segments; shortened or well-developed in *B. baroukianus* (from 15 segments to 1/2–2/3 of cerci length); well developed in *B. melanonyx*, as long as 1/2–2/3 of cerci length (Figs 3, 4, 24, 28; Table 1).

Other differences between the closely related species *B. cypronyx* sp. n. B*, baroukianus* and *B. melanonyx* are summarized in Table 1.

Thomas and Gazagnes (1984) described *B. cyrneus* Thomas & Gazagnes, 1984 from Corsica and placed this species in the *B. alpinus* species-group. *Baetis cyrneus* most probably also is an endemite of the Mediterranean islands (see below). It differs from *B. cypronyx* sp. n. by the arrangement of mouthparts, especially by the shape and setation of mandible with both groups of incisors well developed, segment 2 of maxillary palps with two regular stout setae apically, and by the elongated shape of labial palp segment 3. Additional differences can be observed in the paraproct plate, with numerous scale sockets on its surface, and in the length of paracercus with 10–25 segments.



Figures 29–32. Colour pattern of *Baetis baroukianus* Thomas & Dia, 1984, larvae (material from Iran); male (**29, 30, 32**), female (**31**): **29** body, dorsal view **30** body, lateral view **31, 32** head, dorsal view.

Figures 33–35. Localities of *Baetis* (*Baetis*) *cypronyx* sp. n.: **33** Kryos River [Κρύος ποταμός], app. 1270 m a.s.l., near type locality (photo by Zsuzsa Miskolci, Budapest, Hungary) **34** ibid., app. 1285 m a.s.l. (photo by Philp J Stoate, Somerset, England) **35** Diplos River [Διπλός ποταμός], Chantara [Xantara] Waterfalls, app. 1100 m a.s.l., locality of *Baetis cypronyx* sp. n. (photo by Alexandros Constantinides, Cyprus)

Biological notes

Larvae of *B. cypronyx* sp. n. were found solely on stony substrates (lithal) at depths of 5–40 cm (see also Soldán and Godunko 2008), preferably in stream sections with moderate to fast current (velocity approximately 20–50 cm/s^{-1}) (Figs 33–35). The mac-

Table 2. Checklist of Baetidae in the Mediterranean islands (islands listed from west to east). Abbreviations and symbols: SP – Spain; IT – Italy; FR – France; MT – Malta; GR – Greece; CY – Cyprus. ● – previous records on occurrence of the species confirmed; ○ – occurrence based on our unpublished data; * – data on distribution and / or proper species identification require to be confirmed or clarified.

No. of species	**Species / Mediterranean island Comments in [] see below**	**Baleares (SP)**	**Sardinia (IT)**	**Corsica (FR)**	**Elba (IT)**	**Sicily (IT)**	**Malta (MT)**	**Gozo (MT)**	**Crete (GR)**	**Tasos (GR)**	**Lesbos (GR)**	**Astypalea (GR)**	**Kos (GR)**	**Karpathos (GR)**	**Tilos (GR)**	**Rhodos (GR)**	**Cyprus (CY)**
Genus *Baetis* Leach, 1815																	
Subgenus *Acentrella* Bengtsson, 1912																	
1	*Baetis* (*Acentrella*) *sinaicus* (Bogoescu, 1931)[1]					●											
Subgenus *Baetis* Leach, 1815																	
Baetis alpinus species-group																	
2	*Baetis* (*Baetis*) *cypronyx* **sp. n.**																●
3	*Baetis* (*Baetis*) *cyrneus* Thomas & Gazagnes, 1984[2]		●*	●		●*											
4	*Baetis* (*Baetis*) *melanonyx* (Pictet, 1843)[3]					●											
Baetis buceratus species-group																	
5	*Baetis* (*Baetis*) *buceratus* Eaton, 1870[4]		●	●		●											
6	*Baetis* (*Baetis*) *zdenkae* Soldán & Godunko, 2009[5]															●	
Baetis lutheri species-group																	
7	*Baetis* (*Baetis*) *lutheri* Müller-Liebenau, 1967[6]					●							●*				
8	*Baetis* (*Baetis*) *mirkae* Soldán & Godunko, 2008[7]															●	●
Baetis pavidus species-group																	
9	*Baetis* (*Baetis*) *pavidus* Grandi, 1951[8]					●											
Baetis vernus species-group																	
10	*Baetis* (*Baetis*) *vernus* Curtis, 1834[9]			●*													
Baetis fuscatus species-group																	
11	*Baetis* (*Baetis*) *fuscatus* (Linnaeus, 1761)[10]		●	●		●			●*								
Subgenus *Nigrobaetis* Novikova & Kluge, 1987																	
12	*Baetis* (*Nigrobaetis*) *albinatii* Sartori & Thomas, 1989[11, 12]			●													
13	*Baetis* (*Nigrobaetis*) *digitatus* Bengtsson, 1912[13]												●*			●*	
14	*Baetis* (*Nigrobaetis*) *muticus* (Linnaeus, 1758)[14]		●*	●*		●*											
15	*Baetis* (*Nigrobaetis*) cf. *muticus* (Linnaeus, 1758)																○*

No. of species	Species / Mediterranean island Comments in [] see below	Baleares (SP)	Sardinia (IT)	Corsica (FR)	Elba (IT)	Sicily (IT)	Malta (MT)	Gozo (MT)	Crete (GR)	Tasos (GR)	Lesbos (GR)	Astypalea (GR)	Kos (GR)	Karpathos (GR)	Tilos (GR)	Rhodos (GR)	Cyprus (CY)
16	*Baetis* (*Nigrobaetis*) cf. *navasi* (Müller-Liebenau, 1974)[15]								●*								
17	*Baetis* (*Nigrobaetis*) *niger* (Linnaeus, 1761)[16]			●*													
Subgenus *Rhodobaetis* Jacob, 2003																	
18	*Baetis* (*Rhodobaetis*) *ingridae* Thomas & Soldán, 1987[17]			●*													
19	*Baetis* (*Rhodobaetis*) *irenkae* Soldán & Godunko, 2008[18]																●
20	*Baetis* (*Rhodobaetis*) *rhodani* (Pictet, 1843)[19]	●	●*	●*		●*			○*	●			●*	●*			●*
21	*Baetis* (*Rhodobaetis*) cf. *rhodani* (Pictet, 1843)[19]		●*	●*	●*											○*	
Genus *Centroptilum* Eaton, 1869																	
22	*Centroptilum luteolum* (Müller, 1776)[20]		●	●		●				●			●	●			
Genus *Cloeon* Leach, 1815 Subgenus *Cloeon* Leach, 1815																	
23	*Cloeon* (*Cloeon*) *cognatum* Stephens, 1836[21]	●*	●*			●*											
24	*Cloeon* (*Cloeon*) *dipterum* (Linnaeus, 1761)[22]	●	●	●		●	○*	○*	○*	●		●	●	●	●		○
25	*Cloeon* (*Cloeon*) *inscriptum* Bengtsson, 1917[23]	●*															
26	*Cloeon* (*Cloeon*) *rabaudi* (Verrier, 1949)[24]			●*													
Subgenus *Similicloeon* Kluge & Novikova, 1992																	
27	*Cloeon* (*Similicloeon*) *praetextum* Bengtsson, 1914[25]	●*															
28	*Cloeon* (*Similicloeon*) *schoenemundi* Bengtsson, 1936[26]	●*															
29	*Cloeon* (*Similicloeon*) *simile* Eaton, 1870[27]	●	●	●		●				●							
Genus *Procloeon* Bengtsson, 1915 Subgenus *Procloeon* Bengtsson, 1915																	
30	*Procloeon* (*Procloeon*) *bifidum* (Bengtsson, 1912)[28]		●		●	●											
Subgenus *Pseudocentroptilum* Bogoescu, 1947																	
31	*Procloeon* (*Pseudocentroptilum*) *fascicaudale* (Sowa, 1985)[29]															●	
32	*Procloeon* (*Pseudocentroptilum*) *pulchrum* (Eaton, 1885)[30]					●*											
33	*Procloeon* (*Pseudocentroptilum*) *unguiculatum* (Tshernova, 1941)[31]										●						

[1] Recorded by Belfiore (1983: 57) for the first time; recent data on its distribution summarised by Belfiore and D'Antonio (1991: 260), Belfiore et al. (1991: 32) and Buffagni et al. (2003: 281).

[2] Described by Thomas and Gazagnes (1984: 199) from Corsica. According to Bauernfeind and Soldán (2012: 105) only known from a few localities in terra typica (see also OPIE-benthos data). Nevertheless, Belfiore (1988), Belfiore and D'Antonio (1991), and Buffagni et al. (2003) report *B. cyrneus* also from the Toscana Region and some Mediterranean islands, i.e. Sicily and Sardinia. DNA barcoding (Gattolliat et al. 2015) however revealed that specimens determined as *B. cyrneus* represent four different cryptic species occurring in Corsica and Sardinia. So far no morphological differences have been determined for these putative species. The high intra-specific genetic distance in *B. cyrneus* recently detected by Cardoni et al. (2015) for populations from Corsica and Sardinia also point to cryptic variation.

[3] Recorded by Belfiore and D'Antonio (1991) and Belfiore et al. (1991) for the first time.

[4] Recorded by Belfiore and Gaino (1988: 77) for the first time in Sardinia and later also listed from Sicily (Belfiore and D'Antonio 1991; Buffagni et al. 2003); for Corsica based on OPIE-benthos data.

[5] So far known only from type locality and a single additional locality in Rhodos (Soldán and Godunko 2009: 7–8), considered endemic to the island.

[6] The record from Kos by Belfiore (1990: 266) probably belongs to or other, still undescribed species of the *B. lutheri* species-group.

[7] Considered as probably East Mediterranean (Pontomediterranean) species by Bauernfeind and Soldán (2012: 124); so far known from three localities in Cyprus and from a single locality in Rhodos (Soldán and Godunko 2008: 95).

[8] Recorded by Belfiore (1983) for the first time; recent data on distribution summarized by Belfiore and D'Antonio (1991: 260), Belfiore et al. (1991: 32) and Buffagni et al. (2003: 281).

[9] Most probably missing on Mediterranean islands (Bauernfeind and Soldán 2012: 136). The record for Corsica by Sartori and Thomas (1989: 131) based on earlier data by Verrier (1954: 282 [sub. *Baetis* type *vernus*]; 284 [sub. *Baetis vernus*]) needs to be verified.

[10] Reported from Corsica by Esben-Petersen (1912: 351, 1913: 22) [sub. *Baëtis binoculatus* Linn.]; Kimmins (1930: 186) and Lestage (1922: 275; citation of M. Esben Petersen data) [sub. *Baetis binoculatus* L.] (see also OPIE-benthos data). Verrier (1954: 284; 1956: 95) reported [sub. *B. bioculatus* L.] and [sub. *Baetis*, type *bioculatus* L.] from four localities in Crete, but conspecifity with *B. fuscatus* needs to be verified. For Sicily and Sardinia see summarized data in Belfiore (1983), Belfiore and D'Antonio (1991), Belfiore et al. (1991) and Buffagni et al. (2003). Recent data on DNA barcoding by Cardoni et al. (2015) based on Sardinian material.

[11] The species can be considered endemic to Corsica. This conclusion is confirmed by recent DNA barcoding (Gattolliat et al. 2015; Cardoni et al. 2015). All previous records of *B. muticus* from Corsica refer to *B. albinatii* (see e.g. Hagen 1864: 39 [sub. *Cloe Pumila* Burm.]; Jakobson and Bianki 1905: 875 and Klapálek 1917: 193 [sub. *Baëtis pumilus* (Burm.)]; Esben Petersen 1913: 22 [sub. *Baëtis pumilus* Burm.]; Kimmins 1930: 186 [sub. *Baetis pumilus* Burm.] (citation of previous authors); Belfiore and D'Antonio 1991: 260 [sub. *Baetis muticus* (*L.*)]; see also OPIE-benthos data). Three species reported for Corsica by Hagen (1864: 38) within the genus *Baetis* (orig. *Bætis* Leach.) belong to the genera *Ecdyonurus* Eaton, 1868 and *Electrogena* Zurwerra & Tomka, 1985.

[12] Sartori and Thomas (1991: 224) used the specimens from the type series of *B. albinatii* also to specify distinguishing characters of representatives of the *B. muticus* species-group.

[13] Two records of this species from the islands Kos (Belfiore 1990: 266) and Rhodos (Soldán and Godunko 2009: 9) belong to hitherto undescribed species.

[14] Reported by Grandi (1960), Belfiore et al. (1991), Belfiore and D'Antonio (1991) and Buffagni et al. (2003) from Sicily and Sardinia. The record from Corsica (Belfiore and D'Antonio 1991) in fact refers to *B. albinatii* (see above). The presence of new undescribed endemic species in Sardinia is confirmed based of DNA barcoding by Gattolliat et al. (2015).

[15] Reported by Bauernfeind (2003: 100) based on a single male imago and two subimagines, with remarks on similarities to *B. navasi* Müller-Liebenau, 1974, but with some differences from continental *B. muticus*.

[16] Reported by Esben Petersen (1912) and Kimmins (1930; citation follows data by M. Esben-Petersen); the record by Lestage (1922) also follows data by M. Esben-Petersen; recently reported from Corsica based on published data (see OPIE-benthos). Bauernfeind and Soldán (2012: 154) consider this record questionable.

[17] Most probably endemic to Corsica (Thomas and Soldán 1987: 23; Bauernfeind and Soldán 2012: 167). All previous reports of *B. rhodani* from Corsica (see e.g. Hagen 1864: 39 [sub. *Cloe Rhodani* ? Pictet]; Jakobson and Bianki 1905: 875 [sub. *Baëtis rhodani* (Pict.)]; Lestage 1922: 275 [sub. *Baetis Rhodani* Pict.]; Kimmins 1930: 186 [sub. ? *Baetis rhodani* Pict.] (cited following Hagen 1864); Belfiore and D'Antonio 1991: 260 [sub. *Baetis rhodani* (Pictet)]) most probably belongs to *B. ingridae* (see also OPIE-benthos data). At least a part of the material marked as "*Baetis* sp." by Verrier (1954) from rivers Bevinco, Golo, Restonica, Vecchio, Travo and Rizzanèse in Corsica also belongs to *B. ingridae* Thomas & Soldán, 1987). Recent investigation of DNA barcodes of Corsican mayflies by Gattolliat et al. (2015) clearly showed that it is not possible to assign the separate lineage of this species to a proposed insular Corso-Sardinian lineages; additional investigation of type material is urgently needed to clarify the systematic status of these questionable taxa.

[18] So far only known from Cyprus; probably endemic to the island (Soldán and Godunko 2008: 91).

[19] The records from Corsica might in fact belong to *B. ingridae* and/or new undescribed species (see above). Taxonomical status of larval material reported by Verrier (1956: 95) from Crete [sub. *Baetis*, type *gemellus* Etn.] needs to be clarified. *B. rhodani* was formally listed for Sardinia by Buffagni et al. (2003). Taxonomical status of material from the Mediterranean islands attributed to "*B. rhodani*" remains unclear, since the existence of series of cryptic species among European populations is confirmed by molecular taxonomy (see Williams et al. 2006; Lucentini et al. 2011; Gattolliat et al. 2015). In Italy, 11 potential cryptic species have been recognized, one of these cryptic species clearly has a restricted geographical range within Sicily only (see the position of cryptic species G9 in Lucentini et al. 2011). Gattolliat et al. (2015) documented the existence of two separate insular clades (three clear lineages) for Corso-Sardinian material of *Baetis* gr. *rhodani*. Finally, Bisconti et al. (2016) reported about occurrence of three distinct and deeply divergent species within the "*B. rhodani* species group" in the north-western Mediterranean islands (Sicilia, Corsica and, Elba) based on DNA analysis.

[20] Numerous records from the Mediterranean islands. The record for Tasos was published by Russev (1959: 272) [sub. *Gentroptilum* (sic!) *luteolum* Müller]; first record for Sicily by Grandi (1966: 327); first record for Corsica most probably by Verrier (1954) [sub. *Centroptilum* sp.]; the records for Kos and Karpathos by Belfiore (1990: 267). Recent data on distribution in Sicily, Sardinia and Corsica are summarized by Belfiore and D'Antonio (1991), Belfiore et al. (1991) and Buffagni et al. (2003).

[21] Listed for Sicily and Sardinia by Belfiore and Gaino (1988) and Belfiore and D'Antonio (1991), but absent in the tabular list of Italian species summarized by Buffagni et al. (2003). Original record from Sicily of Belfiore (1983) concerns *Cloeon dipterum* (see Belfiore et al. 1991). The original record from the Balearic Islands needs to be confirmed (Alba-Tercedor and Jáimez-Cuéllar 2003: 92). *Species inquirenda* according to Bauernfeind and Soldán (2012: 189).

[22] Numerous records from Mediterranean islands. Russev (1959: 272) recorded this species from the island of Tasos [sub. *Cloëon rufulum* Eaton]. We collected this species in Malta for the first time (previously unpublished data). However, this findings were generally mentioned in a tabular summary on the distribution of European mayflies (Bauernfeind and Soldán 2012: 639), actual data on respective localities have never been published. These are as follows: Island of Malta: Wied il-Qleja [brook], small artificial reservoirs called Chadwick Lakes, about 15 km west of the town Intarfa, about 110 m a.s.l., N35 89.100 E14 38.580, 238 larvae, 85 males, 15 females, 8 subimagoes, May 12, 2010; Island of Gozo, unnamed brook, about 2 km south of the town Malsarforn, about 10 m a.s.l., N36 07.014 E14 26.010, 22 larvae May 15, 2010 (all material leg. T. Soldán).

[23] The record from the Balearic Islands needs to be confirmed (Alba-Tercedor and Jáimez-Cuéllar 2003). *Species inquirenda* according to Bauernfeind and Soldán (2012: 191).

[24] Verrier (1954: 284) reported larvae from Lake Nino (Corsica) [sub. *Procloeon Rabaudi* Verrier]. According to the online portal Fauna Europaea [http://www.faunaeur.org/] junior subjective synonym of *Cloeon simile*. *Species inquirenda* according to Bauernfeind and Soldán (2012: 194). Taxonomical status and presence in Corsica needs to be clarified.

[25] The record from the Balearic Islands needs to be confirmed (Alba-Tercedor and Jáimez-Cuéllar 2003). Most probably part of material belongs to *C. simile*. *Species inquirenda* according to Bauernfeind and Soldán (2012: 199).

[26] The record from the Balearic Islands needs to be confirmed (Alba-Tercedor and Jáimez-Cuéllar 2003). Most probably part of material belongs to *C. simile*. *Species inquirenda* according to Bauernfeind and Soldán (2012: 199).

[27] Several records from the Western and Eastern Mediterranean Region. The record from Corsica is based on OPIE-benthos data. The information published by Belfiore and D'Antonio (1991: 260) [sub. *Cloeon* gr. *simile*] needs to be clarified. Recently DNA barcoded by Cardoni et al. (2015).

[28] So far known from several localities in Sicily and Sardinia (Belfiore and D'Antonio 1991; Buffagni et al. 2003; Bauernfeind and Soldán 2012). Reported from Elba and Sardinia by Cardoni et al. (2015), with remarks on its possible presence in the Corse-Sardinian biogeographic region; based on DNA barcoding the specimens from Elba and Sardinia may however represent a cryptic endemic species as they differ significantly from specimens of Continental Europe (Cardoni et al. 2015).

[29] So far only known from several localities in Rhodos (see Sowa 1985; Sroka et al. 2010); probably endemic to the island (Bauernfeind and Soldán 2012).

[30] The record from Sicily by Buffagni et al. (2003) refers to an earlier record by Belfiore et al. (1991: 32) [sub. *Pseudocentroptilum* sp. gr. *pulchrum*). According to a tabular summary by Belfiore and D'Antonio (1991). *P. pulchrum* was considered absent from the island. Most probably recorded by Grandi (1966: 327) [sub. *Centroptilum pennulatum* Etn.] from Sicily for the first time. The problem with proper identification of material previously assigned to the *P. pennulatum* species-group is briefly discussed by Belfiore (1988), Belfiore and D'Antonio (1991) and Belfiore et al. (1991). The respective taxonomical status of this material needs to be clarified.

[31] The single record from Lesbos [sub. *Pseudocentroptilum motasi* Bogoescu, 1947] by Keffermüller and Sowa (1984: 334–338, figs 53–55) is based on material collected by H. Malicky.

roinvertebrate taxocene of both localities included several mayfly taxa, viz. *B. irenkae*, *Baetis* (*Baetis*) cf. *muticus* (Linnaeus, 1758), *Epeorus* (*Ironopsis*) sp., and *Electrogena* sp. Flight period probably from May and during first half of summer months, since several nymphs ready to emerge were collected together with younger larvae.

Notes on distribution

As well as *B. irenkae*, a new species so far known only from several localities in Cyprus (type locality at Kryos River within Kalidonian Waterfalls, and another one locality at Diplos River within Chantara Waterfalls), and thus might be considered presently as endemic to this island (Table 2).

Annotated checklist of Baetidae in the Mediterranean islands

The history on the mayfly fauna of the Mediterranean islands dates back to the first published observations by Hagen (1864). In this contribution, seven mayfly species were reported from Corsica, including three species of Baetidae. Significant early publications dealing with the Corsican mayfly fauna and also including the description of new species were contributed by Esben Petersen (1912; 1913). All other publications in the early 20th century (Jakobson and Bianki 1905; Lestage 1922; Kimmins 1930) in fact were just compilations and summaries of H.A. Hagen's and M. Esben-Petersen's earlier investigations. The first records of the mayfly fauna of the Balearic Islands was published by Navás (1914). Literature on the distribution of Baetidae in the Mediterranean Islands however is scattered.

The annotated checklist presented here (Table 2) provides the first comprehensive compilation of records of Baetidae in the Mediterranean islands incorporating also most recent records and findings along with detailed critical comments on previous records.

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RESEARCH ARTICLE

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A new species of the genus *Phaenochilus* Weise from China (Coleoptera, Coccinellidae, Chilocorini)

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Abstract

A new species *Phaenochilus albomarginalis* Li & Wang, **sp. n.** is described. The only other species recorded from China is *P. metasternalis* Miyatake, 1970 and it is described here for comparison. Diagnoses, detailed descriptions, illustrations, and distributions are provided.

Keywords

Coleoptera, new species, *Phaenochilus*, taxonomy, Yunnan

Introduction

Chilocorini is a medium-sized tribe in the Coccinellidae which was placed in the superfamily Coccinelloidea by recent molecular phylogenetic research on Cucujoidea (Robertson et al. 2015). It consists of 26 genera and about 280 species (Łączyński and Tomaszewska 2012). Chilocorini have been shown to be a monophyletic group by some phylogeny works, but the generic relationships within this tribe are ambiguous (Giorgi et al. 2009; Magro et al. 2010; Seago et al. 2011).

Phaenochilus Weise is a small genus of the tribe Chilocorini, the species of which mainly feed on scale insects and a few species of whitefly nymphs. The genus *Phaenochilus* was proposed by Weise (1895). Korschefsky (1932) designated *Phaenochilus punctifrons* as the type species. Giorgi and Vandenberg (2012) revised the genus and described a new species. So far, there are nine species known, distributed mainly in Southeast Asia, China, India and Japan (Giorgi and Vandenberg 2012). Except for *P. metasternalis*, which is widely distributed in China and Southeast Asia, the other species of *Phaenochilus* have more restricted distributions.

The genus was unknown from China until Miyatake (1970) described *P. metasternalis*. Pang and Mao (1979), Cao et al. (1992), and Ren et al. (2009) redescribed this species, but no new species from China have been added to this genus in recent decades.

In this paper, a second species of *Phaenochilus* from China is described and compared with *P. metasternalis*.

Material and methods

Type specimens of the new species are deposited at the Department of Entomology, South China Agriculture University, Guangzhou, China (SCAU).

External morphological characters were observed with a dissecting stereoscope (SteREO Discovery V20). The following measurements were made with an ocular micrometer:

TL	total length, length from apical margin of clypeus to apex of elytra;
TW	total width, width across both elytra at widest point;
TH	height measured across the highest point of the elytra;
HW	head width in frontal view;
PL	pronotal length, from middle of anterior margin to base of pronotum;
PW	pronotal width at widest point;
EL	elytral length, from the apex of the elytra to the base including the scutellum;
EW	elytral width, equal TW.

Male and female genitalia were dissected, cleared in 10% NaOH by boiling for several minutes, and examined with an Olympus BX51 microscope. Genitalic morphological character photographs were generated with digital cameras (AxioCam HRc and Coolsnap-Procf & CRI Micro*Color), attached to the microscopes using AxioVision Rel. 4.8 and Image-Pro Plus 6.0 to capture images from both cameras, and photographs were cleaned up and laid out in plates in Adobe Photoshop CS 8.0.

Morphological terms of Coccinellidae follow Ślipiński (2007) and Ślipiński and Tomaszewska (2010).

Taxonomy

Phaenochilus Weise, 1895

Phaenochilus Weise, 1895: 135. Type species: *Phaenochilus punctifrons* Weise, 1895, by subsequent designation of Korschefsky (1932).

Diagnosis. Members of this genus can be distinguished from other genera of Chilocorini by the following combination of characters: antennae 8-segmented (Fig. 1e); outer margin of mandible slightly curved (Fig. 1f); terminal maxillary palpomere slender and elongate, approximately three times as long as basal width, with sides nearly parallel (Fig. 1g); terminal labial palpomere slender and acuminate, rounded at apex (Fig. 1h); legs without tibial spurs (Fig. 1i–j), tarsal claw stout, with large, rectangular basal tooth about 1/2–2/3 as long as claw (Fig. 1k).

Phaenochilus albomarginalis Li & Wang, sp. n.

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Figs 1a–k, 2a–g, 4

Diagnosis. This new species can be distinguished from *Phaenochilus metasternalis* by the following combination of characters: lateral margin of elytra yellowish white (Fig. 1a–b); penis guide nearly symmetrical in ventral view, parameres slightly shorter than penis guide (Fig. 2b–c). In *P. metasternalis*, lateral margin of elytral yellow or yellowish brown (Fig. 3a–b); penis guide distinctly asymmetrical in ventral view, slightly shorter than parameres (Fig. 3g–h).

Description. TL: 3.67–3.80 mm, TW: 3.60–3.67 mm, TH: 1.87–2.07 mm, TL/TW: 1.02–1.04, PL/PW: 0.66–0.67, EL/EW: 0.96–1.00.

Body roundish, strongly convex (Fig. 1b). Head yellow, sparsely covered with short, greyish pubescence, eyes normally black (Fig. 1c). Pronotum yellow, only anterior angles sparsely covered with short, greyish pubescence. Scutellum and elytra yellow, lateral margin of elytra yellowish white, obvious boundary between two colors (Fig. 1a). Underside entirely yellow, except apex of mandible black with short, greyish pubescence.

Head relatively small, 0.44 times pronotal width, punctures on frons large, 3.0–4.0 diameters apart, surface polished between punctures; eyes subtriangular, densely faceted, widest interocular distance 0.42 times head width (Fig. 1c). Antennae composed of eight antennomeres, scape and pedicel slightly elongate, scape and pedicel of similar length and width, antennomeres 3–5 equal in length, antennomeres 6–8 gradually longer (Fig. 1e). Outer margin of mandible slightly curved (Fig. 1f). Terminal maxillary palpomere slender and elongate, approximately three times as long as basal width, with sides nearly parallel (Fig. 1g). Terminal labial palpomere slender and acuminate, rounded at apex (Fig. 1h). Pronotum 0.53 times elytral width, pronotal punctures

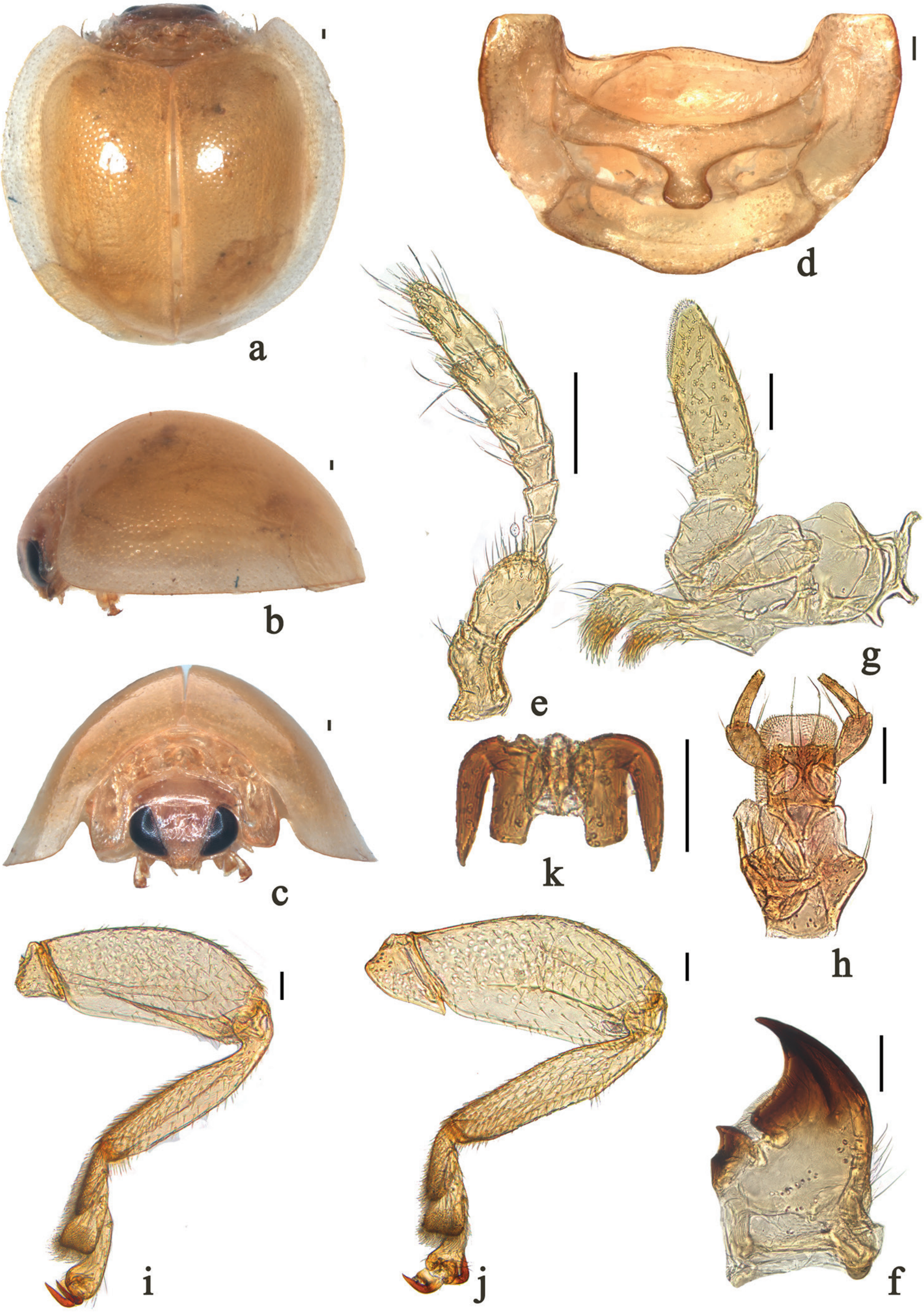

Figure 1. *Phaenochilus albomarginalis* sp. n. **a** dorsal view **b** lateral view **c** frontal view **d** prothorax, ventral **e** antenna **f** mandible **g** maxilla **h** labium **i** front leg **j** hind leg **k** tarsal claws. Scale bars: 0.1 mm.

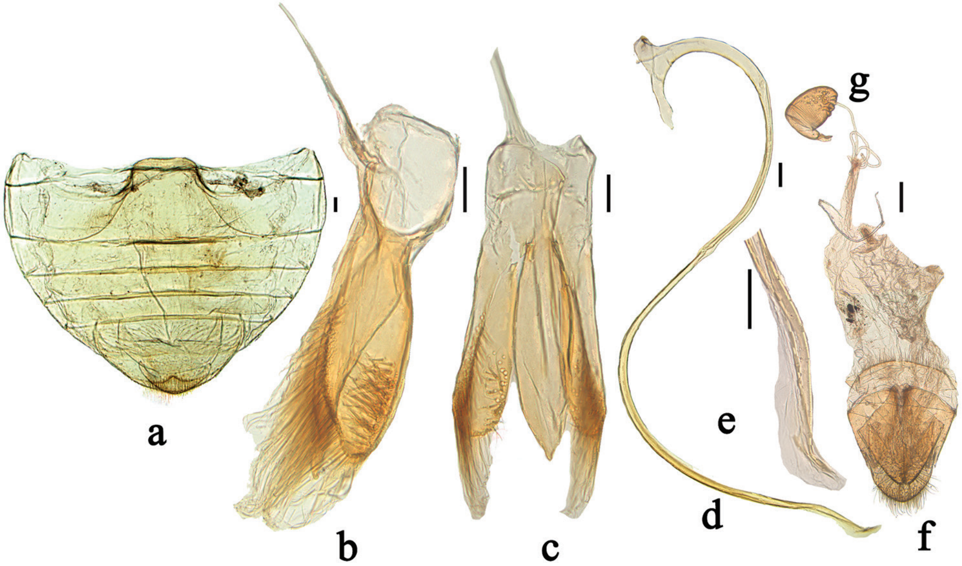

Figure 2. *Phaenochilus albomarginalis* sp. n. **a** abdomen, male, ventral **b** tegmen, lateral view **c** tegmen, ventral view **d** penis **e** apex of penis **f–g** female genitalia: **f** ovipositor **g** spermatheca. Scale bars: 0.1 mm.

fine but larger than those on head, 1.5–2.5 diameters apart, surface polished between punctures. Punctures on elytra fine, similar to those on pronotum, 2.0–4.0 diameters apart. Epipleuron without fovea to reccept mid and hind legs. Prosternal process short, narrow at base, gradually broadened to apex (Fig. 1d). Abdominal postcoxal lines incomplete, reaching posterior margin of abdominal ventrite 1 and running along posterior margin, almost reaching lateral margin. Posterior margin of male abdominal ventrite 5 truncate and ventrite 6 distinctly emarginate medially (Fig. 2a).

Male genitalia: penis slender and long, penis capsule with short outer arm and long inner arm, apex of penis with small protuberance and membranous appendage (Fig. 2d–e). Tegmen stout, penis guide gradually broadened to basal 2/5, subparallel to apical 1/5 thereafter, then gradually converging apically to blunt tip in ventral view; only one lateral margin slightly emarginate at basal 3/5 (Fig. 2c). Parameres slightly shorter than penis guide with dense, long setae at inner sides and apices with group of long setae in lateral view (Fig. 2b).

Female genitalia: coxites elongate, triangular (Fig. 2f). Spermatheca oblong-oval, stout, appendage of cornu well-developed (Fig. 2g).

Types. Holotype, male, CHINA: Yunnan Prov: Tongbiguan, Husa, No. SCAU (E) 15235, [24°37.03'N; 97°39.05'E], *ca.* 1410m, 23.ix.2006, Wang XM leg. Paratypes. 1 male and 4 females with same data as holotype; 1 male, Yunnan Prov: Nanjingli, Ruili, [24°02.54'N; 97°52.10'E], *ca.* 811m, 25.ix.2006, Wang XM leg.

Distribution. China (Yunnan) (Fig. 4).

Etymology. The species name is derived from Latin and refers to the yellowish white lateral margin of elytra.

Phaenochilus metasternalis Miyatake, 1970

Figs 3a–j, 4

Phaenochilus metasternalis Miyatake, 1970: 334; Pang and Mao 1979: 78; Cao 1992: 152; Ren et al. 2009: 138.

Diagnosis. This species can be distinguished from the other species of *Phaenochilus* by the following combination of characters: the elytral bead yellow or yellowish brown (Fig. 3a–b); male abdomen ventrite 6 weakly emarginate at middle (Fig. 3d); penis guide distinctly asymmetrical in ventral view and coxites elongate, triangular (Fig. 3h–i).

Description. TL: 3.33–3.67 mm, TW: 3.13–3.47 mm, TH: 1.67–2.00 mm, TL/TW: 1.04–1.06, PL/PW: 0.72–0.74, EL/EW: 1.00–1.02.

Body roundish, strongly convex (Fig. 3b). Head yellow, sparsely covered with short, greyish pubescence, eyes normally black (Fig. 3c). Pronotum yellowish brown, only anterior angles sparsely covered with short, greyish pubescence. Scutellum, elytra, and elytral bead yellowish brown (Fig. 3a). Underside entirely yellowish brown or brown, except apex of mandible black with short, greyish pubescence.

Head relatively small, 0.56 times pronotal width, punctures on frons large, 2.5–4.0 diameters apart, surface polished between punctures; eyes subtriangular, densely faceted, widest interocular distance 0.40 times head width (Fig. 3c). Antennae composed of eight antennomeres, scape and pedicel slightly elongate, scape and pedicel of similar length and width, antennomeres 3–5 equal in length, antennomeres 6–8 gradually longer. Outer margin of mandible slightly curved. Terminal maxillary palpomere slender and elongate, approximately three times as long as basal width, with sides nearly parallel. Terminal labial palpomere slender and acuminate, rounded at apex. Pronotum 0.52 times elytral width, pronotal punctures fine but larger than those on head, 2.0–3.0 diameters apart, surface polished between punctures. Punctures on elytra fine, similar to those on pronotum, 2.0–4.0 diameters apart. Epipleuron without fovea to reccept mid and hind legs. Prosternal process short, narrow at base, gradually broadened to apex (Fig. 3d). Abdominal postcoxal lines ncomplete, reaching posterior margin of abdominal ventrite 1 and running along posterior margin, almost reaching lateral margin. Posterior margin of male abdominal ventrite 5 truncate and ventrite 6 slightly emarginte medially (Fig. 3d).

Male genitalia: penis slender and long, outer arm of penis capsule slightly longer than inner arm, apex of penis with a small protuberances and membranous appendage inside (Fig. 3e–f). Tegmen stout, penis guide knife-like in ventral view (Fig. 3h). Parameres as long as penis guide with dense short setae at inner sides and apices with patches of short setae visible in lateral view (Fig. 3g).

Female genitalia: coxites elongate, triangular (Fig. 3i). Spermatheca oblong-oval, stout, appendage of cornu well-developed (Fig. 3j).

Material examined. Yunnan: 2 males, Ruili, [24°01.03'N; 97°46.23'E], *ca.* 1159m, 27.vii.2005, Wang XM leg; 1 male, Maku, Dulongjiang, [27°40.57'N;

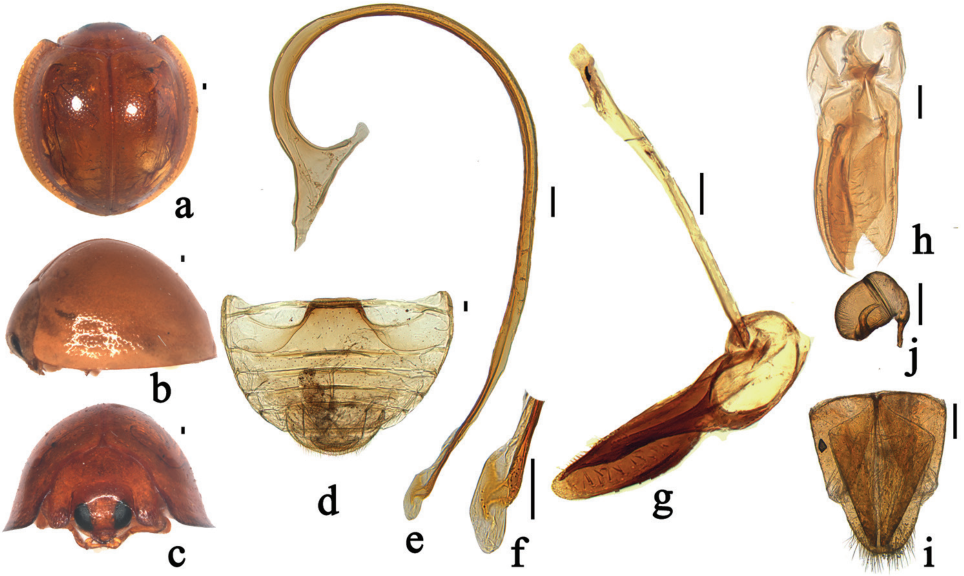

Figure 3. *Phaenochilus metasternalis* Miyatake, 1970. **a** dorsal view **b** lateral view **c** frontal view **d** abdomen, male **e** penis **f** apex of penis **g** tegmen, lateral view **h** tegmen, ventral view **i** ovipositor **j** spermatheca. Scale bars: 0.1 mm.

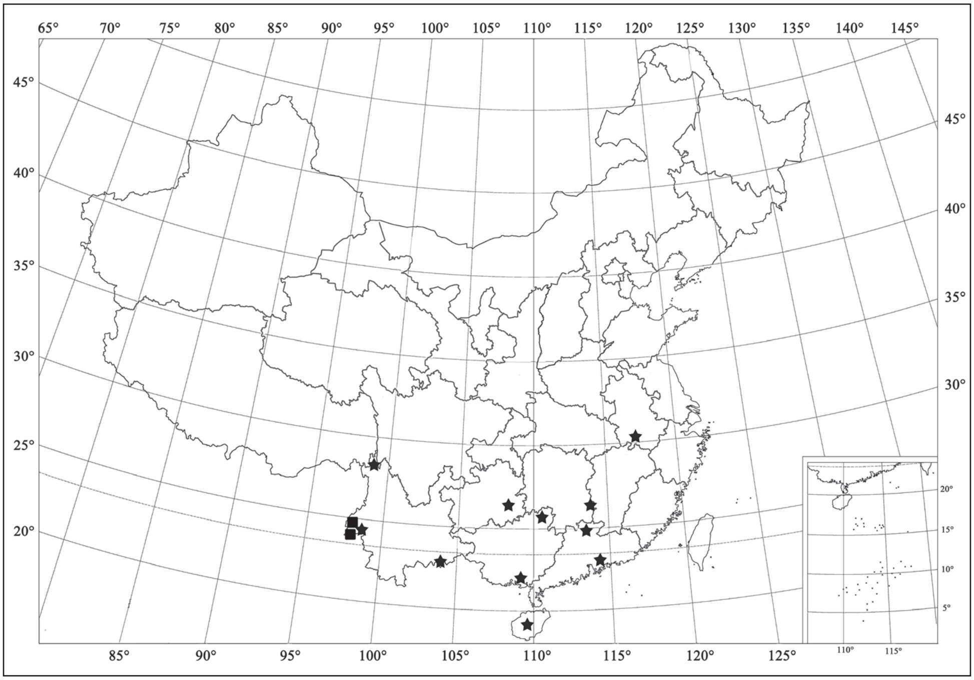

Figure 4. Distribution map. (■) *Phaenochilus albomarginalis* sp. n.; (★) *P. metasternalis* Miyatake, 1970.

98°18.19'E], *ca.* 1600m, 1.viii.2010, Wang XM leg; 2 females, Galaxi, Lianhuatan, Hekou, [22°57.03'N; 103°28.54'E], *ca.* 800m, 21.V.2009, Ren SX leg. Guangdong Prov: 3 males, Huangdong, Shimentai, [24°25.30'N; 113°18.28'E], *ca.* 480m, 31.x.2004, Wang XM leg;1 male, Nankunshan, Huizhou, [23°38.08'N; 113°53.34'E], *ca.* 491m, x.2004, Wang XM leg. Guangxi Prov: 1 male, Daxiagu, Maoershan, [25°50.46'N; 110°29.14'E], *ca.* 406m, 19.x.2004, Wang XM leg; 1 male, Hongqilinchang, Shiwandashan, [21°54.07'N; 107°54.26'E], *ca.* 438m, 11.xi.2004, Wang XM leg. Anhui Prov: 2 males, Huangshan, [38°08.52'N; 118°07.58'E], *ca.* 1250m, 30.vii.2005, Qin ZQ leg; 2 males, Huangshan, [38°08.39'N; 118°08.45'E], *ca.* 1367m, 14–15.ix.2010, Wang XM leg. Hainan Prov: 1 female, Yinggeling, [19°10.26'N; 109°41.08'E], *ca.* 850m, 23.xi.1997, Peng ZQ leg; 1 male, Bawangling, [19°03.51'N; 109°11.47'E], *ca.* 738m, 5.v.2005, Peng ZQ leg. Hunan Prov: 2 males, Shennonggu, Yanling, [26°30.01'N; 114°00.27'E], *ca.* 1100m, 7.x.2010, Wang XM leg. Guizhou Prov: 1 male, Datangwan, Leigongshan, [26°21.28'N; 108°10.01'E], *ca.* 1100m, 5.x.2008, Wang XM leg.

Distribution. China (Anhui, Hunan, Guangdong, Guangxi, Hainan, Guizhou, Yunnan) (Fig. 4); Laos; Vietnam; Singapore; Indonesia.

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RESEARCH ARTICLE

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First record of the genus *Lethades* Davis, 1897 from the Oriental region, with description of a new species (Hymenoptera, Ichneumonidae, Ctenopelmatinae)

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Abstract

A new species of the genus *Lethades* Davis, 1897 (Ctenopelmatinae: Pionini), *L. orientalis* Reshchikov & Xu, **sp. n.**, collected in Heishiding Nature Reserve in Guangdong Province, China, is described. This is new record of the genus from China and for the Oriental region also. The species can be distinguished from all other species of the genus by its black metasoma, the presence of an areolet on the fore wing, distinctly pectinate claws with teeth of the hind claw as high as the claw itself, and a complete longitudinal propodeal carina. A key to the world species of the genus is provided.

Keywords

China, key, new species, Pionini

Introduction

The genus *Lethades* Davis, 1897, is in the tribe Pionini and the subfamily Ctenopelmatinae (Hymenoptera, Ichneumonidae). It formerly comprised 16 described species, two of them reported from the Nearctic Region and the rest from the Palaearctic Region (Yu et al. 2012).

Species of *Lethades* have been reared from Nematinae (Hymenoptera, Thenthredinidae) of the genera *Amauronematus*, *Nematus*, *Pachynematus*, and *Pristiphora* (Hinz 1961, 1976, 1996a, 1996b; Zinnert 1969; Pschorn-Walcher and Zinnert 1971). Only one species, *L. schaffneri* (Hinz) is known to attack *Rhadinocera eanodicornis* Konow, 1886 of the subfamily Blennocampinae (Hinz 1996a).

The European species of *Lethades* Davis were reviewed by Hinz (1996a), who provided a key to the Palaearctic fauna. Afterwards, Kasparyan and Khalaim (2007) developed a key to the species of the Russian Far East based on Hinz's key. Two species, *L. alpinus* (Zetterstedt) and *L. flavifrons* (Zetterstedt) were synonymized with *L. curvispina* (Thomson) by Hinz (1996b) and *L. poloniae* Hinz, 1996 was synonymized with *L. punctatissimus* (Strobl) by Horstmann (2001). Cameron and Wharton (2011) transferred *Hodostates schaffneri* (Hinz) to *Lethades* based on ovipositor characters. In the Nearctic Region one species, *L. kukakensis* (Ashmead), is known from Alaska, and the other species, *L. texanus* (Ashmead) from Texas (Yu et al. 2012). One species, *L. buriator* Aubert, 1987 was described from The Republic of Buryatia (Eastern Russia) and five European species were recorded from the Eastern Palaearctic (Yu et al. 2012). Prior to this paper no species of either genus had been recorded from China or the Oriental Region. Here a new species is described from China, representing the first record of the genus from the Oriental region.

Materials and methods

Specimens were collected using sweep nets in the forests of Heishiding Provincial Nature Reserve, located in Fengkai County, Zhaoqing City, West Guangdong Province, bordering Guangxi, China (23°27'N, 111°53'E, 150–927 m) (Zhang 1997). The reserve consists of subtropical evergreen and broad-leaved forests. The region has a subtropical moist monsoon climate with mean annual temperature 19.6°C and mean monthly temperatures range from 10.6°C in January to 28.4°C in July (Wang and Liu 1987). Annual precipitation is approximately 1743.8 mm, with rainfall occurring mainly between April and September (79% of annual total), there is a pronounced dry season lasting from October to March (Wang and Liu 1987). Species belonging to the Fagaceae and Lauraceae families, which are broadly distributed in subtropical evergreen broadleaved forests, are the dominant tree species (Chan et al. 2004).

The holotype is deposited in the Hymenopteran Collection of South China Agricultural University, Guangzhou (SCAU). Images were taken using AxioCamHRc digital camera attached to Zeiss Discovery V20 microscope and stacked using Helicon Focus®. All images were further processed using various minor adjustment levels in Adobe Photoshop®. Stacked images are available in colour and high resolution at http://www.morphbank.net. Morphological terminology mostly follows Gauld (1991). Wing vein nomenclature follows Ross (1936) and wing vein terminology follows Mason (1986, 1990).

Taxonomy

Lethades Davis, 1897

Lethades Davis, 1897: 204. Type species: *Adelognathus texanus* Ashmead, 1890. Monobasic.

Diagnosis. *Lethades* can be distinguished from all other genera in the Pionini by the combination of the following characters: first flagellomere longer than second; second trochanter of hind leg rounded without a transverse ridge; glymma present; profile of the propodeum nearly rounded with short posterior field; dorsomedian and dorsolateral carinae of the T1 converging at base; ovipositor without subapical notch; cerci parallel-sided and protruding (Townes 1970, Cameron and Wharton 2011). The notaulus varies from absent to deep, but very short, in nearly all described species of *Lethades*. Only *L. schaffneri* Hinz has an elongate notaulus. The latter species was transferred to *Lethades* based on other characters, especially ovipositor morphology (Cameron and Wharton 2011).

Key to world species of the genus *Lethades*

1 Notauli distinctly impressed extending at least over the anterior 0.5 of the mesoscutum. Claws not pectinate .... ***L. schaffneri*** **Hinz**

– Notauli absent or weakly impressed, not extending the anterior 0.5 of the mesoscutum. Claws pectinate **2**

2 Fore wing areolet absent **3**

– Fore wing areolet present **5**

3 Body finely striated and weakly punctate. Fore femur and tibia uniformly red .... ***L. amauroneinati*** **(Hinz)**

– Body distinctly and densely punctate, mesopleuron weakly striated. Fore femur and tibia not uniformly red **4**

4 Epicnemial carina reaching anterior edge of mesopleuron. Metasomal tergites without yellow bands on posterior margins. Fore femur and tibia red, dark apically .... ***L. schmiedeknechti*** **Hinz**

– Epicnemial carina not reaching anterior edge of mesopleuron. Metasomal tergites with yellow bands on posterior margins. Fore femur black, yellowish apically; fore tibia yellow .... ***L. texanus*** **(Ashmead)**

5 Metasomal tergites black, or with narrow posterior margins light colored (Fig. 1 .... **5**

– Middle metasomal tergites red, sometimes with dark maculae **11**

6 Claw distinctly pectinate, teeth of hind claw more than 0.5 times as high as claw (Fig. 7). Longitudinal propodeal carina absent or complete **7**

– Hind claw with teeth less than 0.5 times as high as claw. Longitudinal propodeal carina present **8**

7 Longitudinal propodeal carina mostly absent, only the area apicalis defined ... . ***L. punctatissimus*** **(Strobl)**

– Longitudinal propodeal carina complete (Fig. 4) .... ***L. orientalis*** **Reshchikov & Xu, sp. n.**

8 Head with parallel sides or expanded behind eyes dorsally. T1 with distinct dorsal longitudinal carinae reaching almost to posterior margin.................... .... ***L. erichsonii*** **Hinz, 1996**

– Head narrowed behind eyes dorsally. T1 with weak dorsal longitudinal carinae reaching only 0.7 of length.. **9**

9 Mesopleuron polished ventrally, finely and densely punctate. Propodeum with costula defined. T2 and T3 finely sculptured, polished. Metasomal tergites with narrow yellow posterior margins. Clypeus in female entirely or apically pale. Scape yellow ventrally .... ***L. cingulator*** **Hinz**

– Mesopleuron matt ventrally, shagreened or granulated **10**

10 T2 and T3 with broad reddish-yellow bands on posterior margins. Pronotum, mesonotum, and mesopleuron in male with large yellow maculae. Female with clypeus and scape entirely black........................... ***L. laricis*** **Hinz**

– T2 and T3 black (T3 slightly reddish-brown basally). Male with pronotum, mesonotum, and mesopleuron black. Clypeus in female with yellow maculae on sides.. ***L. buriator*** **Aubert**

11 Ovipositor sheath 2 times as long as first tarsomere of hind leg.................... .... ***L. lapponicus*** **(Holmgren)**

– Ovipositor sheath equal to or shorter than first tarsomere of hind leg **12**

12 Temples and lower part of mesopleuron coriaceous and granulated with fine, dense punctures. T1 very densely punctate and striated, with elongate dorsal carinae reaching to its middle .... ***L. facialis*** **(Brischke)**

– Temples and lower part of mesopleuron striated, punctures not defined. T1 finely shagreened, with short dorsal carinae not reaching middle **13**

13 Ovipositor sheath curved upwards, as long as first tarsomere of hind leg, curved upwards. Antenna with 24–26 flagellomeres; the basal flagellomeres stout, and apical flagellomeres transverse. T1 black; T2–T4 red....... ***L. lapponator*** **Hinz**

– Ovipositor sheath straight, shorter, 0.6–0.8 times as long as first tarsomere of hind leg. Antenna with 23–31 flagellomeres; the basal flagellomeres elongate, the apical flagellomeres cubic. T1 black with posterior margin red............ **14**

14 Antenna with 28–31 flagellomeres. Female with third flagellomere 2.3–2.8 times as long as broad; male with third flagellomere 2.2–2.4 times as long as broad. Mesopleuron finely striated, finely and sparsely punctate. Body black. Palpi, mandibles, posterior edge of pronotum, and tegulae yellow. Legs (except coxae and hind tarsi), posterior margins of T1, and T2–T3 red. Male with clypeus, face, scape and pedicel ventrally, subtegular carina, fore and middle coxae and trochanters yellow.............................. ***L. imperfecti*** **Hinz**

– Antenna with 23–28 flagellomeres. Female with third flagellomere 1.9–2.4 times as long as broad; male with third falgellomere 1.9–2.2 times as long as broad. Mesopleuron distinctly coriaceous **15**

15 Mesonotum and T1–T3 finely striated ....***L. scabriculus* (Thomson)**

– Mesonotum and T1–T3 not striated **16**

16 Mesonotum distinctly matt, finely and densely punctate ....
.... ***L. kukakensis* (Ashmead)**

– Mesonotum distinctly polished, sparsely and indistinctly punctate ....
.... ***L. curvispina* (Thomson)**

***Lethades orientalis* Reshchikov & Xu, sp. n.**

http://zoobank.org/D2D7BFCF-4430-4060-A53B-C52ECC0C0058
Figures 1–7

Type material. *Holotype*, female, CHINA: Guangdong, Fengkai, Heishiding Provincial Nature Reserve (23°27'N, 111°53'E), 150–927 m., sweep net, 1–2.X.2003, leg. Zaifu Xu (SCAU).

Diagnosis. This species can be distinguished from all other species of *Lethades* by a combination of the following characters: metasoma black (Fig. 1); fore wing with areolet; claw distinctly pectinate, teeth of hind claw as high as claw (Fig. 7); longitudinal propodeal carina complete (Fig. 4).

Description. Female. Body length 10.5 mm.

Head. Face and clypeus shagreened and covered with long reddish setae (Fig. 2). Face approximately 1.4 times as wide as high, with distinct, sparse and shallow punctures; median portion weakly and longitudinally convex (Fig. 2). Clypeus convex, gradually raised towards apical margin, with very sparse, fine and distinct punctures. Upper tooth of mandible obviously shorter than lower tooth. Malar space approximately 0.6 times as long as basal width of mandible. Gena, vertex and frons shagreened. Head with parallel sides behind eyes (Fig. 3). Gena in lateral view approximately as long as the width of eye. Postocellar line nearly 0.5 times as long as ocular-ocellar line. Antenna with 40 flagellomeres. Occipital carina complete.

Mesosoma. Pronotum distinctly punctate. Mesoscutum with dense and distinct punctures. Notauli present. Scuto-scutellar groove with weak longitudinal wrinkles. Scutellum convex, with distinct punctures, its basal 0.3 with lateral carina. Mesopleuron (Fig. 5) and metapleuron coriaceous, mat, densely and distinctly punctate. Epicnemial carina distinct, its upper end reaching middle of mesopleuron. Wings slightly brownish, hyaline (Fig. 1). Fore wing with vein 1cu-a interstitial. Hind wing vein 1-cu approximately 1.9 times as long as cu-a. Hind femur 4.4 times as long as broad at its middle. Ratio of length of hind tarsomeres 37 : 14 : 11 : 6 : 16. Claw distinctly pectinate, teeth of hind claw as high as claw (Fig. 7). Propodeum rather short (Fig. 4). Its carinae strongly raised (Fig. 4). Area superomedia and area apicalis fused to form a pentagonal area, costula connecting in front of its middle (Fig. 4). Propodeal spiracle rounded.

Metasoma. Metasomal tergites shagreened, matt, finely punctate. T1 twice as long as apical broad. Dorsal carinae strongly raised, almost reaching posterior margin of T1. T2 transverse. Ovipositor sheath approximately 0.8 times as long as apical depth

Figures 1–7. *Lethades orientalis* Reshchikov & Xu, sp. n., female, holotype. **1** Habitus, lateral view **2** head, frontal view **3** head, dorsal view **4** propodeum, dorsal view **5** mesopleuron **6** apex of metasoma, lateral view **7** claw.

of metasoma, subapical portion distinctly truncated (Fig. 6). Ovipositor moderately stout, without distinct subapical notch (Fig. 6).

Color. Body mostly black (Figs 1–7). Mandibles, palpi, pedicel and basal part of first flagellomere ventrally, ovipositor sheath reddish. Flagellomeres 10–20 and apical tarsomeres white. Metasomal sternites and legs excluding hind coxa, femur, and distal and proximal parts of tibia reddish-yellow.

Male. Unknown.

Etymology. The name of the new species refers to the Oriental Region.

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RESEARCH ARTICLE

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Revision of the genus *Vanenga* Schaus, 1928 (Lepidoptera, Mimallonoidea, Mimallonidae) with the description of a new species

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Abstract

Vanenga Schaus, 1928, like many other Mimallonidae genera being revised in recent years, has not been studied since Schaus (1928) in his revision of the family. This currently monotypic genus is entirely restricted to South America, with no known representatives in Central or North America. Prior to this work, Schaus (1928) and subsequent lists of the family (Gaede 1931, Becker 1996) have mentioned the single species *V. mera* (Dognin, 1924) described from the Brazilian Amazon (Pará state). In Schaus (1928) this species is listed as occurring in both Amazonia and southeastern Brazil.

In completing the present article, numerous "type" specimens have been discovered bearing three different manuscript names associated with the populations of southeastern Brazil and adjacent areas. Despite the fact that these names were written on various labels, the absence of any published descriptions results in them being unavailable (ICZN 1999). Therefore, this distinct southern South American species is now officially recognized and formally described, as well as providing a much more thorough distribution for both *Vanenga* species, including many new records for *V. mera*.

Keywords

Argentina, Brazil, Paraguay, Uruguay, *Vanenga mera*, *Vanenga mediorosea* sp. n.

Introduction

Dissections were performed as in Lafontaine (2004). Morphological, including genitalia, terminology follows Kristensen (2003). Not all genitalia were prepared on slides to allow for three-dimensional analysis of the complex male genitalia. Genitalia and abdomens, when not slide mounted, are preserved in glycerol filled microvials.

Specimens from the following collections were examined:

ADW	Coll. of Andrew D. Warren, Castle Rock, Colorado, USA
CDH	Coll. of Daniel Herbin, Garidech, France
CGCM	Coll. of Carlos G. C. Mielke, Curitiba, Paraná, Brazil
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada
CPAC	Coleção Embrapa Cerrados, Planaltina, Distrito Federal, Brazil
CUIC	Cornell University Insect Collection, Ithaca, New York, USA
DZUP	Collection of Pe. Jesus S. Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
MWM	Museum Witt, Munich, Germany
NHMUK	Natural History Museum, London, U.K.
USNM	National Museum of Natural History [formerly United States National Museum], Washington D.C., USA

The symbol ‡ will be used to represent unavailable names in the text (Fletcher and Nye 1982).

Figures were manipulated with Adobe Photoshop CS4 (Adobe 2008). Male genitalia are figured in natural color with CS4 “auto color” used to improve white backgrounds. All geographical coordinates are approximate, and are based on the localities provided on specimen labels. GPS data were acquired with Google Earth.

Results and discussion

Vanenga Schaus, 1928: 664

Type species. *Perophora mera* Dognin, 1924; Schaus 1928: 664, by original designation.

Diagnosis. The *Vanenga* species are small, relatively plain mimallonids, but can be recognized by the short triangular forewings, straight, preapical or apical postmedial line, pale tan-orange ground color with varying degrees of pink coloration throughout the antemedial and medial areas, which may strongly contrast against the darker orange-brown submarginal area. The male genitalia define the genus by being rather simple with triangular valves, very long and narrow uncus, heavily sclerotized lobe-like gnathos projections, and a short, thick phallus with accessory spiny dorsal projections emanating from the juxta-phallus complex. These juxtal projections may be either long and narrow or short. The male genitalia are reminiscent of some species of *Lacosoma* Grote, 1864, as mentioned by Schaus (1928), but can be distinguished by the longer, narrower uncus and phallic structure. The female genitalia are unique in the absence of a clear lamella antevaginalis and by possessing a very broad ductus bursae, the papillae anales are also quite narrow and elongated, a combination of characters so far seen in no other female Mimallonidae.

Description. Male. *Head*: Varying shades of orange, eyes very large, more than two thirds area of head; antenna coloration as for head, bipectinate to tip, though distal fifth of pectinations much reduced in size; labial palpus highly reduced, three segmented, palpus not extending beyond frons. *Thorax*: Straw colored or with pale pink scales, darker brown-orange scales present on prothoracic collar. *Legs*: Coloration as for thorax, but usually darker orange with rosy scales, vestiture fine. Tibial spurs short, curved, naked or dorsally clothed in scales. *Forewing dorsum*: Forewing length: 10–17 mm, wingspan: 23.0–32.5 mm. Rather short, not elongated, triangular, apically somewhat rounded or more angled. Ground color pale tan-orange, with varying degree of pinkish hue throughout, especially antemedial and medially, overall lightly speckled by dark brown petiolate scales, though may be nearly absent. Antemedial line absent or as faint brown wavy mark. Postmedial line nearly straight, preapical or apical, brown, fading after passing Rs3 or Rs4. Antemedial and medial areas concolorous, either orange-tan or pale pink. Submarginal area always darker than medial area, usually orange-brown with diffuse gray coloration along wing margin, petiolate scales more abundant submarginally. Discal spot may be absent, when present as small dark brown spot. Fringe orange-tan or with light pink hue. *Forewing ventrum*: Similar to dorsum but coloration of medial and submarginal areas more similar, more uniformly orange, becoming gray distally, usually also pink nearer to thorax. Discal spot always present, usually larger than on dorsum (when present there), sometimes more elongated, narrower. Postmedial line somewhat wavy, not as straight as on dorsum, preapical. Petiolate scales more abundant, widely dispersed. *Hindwing dorsum*: Rounded, coloration and patterning as for forewing dorsum, antemedial line absent, postmedial line straight or curved outward, submarginal area broader than on forewing dorsum. *Hindwing ventrum*: Follows same pattern as forewing ventrum. Frenulum as single bristle. *Venation*: Typical of Mimallonidae, similar to *Lacosoma* Grote, 1864 but distal margin of discal cell more slanted. *Abdomen*: Concolorous with thorax, ventrally with pair of darker gray lines of scales, distal tip of abdomen with tuft of black scales, usually upturned in well-preserved specimens. *Genitalia*: Simple; vinculum ovoid, ventrally with lightly sclerotized plate attached to VIII. Uncus simple, acutely triangular but very elongated and narrow, laterally smoothly curving or slightly indented mesally. Gnathos formed by two rather short, unfused arms, as either ovoid, flattened lobe with triangular tooth emanating from center or as more heavily sclerotized downwardly angled cylindrical protuberance. Valves triangular, somewhat angled distally. Valves with baseo-mesal indentation which usually bears patch of thick, heavy setae; base of valves extend past vinculum inward into body cavity as narrow singular or bifurcated extension loosely connected to diaphragm and juxta. Juxta fused to phallus, encircling it as oddly shaped saucer with dorsal spined projections superior to phallus, projections either short and heavily spined or more elongated, curved, and less heavily spined. Phallus short, cylindrical, not much longer than width of juxtal saucer. Vesica bag-like. **Female.** *Head*: As in male but antennae much smaller overall, pectination particularly shorter. *Thorax*: As in male though brown scales along prothoracic collar may be darker. *Legs*: As in male, but tibial spurs shorter. *Forewing dorsum*: Forewing length: 12–15 mm, wingspan: 25–31 mm. Sexual dimorphism reduced, male and female very similar. Maculation similar to male but wing broader, convex mesally, submarginal area broader, apex more sharply acute. Coloration generally more diffuse between antemedial, medial, and submarginal areas, less distinctly bicolored. Submarginal area grayer or pinker overall than medial area relative to males. Postmedial line usually more bowed outward, though may be just as straight as in males. *Forewing ventrum*: Similar to dorsum but darker or paler orange. *Hindwing dorsum*: Coloration and patterning as for forewing dorsum, similar to males but differing in same characters as forewing dorsum. *Hindwing ventrum*: Follows same pattern as forewing ventrum. Frenulum reduced, as multiple bristles. *Abdomen*: Concolorous with thorax, ventrally darker, distal tip with small tuft of elongated scales. *Genitalia*: Small overall, most characters somewhat atrophied, VIII as weakly sclerotized plate, posteriorly curved, laterally VIII more heavily sclerotized. Apophyses anteriores less than half-length of apophyses posteriores or absent, apophyses posteriores elongate, narrower than apophyses anteriories (when present). Lamella antevaginalis membranous. Ductus bursae broad, wrinkled, bag-like. Corpus bursae narrow, elongated, nearly twice length of VIII–IX. Papillae anales somewhat flattened ventrally, elongated and narrow.

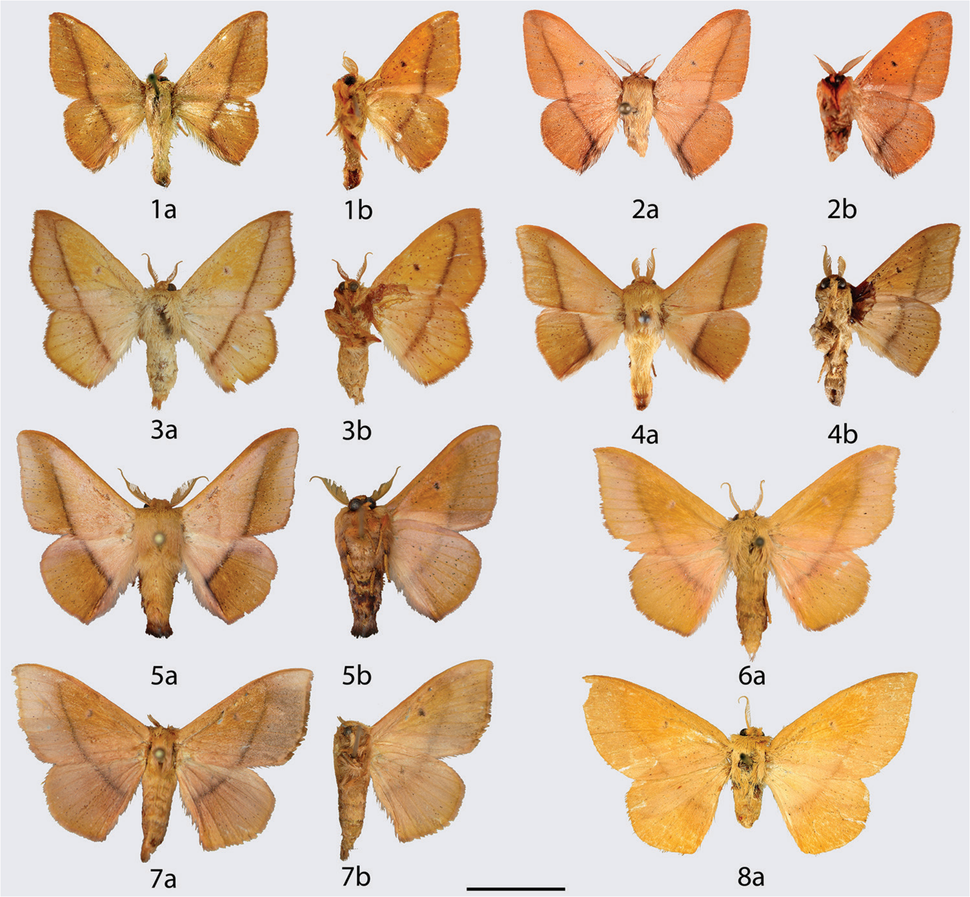
Remarks. The genus *Vanenga* seems to share a close affinity with *Lacosoma* considering the male genitalia (Schaus 1928, St Laurent and Herbin pers. obs.) and small size of these moths overall. However, the female genitalia and external coloration, pattering, and wing shape are all quite distinct from *Lacosoma*. Compare our Figs 10–14 to male/female *Lacosoma* genitalia figured in Herbin and Mielke (2014), Herbin and Monzón (2015), and Herbin (2016).

Vanenga mera (Dognin, 1924)

Figs 1–3, 10, 13, 15

Perophora mera Dognin, 1924: 31
Vanenga mera; Schaus 1928: 664, fig. ♂ 86g [incorrectly labeled as "*asea*" on plate, while the species *Lacosoma asea* Schaus, 1928 is labeled as "*mera*"]
Vanenga mera; Gaede 1931
Vanenga mera; Becker 1996

Type material. Holotype, ♂. BRAZIL: Pará: Obidos, Amazones, Brésil [Óbidos, Pará]/ Dognin Collection/ Spec fig/ *Perophora mera* Type ♂, Dognin/ Type No. 29702 U.S.N.M./ USNM-Mimal: 1100/ (USNM). [examined].



Figures 1–8. *Vanenga* adults, **a** dorsal **b** ventral. **1** *V. mera* holotype ♂, Brazil, Pará, Óbidos (USNM) **2** *V. mera* ♂, French Guiana, Route de Mana PK2 (CDH) **3** *V. mera* ♀, Guyana, Tumatumari, Rio Potaro (CUIC) **4** *V. mediorosea* holotype ♂, Brazil, Santa Catarina, Jaraguá do Sul (CUIC) **5** *V. mediorosea* paratype ♂, Brazil, São Paulo, São José do Barreiro, Bocaina, 1539 m (CGCM) **6** *V. mediorosea* paratype ♀, Argentina, Misiones, Iguazu (MWM) **7** *V. mediorosea* paratype ♀, Brazil, Santa Catarina, São Bento do Sul, Rio Natal, 550 m (CGCM) **8** *V. mediorosea* ♀, "type" of *Macessoga flavirosa*‡ Jones (manuscript name), Brazil, Paraná, Castro (NHMUK). Scale bar: 1 cm.

Additional specimens examined. (4 ♂, 1 ♀ total) **FRENCH GUIANA:** 1 ♂, Route de Mana PK2: 27.VII.2001, M. Laguerre, genitalia prep. D. Herbin ref. H 1118, Bc-Her 2945 (CDH). **GUYANA:** 1 ♂, Tumatumari: I.1908, S.M. Klages, Rothschild Bequest B.M. 1939–1, St Laurent diss.: 7-7-16:2 (NHMUK). 1 ♀, Tumatumari, Rio Potaro, St Laurent diss.: 5-17-16:5 (CUIC). **BRAZIL: Amazonas:** 1 ♂, São Paulo de Olivença, Rio Solimões: 22.II.1930, H. S. Parish, Cornell U. Lot 672, Sub 386 [abdomen missing, no genitalia preparation] (CUIC). **Roraima:** 1 ♂, Ilha de Maracá, Alto Alegre: 26.XI–2.XII.1987, Mielke & Casagrande (DZUP).

Diagnosis. *Vanenga mera* can be distinguished from the following species in both sexes. Usually *V. mera* is smaller, and always bears a distinct discal mark which is often absent in *V. mediorosea* sp. n. In both sexes, the postmedial line terminates apically in *V. mera* but is clearly preapical in *V. mediorosea* sp. n. In males, the forewings are stouter and less sharply angled apically, and the ground color is more tan-orange to fawn, with very little if any pink coloration. Ventrally, the forewing postmedial line is wavier in *V. mera*. The female is much lighter colored dorsally than the female of *V. mediorosea* sp. n., with an almost yellow ground color and a pinkish hue submarginally, unlike the brown to orange-brown females of *V. mediorosea* sp. n. which are usually more grayish brown submarginally. Genitalia are also useful in differentiating these two species. In *V. mera* the uncus is not indented when viewed laterally and the gnathos consists of flattened, ovoid lobes with a single tooth mesally, rather than the heavily sclerotized, thumb-like projections of *V. mediorosea* sp. n. Finally, the valves are broader, and the dorsal projections of the phallus-juxta complex are elongated, curved, and only weakly spined, not short, stout, and heavily spined as in *V. mediorosea* sp. n. The female genitalia can be differentiated from those of *V. mediorosea* sp. n. by the sclerotized ring of VIII, which is incomplete in *V. mera* and complete in *V. mediorosea* sp. n. Furthermore, the apophyses are longer in *V. mera*, with the apophyses anteriores actually being absent in *V. mediorosea* sp. n.

Description. Male. *Head*: As for genus but darker orange to almost red-orange. *Thorax*: As for genus but pale pink scales absent. *Legs*: Coloration as for thorax, but with darker orange scales, especially on tibia and tarsus, similar in coloration to that of head. Tibial spurs short, curved, naked or dorsally clothed in scales. *Forewing dorsum*: Forewing length: 11–13 mm, avg.: 12 mm, wingspan: 24–25 mm, avg.: 24.5 mm [26 mm in Dognin (1924)], n = 2. Short, stout, subtriangular, apically rounded, margin nearly straight to slightly convex. Ground color pale tan-orange, overall lightly speckled by dark brown petiolate scales, particularly submarginally. Antemedial line absent or as faint brown wavy mark. Postmedial line nearly straight, apical, brown. Antemedial and medial areas concolorous, pale orange-tan. Submarginal area darker orange-brown compared to medial area, usually orange-brown with pale diffuse gray coloration near apex. Discal spot always present as small dark gray-brown spot. Fringe orange-tan. *Forewing ventrum*: Similar to dorsum but darker, more uniformly orange, becoming gray distally. Discal spot always present, usually larger, darker than on dorsum. Postmedial line preapical, not as straight as on dorsum. Petiolate scales more abundant, widely dispersed. *Hindwing dorsum*: Rounded, coloration and patterning as for forewing dorsum, antemedial line absent, postmedial line mostly straight, submarginal area broader than on forewing dorsum. *Hindwing ventrum*: Follows same pattern as forewing ventrum. *Abdomen*: As for genus. *Genitalia*: (Fig. 10) n = 2. As for genus but uncus laterally smoothly curving or nearly straight, not indented mesally. Gnathos as pair of ovoid, flattened lobes with sharp tooth emanating from center of lobe. Valves triangular, somewhat angled distally, relatively broad. Valves with baseo-mesal indentation bearing thick patch of heavy setae; base of valves barely extend past vinculum inward into body cavity as narrow, triangular extension loosely connected to diaphragm and juxta.

Juxta fused to phallus, encircling it as oddly shaped saucer with two pairs of elongate, curved, weakly spined projections superior to phallus, one pair longer than the other. Phallus short, cylindrical, not much longer than juxtal extensions. **Female.** *Head*: As in male but broader, antennae much smaller overall, pectinations particularly shorter. *Thorax*: As in male. *Legs*: As in male, but tibial spurs shorter. *Forewing dorsum*: Forewing length: 15 mm, wingspan: 27 mm, n = 1. Similar to male but broader, margin convex mesally, submarginal area broader, apex more acute. Coloration lighter, lemon yellow, more diffuse between antemedial, medial, and submarginal areas, less distinctly bicolored. Submarginal area pinker than medial area. *Forewing ventrum*: Similar to dorsum but generally darker orange. *Hindwing dorsum*: Coloration and pattern as for forewing dorsum. *Hindwing ventrum*: Follows same pattern as forewing ventrum but with more pinkish-gray hue. *Abdomen*: Concolorous with thorax, ventrally darker, distal tip with small tuft of elongated scales. *Genitalia*: (Fig. 13) n = 1. Small overall, most characters atrophied, VIII as weakly sclerotized plate, posteriorly curved, laterally VIII more heavily sclerotized. Apophyses anteriores less than half length of apophyses posteriores but robust, terminating in flat tip, apophyses posteriores elongate, curving outward, narrower than apophyses anteriores. Lamellae absent, replaced by broad membranous area. Ductus bursae broad, bag-like. Corpus bursae narrow, elongated, nearly twice length of VIII–IX. Papillae anales flattened ventrally, elongated and narrow.

Distribution (Fig. 15). This species has an Amazonian distribution, and has so far been collected in Guyana, French Guiana, and the Brazilian states of Amazonas, Pará, and Roraima.

Remarks. Until the present work, all *Vanenga* specimens have been treated as *V. mera* in the literature and various worldwide collections, but external and genital morphology, as well as biogeography, clearly separates the genus into two well-distinct species, with the name *V. mera* only being applicable to the rarely collected Amazonian species. In Schaus's (1928) treatment of Mimallonidae, he considered all populations to be this one species; hence his records for Southeastern Brazil and Paraguay can be attributed to the following new species, now formally described below.

Vanenga mediorosea **sp. n.**

http://zoobank.org/8E8A6963-2C55-4E40-8B71-78AA20BA3DEA
Figs 4–9, 11, 12, 14, 15

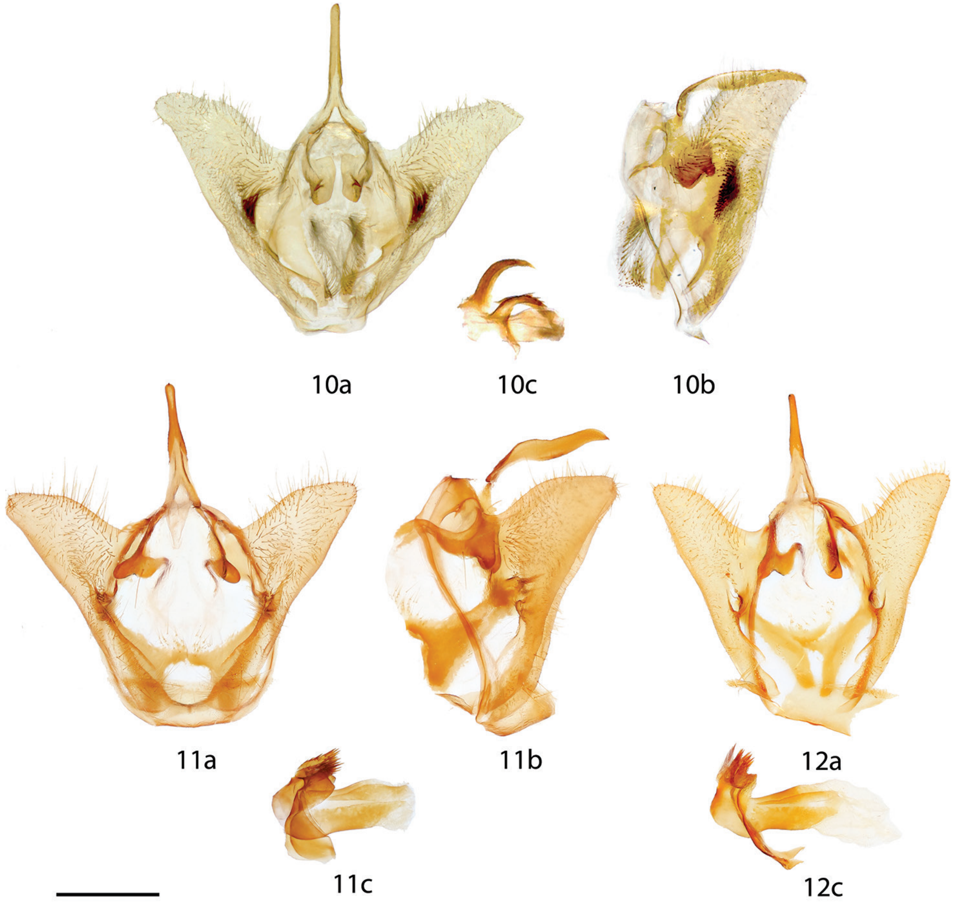
Vanenga mera; Schaus 1928, in part

Type material. Holotype, ♂. **BRAZIL: Santa Catarina:** Jaragua [Jaraguá do Sul], Santa Catarina, Brazil, 5 Dec 1935, Fritz Hoffman/ *Vanenga mera* Dognin [illegible]?/ St Laurent diss.: 5-17-16:1/ HOLOTYPE male *Vanenga mediorosea* St Laurent and Herbin, 2017 [handwritten red label]/ (CUIC).

Paratypes. (103 ♂, 8 ♀ total) **BRAZIL: Bahia:** 1 ♂, Jequié, 13°56'S, 40°11'W: III.2012, H. Thöny leg., genitalia prep. No. 29.240 (MWM). **Espírito Santo:** 7 ♂,

Figure 9. *Vanenga mediorosea* ♂, Brazil, Rio Grande do Sul, Santa Maria, 15.XII.2015, at MV light, photo R. St Laurent (specimen not collected).

Santa Leopoldina, Dorf Tirol, 24°75'S, 40°50'W [coordinates may be incorrect], 700 m: 22–31.X.1996 (2 ♂), 8–20.XII.1996 (3 ♂), genitalia prep. No. 29.237, VI.1998 (1 ♂), X.1999 (1 ♂), H. Thöny leg. (MWM). 1 ♂, Santa Leopoldina, Dorf Tirol, 20°10'S, 40°33'W, 700 m: XI.2000, H. Thöny leg. (MWM). 1 ♂, Aracruz: 12.III.1993, João B. Silva [leg.], Coleção Embrapa-CPAC No. 20903 (CPAC). 8 ♂, Linhares, 40 m: 20–29.II.1992 (2 ♂), 5–9.IV.1992 (5 ♂), 25–30.I.1998 (1 ♂), V.O. Becker col., Col. Becker 80934, 82021, 113494, USNM-Mimal: 2059, 2171–2175, 2185, 2186 (USNM). 2 ♂, No additional locality data: USNM-Mimal: 1683, 2539 (USNM). **Rio de Janeiro:** 1 ♂, 1 ♀, Petrópolis: 4.XII.1928, 24.IV.1960, Gagarin leg., ex. col. Gagarin (DZUP). 1 ♂, Angra-Jussaral: 28.XI.1935, No. 19.200 (DZUP). 1 ♂, Barreira, Teresópolis, 400 m: 26–29.IV.1957, Pearson H. G., No. 19.199 (DZUP). 1 ♀, Indepêndencia, Petrópolis, 900 m: 16.X.1934, Gagarin leg., ex. col. Gagarin (DZUP). 1 ♂, Reserva Ecológica de Guapiaçu, Cachoeiras de Macacu: 25.I.2011, Tangerini Col., Ex. col. Nirton Tangerini (DZUP). 1 ♂, Boca do Mato, Cachoeira de Macacu: 11–20.X.1996, Tangerini leg. (MWM). 7 ♂, Maricá, 5 m: 12–15.I.1985 (5 ♂), 11.X.1995 (2 ♂), V.O. Becker col., Col. Becker 54454, 65200, USNM-Mimal: 2169, 2170, 2177–2181, St Laurent diss.: 8-22-16:5 (USNM). **São Paulo:** 3 ♂, Est. Biol. Boracéia, nr. Salesópolis, 850 m: 13.III.1972 (1 ♂), 14.III.1972 (2 ♂), St Laurent diss.: 5-17-16:2, E.G., I. & E.A. Munroe (CNC). 1 ♂, Salesópolis, Boracea [Boracéia], 850 m: 14–18.II.1950, Trav. Trav. Filho, Pearson, & Rabello coll., Brit. Mus. 1962–112 (NHMUK). 2 ♂, Boracéa [Boracéia], Salesópolis: 8–14.II.1959, Travassos, Kloss, & Pearson leg., HRP 2090, 2091, 2094, *Vanenga mera* Dognin Pearson det., USNM-Mimal: 2182, 2183 (USNM). 3 ♂, Guapiara, Paivinha, 800 m: 2–5.V.2005, 18–21.XII.2005, 3–6.IV.2007, C. Mielke leg., Col. C. Mielke 28.580, 30.041, 32.043 (CGCM). 2 ♂, São José do Barreiro, Bocaina, 22°43'37"S, 44°37'57"W, 1539 m: 2–6.I.2016, C. Mielke leg., Col. C. Mielke 31.330, 31.335, C. Mielke gen. prep. 31.330 (CGCM). 8 ♂, Alto da Serra [Paranapiacaba]: XI.1922, XII.1922, III.1925, II.1926, IV.1926, R. Spitz, Rothschild Bequest, B.M. 1939–1 (NHMUK). 1 ♂, Cantareira: Coll. R. Spitz, Brit. Mus. 1962–112 (NHMUK). 1 ♂, Ypiranga [Ipiranga]: IV.1924, R. Spitz, Rothschild Bequest, BM 1939–1 (NHMUK). 1 ♀, Araçatuba, 450 m: 2.IV.1913, E.D. Jones, E.D. Jones Coll., Brit. Mus. 1919–295, St Laurent diss.: 7-7-16:3 (NHMUK). **Paraná:** 1 ♂, Ponta Grossa: I.1956, Coleção F. Justus Jor, at light (DZUP). 1 ♂, Foz do Iguaçu, 200 m: 16.II.1969, Moure & Mielke (DZUP). 1 ♂, Rolândia: XII.1952, Maller col., Brit. Mus. 1962–112 (NHMUK). 10 ♂, Curitiba, Serra do Mar, Estrada de Castelhanos, 500 m: 30.XI.1997 (2 ♂), III.1998 (3 ♂), IV.1998 (5 ♂), H. Thöny leg. (MWM). 1 ♂, Jaguariaíva, Parque Estadual do Cerrado 24°10'4.98"S, 49°39'59.35"W: 28.II.2015, Andrew D. Warren leg., MV light (ADW). **Santa Catarina:** 1 ♂, Jaragua [Jaraguá do Sul]: 5.XII.1935, Fritz Hoffmann (CUIC). 2 ♂, Blumenau: X, Br. Pohl, Cornell U. Lot 819, Sub 322, "Paratype" [blue label], *Cicinnus roseatincta*‡ Schaus No. 697 Paratype [manuscript name], St Laurent diss.: 5-17-16:3 (CUIC). 1 ♂, Blumenau: "671," USNM-Mimal: 2538 (USNM). 1 ♀, São Bento do Sul, Rio Natal, 550 m: XI.2013, A. Rank leg., Col. C. Mielke 28.007 (CGCM). 2 ♂, São Bento do Sul, Serra Rio Natal, 850 m: VII.1998, XI.1998, H. Thöny leg., genitalia prep. No. 29.238, 29.239 (MWM). 3 ♂, No additional locality data: F. Hoffman, USNM-Mimal: 2534, 2535, 2537, specimen 2537 with label "Saturniidae ?" (USNM). 1 ♂, Hansa Humbolt [Corupá]: "10," USNM-Mimal: 2540, St Laurent diss.: 8-22-16:4 (USNM). 1 ♂, Joinville, 500 m: 3.I.1989, V.O. Becker [leg.], Col. Becker 60597, USNM-Mimal: 2176 (USNM). **Rio Grande do Sul:** 5 ♂, Pelotas: 5.IV.1954, 27.III.1959, no date, C.M. Biezanko, B.M. 1954–395, 1961–209 (NHMUK); 18.III.1953, 15.IV.1953, C.M. de Biezanko, No. 753, St Laurent diss.: 5-17-16:4 (CUIC). 2 ♂, Guarani [das Missões]: 3.III.1932, C.M. de Biezanko, No. 753, St Laurent diss.: 2-26-16:5 (CUIC). **PARAGUAY: Guairá:** 1 ♀, Villarica: XI.1927, F. Schade [leg.], Joicey Bequest, Brit. Mus. 1934–120 (NHMUK). 1 ♀, Villarica: 18.IV.1925, F. Schade Coll., Collection Wm Schaus, USNM-Mimal: 2541, [handwritten label in Schaus's handwriting:] "*Cicinnus meroides*‡ [or *meroidea*‡] type Schaus mss" (USNM). **Caazapá:** 1 ♂, Cristal, San Juan de Nepomuceno: XII.1998 (MWM). **Alto Paraná:** 1 ♂, Reserva Biológica Limoy, 24°47'S, 54°26'W: 17–20.IV.1986, M. Pogue & M. Solis [leg.], USNM-Mimal: 2407 (USNM). 1 ♂, Limoy, 24°45'S, 54°27'W, 245 m: 01–05.XI.2009, U. Drechsel [leg.] (CDH). 1 ♂, 1 ♀, Estancia Dimas, 25°33'S, 55°13'W, 200 m: 24–26.III.2011 (1 ♂), 26–31.I.2012 (1 ♀), U. Drechsel [leg.] (CDH). **Canindeyú:** 4 ♂, Armisticio, 24°34'S, 54°32'W, 290 m: 26–30.XI.2009, U. Drechsel [leg.] (CDH). 1 ♂, Carapá, 24°22'S, 54°23'W, 240 m: 1–4.IV.2009, U. Drechsel [leg.] (CDH). **Ñeembucú:** 1 ♂, Zanjita, 26°03'S, 57°56'W, 50 m: 1–3.III.2013, U. Drechsel [leg.] (CDH). **Paraguarí:** 1 ♂, Mbatoví, 25°35'S, 57°05'W, 383 m: 17–18.IV.2014, U. Drechsel [leg.], genitalia prep. D. Herbin ref. H 1120, Bc-Her4967 (CDH). **Amabay:** 1 ♂, Parque nacional Cerro



Figures 10–12. *Vanenga* male genitalia, **a** ventral **b** lateral **c** phallus. **10** *V. mera*, Guyana, Tumatumari, St Laurent diss.: 7-7-16:2 (NHMUK) **11** *V. mediorosea* holotype, Brazil, Santa Catarina, Jaraguá do Sul, St Laurent diss.: 5-17-16:1 (CUIC) **12** *V. mediorosea* paratype, Brazil, Rio Grande do Sul, Guarani das Missões, St Laurent diss.: 2-26-16:5 (CUIC). Scale bar: 1 mm.

Corá, 22°39'S, 56°01'W: 7–10.IV.1986, M. Pogue & M. Solis [leg.], USNM-Mimal: 2757, St Laurent diss.: 8-22-16:6 (USNM). **ARGENTINA: Misiones:** 1 ♂, 1 ♀, Iguazu: 23–26.XI.1993, J.R., genitalia prep. no. 29.236 [♀] (MWM). **Santa Fe:** 4 ♂, Villa Ana, Ferrocarril Provincial de Santa Fe: III.1924, K.J. Hayward [leg.], Brit. Mus. 1924–203, [genitalia] vial NHMUK010402135, NHMUK010318285 (NHMUK). **URUGUAY: Maldonado:** 1 ♂, Piriápolis: 8.II.59 [interpretation of "8/11/59"], F. Penades [leg.] (NHMUK). – All paratypes with the following yellow label: PARATYPE male/female *Vanenga mediorosea* St Laurent and Herbin, 2017.

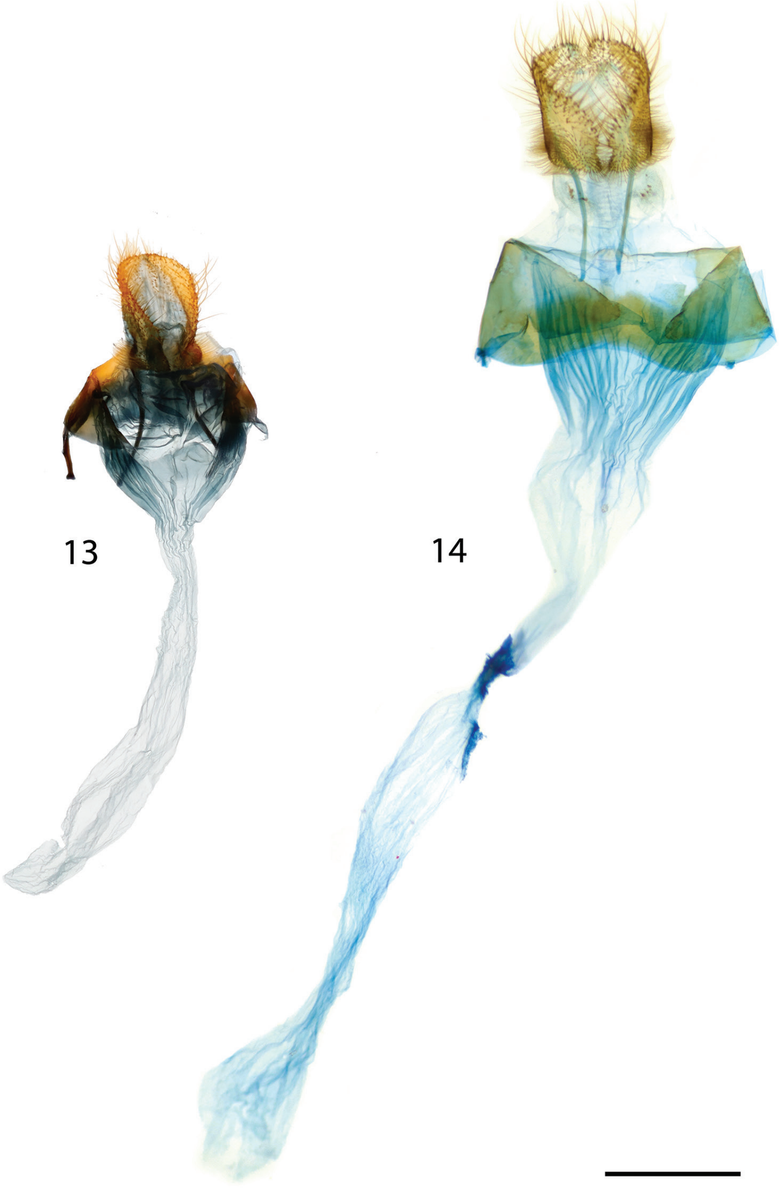
Additional specimens examined. [not to be included in type series] (1 ♂, 1 ♀ total) **BRAZIL: Rio Grande do Sul:** 1 ♂, Pelotas: 18.III.1953, C.M. de Biezanko [leg.], No. 753 (ex. CUIC donated to CMNH). **Paraná:** 1 ♀, Castro, 950 m: E.D.

Jones, E.D. Jones Coll. Brit. Mus. 1919–295, "*Perophora flavirosa*‡ Type ♀ D-Jones" [manuscript name], "*Macessoga flavirosa*‡ (Jones) type genit. pr. No 9, Mimallonidae" [genitalia prep. lost], NHMUK010354541 (NHMUK).

Photo of living specimen examined. [not to be included in type series] **BRAZIL: Rio Grande do Sul:** 1 ♂, Santa Maria, -29.697441°, -53.920125°, 119 m: 15.XII.2015, R.A. St. Laurent & A.P.S. de Carvalho leg., at MV light (Fig. 9).

Diagnosis. For characters differentiating this new species from the previous one, see the diagnosis of *V. mera*.

Description. Male. *Head*: As for genus, varying shades of orange fading to pale tan. *Thorax*: Straw colored, usually with pale pink scales, darker brown-orange scales may be present on prothoracic collar. *Legs*: Coloration as for thorax, but usually darker orange with rosy scales, vestiture fine, tibial spurs short, curved, naked or dorsally clothed in scales. *Forewing dorsum*: Forewing length: 10–17 mm, avg. 13.7 mm, wingspan: 23.0–32.5 mm, avg. 27.2 mm, n = 50. Triangular, apically angled, margin nearly straight though may be barely concave or convex. Ground color pale tan-orange to gray-salmon, with varying degree of pale to strong pink coloration antemedial and medially, overall lightly speckled by dark brown petiolate scales, though petiolate scales often absent medially. Antemedial line absent or as faint brown or gray wavy mark. Postmedial line preapical, faint, straight, dark brown to black, distally curved to costa, fading after passing Rs3 or Rs4. Antemedial and medial areas concolorous, pale pink. Submarginal area always darker than medial area, usually orange-brown with diffuse gray coloration along wing margin, petiolate scales more abundant. Discal spot usually absent, though sometimes present as small, dark brown or black spot. Fringe orange-tan with light pink hue. *Forewing ventrum*: Similar to dorsum but coloration of medial and submarginal area more similar, more uniformly darker orange, becoming gray distally, usually also pink nearer to thorax. Discal spot always present, oblong or circular. Postmedial line may be somewhat wavy or very faint. Petiolate scales more abundant, widely dispersed. *Hindwing dorsum*: Rounded, coloration and patterning as for forewing dorsum, antemedial line absent, postmedial line straight, submarginal area broader than on dorsum. *Hindwing ventrum*: Follows same pattern as forewing ventrum, but rosier pink overall than orange, especially antemedial and medially. *Abdomen*: As for genus. *Genitalia*: (Figs 11, 12) n = 15. As for genus but uncus indented mesally when viewed laterally. Gnathos as pair of heavily sclerotized, downward angled protuberances of variable thickness and length. Valves triangular, somewhat angled distally, relatively narrow, acute. Valves with baseo-mesal indentation usually bearing small patch of heavy setae; base of valves extend well past vinculum inward into body cavity as singular bifurcated extension loosely connected to diaphragm and juxta. Juxta fused to phallus, encircling it as oddly shaped saucer with two pairs of dorsal projections superior to phallus, projections short and heavily spined. Phallus short, cylindrical, not much longer than width of juxtal saucer. Vesica bag-like, small. **Female.** *Head*: As in male but antennae much smaller overall, pectinations particularly shorter. *Thorax*: As in male though may be darker brown overall. *Legs*: As in male, but tibial spurs shorter. *Forewing dorsum*: Forewing length: 12.0–14.5 mm, avg. 13.9 mm, wingspan:



Figures 13, 14. *Vanenga* female genitalia. **13** *V. mera* Guyana, Tumatumari, Rio Potaro, St Laurent diss.: 5-17-16:5 (CUIC) **14** *V. mediorosea* paratype, Argentina, Missiones, Iguazu, genitalia prep. No. 29.236 (MWM). Scale bar: 1 mm.

26–31 mm, avg. 28.5, n = 4. Forewing broader than in male, more elongated, convex mesally, submarginal area broader, apex more acute. Coloration generally more diffuse between antemedial, medial, and submarginal areas, less distinctly bicolored. Overall darker orange-brown antemedial and medially, submarginal area lighter gray compared to medial area. Postmedial line usually more bowed outward than in male. *Forewing ventrum*: Similar to dorsum but generally paler orange. *Hindwing dorsum*: Coloration and pattern as for forewing dorsum. *Hindwing ventrum*: Follows same pattern as forewing ventrum. *Abdomen*: As for genus. *Genitalia*: (Fig. 14) n = 2. Small overall, most characters atrophied, VIII as moderately sclerotized ring, posteriorly curved, ventrally angled inward forming anteriorly directed angle with ostium at apex. Apophyses anteriores absent, apophyses posteriores elongate, but not much longer than length of extended IX. Sclerotized lamella antevaginalis absent, replaced by broad membranous area. Ductus bursae broad, bag-like. Corpus bursae narrow, elongated, more than twice length of VIII–IX. Papillae anales flattened ventrally, elongated and narrow.

Distribution (Fig. 15). This new species is broadly distributed in the Brazilian Atlantic Forest in the states of Bahia south through Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul. *Vanenga mediorosea* is also found in the Pampa biome of Rio Grande do Sul (Brazil) and Uruguay, and is found in neighboring Paraguay and Argentina in various habitats, particularly in inland forests (Alta Paraná) and Humid Chaco.

Etymology. This species is named for the pink-flushed (*rosea* meaning pink, Latin) medial (*medio* Latin) area of the forewings.

Remarks. As previously mentioned, *V. mediorosea* is much more commonly collected than *V. mera*, and thus the vast majority of *Vanenga* specimens are mislabeled as *V. mera* in major collections. Furthermore, *V. mediorosea* is often present in series in collections rather than singletons as is *V. mera*.

In performing the research necessary for this revision, we have discovered "types" of *Vanenga* specimens bearing manuscript names, but which were apparently never described. In the NHMUK there is a single female specimen labeled as a type of *Perophora flavirosa*‡ Jones from Brazil, Paraná, (Fig. 8), curated together with other females of *V. mediorosea*, and clearly this "type" belongs to the species that we describe herein. This specimen is also labeled as a "type" of *Macessoga flavirosa*‡ (Jones). However, we are unaware of any publication using this name in either combination by Jones from the period of time when he was describing Mimallonidae, and thus it is a manuscript name without an associated formal description. The genitalia preparation associated with this species is lost; therefore we omit it from the type series of *V. mediorosea*.

Additionally, in the CUIC there are two specimens labeled as "paratypes" of *Cicinnus roseatincta*‡ Schaus, apparently from prior to 1928 since Schaus did not label these as *Vanenga* specimens (a genus he described for *V. mera* in 1928). A holotype bearing this name has not been located. In Schaus (1928), he lists *V. mera* as being present in Blumenau, Santa Catarina, Brazil, which incidentally, is the locality of these two "paratypes." Therefore, we can infer that Schaus never formally described this species; otherwise the Brazilian specimens would not have been listed under *V. mera* in his revision. Similarly, there is a female specimen at the USNM labeled as a "type" (in Schaus's handwriting) of *Cicinnus meroides*‡ (or *meroidea*‡, the final letter is illegible, regardless in reference to "near *mera*"). This label bears the letters "mss" subsequently written in pencil over the name. Therefore, this seems to be yet a third manuscript name associ-

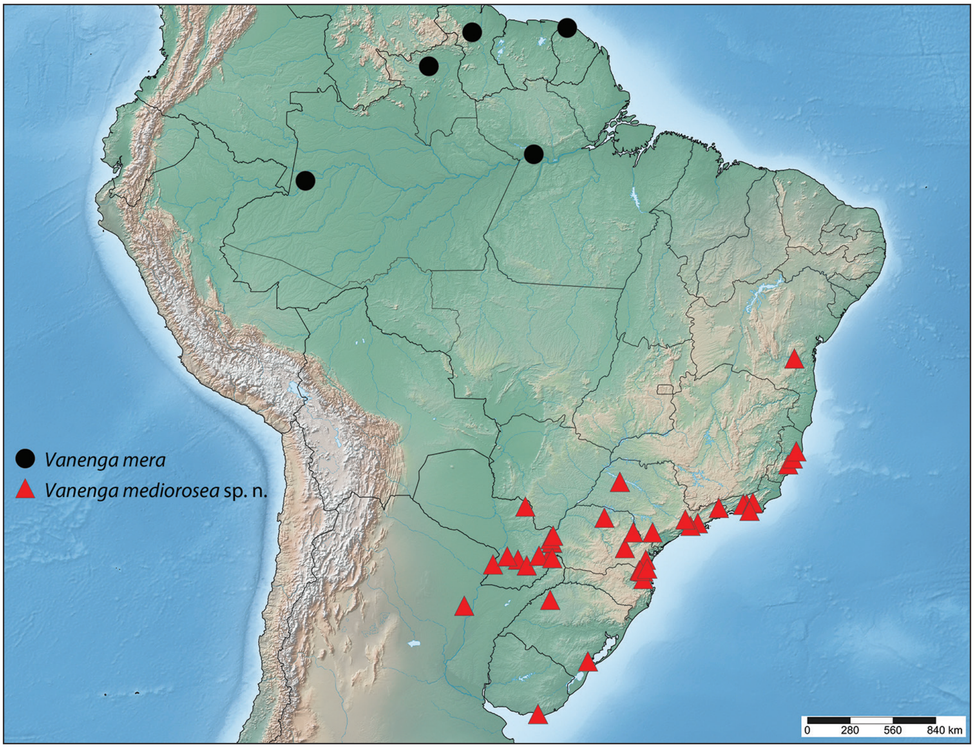


Figure 15. Known distribution of *Vanenga*.

ated with this species, though again, never formally described for the same reasons as mentioned previously.

If any or all of these hereby-unavailable names is/are located in the literature, it would be necessary to treat *V. mediorosea* as a synonym of the most senior name.

Vanenga mediorosea is rather consistent in coloration and markings across its range, though occasionally some specimens are darker brown-orange submarginally and more salmon colored medially. We also note some geographic variation in the length of the gnathos protuberance, which is shorter at the northern and southern extremities of the range (Bahia and Rio Grande do Sul respectively) than centrally along the distribution, such as those from Santa Catarina and São Paulo. There seems to also be some size variation depending on elevation, with larger specimens coming from higher elevations. Two male specimens (Brazil, São Paulo, near São José do Barreiro, 1539 m) from higher elevation than all other examined material are the largest of the examined specimens (Fig. 5). Additional specimens from Salesópolis (also São Paulo state) are also quite large in comparison with lower elevation material from coastal Brazil (such as Rio de Janeiro, Maracá and Espírito Santo, Linhares for example) and Paraguay. Genitalia of specimens from various elevations however, are consistent. It is interesting to note that the higher elevation specimens are actually larger than many from lower elevations.

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The mammalian faunas endemic to the Cerrado and the Caatinga

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Abstract

We undertook a comprehensive, critical review of literature concerning the distribution, conservation status, and taxonomy of species of mammals endemic to the Cerrado and the Caatinga, the two largest biomes of the South American Dry-Diagonal. We present species accounts and lists of species, which we built with criteria that, in our opinion, yielded results with increased scientific rigor relative to previously published lists – e.g., excluding nominal taxa whose statuses as species have been claimed only on the basis of unpublished data, incomplete taxonomic work, or weak evidence. For various taxa, we provided arguments regarding species distributions, conservation and taxonomic statuses previously lacking in the literature. Two major findings are worth highlighting. First, we unveil the existence of a group of species endemic to both the Cerrado and the Caatinga (i.e., present in both biomes and absent in all other biomes). From the biogeographic point of view, this group, herein referred to as Caatinga-Cerrado endemics, deserves attention as a unit – just as in case of the Caatinga-only and the Cerrado-only endemics. We present preliminary hypotheses on the origin of these three endemic faunas (Cerrado-only, Caatinga-only, and Caatinga-Cerrado endemics). Secondly, we discovered that a substantial portion of the endemic mammalian faunas of the Caatinga and the Cerrado faces risks of extinction that are unrecognized in the highly influential Red List of Threatened Species published by the International Union for Conservation of Nature (IUCN). “Data deficient” is a category that misrepresents the real risks of extinction of these species considering that (a) some of these species are known only from a handful of specimens collected in a single or a few localities long ago; (b) the Cerrado and the Caatinga have been sufficiently sampled to guarantee collection of additional specimens of these species if they were abundant; (c) natural habitats of the Cerrado and the Caatinga have been substantially altered or lost in recent decades. Failures either in the design of the IUCN criteria or in their application to assign categories of extinction risks represent an additional important threat to these endemic faunas because their real risks of extinctions become hidden. It is imperative to correct this situation, particularly considering that these species are associated to habitats that are experiencing fast transformation into areas for agriculture, at an unbearable cost for biodiversity.

Keywords

Brazil, Bolivia, biogeography, checklist, conservation, Dry Diagonal, evolution, habitat, mammals, nomenclature, savannas, taxonomy

Introduction

The Caatinga and the Cerrado are the two largest biomes of the so-called Dry Diagonal of South America – a massive belt of land characterized by low precipitation and high seasonality – and together they occupy more than 30% of the Brazilian territory. The latter constitutes a vast (2 million km^2) mosaic of xeromorphic vegetation types, from either dry (*campo limpo*) or humid (*campo úmido*) grasslands to woodlands (*cerradão*), and also harboring gallery forests, and patches of deciduous and semideciduous forests (Silva and Bates 2002, Voss et al. 2009, Carmignotto et al. 2012). The Cerrado encompasses areas from northeastern to southwestern Brazil, eastern Bolivia, and northern Paraguay. With deep soils rich in Aluminum, the Cerrado is irrigated by perennial watercourses (Coutinho 2006); its dry season lasts four months per year, with the rainfall concentrated in the wet season, and averaging annual values of 800–2000 mm (Ab'Sáber 1974, Nimer 1989). Neighboring the Cerrado is the Caatinga, a biome that occupies an extensive area (800,000 km^2) of northeastern Brazil (Prado 2008). Its predominant habitat types are dry forests and xeric scrubs, although it also harbors patches of savannas (Andrade-Lima 1981). The climate of the Caatinga is markedly hot and dry, with highly erratic rainfall ranging from 240 to 1500 mm (Sampaio 1995, Prado 2008), and a severe period of drought lasting at least 5 months with high temperatures (Nimer 1989).

The Caatinga and the Cerrado harbor unique mammalian faunas whose evolutionary origin, biogeography, and conservation status remain poorly understood. Contrary to the mammalian fauna from open vegetation formations of northern South America (see Gutiérrez et al. 2014 and references therein), the mammals of the Caatinga and Cerrado biomes in northeastern, central, and southwestern South America have received some attention. New species either endemic to or predominantly distributed in these two biomes have been described (e.g., Sazima et al. 1978, Moojen et al. 1997, Bonvicino 2003, Bonvicino et al. 2003); data on the distribution of members of these faunas have been published (e.g., Marinho-Filho and Veríssimo 1997, Bezerra et al. 2007, 2010, Sá-Neto and Marinho-Filho 2013); patterns of phylogeographic variation have been detected (e.g., Carvalho et al. 2011, Nascimento et al. 2013); and assessments of their extinction risks have been conducted (e.g. Zimbres et al. 2012). In addition, a few studies have synthetized various kinds of ecological and biogeographic information of the mammalian faunas from the Caatinga and the Cerrado (Marinho-Filho et al. 2002, Oliveira et al. 2008, Carmignotto et al. 2012). Despite these valuable contributions, the study of these unique faunas remains in its infancy.

In order to facilitate further research, herein we provide lists and species accounts of the mammal species endemic to the Caatinga and the Cerrado. These species account focus on geographic distributions and conservation statuses according to published assessments. Due to the importance of clarifying taxonomic issues for biodiversity conservation (Gutiérrez and Helgen 2013), we provide discussions for taxa with unclear taxonomic statuses integrating all sources of relevant information currently available in the literature. We also conducted a critical discussion of the conservation status of our focal faunas. This aspect is particularly important taking into account that, due to expansion of land used for agriculture, only 47% of the original vegetation of the Cerrado remains (Beuchle et al. 2015), and its protected areas cover about 2% of this biome (Klink and Machado 2005), and that whereas the Caatinga preserves a larger portion of its original vegetation (63%; Beuchle et al. 2015), only ca. 1% of it is under strict federal protection, and it is being affected by accelerated desertification (Albuquerque et al. 2012).

Methods

We conducted a critical review of literature concerning the distribution and conservation of mammalian species endemic to the Cerrado and the Caatinga. We used four main sources for constructing a preliminary list of focal species. These sources are the modern syntheses of the mammals of the Cerrado (Marinho-Filho et al. 2002) and the Caatinga (Oliveira et al. 2008), and their most recent update (Carmignotto et al. 2012); the most recent list of the mammals of Brazil (Paglia et al. 2012); and the two currently available volumes of the book series Mammals of South America (Gardner 2008, Patton et al. 2015). The preliminary list was then refined to obtain a final list by: (1) considering information from a plethora of studies published in peer-reviewed journals and books; (2) removing species for which no enough evidence of their nature as either endemic or valid species have been published – this applied also to cases in which authors mentioned the existence of unpublished data or manuscripts in support of their views, but such information remain unavailable for scientific scrutiny.

Two considerations regarding the scope of the present study need to be made. First, the geographic scope of our study differs from some of those used in previous studies. For example, contrary to Carmignotto et al. (2012), we did not regard the Pantanal as part of the Cerrado, as we consider it to be a biome itself, with particular influences from other humid biomes (see Werneck 2011 and references therein).

Second, although differentiated, isolated populations that are often recognized as subspecies can be of importance from the conservation point of view, given the limited knowledge currently available about these faunas, we herein focused only on taxa recognizable at the species level.

We constructed species accounts composed primarily of two sections, distribution and conservation, but when necessary we also included an additional section devoted to taxonomic and nomenclatural considerations. For the distribution section, we indicated whether the species is endemic to the Cerrado, the Caatinga, or both, and presented a list of the administrative entities for which records supported by voucher specimens exist – with the only exceptions of *Cebus libidinosus* and *Lycalopex vetulus*, species for which some of the literature cited included ecological studies and direct observations made by mammalogists on free ranging individuals. We refer to publications that reported such records. We considered species as "endemic" in a strict way. That is, we excluded from our list of endemic species those that despite being predominantly distributed in the Cerrado, the Caatinga, or both, also occur in other biomes in areas that do not match patches of Caatinga or Cerrado vegetation. To do so, we followed the limits of the Brazilian biomes as defined by the *Instituto Brasileiro de Geografia e Estatística* (IBGE 2004a) and information reported in the literature regarding habitat types at collection localities. We did include in our list of endemics those species for which marginal records exist in the ecotones between our focal biomes (the Cerrado and the Caatinga) and other biomes, or in patches of Cerrado or Caatinga vegetation nearby the current contact zones between these and their neighbor biomes. Similarly, in cases in which a species was predominantly distributed in one of our focal biomes (e.g., the Caatinga) and transitional areas/ecotones with our other focal biome (i.e., the Cerrado, in this example), we considered that species endemic to the focal biome in which it is predominantly distributed (i.e. the Caatinga, in this example). In addition, we flag cases in which species have been regarded in the literature as endemics to our focal biomes, but that either more recent or revisited information demonstrate that they are not. We also flag the existence of species only known from transitional areas between our focal biomes and other biomes, as well as known undescribed species that might be endemic to our focal biomes, but for which further research is necessary to understand their distribution. In addition to the geographic distribution, for each species we indicate whether it has been recorded in open vegetation formations, forest, or both types of habitat.

For the conservation section, we used two sources: (1) the IUCN Red List of Threatened Species (available at http://www.iucnredlist.org), consulted in October–December 2016 (see citations relevant to each species under *Species accounts*); and (2) the official national list of threatened species published by the Brazilian government (ICMBIO-MMA 2016). The latter list only mentions species to which a category of threat has been assigned (i.e., it does not include species that are not threatened). We compared the conservation status (risk of extinction) that these two sources assigned to each species, and provided recommendations to improve their accuracy with regard to the focal species of this study.

Results

Species accounts

Didelphimorphia, Didelphidae, Didelphinae, Thylamyini

Cryptonanus agricolai (Moojen, 1943)

Distribution. *Cryptonanus agricolai* is endemic to the Cerrado and the Caatinga, and has also been collected in contact zones between these biomes and the Amazon in northern Mato Grosso and southwestern Piauí states (Bezerra et al. 2009). Records of *C. agricolai* in the Atlantic forest were obtained from pellets of *Tyto alba* and might actually correspond to individuals captured in the Cerrado, the Caatinga, or both (Souza et al. 2010), as these owls can potentially forage through long distances (up to ~31 km; Hegdal and Blaskiewicz 1984). According to Bezerra et al. (2014), unpublished molecular data suggest that *C. agricolai* is absent from the Cerrado; however, we will refrain from adopting this view until these data become publicly available (contra Carmignotto et al. 2012). The current, known distribution of *C. agricolai* includes the Brazilian states of Ceará, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pernambuco, Piauí, Sergipe, and Tocantins (Voss et al. 2005, Bezerra et al. 2009, 2014, Carmignotto and Aires 2011, Bonvicino et al. 2012, Gómes et al. 2015, Gurgel-Filho et al. 2015, Hannibal and Neves-Godoi 2015, de la Sancha and D'Elía 2015). Alleged records from a locality in São Paulo state have been mentioned in the literature (see Martin et al. 2012), but they were made based on animals that were released (i.e., no voucher specimens are available) and identified using unreported criteria.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Cryptonanus agricolai* (see Carmignotto et al. 2016a). The species was not included in the official list of threatened species of Brazil (ICMBio-MMA 2016).

Thylamys (*Xerodelphis*) *karimii* (Petter, 1968)

Distribution. *Thylamys karimii* is endemic to the Cerrado and the Caatinga, and has been recorded in the Brazilian states of Bahia, Goiás, Mato Grosso, Minas Gerais, Pernambuco, Piauí, Rondônia, Sergipe, and Tocantins, and in the Distrito Federal (Carmignotto and Monfort 2006, Carvalho et al. 2009, Bruna et al. 2010, Carmignotto and Aires 2011, Bonvicino et al. 2012, Bezerra et al. 2014). The species has not been reported for Bolivia, but its presence on the Serranía de Huanchaca in the Santa Cruz department of that country might be expected (Giarla et al. 2010).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Vulnerable" to *Thylamys karimii* (see Carmignotto et al. 2016b). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

***Thylamys* (*Xerodelphis*) *velutinus* (Wagner, 1842)**

Distribution. *Thylamys velutinus* is endemic to the Cerrado, and has been recorded in the Brazilian states of Bahia, Minas Gerais, São Paulo, and in the Distrito Federal (Vieira and Palma 1996, Bonvicino and Bezerra 2003, Giarla et al. 2010, Bonvicino et al. 2014). Marginal records are known from transitional areas that harbor isolated patches of Cerrado vegetation embedded within the Atlantic Forest biome (see Caceres 2012 and references therein).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Near Threatened" to *Thylamys velutinus* (see Carmignotto and Astúa 2016). The species appears in the official list of threatened species of Brazil with the category "Vulnerable" (ICMBIO-MMA 2016).

Cingulata, Dasypodidae, Tolypeutinae, Tolypeutini

***Tolypeutes tricinctus* (Linnaeus, 1758)**

Distribution. *Tolypeutes tricinctus* is endemic to the Cerrado and the Caatinga (contra Wetzel et al. 2007), and has been recorded in the Brazilian states of Alagoas, Bahia, Ceará, Goiás, Maranhão, Paraíba, Pernambuco, Piauí, Sergipe, and Tocantins (Sanborn 1930, Moojen 1943; Silva and Oren 1993, Santos et al. 1994, Oliveira 1995, Marinho-Filho et al. 1997, Zimbres et al. 2012, 2013, Feijó et al. 2015a). The species had been traditionally considered an endemic of the Caatinga biome, however records of the species well within the Cerrado biome and in native Cerrado habitat type have been reported (Marinho-Filho et al. 1997; see also figure 2 in Feijó et al. 2015a).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Vulnerable" to *Tolypeutes tricinctus* (see Miranda et al. 2014). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Chiroptera, Phyllostomidae, Lonchophyllinae

***Lonchophylla bokermanni* Sazima, Vizotto & Taddei, 1978**

Distribution. *Lonchophylla bokermanni* is endemic to the Cerrado, where it has been collected in the Brazilian state of Minas Gerais (Dias et al. 2013, Teixeira et al. 2014, Almeida et al. 2016). Specimens collected in the Atlantic Forest of Brazil and previously identified as *L. bokermanni* (by Nascimento et al. 2013) actually correspond to the recently described *Lonchophylla peracchii* (Dias et al. 2013).

Conservation. The red list of the IUCN ver. 3.1 assigned the category "Endangered" to *Lonchophylla bokermanni* (see Aguiar et al. 2016; see also Teixeira et al. 2014). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Lonchophylla dekeyseri Taddei, Vizotto & Sazima, 1983

Distribution. *Lonchophylla dekeyseri* is endemic to the Cerrado (contra Leal et al. 2013), and has been collected in the Brazilian states of Goiás, Mato Grosso do Sul, Minas Gerais, and in the Distrito Federal (Taddei et al. 1983, Coelho and Marinho-Filho 2002, Aguiar et al. 2014, Moratelli and Dias 2015, Almeida et al. 2016). Additional specimens assigned to *L. dekeyseri* exist for the Bolivian state of Santa Cruz (in the Cerrado), and for the Brazilian states of Piauí (in the Cerrado-Caatinga ecotone) and Paraíba (in the Caatinga) (Woodman and Timm 2006, Leal et al. 2013). However, the taxonomic identifications of these specimens need to be reevaluated based on the morphological criteria recently proposed by Moratelli and Dias (2015), who noted the following: "*We are not convinced that L. dekeyseri occurs in the Bolivian savannah and in the Cerrado–Caatinga ecotone in NE Brazil. One of the specimens supporting these records was examined a long time ago (DZSJRP 11459), and the other two (USNM 584472, 584473) are distinct from other samples of L. dekeyseri as determined in a previous discriminant function analysis. These specimens are not included in this analysis because we were not able to compare them with samples from other localities.*" We provisionally regard *L. dekeyseri* as endemic to the Brazilian Cerrado until further studies determine the taxonomic identity of specimens collected in Bolivia, the Cerrado-Caatinga ecotone, and the Caatinga.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Endangered" to *Lonchophylla dekeyseri* (see Aguiar and Bernard 2016). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Lonchophylla inexpectata Moratelli & Dias, 2015

Distribution. *Lonchophylla inexpectata* is endemic to the Caatinga, and has been recorded in the Brazilian states of Pernambuco and Bahia (Moratelli and Dias 2015).

Conservation status. The red list of the IUCN ver. 3.1 has not yet evaluated the extinction risk of *Lonchophylla inexpectata*. The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016). Confirmed specimens of *L. inexpectata* are currently known from only three localities. Although an exhaustive revision of specimens housed in zoological collections might reveal a higher number of localities for the species, a provisional conservation status denoting some risk of extinction seems a sensible action considering the extremely low number of confirmed localities, particularly considering trends of habitat loss in the Caatinga (Albuquerque et al. 2012).

Xeronycteris vieirai Gregorin & Ditchfield, 2005

Distribution. *Xeronycteris vieirai* is endemic to the Caatinga, and has been recorded in the Brazilian states of Bahia, Minas Gerais, Paraíba, and Pernambuco (Gregorin and Ditchfield 2005, Nogueira et al. 2007, 2014a, 2015, Astúa and Guerra 2008).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Xeronycteris vieirai* (see Solari 2015). The species appears in the official list of threatened species of Brazil with the category "Vulnerable" (ICMBIO-MMA 2016). Eleven years after its description (Gregorin and Ditchfield 2005), *X. vieirai* is known from only eight specimens and seven localities from the Caatinga (Gregorin and Ditchfield 2005, Nogueira et al. 2007, 2014a, 2015, Astúa and Guerra 2008), a biome with large disturbed areas as well as areas undergoing desertification (Albuquerque et al. 2012). Considering habitat loss, the specialized diet and the endemic nature of *X. vieirai*, Gregorin and Ditchfield (2005) noted that the species might be one of most threatened species of mammals in Brazil. We agree with this view, and strongly encourage NGOs and governmental agencies in charge of producing influential "red lists of threatened species" to revaluate the conservation status they have assigned to *Xeronycteris vieirai*; a realistic category for the species should reflect at the very least a moderate risk of extinction, particularly considering trends of habitat loss in the Caatinga (Albuquerque et al. 2012).

Chiroptera, Phyllostomidae, Micronycterinae

Micronycteris sanborni Simmons, 1996

Distribution. *Micronycteris sanborni* is endemic to the Cerrado and the Caatinga, and has been recorded in the Brazilian states of Ceará, Minas Gerais, Paraíba, Piauí, Pernambuco, and Tocantins (Simmons 1996, Gregorin et al. 2008, Cunha et al. 2009, Feijó et al. 2010, 2015b, Nogueira et al. 2015, Silva et al. 2015). An alleged record of the species for the Amazon biome has been recently published (López-Baucells et al. 2013), but no voucher specimen supports this claim and the individual that forms the basis of this record lacked the pure white ventral pelage coloration that seems to be characteristic of *M. sanborni* (see Simmons 1996, Feijó et al. 2015b). Applying Hitchens' razor, we dismiss the alleged record for the Amazon biome (contra López-Baucells et al. 2013), a view we share with other authors (see Nogueira et al. 2014b, Feijó et al. 2015b). In addition, as noted by Feijó et al. (2015b), alleged records from the state of Mato Grosso do Sul need to be confirmed. One of the two specimens that formed the basis of these records (see Santos et al. 2010) lacks the pure white ventral pelage coloration typical of confirmed vouchers of *M. sanborni* (see above) – and according to Siles et al. (2013) it might actually correspond to *M. yatesi*. No information about the morphology of the other specimen has been published (see Cunha et al. 2009).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Micronycteris sanborni* (see Tavares and Aguirre 2008). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Chiroptera, Phyllostomidae, Stenodermatinae

Chiroderma vizottoi Taddei & Lim, 2010

Distribution. *Chiroderma vizottoi* is endemic to the Caatinga, and has been recorded in the Brazilian states of Ceará and Piauí (Gregorin et al. 2008, Taddei and Lim 2010, Silva et al. 2015).

Conservation status. The red list of the IUCN ver. 3.1 has not yet evaluated the status of *Chiroderma vizottoi*. The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Primates, Cebidae, Callitrichinae

Callithrix penicillata (É. Geoffroy in Humboldt, 1812)

Distribution. *Callithrix penicillata* is endemic to the Cerrado, and has been recorded in the Brazilian states of Bahia, Goiás, Maranhão, Minas Gerais, Piauí, São Paulo, and in the Distrito Federal (de Vivo 1991, Miranda and Faria 2001, Rylands et al. 2009, Coimbra-Filho et al. 2006, Bruna et al. 2010, Vilela and Del-Claro 2011, Garbino 2015b). However, according to Rylands et al. (2009 p. 36) the records from Maranhão, which were reported by de Vivo (1991) based on skins deposited at the Museu Nacional (Rio de Janeiro), likely correspond to introductions of the species in areas far away from the native range of the species. Similarly, translocations of individuals out of their native range have been considered as a possible causal explanation for the existence of a hybrid zone between *C. penicillata* and *C. geoffroyi* in the Atlantic Forest (Fuzessy et al. 2014). Rylands et al. (2009) also commented that habitat transformation (with loss of forest) and introductions (resulting from misguided release of confiscated animals) have led *C. penicillata* to occupy, and perhaps replace other species of *Callithrix,* at localities south and east of its native range.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Callithrix penicillata* (see Rylands and Mendes 2008). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Primates, Cebidae, Cebinae

Cebus (*Sapajus*) *libidinosus* Spix, 1823

Distribution. *Cebus libidinosus* is endemic to the Cerrado and the Caatinga, and has been recorded in the Brazilian states of Bahia, Ceará, Goiás, Maranhão, Minas Gerais, Paraíba, Piauí, Pernambuco, Rio Grande do Norte, São Paulo, Tocantins, and Distrito Federal (Pontes et al. 2006, Vilela 2007, Canale et al. 2009, Bruna et al. 2010, Lynch-Alfaro et al. 2012a, 2014, Feijó and Langguth 2013, Fragaszy et al. 2013, Gomes et al. 2015, Mendes et al. 2015, Nova et al. 2015).

Nomenclature. We regard *libidinosus* as a member of the genus *Cebus*, subgenus *Sapajus*, and advocate for the use of the name *Sapajus* at the subgenus-level (contra Lynch-Alfaro et al. 2012a, 2012b, 2014). The division between the gracile (untufted) and robust (tufted) groups of capuchin monkeys has been known for over a century (see Elliot 1913, Hershkovitz 1949, 1955), and the names *Cebus* and *Sapajus* have been applied to them at the subgenus-level, respectively (e.g., Silva-Junior 2001, Ferreira et al. 2009, Casado et al. 2010). Lynch-Alfaro et al. (2012a) recommended elevating *Sapajus* to the genus-level based on their estimated age for the split between the gracile and robust lineages of *Cebus* (95% highest posterior density = 4.21–7.86 Ma). This estimate resulted from the analysis of sequence data from two mitochondrial genes. Subsequently, Lynch-Alfaro et al. (2012b) summarized known morphological and behavioral differences between gracile and robust lineages, restated the gene-tree argument of Lynch-Alfaro et al. (2012a), and advocated for elevating *Sapajus* at the genus level; 'expert opinions' have been invoked to promote this view (Lynch-Alfaro et al. 2014). Although several NGOs, ecologists, and ethologists started to adopt this proposal, dissent exists (e.g., Rosenberger 2012, Feijó and Langguth 2013, this study). Clearly, the differences and phylogenetic split between the two lineages of capuchin monkeys should be recognized with Linnean nomenclature; however, the most suitable action to do so, at least provisionally, is to use *Sapajus* and *Cebus* as subgenera of *Cebus*. At least three reasons support this view, as follows (see also Voss et al. 2014, Garbino 2015a):

(1) Elevating *Sapajus* to the genus level is unnecessary, as it does not accomplish anything than using the name at the subgenus level could not.

(2) At least for now, using the age since the split between *Sapajus* and *Cebus* as an argument to elevate *Sapajus* at the genus level is flawed for two reasons. First, because the age of that split, as estimated by Lynch-Alfaro et al. (2012a), was inferred based on data from a single locus, it should be considered a preliminary one (i.e., a working hypothesis). Secondly, the artifactual current taxonomy of platyrrhine monkeys (see Rosenberger and Matthews 2008, Rosenberger 2012, Garbino 2015a and references therein) prevents sensible comparisons of age of splits among pairs of platyrrhine sister genera. This is a consequence of the wide, dogmatic acceptance of genera that have been proposed on the basis of criteria that are typically used to recognize species (at best) in most other groups of mammals. A recent example of this

phenomenon is provided by the recent proposal to validate the name *Leontocebus* as a genus, to contain the *nigricollis* group of *Saguinus,* using as an argument the fact that it is sympatric with other tamarin lineage (Rylands et al. 2016) – note that this same unacceptable criterion (i.e., sympatry) and divergence-time have been used by Byrne et al. (2016) to propose the recognition of *Cheracebus* as a "genus" and without even considering the more sensible option of regarding *Cheracebus* as a subgenus of *Callicebus*; we herein propose to use *Cheracebus* at the subgenus level only. Clearly, the currently inflated taxonomy of New World primates should be fixed, and several proposed genera should be lumped into fewer ones. This process has already begun (e.g., Garbino 2015a, this study), but it is far from completion.

(3) Continuing to recognize the long established, monophyletic genus *Cebus*, and subgenera *Sapajus* and *Cebus* within it, allows for more efficient communication among scientists. First, the use of the genus-(subgenus)-species format (i.e. using the subgenus name, when pertinent) readily confers phylogenetic information. In this case, the genus name *Cebus* informs about the sister-taxon relationship between the subgenera *Sapajus* and *Cebus* – supported by a number of synapomorphies (see Lynch-Alfaro et al. 2012b) – whereas the subgenera names, *Sapajus* and *Cebus*, recognize the differences between the two lineages that underwent different evolutionary histories. Furthermore, association of the genus name *Cebus* with the species epithets of both linages of capuchin monkeys have existed for decades, and unnecessarily disrupting this association (by elevating *Sapajus* to the genus level) might pose difficulties in scientific communication, for example for literature searches or for merging data from public repositories (e.g., GenBank, Global Biodiversity Information Facility).

We take the opportunity to emphasize the importance of using the subgenus rank to preserve nomenclatural stability, similar to what have been recently done for other groups of mammals (Giarla et al. 2010, Voss et al. 2014, Díaz-Nieto et al. 2016, Teta et al. 2016). This aspect is especially important for New World primates, whose generic and alpha-level taxonomy should be rectified in the upcoming decades.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Cebus* (*Sapajus*) *libidinosus* (see Rylands and Kierulff 2015). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Primates, Pitheciidae, Callicebinae, Callicebini

***Callicebus* (*Callicebus*) *barbarabrownae* Hershkovitz, 1990**

Distribution. *Callicebus barbarabrownae* is endemic to the Caatinga, and has been recorded in the Brazilian states of Bahia and Sergipe (Hershkovitz 1990b, Marinho-Filho and Veríssimo 1997, Printes et al. 2011 and 2013, Marques et al. 2013, Corsini and Moura 2014).

Nomenclature. We regard *barbarabrownae* as a member of the genus *Callicebus*, subgenus *Callicebus.* The arguments presented by Byrne et al. (2016) to propose splitting *Callicebus* (as traditionally understood) into different genera are flawed for the same reasons we have already discussed under the account of *Cebus libidinosus* (see above).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Critically Endangered" to *Callicebus barbarabrownae* (see Veiga et al. 2008). The species appears in the official list of threatened species of Brazil with the category "Critically Endangered" (ICMBIO-MMA 2016).

Carnivora, Canidae, Caninae, Canini

Lycalopex vetulus (Lund, 1842)

Distribution. *Lycalopex vetulus* is endemic to the Cerrado and the Caatinga, and has been recorded in the Brazilian states of Bahia, Ceará, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Piauí, São Paulo, and in the Distrito Federal (Costa and Courtenay 2003, Courtenay et al. 2006, Dalponte 2009, Bocchiglieri et al. 2010, Ribeiro et al. 2010, Olifiers and Delciellos 2013; see also Supplementary Material of Bubadué et al 2016). The species has also been observed in the Brazilian state of Tocantins (Carmignotto and Aires 2011).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Lycalopex vetulus* (see Dalponte and Courtenay 2008). The species appears in the official list of threatened species of Brazil with the category "Vulnerable" (ICMBIO-MMA 2016).

Rodentia, Caviidae, Caviinae

Galea spixii (Wagler, 1831)

Distribution. *Galea spixii* is endemic to the Caatinga, and has been recorded in the Brazilian states of Alagoas, Bahia, Ceará, Minas Gerais, Pará, Pernambuco, São Paulo (Bezerra 2008, Norgueira et al. 2015, Dunnum 2015 and references therein).

Taxonomy. Some authors have regarded *Galea spixii* and *G. flavidens* as different species (Ellerman 1941, Bonvicino et al. 2005, Weksler and Bonvicino 2008a, Dunnum 2015); however the latter species has never been incorporated into a phylogenetic study based on molecular data (e.g., Dunnum and Salazar-Bravo 2010), and a modern morphological study that included all extant species in the genus did not find differences to distinguish *G. flavidens* from *G. spixii* (Bezerra 2008; but see Bonvicino et al. 2008). We follow Bezerra (2008) in treating *Galea flavidens* as a junior synonym of *Galea spixii*. The same author also found that populations currently referred to as *Galea spixii* actually might be composed by multiple valid species (Bezerra 2008).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Galea spixii* (see Catzeflis et al. 2016a). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Rodentia, Caviidae, Hydrochoerinae

Kerodon acrobata Moojen, Locks & Langguth, 1997

Distribution. *Kerodon acrobata* is endemic to the Cerrado, and has been recorded only in the Brazilian states of Goiás and Tocantins (Moojen et al. 1997, Bezerra et al. 2010, Zappes et al. 2014).

Conservation status. The red list of the IUCN ver 3.1 assigned the category "Data Deficient" to *Kerodon acrobata* (see Roach 2016). The species appears in the official list of threatened species of Brazil with the category "Vulnerable" (ICMBIO-MMA 2016).

Kerodon rupestris (Wied-Neuwied, 1820)

Distribution. *Kerodon rupestris* is endemic to the Caatinga, and has been recorded in the Brazilian states of Alagoas, Bahia, Ceará, Minas Gerais, Paraiba, and Pernambuco (Moojen et al. 1997, Lessa et al. 2005, Dunnum 2015 and references therein). Indications of the species presence in the Cerrado (e.g., Marinho-Filho et al. 2002, Carmignotto et al. 2012) do not seem to be supported by voucher specimens.

Conservation status. The red list of the IUCN ver 3.1 assigned the category "Least Concern" to *Kerodon rupestris* (see Catzeflis et al. 2016b). The species appears in the official list of threatened species of Brazil with the category "Vulnerable" (ICMBIO-MMA 2016).

Rodentia, Cricetidae, Sigmodontinae, Akodontini

Gyldenstolpia planaltensis (Avila-Pires, 1972)

Distribution. *Gyldenstolpia planaltensis* is endemic to the Cerrado, and has been recorded in the Brazilian state of Mato Grosso, and in the Distrito Federal (Bezerra et al. 2011, Pardiñas and Bezerra 2015).

Conservation status. The red list of the IUCN ver. 3.1 has not yet attempted to evaluate the extinction risk of *Gyldenstolpia planaltensis*. The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Juscelinomys candango Moojen, 1965

Distribution. *Juscelinomys candango* is endemic to the Cerrado, and is only known from its type locality in the Brazilian Distrito Federal (Moojen 1965, Emmons 2015).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Extinct" to *Juscelinomys candango* (see Leite and Patterson 2008). The species appears in the official list of threatened species of Brazil with the category "Critically Endangered (Likely Extinct)" (ICMBIO-MMA 2016).

Juscelinomys huanchacae Emmons, 1999

Distribution. *Juscelinomys huanchacae* is endemic to the Cerrado, and is only known from the Bolivian department of Santa Cruz (Emmons 2015).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Juscelinomys huanchacae* (see Dunnum et al. 2008). Since the known records are restricted to Bolivian cerrado, the species was not considered to be included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Oxymycterus delator Thomas, 1903

Distribution. *Oxymycterus delator* is endemic to the Cerrado and the Caatinga, and has been recorded in the Brazilian states of Bahia, Ceará, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Piauí, São Paulo, and Tocantins, and in the Distrito Federal; and in the Paraguayan departments of Canindeyú and Paraguarí (Emmons 1999, Hoffmann et al. 2002, Andrade et al. 2004, Bonvicino et al. 2005, 2008, 2012, 2014, Bruna et al. 2010, Ribeiro et al. 2010, Carmignotto and Aires 2011, Owen 2013, Gurgel-Filho et al. 2015, Oliveira and Gonçalves 2015, Stumpp et al. 2016). It has been indicated that the species occurs also in the Chaco biome (Carmignotto et al. 2012), but we are not aware of reported specimens that support this notion. D'Elía et al. (2008) noted that in Paraguay the species is restricted to the Oriental Region (east of the Paraguay River), where areas with Chaco's physiognomy are absent and, instead, isolated patches of Cerrado can be found (Owen 2013).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Oxymycterus delator* (see Patterson et al. 2008). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Thalpomys cerradensis Hershkovitz, 1990

Distribution. *Thalpomys cerradensis* is endemic to the Cerrado, and has been recorded in the Brazilian states of Bahia, Goiás, Mato Grosso, Tocantins, and in the

Distrito Federal (Hershkovitz 1990a, Andrade et al. 2004, Gonçalves et al. 2006, Ribeiro et al. 2010, Carmignotto and Aires 2011, Bonvicino et al. 2012, Pardiñas and Teta 2015).

Conservation status. The red list of the IUCN ver 3.1 assigned the category "Least Concern" to *Thalpomys cerradensis* (see Marinho-Filho et al. 2016a). The species appears in the official list of threatened species of Brazil with the category "Vulnerable" (ICMBIO-MMA 2016).

Thalpomys lasiotis Thomas, 1916

Distribution. *Thalpomys lasiotis* is endemic to the Cerrado, and has been recorded in the Brazilian states of Bahia, Minas Gerais, Rondônia, and São Paulo, and in the Distrito Federal (Hershkovitz 1990a, Ribeiro et al. 2010, 2011, Rocha et al. 2011a, Pardiñas and Teta 2015).

Conservation status. The red list of the IUCN ver 3.1 assigned the category "Least Concern" to *Thalpomys lasiotis* (see Marinho-Filho et al. 2016b). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Rodentia, Cricetidae, Sigmodontinae, Oryzomyini

Cerradomys marinhus (Bonvicino, 2003)

Distribution. *Cerradomys marinhus* is endemic to the Cerrado, and has been recorded in the Brazilian states of Bahia and Minas Gerais (Carmignotto and Aires 2011, Percequillo 2015, Tavares et al. 2016).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Cerradomys marinhus* (see Bonvicino and Percequillo 2008). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Euryoryzomys lamia (Thomas, 1901)

Distribution. *Euryoryzomys lamia* is endemic to the Cerrado, and has been recorded in the Brazilian states of Minas Gerais and Goiás (Prado and Percequillo 2013).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Endangered" to *Euryoryzomys lamia* (see Percequillo and Weksler 2008). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Microakodontomys transitorius Hershkovitz, 1993

Distribution. *Microakodontomys transitorius* is endemic to the Cerrado, and has been recorded in the Brazilian Distrito Federal (Hershkovitz 1993, Bonvicino et al. 2014, Paresque and Hanson 2015).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Endangered" to *Microakodontomys transitorius* (see Marinho-Filho and Vieira 2010). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Oecomys cleberi Locks, 1981

Distribution. *Oecomys cleberi* is endemic to the Cerrado, and has been recorded in the Brazilian Distrito Federal (Locks 1981, Rocha et al. 2012, Carleton and Musser 2015).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Oecomys cleberi* (see Costa et al. 2008). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Oligoryzomys moojeni Weksler & Bonvicino, 2005

Distribution. *Oligoryzomys moojeni* is endemic to the Cerrado, and has been recorded in the Brazilian states of Goiás and Tocantins (Miranda et al. 2009, Weksler and Bonvicino 2005, Carmignotto and Aires 2011, Di-Nizo et al. 2015, Gomes et al. 2015).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Oligoryzomys moojeni* (see Weksler and Bonvicino 2008b). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Oligoryzomys rupestris Weksler & Bonvicino, 2005

Distribution. *Oligoryzomys rupestris* is endemic to the Cerrado, and has been recorded in the Brazilian states of Bahia, Goiás, and Minas Gerais (Weksler and Bonvicino 2005, Pereira and Geise 2009, Di-Nizo et al. 2015).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Oligoryzomys rupestris* (see Weksler and Bonvicino 2008c). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Oligoryzomys stramineus Bonvicino & Weksler, 1998

Distribution. *Oligoryzomys stramineus* is endemic to the Cerrado and the Caatinga, and has been recorded in the Brazilian states of Bahia, Ceará, Goiás, Minas Gerais, Paraíba, Pernambuco and Piauí (Bonvicino and Weksler 1998, Weksler and Bonvicino 2005, 2015, Geise et al. 2010, Fernandes et al. 2012).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Oligoryzomys stramineus* (see Weksler and Bonvicino 2008d). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Rodentia, Cricetidae, Sigmodontinae, Phyllotini

Calassomys apicalis Pardiñas, Lessa, Salazar-Bravo & Câmara, 2014

Distribution. *Calassomys apicalis* is endemic to the Cerrado, and has been recorded only in the Brazilian state of Minas Gerais (Pardiñas et al. 2014).

Conservation status. The red list of the IUCN ver. 3.1 has not yet attempted to evaluate the extinction risk of *Calassomys apicalis*. The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Calomys expulsus (Lund, 1840)

Distribution. *Calomys expulsus* is endemic to the Cerrado and the Caatinga (contra Gurgel-Filho et al. 2015). All but one known records attributable to this species are located within these biomes; the exceptional record comes from a site likely harboring transitional conditions, in terms of physiognomy and climate, between those of the Caatinga and Atlantic Forest, in the Brazilian state of Pernambuco (see Gurgel-Filho et al. 2015, who referred to this species as *C. mattevii*, which we consider a junior synonym of *C. expulsus*; see "Taxonomy", below). Specimens attributed to *C. expulsus* have been recorded in the Brazilian states of Bahia, Goiás, Minas Gerais, Pernambuco, Piauí, Sergipe, and in the Distrito Federal (Bonvicino and Almeida 2000, Bonvicino et al. 2003, Almeida et al. 2007, Haag et al. 2007, Bonvicino et al. 2012, Bezerra et al. 2014, Gurgel-Filho et al. 2015 and references therein, Nogueira et al. 2015). According to Gurgel-Filho et al. (2015), unpublished results of a phylogenetic study recovered samples of "*C. mattevii*" (=*C. expulsus*) in a clade in which samples from the states of Ceará and Tocantins – for which we presume no karyotype were available – were also included.

Taxonomy. We provisionally consider the recently described *Calomys mattevii* as a junior synonym of *Calomys expulsus*. Gurgel-Filho et al. (2015) asserted that two specimens karyotyped by Geise et al. (1996), collected in Lagoa Santa (the type locality of *Calomys expulsus*), Minas Gerais, with 2n=36/FN=66, correspond to *C. expulsus*; however, Gurgel-Filho et al. (2015) did not examine these specimens. These authors alleged that the karyotype 2n=66/FN=68, widely attributed by authors to *C. expulsus* (e.g., Bonvicino and Almeida 2000, Mattevi et al. 2005, Haag et al. 2007, Bezerra et al. 2014, Salazar-Bravo 2015), would have to correspond to a different species (other than *C. expulsus*), which they described as *C. mattevii*. Although it is plausible that the specimens reported by Geise et al. (1996) were indeed *C. expulsus*, this cannot be assumed as certain because multiple species of *Calomys* might occur in Lagoa Santa (not only *C. expulsus*). In fact, Lagoa Santa is also the type locality of *C. tener* (see Winge 1887, Salazar-Bravo 2015), and the identity of the specimens from Lagoa Santa that were the basis of Geise et al.'s (1996) report has also been attributed to *C. cerqueirai* (Bonvicino et al. 2010; see also Colombi and Fagundes 2015, Salazar-Bravo 2015 and citations therein). Examination of the specimens from which Geise et al. (1996) obtained the reported karyotypes, and comparisons of their morphologies with respect to type material of *C. expulsus*, would be necessary to evaluate whether Gurgel-Filho et al.'s (2015) conjecture is correct. Unfortunately, it is unclear whether the specimens karyotyped by Geise et al. (1996) were ever deposited in a zoological collection, and whether their morphology matches that of *C. expulsus* – see similar concern expressed by Bonvicino and Almeida (2000, p. 347). Moreover, the karyotype reported by Geise et al. (1996) was not ever part of a formal peer-reviewed publication; it was rather reported as an abstract from a presentation at a scientific meeting – the 42th National Congress of Genetics of the *Sociedade Brasileira de Genética* – that have permeated into the literature. In addition, to support their conjecture and decision to describe *C. mattevii*, Gurgel-Filho et al. (2015) disregarded the use of morphological data as relevant to assess the taxonomic status of *C. mattevii*. However, we argue that it is possible to use morphometrics to discriminate among some species of *Calomys*; albeit not an easy task, and might not always lead to evidence that allow unambiguous discrimination among the studied species, several authors have accomplished it in the past (e.g., Bonvicino and Almeida 2000, Bonvicino et al. 2003, Cordeiro-Estrela et al. 2006).

In summary, given the aforementioned uncertainties in the description of *Calomys mattevii*, we provisionally consider it a junior synonym of *C. expulsus.* Collecting, karyotyping, and sequencing *Calomys* from the type locality of *C. expulsus* (see above), and using this material in comparative analyses that should include typical, or at least topotypical, material of other members of the large-size group of the genus (i.e., *C. callidus*, *C. callosus, C. cerqueirai*, and *C. tocantinsi*) is a necessary step to evaluate the taxonomic status of *C. mattevii*. On the meantime, we consider that karyotype 2n=66/FN=68 corresponds to *C. expulsus*, following Bonvicino and Almeida (2000), who asserted that the morphology of their karyotyped specimens is congruent with morphological characters and measurements of the holotype of *C. expulsus* as reported by Winge (1887) and Hershkovitz (1962), respectively.

Conservation status. The red list of the IUCN ver 3.1 assigned the category "Least Concern" to *Calomys expulsus* (see Bonvicino and Geise 2008a). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Calomys tocantinsi Bonvicino, Lima & Almeida, 2003

Distribution. *Calomys tocantinsi* is endemic to the Cerrado, and has been recorded in the Brazilian states of Mato Grosso and Tocantins (Bonvicino et al. 2003, 2010, Cordeiro-Estrela et al. 2006, Rocha et al. 2011a).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Calomys tocantinsi* (see Bonvicino and Marinho-Filho 2008a). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Rodentia, Cricetidae, Sigmodontinae, Thomasomyini

Rhipidomys cariri Tribe, 2005

Distribution. *Rhipidomys cariri* is endemic to the Caatinga, and has been recorded in the Brazilian states of Bahia, Ceará, and Pernambuco (Tribe 2005, 2015, Geise et al. 2010, Fernandes-Ferreira et al. 2015, Gurgel-Filho et al. 2015).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Rhipidomys cariri* (see Patton et al. 2008a). The species appears in the official list of threatened species of Brazil with the category "Vulnerable" (ICMBIO-MMA 2016).

Rodentia, Cricetidae, Sigmodontinae, Wiedomyini

Wiedomys cerradensis Gonçalves, Almeida & Bonvicino, 2005

Distribution. *Wiedomys cerradensis* is endemic to the Cerrado, and has been recorded in the Brazilian states of Bahia, Ceará, Goiás, and Tocantins (Gonçalves et al. 2005, Bezerra et al. 2013, Bonvicino 2015, Gurgel-Filho et al. 2015). Gurgel-Filho et al. (2015) indicated that the species also occurs in the Brazilian states of Piauí, Maranhão, Paraíba, and Pernambuco, but did not provide evidence supporting this assertion.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Wiedomys cerradensis* (see Bonvicino and Marinho-Filho 2008b). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Wiedomys pyrrhorhinos (Wied-Neuwied, 1821)

Distribution. *Wiedomys pyrrhorhinos* is endemic to the Caatinga, and has been recorded in the Brazilian states of Alagoas, Bahia, Minas Gerais, Paraíba, and Pernambuco

(Maia and Langguth 1987, Pereira and Geise 2009, Souza et al. 2011a, Bonvicino 2015, Nogueira et al. 2015). Bonvicino (2015) indicated that the species is also present in the state of Sergipe, but this assertion is based on an abstract presented at the XXIV Jornadas Argentinas de Mastozoología. Citation of this abstract is as follows:

Souza ALG, Pessôa LM, Menezes AN, Bezerra AMR, Bonvicino CR (2011) O rio São Francisco como provável barreira geográfica para as duas espécies do gênero *Wiedomys* (Rodentia). Revista del Museo de La Plata, Zoología 18(172): 163R. [abstract presented in the XXIV Jornadas Argentinas de Mastozoología, La Plata, Argentina, November 8–11, 2011].

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Wiedomys pyrrhorhinos* (see Marinho-Filho and Langguth 2016). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Rodentia, Echimyidae, Eumysopinae

Carterodon sulcidens (Lund, 1838)

Distribution. *Carterodon sulcidens* is endemic to the Cerrado, and has been recorded in the Brazilian states of Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, and in the Distrito Federal (Ribeiro et al. 2010, Bezerra et al. 2011, Bezerra and Bonvicino 2015a and references therein).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Data Deficient" to *Carterodon sulcidens* (see Lacher 2016). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Phyllomys brasiliensis Lund, 1840

Distribution. *Phyllomys brasiliensis* is endemic to the Cerrado, and has been recorded in the Brazilian state of Minas Gerais (Emmons et al. 2002, Leite 2003, Leite and Loss 2015).

Conservation. The red list of the IUCN ver. 3.1 assigned the category "Endangered" to *Phyllomys brasiliensis* (see Loss and Leite 2016). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Thrichomys apereoides (Lund, 1839)

Distribution. *Thrichomys apereoides* is endemic to the Cerrado (contra Oliveira and Langguth 2004, Paglia et al. 2012), and has been recorded in the Brazilian state of Minas Gerais (Nogueira et al. 2015, Pessôa et al. 2015, Stumpp et al. 2016; but see "Taxonomy", below).

Taxonomy. Based on karyological data, Bonvicino et al. (2002) changed the traditional notion that the genus *Thrichomys* was monotypic (*T. apereoides*). Subsequently, two other studies gave support to the polytypic nature of *Thrichomys*, one based on karyological data and morphometric analyses (Pessôa et al. 2004), and the other on karyological data and phylogenetic (maximum parsimony, maximum likelihood) and phenetic (neighbor joining) analyses of cytochrome-*b* sequences (Braggio and Bonvicino 2004). A synthetic view of progress made since then has been recently published (by Pessôa et al. 2015a), and restricted species names to populations from type localities and nearby areas. In absence of a comprehensive systematic review for the genus *Thrichomys*, we provisionally adhere to that synthesis, according to which *T. apereoides* is restricted to a few localities in the state of Minas Gerais. Nevertheless, records potentially attributable to this species exist for localities corresponding to the Cerrado biome in the Brazilian states of Goiás and Tocantins (Bezerra et al. 2013, Gomes et al. 2015). Clearly, a systematic review including karyotyped and sequenced samples from throughout the distribution of all currently recognized species and their type localities is needed to establish species boundaries and distributions.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Thrichomys apereoides* (see Roach and Naylor 2016b). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Thrichomys inermis (Pictet, 1843)

Distribution. *Thrichomys inermis* is endemic to the Caatinga (contra Carmignotto et al. 2012, Paglia et al. 2012), and has been recorded in the Brazilian state of Bahia (Pereira and Geise 2009, Pessôa et al. 2015a). Alleged records of the species for the Brazilian state of Tocantins, from what seems to correspond to the Cerrado biome, reported in abstracts of meeting presentations have permeated through the literature – e.g., cited by Oliveira and Bonvicino (2006), Bonvicino et al. (2008), Pessôa et al. (2015a) – but, to the best of our knowledge, tangible evidence of the species being present in states and biomes other than Bahia and the Caatinga, respectively, is still lacking. The aforementioned abstracts are as follows:

Carvalho AH, Fagundes V (2005) Área de ocorrência de três táxons do gênero *Thrichomys* (Echimyidae, Rodentia) baseados em identificação cariotípica. In: Fagundes V, Costa LP, Leite YLR, Mendes SL (Eds), Livros de resumos, III Congresso Brasileiro de Mastozoologia. Espírito Santo, Aracruz, p. 102.

Carvalho AH, Lopes MOG, Svartman M (2008) Cariótipo de *Thrichomys inermis* (Rodentia, Echimyidae) do Tocantins. XXVII Congresso Brasileiro de Zoologia, Curitiba.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Thrichomys inermis* (see Bonvicino and Geise 2008b). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Trinomys albispinus (I. Geoffroy, 1838)

Distribution. *Trinomys albispinus* is endemic to the Cerrado and the Caatinga (contra Carmignotto et al. 2012, Paglia et al. 2012), and has been recorded in the Brazilian states of Bahia, Minas Gerais, and Sergipe (Souza et al. 2006, Pessôa et al. 2015b).

Taxonomy. The recently published synopsis of the genus *Trinomys* by Pessôa et al. (2015b) followed the views of Reis and Pessôa (1995) and Souza et al. (2006) in treating *Trinomys minor* as a subspecies of *T. albispinus* (i.e., *T. a. minor*). Reis and Pessôa (1995) did not discuss the biogeographic context they presumably considered to designate *minor* as a subspecies of *T. albispinus* (then allocated in the genus *Proechimys*) instead of a valid species. Souza et al. (2006) considered *minor* as a subspecies of *T. albispinus* due to the fact that karyotypes that they and Leal-Mesquita et al. (1992) attributed to *albispinus* and *minor*, respectively, shared the same diploid and autosomal fundamental numbers (2n=60, FN_a=116), morphology of the sex chromosomes, and size of the first and second pairs of autosomes. Pessôa et al. (2015b) textually described a topology presumably resulting from phylogenetic analyses based on cytochrome-*b* sequences by Souza (2011 [an unpublished Ph.D. dissertation]) in which samples attributed to *minor* were nested within a haplogroup formed by samples attributed to *T. albispinus sertonius* (= *T. a. albispinus* [sensu Pessôa et al. 2015b and references therein]). We currently lack access to both the sequence data and the analyses that formed the basis of Pessôa et al.'s (2015b) views. Regardless, we argue that *T. minor* and *T. albispinus* represent different, valid species, for the following reasons: (1) the two species occur in a geographic context in which no clear barrier to dispersal separate them (see map in Pessôa et al. 2015b: 1004), and records of both species exists at only 30 km away from each other (see Souza et al. 2006); (2) the two species present well marked morphological differences (Reis and Pessôa 1995, Pessôa and Strauss 1999, Souza et al. 2006), and specimens with intermedium morphological characteristics have not been reported. These aspects strongly suggest that *minor* and *albispinus* do not constitute different subspecies of a single species, but rather that they are valid biological species, able to maintain their morphological differences in close geographic proximity and in absence of barriers to dispersal (i.e., virtually in sympatry) – even if they share the same karyotype and shallow genetic divergences. According to Pessôa et al. (2015b), Iack-Ximenes (2005 [an unpublished Ph.D. dissertation]) also recommends treating *T. minor* as a species rather than as a subspecies of *T. albispinus*. A number of potential causes could explain the yet-to-be-confirmed topology described in the species account by Pessôa et al. (2015b), including incomplete lineage sorting and other more technical aspects of the analyses and/or data (e.g., saturation of sequences, biases in nucleotide composition). Addressing these possibilities is pending from future publication of the sequence data used in those analyses and from future efforts to obtain nuclear sequence data from populations of *T. minor* and *T. albispinus*.

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Least Concern" to *Trinomys albispinus* (see Bonvicino et al. 2016). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Trinomys minor (Reis & Pessôa, 1995)

Distribution. *Trinomys minor* is endemic to the Cerrado and the Caatinga (not Carmignotto et al. 2012, Paglia et al. 2012), and has been recorded in the Brazilian state of Bahia (Pessôa et al. 2015b).

Taxonomy. See the Taxonomy section of *Trinomys albispinus* (above).

Conservation status. The red list of the IUCN ver. 3.1 has not yet attempted to evaluate the extinction risk of *Trinomys minor*, and although the IUCN acknowledged that the Iack-Ximenes's (2005) unpublished Ph.D. dissertation concluded that *minor* merited species-level recognition, it treated *minor* as a subspecies of *T. albispinus* (see Bonvicino et al. 2016). The species was not included in the official list of threatened species of Brazil (ICMBIO-MMA 2016).

Trinomys yonenagae (Rocha, 1996)

Distribution. *Trinomys yonenagae* is endemic to the Caatinga, and has been recorded in the Brazilian state of Bahia (Rocha 1995, Pessôa et al. 2015b, Tavares et al. 2016).

Conservation status. The red list of the IUCN ver. 3.1 assigned the category "Endangered" to *Trinomys yonenagae* (see Roach and Naylor 2016a). The species appears in the official list of threatened species of Brazil with the category "Endangered" (ICMBIO-MMA 2016).

Discussion

Endemic faunas and taxonomic richness. Three endemic mammalian faunas can be recognized in our results: one endemic to the Caatinga (ten species that are currently allocated in ten genera; hereafter "Caatinga-only endemics"), other endemic to the Cerrado (22 species that are currently allocated in 18 genera; hereafter "Cerrado-only endemics"), and another endemic to the Caatinga and the Cerrado in combination (i.e., formed by taxa with presence in both biomes; eleven species that are currently allocated in ten genera; hereafter "Caatinga-Cerrado endemics"). Altogether, these faunas encompass 43 species (allocated in 31 genera) that are only found in either the Caatinga, or the Cerrado, or both (Tables 1 and 2). Discrepancies between these figures – as well as the taxonomic identity of the taxa that form their basis – with respect to those from previous syntheses (e.g., Marinho-Filho et al. 2002, Ribeiro et al. 2010, Carmignotto et al. 2012) can be explained by the following factors: (1) some of the currently available data on the taxonomy and distribution of these faunas were not available when previous syntheses were conducted (see under Species Accounts); (2) the geographic scope considered in the present study differ from some of those used in previous studies – e.g., contrary to Carmignotto et al. 2012, we did not regard the Pantanal as part of the Cerrado, as we consider it to be a biome itself, with particular in-

Table 1. List of mammal species endemic to the Caatinga, the Cerrado, or both, and their habitat and conservation statuses. Biome: Caatinga (Ca), Cerrado (Ce). Habitat: forest (F), open (O; e.g., campo limpo, cerrado *sensu stricto*; Oliveira and Marquis 2002), Locs: approximate number of localities for which voucher specimens exist according to the literature (see Species Accounts). IUCN: conservation status according to the International Union for the Conservation of Nature (Red List of Threatened Species version 3.1). ICMBio-MMA: conservation status according to the *Instituto Chico Mendes de Conservação da Biodiversidade-Ministério do Meio Ambiente* of Brazil (ICMBio-MMA 2016). Categories for conservation statuses: Data Deficient (DD), Low Concern (LC), Vulnerable (VU), Near Threatened (NT), Endangered (EN), Critically Endangered (CR), Extinct (EX); species that have not been evaluated by the IUCN or the ICMBio-MMA are indicated with m-dashes. Differences with respect to previous lists (from the literature) are discussed in the Results section.

Order, Family	Species	Biome	Habitat	Locs.	IUCN	ICMBio-MMA
Chiroptera, Phyllostomidae	*Chiroderma vizottoi*	Ca	F	4	–	–
	Lonchophylla inexpectata	Ca	F, O[1]	3	–	–
	Xeronycteris vieirai	Ca	O[2]	6	DD	VU
Primates, Pitheciidae	*Callicebus barbarabrownae*	Ca	F	>15	CR	CR
Rodentia, Caviidae	*Galea spixii*	Ca	O	>15	LC	–
	Kerodon rupestris	Ca	O	>15	LC	VU
Rodentia, Cricetidae	*Rhipidomys cariri*	Ca	F	10	DD	VU
	Wiedomys pyrrhorhinos	Ca	F, O	14	LC	–
Rodentia, Echimyidae	*Thrichomys inermis*	Ca	F, O	12	LC	–
	Trinomys yonenagae	Ca	O	2	EN	EN
Didelphimorphia, Didelphidae	*Thylamys* (*Xerodelphis*) *velutinus*	Ce	O	7	NT	VU
Chiroptera, Phyllostomidae	*Lonchophylla bokermanni*	Ce	F, O[1]	4	EN	–
	Lonchophylla dekeyseri	Ce	F, O	6	EN	EN
Primates, Cebidae	*Callithrix penicillata*	Ce	F, O	>15	LC	–
Rodentia, Caviidae	*Kerodon acrobata*	Ce	F, O	5	DD	VU
Rodentia, Cricetidae	*Calassomys apicalis*	Ce	O	2	–	–
	Calomys tocantinsi	Ce	F, O	10	LC	–
	Cerradomys marinhus	Ce	F, O	2	DD	–
	Euryoryzomys lamia	Ce	F[3]	3	EN	EN
	Gyldenstolpia planaltensis	Ce	O	3	–	–
	Juscelinomys candango	Ce	O	1	EX	CR/EX
	Juscelinomys huanchacae	Ce	O	4	DD	–
	Microakodontomys transitorius	Ce	F, O	2	EN	EN
	Oecomys cleberi	Ce	F	4	DD	–
	Oligoryzomys moojeni	Ce	F, O	7	DD	–
	Oligoryzomys rupestris	Ce	O	3	DD	EN
	Thalpomys cerradensis	Ce	O	>15	LC	VU
	Thalpomys lasiotis	Ce	O	10	LC	EN
	Wiedomys cerradensis	Ce	F, O	3	DD	–
Rodentia, Echimyidae	*Carterodon sulcidens*	Ce	O	12	DD	–
	Phyllomys brasiliensis	Ce	F, O	2	EN	EN
	Thrichomys apereoides	Ce	O	15	LC	–
Didelphimorphia, Didelphidae	*Cryptonanus agricolai*	Ca, Ce	F, O[4]	10	DD	–
	Thylamys (*Xerodelphis*) *karimii*	Ca, Ce	F, O	>15	VU	–

Order, Family	Species	Biome	Habitat	Locs.	IUCN	ICMBio-MMA
Cingulata, Dasypodidae	*Tolypeutes tricinctus*	Ca, Ce	F, O	>15	VU	EN
Chiroptera, Phyllostomidae	*Micronycteris sanborni*	Ca, Ce	F, O	13	DD	–
Primates, Cebidae	*Cebus* (*Sapajus*) *libidinosus*	Ca, Ce	F, O	>15	LC	–
Carnivora, Canidae	*Lycalopex vetulus*	Ca, Ce	O	>15	LC	VU
Rodentia, Cricetidae	*Calomys expulsus*	Ca, Ce	F, O	>15	LC	–
	Oligoryzomys stramineus	Ca, Ce	F, O	>15	LC	–
	Oxymycterus delator	Ca, Ce	O	>15	LC	–
Rodentia, Echimyidae	*Trinomys albispinus*	Ca, Ce	F	12	LC	–
	Trinomys minor	Ca, Ce	O	3	–	–

[1] Unpublished observations suggest that *Lonchophylla inexpectata*, *L. bokermanni,* and *L. dekeyseri* occur in open and forest habitat types (R. Moratelli *in litt.* for *L. inexpectata* and *L. bokermanni*; personal observations for *L. dekeyseri*).

[2] *Xeronycteris vieirai* is associated to outcroppings in open habitats; however, some of this outcroppings are located near forests, and it is likely that the species forages in them (M. Nogueira *in litt.*).

[3] Two of the three known localities known for *Euryoryzomys lamia* correspond to transitional areas between gallery forest and open habitats (see Bonvicino et al. 1998).

[4] Currently available records for *Cryptonanus agricolai* suggest that it occurs in open habitats as well as in enclaves of moist forests within the Caatinga locally known as *brejos de altitude*.

Table 2. Number of genera and species endemic to the Caatinga, the Cerrado, or both, per mammalian order. The column "Caatinga-Cerrado" corresponds to endemic taxa with presence in both biomes, whereas the column "all endemics" corresponds to taxa either endemic to the Caatinga, or to the Cerrado, or endemic to both in combination.

	Caatinga-only		Cerrado-only		Caatinga-Cerrado		All endemics	
	Genera	Species	Genera	Species	Genera	Species	Genera	Species
Didelphimorphia	0	0	0	1	0	2	0	3
Cingulata	0	0	0	0	0	1	0	1
Chiroptera	1	3	0	2	0	1	1	6
Primates	0	1	0	1	0	1	0	3
Carnivora	0	0	0	0	1	1	1	1
Rodentia	0	6	5	18	2	5	7	29
Total	1	10	5	22	3	11	9	43

fluences from other humid biomes (see Werneck 2011 and references therein); (3) we disregarded information that has not ever been published, but that had permeated into the literature in the form of cited abstracts that merely correspond to presentations in scientific meetings, personal observations, or unpublished data (with the only exception of habitat information for three species of *Lonchophylla* and *Xeronycteris vieirai*; see Table 1). Current and future fieldwork and taxonomic research will undoubtedly alter our current list of endemic species (Table 1). For instance, future research might reveal that the distributions of species currently known only from transitional zones between our focal and neighboring biomes are larger than currently understood, which might render some of these species as endemic to our focal biomes (see section "Species currently only known from transitional areas", below).

Species richness was the highest in the Cerrado-only endemics, followed by the Caatinga-Cerrado endemics, and then by the Caatinga-only endemics. The order with highest species richness in all three faunas aforementioned was rodents; all other orders were represented by only one to three species (Tables 1 and 2). Pooling together the three faunas, bats were the second most important order, with six species. These results are congruent with patterns found in earlier studies (e.g., Marinho-Filho et al. 2002, Carmignotto et al. 2012 and references therein). The fact that the Caatinga-Cerrado endemics present an intermedium level of species richness between that of the Caatinga-only and the Cerrado-only endemics suggests the possibility that the Cerrado might have functioned as a source of ancestral populations for the Caatinga. This process might be explained by (1) the chronological order in which the Caatinga and the Cerrado established in the region, with the Cerrado being established substantially earlier than the Caatinga, and (2) by the larger size and higher habitat heterogeneity of the Cerrado (see Werneck 2011 and references therein; Carmignotto et al. 2012). Nevertheless, this process and its potential causal explanations remain as hypotheses to be tested employing other sources of information and considering additional factors, as the possible effect of species extinction masking past patterns of species richness in the focal biomes.

As demonstrated, from the biogeographic point of view, the Caatinga-Cerrado endemics deserve attention as a unit, as is the case for the Caatinga-only and the Cerrado-only endemics (e.g. Carmignotto et al. 2012). The Caatinga-Cerrado endemic fauna is composed of two marsupials (*Cryptonanus agricolai*, *Thylamys karimii*), one xenarthran (*Tolypeutes tricinctus*), one bat (*Micronycteris sanborni*), one primate (*Cebus libidinosus*), one carnivore (*Lycalopex vetulus*), and five rodents (*Calomys expulsus*, *Oligoryzomys stramineus*, *Oxymycterus delator*, *Trinomys albispinus*, *Trinomys minor*). Two genera are currently known to be endemic to the Caatinga-Cerrado unit (the marsupial genus *Cryptonanus* and the rodent genus *Kerodon*). Among Caatinga-Cerrado endemics, only *Trinomys albispinus* seems to be strictly associated to forest habitat, whereas *Lycalopex vetulus*, *Oxymycterus delator*, and *Trinomys minor* seem strictly associated to open habitat. The remaining seven species are likely associated to both open and forest habitats (Table 2; see also Species Accounts). This heterogeneity in habitat association suggests a complex biogeographic history. To dig into this history, it is necessary to revise the phylogenetic information existing for each of these species, and integrate it with that for Caatinga-only and Cerrado-only endemics. Such a task is out of the scope of the present study, which aims to set a baseline, regarding the distribution, taxonomy, and conservation statuses of the focal species, upon which further studies could be built. However, we stress that delimiting these three faunas (Caatinga-only, Cerrado-only, and Caatinga-Cerrado endemics) as discrete study subjects – rather than focusing only on two of them, those of the Caatinga and the Cerrado – and then integrating information about their corresponding biogeographic patterns, might provide novel information regarding the evolutionary origin of the biota of open dry habitats of central and northeastern South America.

Species currently only known from transitional areas. A group of species are currently known only from transitional areas between our focal biomes and other adjacent biomes. These species include *Oligoryzomys utiaritensis*, *Rhipidomys ipukensis*, and an undescribed species of *Akodon*, all of which occur in transitional areas between the Brazilian Cerrado and the Amazon (Rocha 2011b, Pardiñas et al. 2015, Weksler and Bonvicino 2015); it is unclear whether they are restricted to those transitional areas, or if they are rather Cerrado, or Amazon, endemics with presence in the contact zones between these two biomes. Similarly, *Calomys cerqueirai* and *Phyllomys brasiliensis* are known from transitional areas between the Cerrado and the Atlantic Forest (Bonvicino et al. 2010, Leite and Loss 2015, Salazar-Bravo 2015); it remains to be investigated whether these species are restricted to those transitional areas, or if they are rather Cerrado, or Atlantic Forest, endemics with presence in the contact zones between these biomes.

A howler monkey endemic to the Cerrado and the Caatinga? A case that deserves special discussion is that of a group of populations of howler monkeys from the northern part of the Brazilian states of Ceará, Maranhão, and Piauí. These populations have been regarded as a valid species, *Alouatta ululata* (e.g., Elliot 1912, 1913, Gregorin 2006), or as either a subspecies (Bonvicino et al. 1989) or a junior synonym (Groves 2001, 2005) of *Alouatta belzebul*. The primary argument based on which recognizing "*ululata*" as a valid taxon (either a species or a subspecies of *A. belzebul*) has been advocated is the existence of sexual dimorphism on pelage coloration in this form; however, there is a wide variation in color pelage within *A. belzebul*, and some variation exists even among samples of "*ululata*" (see Gregorin 2006). In fact, in his review of Brazilian species of *Alouatta*, Gregorin (2006) acknowledged to have defined "*Alouatta ululata*" based on its "*… sexual dicromism* [sic] *on pelage, but this character can be an artefate* [sic] *due the small sample*", and that this taxon needs to be further studied to confirm its validity. One such study was recently published based on analyses of sequence data from the mitochondrial cytochrome-*b* gene (CYTB) and karyotypes (Viana et al. 2015). This study found no karyological differences between *A. belzebul* and "*ululata*", and its phylogenetic analyses recovered "*ululata*" nested within a haplogroup formed by all analyzed samples of *A. belzebul*. Given that karyological and CYTB data have proven to be taxonomically informative in *Alouatta* (e.g., Bonvicino et al. 1995, Cortés-Ortiz et al. 2003), the results just described suggest that "*ululata*" might just be a junior synonym of *A. belzebul*. The Principal Component Analysis conducted by Gregorin (2006) on the basis of linear measurements taken on skulls and mandibles support this view, as no morphometric discontinuities between "*ululata*" and samples of *A. belzebul* were detected. Nevertheless, considering that only one sample of "*ululata*" was analyzed in the study by Viana et al. (2015), and that future efforts based on more samples and the use of faster evolving parts of the genome – e.g., the mitochondrial control region, nuclear introns, or some flanking regions of ultra conserved elements – could potentially reveal that "*ululata*" represent a linage worth nomenclatural recognition, we conservatively treat "*ululata*" as a subspecies of *A. belzebul* (i.e., *A. b. ululata*), a status also considered by Bonvicino et al. (1989). Future efforts to clarify the taxonomic status of populations that have been referred to as "*ululata*" should test for an additional possibility, which is that population that have been referred to as corresponding to "*ululata*" could represent hybrids between *A. belzebul* and *A. caraya* (Garbino *in litt.*). With respect to the distribution of *A. b. ululata,* some authors regarded it as endemic to the Cerrado and the Caatinga (Carmignotto et al. 2012), whereas others regarded it as restricted to the Amazonia and the Caatinga (Paglia et al. 2012). Using Geographic Information Systems, we determined that occurrence localities of *A. b. ululata* (from Gregorin 2006, Viana et al. 2015) are within the borders of Cerrado and the Caatinga biomes as defined by the *Instituto Brasileiro de Geografia e Estatística* (IBGE 2004b) (Figure 1). Within these biomes, *A. b. ululata* inhabits predominantly transitional areas between dry, open vegetation and Amazon rain forest (*floresta pluvial amazônica*; Gregorin 2006). Whereas assessing the real taxonomic status of populations currently attributed to *A. b. ululata* remains to be accomplished, conservation efforts should be invested in protecting its endangered populations (see de Oliveira and Kierulff 2008).

A porcupine endemic to the Caatinga? Feijó and Langguth (2013) described an alleged new species of porcupine, *Coendou baturitensis*, on the basis of four specimens from the Baturité Range in the Brazilian state of Ceará, in the Caatinga biome. These authors mentioned that the [alleged] new species differs from *C. prehensilis* in the color pattern of quills and in having a darker general appearance. In absence of a larger sample and quantitative analyses that take into account the geographic and non-geographic variation within *C. prehensilis* and other species of *Coendou*, we are not convinced that *C. baturitensis* represents a valid species. Therefore, herein we provisionally treat *C. baturitensis* as a junior synonym of *C. prehensilis* (see also Voss 2015b).

Species previously regarded as endemic. A number of species that were previously considered as endemic to the Caatinga, the Cerrado, or both, are not considered endemic to those geographic units in this study because: (1) our criterion to deem a species as endemic is stricter than that used by other authors (see Methods); or (2) recently published information demonstrate that these species are present in biomes other than the Caatinga and the Cerrado; or because (3) we do not consider them valid species. Due to either of the former two criteria, we excluded the following species from our list of endemics: *Calomys tener*, *Cerradomys langguthi*, *Cerradomys vivoi*, *Cerradomys maracajuensis*, *Cerradomys subflavus*, *Ctenomys brasiliensis*, *Ctenomys nattereri, Clyomys laticeps*, *Dasyprocta azarae, Guerlinguetus poaiae*, *Kunsia tomentosus*, *Phyllomys blainvillii, Pseudoryzomys simplex*, *Rhipidomys macrurus*, *Thrichomys laurentius* (see Cordeiro-Estrela et al. 2006, de la Sancha et al. 2011, Bezerra 2015, Bezerra and Bonvicino 2015b, Bidau 2015, Patton and Emmons 2015, Percequillo 2015, Pessôa et al. 2015a, Salazar-Bravo 2015, de Vivo and Carmignotto 2015, Voss 2015a, Caccavo and Oliveira 2016). Besides the cases of *Alouatta ululata* and *Coendou baturitensis*, which we do not consider valid species (see discussion of cases above), we adhere to recent synopses of mammal genera provided by various authors, and do not recognize the following names as corresponding to valid species: *Guerlinguetus poaiae*, *Urosciurus urucumus*, *Dasyprocta nigriclunis*, and *Rhipidomys cearanus* (see Patton and Emmons 2015, Tribe 2015, de Vivo and Carmignotto 2015).

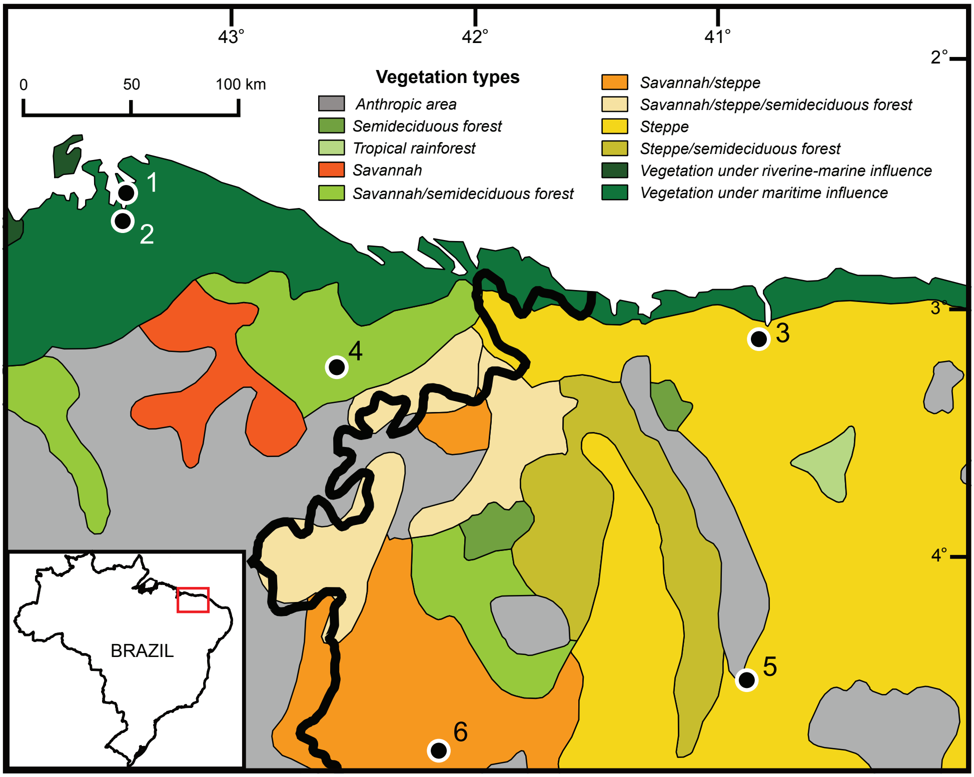

Figure 1. Localities of *Alouatta belzebul ululata* reported in the literature (Viana et al. 2015). Borders of biomes and habitat types as regarded by the *Instituto Brasileiro de Geografia e Estatística* (IBGE 2004a, b). Thick line represents the borders of the Cerrado (left) and the Caatinga (right) according to the IBGE (2004a). Localities: **1** Maranhão, Primeira Cruz (Igarapé das Palmeiras) (2.50°S, 43.33°W; Gregorin 2006) **2** Maranhão, Humberto de Campos (antiga Miritiba) (2.62°S, 43.45°W; Gregorin 2006) **3** Ceará, Granjá (Goiabeira) (3.10°S, 40.83°W; Gregorin 2006) **4** Maranhão, Boa Vista (3.22°S, 42.57°W; Gregorin 2006) **5** Ceará, São Benedito (Bom Jardim) (4.50°S, 40.88°W; Gregorin 2006); Piauí, Campo Maior [4.50°S, 40.88°W; description of locality from Viana et al. (2015); coordinates assigned by us and assessed via Google Earth version 7.1.7.2602]. Geographic coordinates in decimal degrees rounded to the nearest tenth. The original names in Portuguese for the vegetation types as reported by the IBGE (2004b) and their corresponding translation into English are as follows: *área antropizada* (anthropic area); *floresta estacional semidecidual* (semideciduous forest or dry forest); *floresta ombrófila aberta* (tropical rainforest); *savana* (savannah); *savana/floresta estacional* (savannah/semideciduous forest); *savana/savana estépica* (savannah/steppe); *savana/savana estépica/floresta estacional* (savannah/steppe/semideciduous forest); *savana estépica* (steppe); *savana estépica/floresta estacional* (steppe/semideciduous forest); *vegetação com influência fluviomarinha* (vegetation under riverine-marine influence); *vegetação com influência marinha* (vegetation under maritime influence).

Conservation. A substantial portion of the endemic mammalian faunas of the Caatinga and the Cerrado faces high risk of extinction; however, this fact has been dangerously overlooked. Considering the information published by the International Union for Conservation of Nature (IUCN; see Methods and Species Accounts), the great majority of members of the endemic faunas of the Caatinga and the Cerrado are either of low concern, lack data for assessing their extinction risk, or have not been considered yet by the IUCN (Table 3). According to IUCN data, these three categories (Low Concern, Data Deficient, not evaluated) conform 80% of the Caatinga-only endemics (8 out of 10 species), 68% of the Cerrado-only endemics (15 out of 22 species), 82% of the Caatinga-Cerrado endemics (9 out of 11 species), and 74% of all endemics (32 out of 43 species). We argue that this situation does not reflect the reality of these faunas. Our reasons are as follows:

For mammals, the Caatinga and the Cerrado have been relatively well sampled; yet several of their endemic species are known only from a handful of localities. Since the second half of the 20th century, surveys of mammals in both the Caatinga and the Cerrado covered numerous sites (Mares et al. 1989, Marinho-Filho and Veríssimo 1997, Marinho-Filho et al. 1997, Bonvicino and Bezerra 2003, Bonvicino et al. 2005, 2012, Bezerra et al. 2007, 2009, 2010, 2014, Astúa and Guerra 2008, Oliveira et al. 2008, Bocchiglieri et al. 2010, Bruna et al. 2010, Silva et al. 2015; see also Marinho-Filho et al. 2002, Carmignotto et al. 2012 and references therein; see also citations under Species Accounts). Although biodiversity inventories in the Caatinga and the Cerrado are far from being complete, both biomes are relatively well sampled when compared to other biomes (e.g., the Amazon). A map (Figure 2) showing localities where sampling of mammals have taken place in the Caatinga and the Cerrado, based on data from both the Global Biodiversity Information Facility (GBIF) and the contribution by Ribeiro et al. (2010), documents that our focal biomes have been relatively well sampled. The sampling shown on this map is a quite conservative proxy of the degree of sampling conducted in these biomes, as it lacks data from Brazilian and several North American collections that are not yet available through GBIF or that were not included in the publication by Ribeiro et al. (2010) – this latter study used data from some of the Brazilian collections and focused on endemic and threatened species of the Cerrado, lacking data for species that did not meet either of these conditions. Given the sampling effort achieved in the last decades, we argue that most, if not all, of the endemic species of the Caatinga and the Cerrado to which the IUCN assigned the category "Data Deficient" are rather species with recognizable risks of extinction. The category "Data Deficient" implies the possibility that future efforts (i.e., museum work, fieldwork, or both) might demonstrate that these species are sufficiently common to be of Low Concern; however, the sampling already conducted should have yielded enough distributional records if the species did not have very low population sizes, extremely restricted distributions, or both. The application of the IUCN criteria for assigning conservation statuses globally are clearly inadequate when applied to species that are known from few records and are endemic to regions that have been well sampled.

Natural habitat loss has been pervasive in the Caatinga and the Cerrado. Due to agriculture or transformation of rural areas into urban areas, both of these biomes have lost enormous amounts of their natural habitats (Klink and Machado 2005, Leal et al. 2005, Beuchle et al. 2015). In addition to agriculture, the Caatinga suffer of high degrees of habitat transformation due to human occupation, with replacement of gallery and dry

Table 3. Representation of species endemic to the Caatinga, the Cerrado, or both, in each category of conservation status. The column "Caatinga-Cerrado" corresponds to taxa with presence in both biomes, whereas the column "all endemics" corresponds to taxa either endemic to the Caatinga, or to the Cerrado, or endemic to both in combination. s: number of species; IUCN: conservation status according to the International Union for the Conservation of Nature (Red List of Threatened Species version 3.1); ICMBio-MMA: conservation status according to the *Instituto Chico Mendes de Conservação da Biodiversidade-Ministério do Meio Ambiente* of Brazil (ICMBio-MMA 2016). Categories for conservation statuses: Data Deficient, Low Concern, Vulnerable, Near Threatened, Endangered, Critically Endangered, and Extinct. See Methods for descriptions of each of these categories.

Category	**Caatinga-only**				**Cerrado-only**				**Caatinga-Cerrado**				**All endemics**			
	IUCN		**ICMBio-MMA**		**IUCN**		**ICMBio-MMA**		**IUCN**		**ICMBio-MMA**		**IUCN**		**ICMBio-MMA**	
	s	**%**	**s**	**%**	**s**	**%**	**s**	**%**	**s**	**%**	**s**	**%**	**s**	**%**	**s**	**%**
Not evaluated	2	20	5	50	2	9	12	55	1	9	9	82	5	12	26	60
Data Deficient	2	20	0	0	8	36	0	0	2	18	0	0	12	28	0	0
Low Concern	4	40	0	0	5	23	0	0	6	55	0	0	15	35	0	0
Near Threatened	0	0	0	0	1	5	0	0	0	0	0	0	1	2	0	0
Vulnerable	0	0	3	30	0	0	3	14	2	18	1	9	2	5	7	16
Endangered	1	10	1	10	5	23	6	27	0	0	1	9	6	14	8	19
Critically Endangered[1]	1	10	1	10	0	0	1	5	0	0	0	0	1	2	2	4
Extinct	0	0	0	0	1	5	0	0	0	0	0	0	1	2	0	0
Total number of species	10		10		22		22		11		11		43		43	

[1] ICMBio-MMA regards some species as Critically Endangered or Extinct; for simplicity, in this table one species (*Juscelinomys candango*; see Table 1) with that combination of two categories was treated as Critically Endangered.

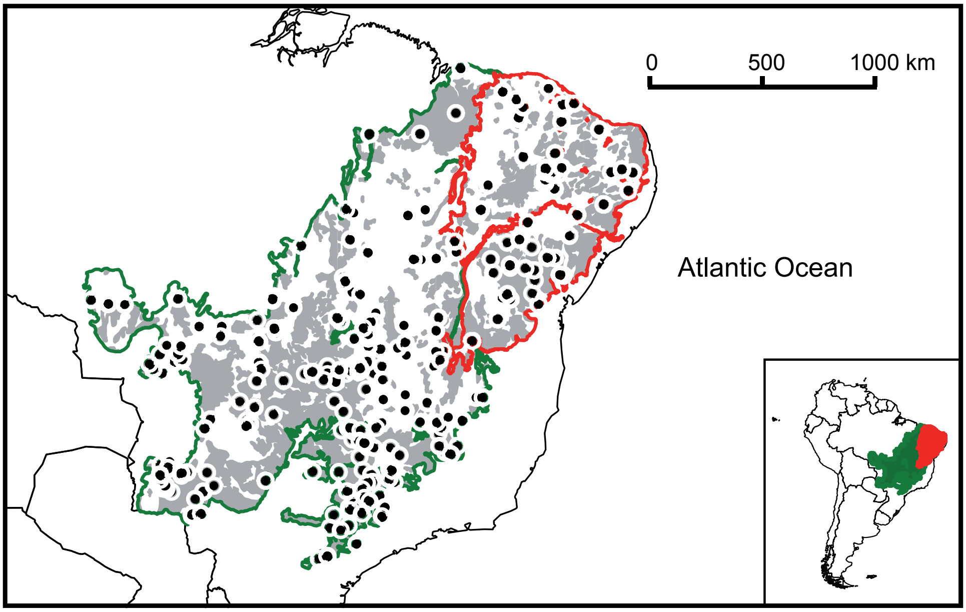

Figure 2. Sampling conducted for mammals and habitat lost due to human activities in the Caatinga and the Cerrado. Dots represent sites where sampling has been conducted according to data from the Global Information Biodiversity Facility (GBIF) and Ribeiro et al. (2010). These data represent a highly conservative proxy of the sampling conducted in these biomes (see Discussion). Areas in grey represent areas where habitat loss has occurred due to human activities. Borders of the Caatinga (red) and the Cerrado (green) are restricted to Brazil (i.e., does not include the small portions of the Cerrado in Bolivia and Paraguay). The plotted data for habitat loss and biome borders were obtained from the *Instituto Brasileiro de Geografia e Estatística*.

forests by open vegetation via charcoal production, timber and cattle ranching (Sampaio 1995, Leal et al. 2005, Miles et al. 2006, Pennington et al. 2006, Werneck 2011); and in the Cerrado invasive African grasses and uncontrolled fire also contribute to the elimination of natural habitats (Klink and Machado 2005). Using data from the *Instituto Brasileiro de Geografia e Estatística* (http://www.ibge.gov.br), we generated a map that shows extensive areas of the Cerrado and the Caatinga that have suffered of habitat transformation due to human activities (Figure 2). The extent and accelerated trend of habitat loss in both biomes make it even more likely that species for which only a handful of localities are known are facing high risks of extinction, therefore deserving conservation categories that indicate such a situation (rather than the category "Data Deficient").

The Red List published by the IUCN is highly influential in conservation planning initiatives; hence, a review and improvement of the IUCN criteria, and of how are they applied, based on the issues we just described, represents an imperative task for the conservation of these and other endemic faunas. Sensible assessments of their conservation statuses should reflect realities of species, which is not currently the case of several of our focal species, including eleven rodents (*Calassomys apicalis*, *Cerra-*

domys marinhus, *Gyldenstolpia planaltensis*, *Juscelinomys huanchacae*, *Kerodon acrobata*, *Oligoryzomys moojeni*, *Oligoryzomys rupestris*, *Thalpomys cerradensis*, *Trinomys minor*, *Trinomys yonenagae*, *Wiedomys cerradensis*) and two bats (*Xeronycteris vieirai* and *Lonchophylla inexpectata*). Both bat species have been recently described; hence, because future reexamination of museum specimens might reveal that these species are more common than currently thought, the category "Data Deficient", which has been assigned to them, might be justifiable. All other cases are undoubtedly facing certain recognizable risk of extinction.

When compared with the IUCN assessment, the Brazilian national assessment of the conservation statuses yielded categories that seem more congruent with the high risks of extinction these species face. Nevertheless, many of the species evaluated by the IUCN have not been considered in this national assessment, indicating the need for a larger and more expedite effort by Brazil's *Ministério do Meio Ambiente* (ICMBIO-MMA 2016) to assure the conservation of the unique fauna Brazil harbors in the Caatinga and the Cerrado. This is an urgent task because many of these endemic species are associated to habitats that are experiencing fast transformation into areas for agriculture, at an unbearable cost for biodiversity.

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