

UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM ENTOMOLOGIA

**A comparative morphology of Oscinellinae genera (Diptera:
Chloropidae): a framework towards a phylogeny of the subfamily**

**"Morfologia comparada dos gêneros de Oscinellinae (Diptera: Chloropidae):
estrutura para uma filogenia da subfamília"**

Zeinab Bazyar

Thesis presented to the Faculty of Philosophy, Sciences and Letters of Ribeirão Preto of the University of São Paulo, part of the requirements for obtaining the title of Doctor of Philosophy (Ph.D), obtained in the Postgraduate Program in Entomology.

Ribeirão Preto - SP

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هیچ وقت دوست نداشتم که خیلی رسمی صحبت کنم چون هیچ چیزی زیباتر و راحت تر از سادگی نیست و در سادگی، نمی‌گم تمام احساسات، اما بیشترین و وافعی ترین احساسات رو میشه نشون داد.

مادر و پدر عزیزم، من همیشه قدردان تمام زحمات و محبتهاش شما هستم.
تمام لحظاتی که شما می‌تونستید به راحتی داشته باشید ولی خالصانه، صادقانه و بدون هیچ چشمداشتی از خودتون و از آرامش خودتون گذشتید و به ما دادید.

این نتیجه چهار سال دوری و تلاش هست. چهار سال دویدن، جنگیدن با نامالیمات و سختیها و چهار سال عشق به رسیدن به آینده ای که آرزو شو داشتم. می‌دونم واسه شما هم این دوری بسیار سخت بوده و هست و حتی گاهی غیرقابل تحمل. اما تو این چهار سال خیلی چیزها یاد گرفتم، که ارزش تمام این تلاشها رو داشت. اما دو چیز که یاد گرفتم و واسم از همه مهمتر بود، این بود که خانواده همه چیز هست و هیچ وقت و هیچ جا جایگزینی برآش نیست، و دیگه اینکه تمام لذت زندگی در تلاشها و پشتکارهایی هست که داریم و نه تنها در رسیدن به آرزوها.

خیلی دوستون دارم، عاشقانه می‌پرستمتوون. شما عشق من، دنیای من، آرزوی من و همه چیز و کس من هستید. همتوون رو دوست دارم، با تمام وجودم و حضورم، همیشه.

سپاسگزار تمام زحمات و تلاشها، دعاهای بی‌منت و آرزوهای عاشقانتون هستم.

دوستون دارم، دوستون دارم، دوستون دارم.....

TO MY LOVING PARENTS AND LOVES OF MY LIFE. JUST LOVE YOU!



Abstract

The Chloropidae have about 3,000 described species and are often known as “grass flies”: most members of the family are phytophagous and can be important pests of cereals and cultivated forage grasses. The Chloropidae have been often divided into four subfamilies Siphonellopsinae, Chloropinae, Rhodesiellinae, and Oscinellinae. The oscinellines include 124 genera in the world. This project intends to provide a systematic comparasion of the morphology of the oscinelline genera to test of the monophyly of the subfamily and the monophyly of the Rhodesiellinae, and begin to build a phylogenetic framework for the group. A total of 55 species of 50 genera of oscinellines were used as terminals, with five species of three genera of rhodesiellines, 12 species of 11 genera of chloropines, three species of two genera of siphonellopsines, two species of milichiids and one species of carnid used as outgroups. A total of 167 characters from external adult morphology (head, thorax, wing, legs, and abdomen) and from male and female genitalia have been coded and used to build a data matrix. A phylogenetic analysis was performed to reconstruct the relationships among the taxa using two different analytical parameters—implied weight with $k = 3$ and a k value ($k = \sim 17$). Both analyses resulted in one most parsimonious tree, with important differences between them on the position of many genera. The Rhodesiellinae is shown to be paraphyletic in relation to the Oscinellinae, with the Stenoscinini, a rhodesielline tribe, being sister to all remaining Oscinellinae. A large stable clade includes most Fiebriegellini and genera previously included in the Siphonellini, Tricimbini, Oscinisomatini, Liparaini, and Botanobiini. It was corroborated that the Neotropical group *blanda* of *Oscinella* does not fit together with the type-species of *Oscinella* and needs a group of generic rank. A large group of genera belonging to different tribes have no reliable position in the tree, suggesting that the Incertellini, Hippelatini, Oscinellini, and Siphonellini may not correspond to clades. Another large, stable clade (the “higher oscinellines”) bring together the Dicraeini, and genera of the Botanobiini, Elachipterini, Liparaini, and Hippelatini. Information in the literature gives support to the idea of a clade that gathers these tribes. The use of a considerably large list of characters to analyse a larger generic taxon sampling of the subfamily will certainly help bringing stability to the classification of the group.

Key words: Acalyptratae, Chloropidae, Diptera, Phylogeny, Oscinellinae, Worldwide.

Resumo

A família Chloropidae, têm cerca de 3.000 espécies descritas e são muitas vezes conhecidos como "moscas da grama": a maioria dos membros da família são fitófagos e podem ser importantes pragas de cereais e cultivos de gramíneas forrageiras. Essa família em sido freqüentemente dividida em quatro subfamílias: Siphonellopsinae, Chloropinae, Rhodesiellinae e Oscinellinae. Os Oscinellines incluem 124 gêneros no mundo. Este projeto pretende fornecer uma comparação sistemática da morfologia e monofilia do gênero de Oscinellinae e de Rhodesiellinae, bem como construir uma estrutura filogenética para o grupo. Um total de 55 espécies de 50 gêneros de oscinellines foram utilizados como taxon terminais, sendo cinco espécies de três gêneros de Rhodesiellines, doze espécies de onze gêneros de Chloropines, três espécies de dois gêneros de Siphonellopsines, duas espécies de Milichiideos e uma espécie de carnidos usada como grupo externo. Um total de 167 caracteres da morfologia externa de adultos (cabeça, tórax, asa, pernas e abdômen) e das genitálias masculina e feminina foram codificadas e usadas para construir uma matriz de dados. Uma análise filogenética foi realizada para reconstruir as relações entre os táxons usando dois parâmetros analíticos diferentes - peso implícito sendo $k = 3$ e um valor k ($k = \sim 17$). Ambas as análises resultaram em uma árvore mais parsimoniosa, com diferenças importantes entre si e em muitos gêneros. Rhodesiellinae mostrou-se parafilético em relação a Oscinellinae, e Stenosciniini, uma tribo de rhodesielline, irmã de todos os restantes de Oscinellinae. Um grande clado estável inclui a maioria dos gêneros Fiebriegellini anteriormente incluídos nos Siphonellini, Tricimbini, Oscinisomatini, Liparaini e Botanobiini. Isso reafirmou que o grupo neotropical *blanda* de *Oscinella* não se encaixa com as espécies-tipo de *Oscinella* necessitando de uma classificação genérica para grupo. Um numeroso grupo de gêneros pertencentes a diferentes tribos não possuem uma posição confiável na árvore, sugerindo que os Incertellini, Hippelatini, Oscinellini e Siphonellini podem não corresponder aos respectivos clados. Outro amplo e estável clado (os "oscinelines superiores") reúne os Dicraeini e os gêneros de Botanobiini, Elachipterini, Liparaini e Hippelatini. Informações na literatura dão suporte à idéia de um clado que reúna essas tribos. O uso de uma lista de caracteres consideravelmente ampla que permita analisar uma amostragem genérica maior de taxons da subfamília, certamente, auxiliará e trará mais estabilidade à classificação do grupo.

Palavras-chave: Acalyptratae, Chloropidae, Diptera, Filogenia, Oscinellinae, Universal.

Introduction

The Chloropidae correspond to a considerably large family of acalyprate flies, with about 3,000 described species (Nartshuk 2014). Some authors estimate between 5,000 and 10,000 the real number of chloropid species worldwide (Ismay 2014). They are found in all regions of the world except Antarctica.

In temperate regions, many species are associated with grassland habitats (Ismay & Nartshuk 2000). They are minute to small in size (1.0 to 4.0 mm), rarely larger (6.0 to 9.0 mm). They are mostly blackish, but some species may be greyish, largely yellow, or greenish. In many genera, the mesonotum often has a pattern with three to five dark longitudinal stripes against a lighter background (Nartshuk *et al.* 1988, Ismay 2014).

The family is often referred to as “grass flies” and has members with highly specialized biologies. Most members of the family are phytophagous and some species are important pests of cereals and cultivated forage grasses (Nartshuk 2006). Different genera have species that infest the shoots of cereal crops and grasses. Among these species, *Chlorops* Meigen, *Elachiptera* Macquart and *Oscinella* Becker are best known for the damage their larvae cause (Deeming & Al-Dhafer 2012). The most important economic damages are of the Poaceae stem miners. They can live in different parts of the plant, deforming them in various ways, even producing galls (Ismay & Nartshuk 2000). Alternatively, some species are saprophagous and live in decaying plant tissues (Ismay & Nartshuk 2000) or in fungi (Deeming & Al-Dhafer 2012). There are as well parasites and parasitoids of other insects and arthropods. Larvae of species of *Thaumatomyia* Zencker prey upon root-aphids, larvae of *Batrachomyia* Krefft are subdermal parasites of frogs, and larvae of *Speccafrons* Sabrosky develop in spider egg capsules (Deeming & Al- Dhafer 2012).

A few genera of the family are considered vectors of diseases between animals and humans. The so-called “eye gnats” (*Hippelates* spp. and *Liohippelates* spp.) constitute important vectors, swarming around eyes and body secretions. In Brazil they may transmit purpuric fever, which initial symptom is acute conjunctivitis (Reilly *et al.* 2007, Deeming & Al-Dhafer 2012).

McAlpine’s (1989) study of the phylogeny of the Acalyptratae included Chloropidae as a monophyletic group. In his system, the Chloropidae fit into the Carnoidea, in which they

are more closely related to the families Cryptochetidae and Milichiidae, what is supported by synapomorphies of the head capsule, proboscis, wing venation and spermathecae (Buck 2006). Chloropidae and Milichiidae are well-supported as sister groups due to the presence of a well developed ventral receptacle and a bare, truncate distiphallus in the male terminalia (Buck 2006).

The relationships within the Chloropidae remain in a large extent unsettled. Besides the considerably large number of species and taxa of generic rank in the family in a worldwide scale (Nartshuk & Andersson 2013), some of the genera in the family are probably paraphyletic, thus tending to obscure the real affinities between the groups (Sabrosky 1951).

Great advance in the systematics of the Chloropidae was obtained from experts such as Andersson (1977), Kanmiya (1983), Sabrosky (1984), Nartshuk (1983), Ismay (1993), and Nartshuk & Andersson (2013), providing the basis for the current tribal and subfamily classification of the family (Mlynarek & Wheeler 2018). Andersson (1977, 1979) and Nartshuk (1983, 1987) presented some ideas on the phylogeny of the Chloropidae, but stressed that much further work was needed. Andersson (1977, 1979) remarked that the Chloropidae evolved relatively recently and, combined with the size of the chloropids, a morphology-based cladistic analysis would render difficult.

Becker (1910) divided the family Chloropidae in two main groups, now referred to the Oscinellinae and Chloropinae. Duda (1930a) divided the family into three subfamilies, Oscinellinae, Chloropinae and Paleoscinellinae (including *Hippelates* and related genera) (Sabrosky 1941). Later Duda (1932) changed his classification of the group to include two subfamilies, Siphonellopsinae and Chloropinae, dividing the latter into three tribes Chloropoidea, Oscinelloidea and Hippelatoidea (Sabrosky 1941). Sabrosky (1941) kept four chloropid subfamilies, Chloropinae, Oscinellinae, Siphonellopsinae and Heringiinae.

In a modern stage of the systematics of the family, Andersson (1977) recognized three subfamilies, Siphonellopsinae, Chloropinae and Oscinellinae, a position followed by Ismay & Nartshuk (2000) and Mlynarek & Wheeler (2009, 2018). Nartshuk & Andersson (2013), in the phylogenetic section of their study, proposed the Siphonellopsinae to be sister to the set of remaining members of chloropids.

There are some synapomorphies that sustain that the Siphonellopsinae should be sister to the remaining chloropids. This subfamily often has more extensive bristling on the

thorax, and the arrangement and orientation of cephalic setae are more similar (in terms of a plesiomorphic condition) to related families such as Milichiidae (Nartshuk & Andersson 2013). The male genitalia is asymmetrical, which is assumed by Brake (2000) to be relatively plesiomorphic to the other chloropids. Only four genera are included by Nartshuk (2012) in this subfamily, *Apotropina* Hendel, *Protohippellates* Andersson, *Siphonellopsina* Andersson and *Siphonellopsis* Strobl. Mlynarek & Wheeler (2018) discussed the morphological variation and the generic limits in this subfamily.

The Chloropinae contain 66 genera distributed and it has been unanimously accepted as monophyletic. The relationships within the Chloropinae have been addressed informally by Andersson (1977), Nartshuk (1983, 2012), Nartshuk & Andersson (2013), and formally by Paganelli (2002), Riccardi (2016) and Riccardi & Amorim (submitted). In Riccardi & Amorim (submitted), the monophyly of the Chloropinae was corroborated and a group of stable clades has been ranked as tribes.

Nartshuk & Andersson (2013) gave subfamily rank to the Rhodesiellinae, previously proposed as a tribe of Oscinellinae by Nartshuk (1983). Nartshuk & Andersson (2013), in the phylogenetic section of their study, presented two alternative scenarios for the relationships in the chloropids except the Siphonellopsinae: (Chloropinae + (Rhodesiellinae + Oscinellinae)) or (Oscinellinae + (Rhodesiellinae + Chloropinae)). The number of features and the taxon sampling in their study is small and the monophyly of the Oscinellinae still needed further evidence. In other words, it was not actually clear if the “Rhodesiellini” would fit into the Oscinellinae or if it should be a clade sister to one of these two subfamilies. Nartshuk (2012) recognized three groups of genera within the Rhodesiellinae to which was given tribe rank.

The Oscinellinae now include 124 genera. For a long time, this group was referred to as Oscininae (Sabrosky 1941). This name of the group of the family was replaced by Oscinellinae, since *Oscinis* Laterille has been synonymized to *Chlorops* (Sabrosky 1941). Sabrosky (1980a) recorded about 245 described species for the Oscinellinae. Most species are 1 to 5 mm long, rather blackish, uniformly colored, with the costal vein extending to M_{1+2} and usually with the presence of a male femoral organ. There is a wide variation in the subfamily, including size and color (Andersson 1977, Mlynarek & Wheeler 2018).

Andersson (1977), as mentioned above, divided the Oscinellinae into two tribes, Oscinellini and Rhodesiellini. Andersson (1977) concentrated his taxon sampling mostly on

the Old World fauna and did not examine many of the New World genera of the subfamily. The tribes Rhodesiellini and the Oscinellini were subdivided by Andersson (1977) into nine genus-groups: *Javanoscinis*, *Elachiptera*, *Gaurax*, *Dicraeus*, *Lipara*, *Polyodaspis*, *Aphanotrigonum*, *Oscinella* and *Eribolus* groups. Sabrosky (1984) dealt with most of Andersson's genus-groups as taxa without tribal rank.

Ismay (1993) addressed the question of the tribes Tricimbini and Incertellini, including a phylogenetic discussion of the relationships between groups of species of *Tricimba* and of *Aprometopis*, and of shared features between *Tricimba* and related genera.

More recently, Nartshuk (2012) divided the subfamily Oscinellinae in 11 tribes, but the affiliation of many genera of the subfamily into the tribes were not established. The tribes are:

- (1) Tribe Botanobiini Malloch, 1913: *Cestoplectus* Lamb, *Gampsocera* Schiner, *Gaurax* Loew, *Hapleginella* Duda, *Leucochaeta* Becker, *Pselaphia* Becker, *Pseudogaurax* Malloch, *Pterogaurax* Duda;
- (2) Tribe Dicraeini Nartshuk, 1983: *Dicraeus* Loew;
- (3) Tribe Elachipterini Lioy, 1864: *Alombus* Becker, *Anatrichus* Loew, *Ceratobarys* Coquillett, *Cyrtomomyia* Becker, *Disciphus* Becker, *Elachiptera* Macquart, *Lasiochaeta* Corti, *Melanochaetomyia* Cherian, *Sepsidoscinis* Hendel, *Togeciphus* Nishijima;
- (4) Tribe Fiebrigellini Nartshuk, 1983: *Anacamptoneurum* Becker, *Chaetochlorops* Malloch, *Epimadiza* Becker, *Fiebrigella* Duda, *Lasiambia* Anonymous, *Heteroscinis* Lamb, *Heteroscinoides* Cherian, *Polyodaspis* Duda;
- (5) Tribe Hippelatini Duda, 1932: *Chaethippus* Duda, *Hippelates* Loew, *Liohippelates* Duda, *Lioscinella* Duda;
- (6) Tribe Incertellini Nartshuk, 1983: *Apallates* Sabrosky, *Aphanotrigonum* Duda, *Biorbitella* Sabrosky, *Incertella* Sabrosky, *Malloevia* Sabrosky, *Meijerella* Sabrosky, *Microcercis* Beschovski, *Parameijerella* Cherian, *Parapallates* Cherian & Tilak;
- (7) Tribe Liparaini Camero & Tubbs, 1990: *Anomoeoceros* Lamb, *Calamoncosis* Enderlein, *Dasyopa* Malloch, *Lipara* Meigen, *Pseudeurina* Meijere;
- (8) Tribe Oscinellini Becker, 1910: *Camptoscinella* Sabrosky, *Conioscinella* Duda, *Olcella* Enderlein, *Oscinella* Becker, *Oscinimorpha* Lioy, *Neolcella* Cherian, *Neoscinella* Sabrosky;

(9) Tribe Oscinisomatini Enderlein, 1911: *Eribolus* Becker, *Oscinisoma* Lioy, *Rhopalopterum* Duda, *Sabroskyina* Beschovski;

(10) Tribe Siphonellini Lioy, 1864: *Kurumemyia* Kanmiya, *Siphonella* Macquart, *Speccafrons* Sabrosky;

(11) Tribe Tricimbini Nartshuk, 1983: *Aphanotrigonella* Nartshuk, *Aprometopis* Becker, *Indometopis* Cherian, *Siphunculina* Rondani, *Pseudotricimba* Ismay, *Tricimba* Lioy, *Tricimbomyia* Cherian.

Mlynarek & Wheeler (2018) for the first time made a formal phylogenetic analysis in the subfamily, with a study of 75 species of nine genera of Elachipterini, with some of the genera of oscinellines as outgroups. Two major clades were recognized, the group *Anathricus* and the group *Elachiptera*. In Appendix I, we provide a comparison of Andersson's (1977), Kanmiya's (1983), Nartshuk's (1983, 2012), and Mlynarek & Wheeler's (2018) systems concerning the position of the Oscinellinae and Rhodesiellinae genera into genus groups or tribes.

Andersson (1977), Kanmiya (1983), Nartshuk (1983) and Mlynarek & Wheeler (2018) worked on the question of the position and relationships of genera within the system of the Oscinellinae/Rhodesiellinae. The picture drawn out from their papers is that a global approach of the Oscinellinae has not been possible so far. Many genera have not been dealt in each of these studies, there is considerable inconsistency between their conclusions, and strict phylogenetic inference was used only by Mlynarek & Wheeler (2018). This strongly points to the need of a consistent comparative study of the genera of Oscinellinae and of their relationships so monophyly of the subfamily (including or excluding the Rhodesiellinae) can be verified and major clades within them can be detected.

Goals

This study intends to perform a careful comparative study of the morphology of the genera of Oscinellinae to develop the basis for a formal phylogenetic analysis of the subfamily. Hence, the main goals of the thesis are:

- (1) to describe in considerable detail morphological features not addressed in the literature for many genera and as much as possible convert this information into characters;
- (2) to test of the monophyly of the Oscinellinae, which basically means to check the position of the Rhodesiellinae relative to the Oscinellinae;
- (3) to establish the phylogenetic relationships between the genera of oscinellines, trying to recover major clades; and
- (4) within the limits of the taxon sampling, to verify the existence of paraphyletic genera in the system.

Material and Methods

A complete list of the genera of Oscinellinae and Rhodesiellinae is in Appendix II, with indication of the geographic distribution of each genus and the origin of the type-species. We tried to use representatives of as many genera as possible. Whenever available, we preferred to examin the type-species of the genus. The Neotropical fauna of the subfamily was the easiest source of material from the oscinelline genera, but material from other regions have been requested and included in the analysis when made available.

A list of the specimens received for this project is presented in Appendix III, indicating gender and corresponding depositary institutions.

Abbreviations of institutions from which material was obtained are indicated below:

- Australian Museum (NSW);
- British Museum of Natural History, London, England (NHM);
- Diptera Morphology and Evolution Lab, Depto. de Biologia, FFCLRP, Universidade de São Paulo (DMEL);
- Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP);
- Smithsonian Institution National Museum of Natural History, Washington DC, United States (USNM);
- Dr. John Waland Ismay personal collection (JIPC), from which Barbara Ismay very kindly made photos of some species (referred to ahead);
- Museum für Naturkunde an der Humboldt Universität, Berlin, Germany (ZMHU);
- California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, USA (CDFA);
- Naturhistorisches Museum Wien, Viena, Austria (NHMW);
- Queensland Museum (QM);
- Canadian National Collection of Insects, Arachnids and Nematodes (CNC);
- Michael von Tschirnhaus private collection, Bielefeld University, Germany (MVTPC);
- Jari Flinck private collections, Finland (JFPC)
- Zeinab Bazyar private collection of material from Iran and from donations from countries other than Brazil (ZBPC).

This analysis is based on the study of the morphology of more than 5.000 specimens of the Diptera Morphology and Evolution Lab and on loan of material from different museums and collections of the world. The material in our data matrix includes males and/or females of 61 species of 54 genera of Oscinellinae (including the type-species of 38 genera), six species of four genera of Rhodesiellinae (including the type-species of one genus), 14 species of 13 genera of Chloropinae, three species of two genera of Siphonellopsinae, three species of two genera of Milichiidae, and one species of Carnidae. Some species were made available only through photos sent by museum curators. Part of the data was obtained or confirmed from the literature, particularly Andersson (1977), Chvala *et al.* (1974), Cherian & Emiliyamma (1999), Kanmiya (1983, 1994), Kubik & Bartak (2010), Liu *et al.* (2017), Malloch (1913b, 1928, 1938), Mlynarek & Wheeler (2009, 2018), Sabrosky (1941, 1947), Spencer (1978), Walker (1860). The entire tree was rooted on the species of Carnidae.

Some of the illustrations were made vectorizing Dr. Paula Raile Riccardi's original drawings with her consent.

The dissection of specimens followed procedures that are standard for some groups of Diptera. The male terminalia was removed from the abdomen and placed into warm 10% KOH for 2–3 minutes. They were then transferred to acetic acid and, afterwards, to ethanol 70% for a few seconds. After dissection, the wing, abdomen, and the terminalia were stored in a microvial containing glycerol and pinned together with the specimen. In some cases, wings were mounted between cover slips with Euparal and pinned together the specimen. The female terminalia were removed from the abdomen and placed into cold KOH for 5–15 hours and then transferred to acetic acid. They were then transferred to ethanol 70% for a few seconds where the ovipositor was pulled out. The abdomen was transferred to a microvial with glycerol, which was pinned under the specimen.

Photos were taken using a DC500 Leica camera coupled to a Leica MZ16 stereomicroscope. Helicon Focus Software 6 was used for stacking. Photoshop CC was used for further editing of images. Initial drawings were made using a camera lucida coupled to a Leica DM2500 microscope, vectorized with Illustrator CC.

Morphology and terminology basically follows Cumming & Wood (2009), except for particular chloropid features, that follow Andersson (1977), Kanmiya (1983) and Nartshuk & Andersson (2013).

The morphological matrix was constructed with WinClada (Nixon 1999-2002). All multistate characters were treated as unordered. Characters were polarized through the rooting between outgroups (Nixon & Carpenter, 1993), in this case, specifically on Carnidae. Matrix analysis followed the cladistic method under the principle of parsimony (Lipscomb 1998, Schuh & Brower 2009), carried out with the software TNT ver. 1.1 (Goloboff *et al.* 2008b). Both equal and implied weighting schemes (Goloboff 1993, Goloboff *et al.* 2005) were conducted with the "New Technology Search" option (random seed 0, irritation level 75, initial addseqs 11, finding minimum tree length 10 times, default values for Ratchet, Drift, Sectorial search and Tree fusion) saving the most parsimonious trees (MPTs). There is a major loss of information using equal weight and the trees obtained therefore were not used. The tree from both implied weight strategies had better resolution and are able to recognize and underscore highly incongruent characters. We used two different implied weighting schemes, one with $k = 3$, and the other with $k = \sim 17$ using the setk.run script. Both trees represented in the results (Figures 1, 2).

Results

The complete data matrix has 167 morphological characters for 84 terminal taxa. Along the stage of the analysis of the matrix, six terminals had a large amount of missing data—*Cadrema lonchopterooides* (NHM), *Camptoscinella annulitibia* (NHM), *Deltastoma unipunctatum* (NSW), *Eugaurax floridensis* (USNM), *Meijerella cavernae* (ZMHU) and *Pterogaurax* sp. nov. (DMEL)—and were removed from the final analyses. Part of the characters come from published morphological studies—as Andersson (1977), Kanmiya (1983), Nartshuk (1983), Nartshuk (2012)—or from phylogenetic analyses—Mlynarek & Wheeler (2018) and Riccardi & Amorim (submitted)—, sometimes with slightly different coding and the sources are duly recognized.

List of characters

Head

1. Connection of head capsule with thorax (Figure 9a-c): (0) ventrally; (1) posteriorly; (2) medially.
2. Frons (in dorsal view) (Figure 10a-c): (0) wider than long; (1) as wide as long; (2) longer than wide. Riccardi & Amorim (submitted), Mlynarek & Wheeler (2018)
3. Occiput: (0) convex (Figure 11a-b): (1) straight, angulated with frons. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
4. Occiput with pair of setae, basally (supercervial setae) (Figure 12a-b): (0) absent; (1) present.
5. Head in lateral view (Figure 13a-c): (0) longer than wide; (1) as wide as long; (2) wider than long. Mlynarek & Wheeler 2018
6. Ocellar triangle (Figure 14a-c): (0) well marked, margins of ocellar triangle conspicuous; (1) not well marked, margins not clear or entirely absent. Riccardi & Amorim (submitted)
7. Texture of ocellar triangle (Figure 15a-c): (0) opaque, rugose; (1) shining. Mlynarek & Wheeler (2018)
8. Pruinosity of ocellar triangle without tubercle (Figure 16a-f): (0) almost entirely pubescent; (1) posterior two third pubescent; (2) posterior third pubescent; (3) almost

- bare; (4) anterior two third pubescent; (5) anterior third pubescent; (6) anterior tip of triangle bare; (7) anterior tip of triangle pubescent. Riccardi & Amorim (submitted)
9. Anterior end of ocellar triangle (Figure 17a-c): (0) reaching or almost reaching anterior margin of frons; (1) between anterior margin of frons and middle of frons; (2) at most reaches middle of frons. Riccardi & Amorim (submitted), Mlynarek & Wheeler (2018)
 10. Ocellar triangle width at posterior margin (Figure 18a-c): (0) hardly wider than the tubercle itself; (1) wider than tubercle, reaching halfway to eye margin; (2) getting close or laterally reaching the eye margins. Riccardi & Amorim (submitted)
 11. Lateral margins of ocellar triangle (Figure 19a-c): (0) convex; (1) concave; (2) straight. Mlynarek & Wheeler (2018)
 12. Color of ocellar triangle (Figure 20a-l): (0) light brown to yellow entirely; (1) dark brown to black entirely; (2) anterior end light, the rest dark; (3) anterior half light, posterior half dark; (4) posterior end light, the rest dark; (5) posterior light, anterior dark; (6) middle (oval or linear) light, around dark; (7) posterior end dark, the rest light; (8) anterior fifth and a median band dark, with dark yellow background; (9) dark tubercle with darker lateral areas over lighter background.
 13. Ocellar triangle (Figure 21a-e): (0) concolor; (1) with spot; (2) with band.
 14. Posterior ocelli (Figure 22a-b): (0) yellow or light brown; (1) black or dark brown.
 15. Anterior ocellus (Figure 23a-b): (0) yellow or light brown; (1) black or dark brown.
 16. Density of setation on frons (Figure 24a-c): (0) bare; (1) dense; (2) scattered.
 17. Anterior margin of frons in dorsal view (in comparison of the level of eyes) (Figure 25a-d): (0) straight or slightly projected; (1) projected moderately beyond the anterior margin of eyes; (2) concave, medially with projection; (3) concave, medially straight. Riccardi & Amorim (submitted)
 18. Lateral margins of frons in dorsal view (Figure 26a-c): (0) converging towards anterior margin; (1) diverging towards anterior margin; (2) almost parallel. Riccardi & Amorim (submitted), Mlynarek & Wheeler (2018)
 19. Ground color of frons (Figure 27a-h): (0) anterior third yellow; (1) anterior half yellow; (2) anterior two third yellow; (3) entirely yellow; (4) entirely dark; (5) anterior third dark; (6) anterior two third dark; (7) anterior half dark.
 20. Length of orbital setae (Figure 28a-b): (0) long; (1) short. Riccardi & Amorim (submitted)

21. Comparison of length of orbital setae to each other (Figure 29a-b): (0) of same length; (1) some clearly longer than others. Mlynarek & Wheeler (2018)
22. Direction of orbital setae (Figure 30a-c): (0) all reclinate; (1) all proclinate; (2) anterior one proclinate, posterior two reclinate. Riccardi & Amorim (submitted)
23. Number of orbital setae (Figure 31a-c): (0) less than five; (1) between five and ten; (2) more than ten. Riccardi & Amorim (submitted)
In all cases the last posterior seta, which was different to the rest, was ignored.
24. Inner vertical seta (Figure 32a-b): (0) conspicuous and strong; (1) absent or not distinguishable. Mlynarek & Wheeler (2018)
25. Length of ocellar setae (Figure 33a-b): (0) shorter than or as long as ocellar tubercle; (1) longer than ocellar tubercle. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
26. Direction and orientation of ocellar setae (Figure 34a-f): (0) proclinate and convergent; (1) proclinate and divergent; (2) proclinate and parallel; (3) reclinate and convergent; (4) reclinate and parallel; (5) reclinate and divergent. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
27. Length of post-ocellar setae (Figure 35a-b): (0) shorter or as long as the ocellar tubercle; (1) longer than the ocellar tubercle.
28. Orientation of postocellar setae (Figure 36a-c): (0) convergent; (1) divergent; (2) parallel.
29. Anterior interfrontal setae (Figure 37a-b): (0) longer than remaining interfrontal setae; (1) shorter or as long as remaining interfrontal setae.
30. Interfrontal setae relative to the frontal setae (Figure 38a-c): (0) absent; (1) present, as long as frontal setae; (2) present, conspicuous. Riccardi & Amorim (submitted)
31. Direction of interfrontal seta (Figure 39a-d): (0) all proclinate; (1) all inclinate; (2) anteriorly proclinate and posteriorly inclinate; (3) all straight.
32. Height of gena relative to the height of first flagellomere of antenna (Figure 40a-c): (0) shorter; (1) almost as long; (2) longer. Riccardi & Amorim (submitted)
33. Color of gena (Figure 41a-i): (0) all over yellow or light brown; (1) posterior half yellow; (2) anterior half yellow; (3) dark color; (4) posterior third yellow; (5) anterior third yellow; (6) posterior two third yellow; (7) anterior two third yellow; (8) all over yellow except anterior tip dark.

34. Color of postgena (Figure 42a-b): (0) black or dark brown; (1) yellow or light brown.
35. Vibrissal seta (Figure 43a-b): (0) present; (1) absent.
36. Parafacialia (related to the broadness of first flagellomere of antenna) (Figure 44a-c): (0) absent; (1) narrow; (2) wider. Riccardi & Amorim (submitted)
37. Pilosity of eye (Figure 45a-b): (0) bare; (1) hairy.
38. Dispersal pilosity of eye (Figure 46a-b): (0) scattered; (1) dense.
39. Posterior margin of eye, $\frac{1}{4}$ ventral (Figure 47a-b): (0) continues; (1) with notch.
40. Rate of eye compared with head capsule vertically in lateral view (Figure 48): (0) smaller than 1.3; (1) between 1.3 and 1.4; (2) between 1.41 and 1.5; (3) between 1.51 and 1.6; (4) bigger than 1.6.
41. Proboscis (Figure 49a-b): (0) geniculate; (1) not geniculate.
42. Length of palpus in comparison with the oral cavity (lower margin of the face) (Figure 50a-b): (0) at most at the margin of oral cavity; (1) longer than the margin of oral cavity. Mlynarek & Wheeler (2018)
43. Shape of facial carina (Figure 51a-b): (0) wide dorsally and ventrally; (1) narrow ventrally and wide or narrow dorsally.
44. Facial carina (Figure 52a-b): (0) complete, reaching to the epistomal margin or very close; (1) incomplete, extending almost halfway to epistomal margin. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
45. Rate of first antennal flagellomere (length/wide) (Figure 53): (0) 1; (1) between 1.1 and 1.5; (2) more than 1.5.
46. First antennal flagellomere distally (Figure 54a-d): (0) pointed; (1) angulated; (2) rounded. Riccardi & Amorim (submitted)
47. Color of first antennal flagellomere (Figure 55a-g): (0) posterior half yellow or light; (1) entirely yellow or light brown; (2) entirely dark brown or black; (3) posterior two third yellow or light brown; (4) entirely yellow or light brown except at base of arista; (5) yellow or light brown, dark dorsobasally; (6) posterior third yellow or light brown; (7) dark with yellow ventral margin. Riccardi & Amorim (submitted)
48. Posterior end of first antennal flagellomere, in frontal view (Figure 56a-b): (0) straight; (1) concave (reniform). Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
49. Color of basal segment of arista (Figure 57a-b): (0) dark; (1) yellow.

50. Color of distal segment of arista (Figure 58a-b): (0) dark; (1) yellow. Riccardi & Amorim (submitted)
51. Width of distal half arista (Figure 59a-b): (0) thin; (1) thick. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
52. Position of arista on first antennal flagellomere (Figure 60a-b): (0) placed at most equal with arista base; (1) more than arista base, at least twice. Riccardi & Amorim (submitted)
53. Pilosity of entire arista comparing with the stem of arista (Figure 61a-b): (0) short hairs; (1) long hairs. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018

Thorax

54. Anterior part of mesonotum (Figure 62a-b): (0) not projected; (1) projected (neck form).
55. Length of scutum dorsally (Figure 63): (0) as long as wide; (1) longer than wide; (2) wider than long. Mlynarek & Wheeler (2018)
56. Acrostical seta (Figure 64a-b): (0) present; (1) absent.
57. Dorsocentral seta (Figure 65a-b): (0) present; (1) absent. Riccardi & Amorim (submitted)
58. Pruinosity all over the scutum (Figure 66a-b): (0) present; (1) absent. Riccardi & Amorim (submitted)
59. Color of pruinosity on scutum (Figure 67a-b): (0) dark brown or black; (1) yellow or whitish.
60. Scutum (Figure 68a-b): (0) no longitudinal sulcus; (1) with 1-3 longitudinal sulcus. Riccardi & Amorim (submitted)
61. Area over dc (Figure 69a): (0) dark; (1) yellow.
62. Area over ac (Figure 69a): (0) dark; (1) yellow.
63. Lateral area, dorsal to margin on scutum (Figure 69a): (0) dark; (1) yellow.
64. Lateral most area on scutum (Figure 69a): (0) dark; (1) yellow.
65. Scutum dorsal to wing base (Figure 69a): (0) dark; (1) yellow.
66. Scutum posterior end (Figure 69a): (0) dark; (1) yellow.
67. Scutum area between ac and dc (Figure 69a): (0) dark; (1) yellow. Riccardi & Amorim (submitted)

68. Scutum area, external line to the dorso-lateral to dc (Figure 69a): (0) dark; (1) yellow.
69. Scutum area, external line to the ventro-lateral to dc (Figure 69a): (0) dark; (1) yellow.
70. Scutum anterior half (Figure 69b): (0) dark; (1) yellow.
71. Scutum area posterior half (Figure 69b): (0) dark; (1) yellow.
72. Propleuron (Figure 70a-b): (0) well developed; (1) weakly developed.
73. Postpronotal seta (Figure 71a-b): (0) 0 or 1; (1) 2 or more. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
74. Postpronotal seta orientation, in case of 2 or more setae (Figure 72a-b): (0) only lateroclinate; (1) reclinate and lateroclinate.
75. Postpronotal lobe (Figure 73a-b): (0) mostly yellow; (1) mostly brown or black.
76. Anepisternum (Figure 74a-b): (0) purinosity; (1) bare. Riccardi & Amorim (submitted)
77. Anepisternum setaceous (Figure 75a-b): (0) present; (1) absent.
78. Anepisternum color (Figure 76a-c): (0) entirely yellow(ish); (1) entirely brown or black; (2) mostly yellow with brown marketing ventrally.
79. Katepisternum color (Figure 77a-c): (0) entirely yellow(ish); (1) entirely brown or black; (2) mostly yellow with brown marketing.
80. Meron color (Figure 78a-c): (0) yellow or light brown; (1) brown or black; (2) yellow(ish), dark marketing.
81. Number of distinct anterior notopleural setae (Figure 79a-d): (0) 1; (1) 2; (2) more; (3) 0. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
82. Number of distinct posterior notopleural setae (Figure 80a-c): (0) 1; (1) 2; (2) more. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
83. Purinosity on postpronotal lobe (Figure 81a-b): (0) present; (1) absent.
84. Numbers of supraalars (Figure 82a-c): (0) 0; (1) 1; (2) 2. Mlynarek & Wheeler (2018)
85. Numbers of postalars (Figure 83a-c): (0) 1; (1) 2; (2) more. Riccardi & Amorim (submitted)
86. Intrapostalar (Figure 84a-b): (0) absent; (1) present. Mlynarek & Wheeler (2018)
87. Length of scutellum (Figure 85a-c): (0) longer than wide; (1) wider than long; (2) almost as long as wide. Mlynarek & Wheeler (2018)
88. Tip of scutellum in dorsal view (Figure 86a-b): (0) apically rounded or slightly pointed; (1) apically straight (flattened).
89. Laterals of scutellum in dorsal view (Figure 87a-b): (0) convex; (1) straight.

90. Scutellar finger-like tubercles (Figure 88a-c): (0) absent; (1) present, only apicals; (2) present, apicals and subapicals. Mlynarek & Wheeler (2018)
91. Scutellar large setae position (Figure 89a-b): (0) marginal; (1) ventral.
92. Scutellum color (Figure 90a-d): (0) entirely dark brown or black; (1) entirely yellow or light brown; (2) apically and laterally yellow or brown; (3) black or dark brown anteriorly; (4) laterally yellow or light brown; (5) basally yellow or brown; (6) apically and basally yellow or brown; (7) laterally black or dark brown; (8) yellow or light brown anteriorly.

Wing

93. Wing length compared to the abdomen length (Figure 91): (0) longer or as long; (1) shorter. Mlynarek & Wheeler (2018)
94. Costal (Figure 92a-d): (0) ending at R_{4+5} ; (1) ending at M_{1+2} ; (2) ending between R_{4+5} and M_{1+2} ; (3) ending before R_{4+5} . Riccardi & Amorim (submitted)
95. Anal lobe (Figure 93a-b) (0) present; (1) absent. Riccardi & Amorim (submitted), Mlynarek & Wheeler, 2018
96. Alula (length/width) (Figure 94): (0) lesser than 3; (1) between 3 to 5; (2) more than 5.
97. Pattern on the wing, apically (Figure 95): (0) translucent; (1) marked. Mlynarek & Wheeler (2018)
98. Pattern on the wing, basally (Figure 95): (0) translucent; (1) marked.
99. Pattern on the wing, medially (Figure 95): (0) translucent; (1) marked.
100. Shape of pattern on the wing, apically (Figure 96): (0) restricted between veins; (1) unrestricted.
101. Basal radial cell relating to the basal medial cell (Figure 97a-b): (0) reaches before middle of basal medial cell; (1) at least at the medium of basal medial cell. Riccardi & Amorim (submitted)
102. Height of basal radial cell (Figure 98): (0) no modification; (1) projecting dorsally.
103. Sinusoidal of CuA (Figure 99a-b): (0) absent (straight or slightly inward); (1) present (notably inward). Riccardi & Amorim (submitted)
104. R_1 (Figure 100a-b): (0) slightly distally; (1) with a short bump.
105. Sc (Figure 101a-c): (0) almost entirely independent from R_1 ; (1) distinct from R_1 basally; (2) entirely indistinctive.

106. Costal break on Sc part (Figure 102a-b): (0) present; (1) absent. Riccardi & Amorim (submitted)
107. Costal break on humeral part (Figure 103): (0) present; (1) absent. Riccardi & Amorim (submitted)
108. Shape of anterior end of R_{2+3} (Figure 104a-b): (0) curved to the C; (1) about straight to the C.
109. Shape of basal half of M_{1+2} (Figure 105): (0) convex anteriorly; (1) straight.
110. Shape of dm-cu (Figure 106): (0) convex; (1) straight.
111. Position of dm-cu in relation to CuA_1 (Figure 107a-b): (0) more than 100°; (1) about 90° or less.
112. C2 (Figure 108a-c): (0) at most reaches to the middle of the wing; (1) between middle and tip of the wing; (2) at the tip of the wing. Riccardi & Amorim (submitted)
113. C4 (Figure 109a-b): (0) ending below the apical margin of the wing; (1) ending at the apical margin of the wing.
114. M_{1+2} thickness (Figure 110a-b): (0) as thick as R_{4+5} ; (1) thinner than R_{4+5} . Riccardi & Amorim (submitted)
115. Halter color (knob) (Figure 111a-b): (0) black or dark brown; (1) yellow-ish or light brown. Riccardi & Amorim (submitted)
116. Halter color (stem) (Figure 111a-b): (0) black or dark brown; (1) yellow-ish or light brown.

Legs

117. Male mid femoral organ (Figure 112): (0) present; (1) absent. Mlynarek & Wheeler (2018)
118. Tibial organ (Figure 113): (0) absent; (1) present; (2) not developed well. Riccardi & Amorim (submitted)
119. Hind tibial spur (Figure 114a-b): (0) shorter or slightly longer than hind tibia diameter; (1) clearly longer; (2) absent. Mlynarek & Wheeler (2018)
120. Hind tibia color: (0) yellow or light brown entirely; (1) black or dark brown entirely; (2) dorsal tip yellow, the rest dark; (3) dorsal and ventral tips yellow, the rest dark; (4) dorsal and ventral tips dark, the rest yellow; (5) around tibial organ dark, the rest yellow; (6) dorsally, medially and ventrally yellow, the rest dark.

121. Hind tibial organ: (0) dark color; (1) yellow or white.
122. First hind tarsal segment: (0) yellow or light brown; (1) black or dark brown; (2) dorsally yellow, ventrally dark.
123. Fore tibia color: (0) yellow or light brown entirely; (1) black or dark brown entirely; (2) small part at the middle dark, the rest yellow; (3) dorsal tip yellow, the rest dark; (4) dorsally, medially and ventrally yellow, the rest dark.
124. First fore tarsal segment: (0) yellow or light brown entirely; (1) black or brown; (2) dorsal tip yellow, the rest dark.
125. Fore coxa color: (0) yellow or light brown entirely; (1) black or dark brown entirely; (2) ventral half yellow, dorsal half dark; (3) dorsal and ventral tip yellow, the rest dark; (4) ventral tip yellow, the rest dark.

Abdomen

126. Abdominal tergites (Figure 115): (0) no modification; (1) syntergites 1+2 expanded comparing with other tergites. Mlynarek & Wheeler (2018)
127. Sclerotization of tergite (Figure 116a-b): (0) syntergites 1+2 slightly sclerotized; (1) syntergites 1+2 firmly sclerotized; (2) syntergites 1+2 and tergite 3 firmly sclerotized. Mlynarek & Wheeler (2018)
128. Color of 5th tergit of abdomen: (0) entirely yellow; (1) entirely black or dark brown; (2) dark in 2 or 3 vertical lines; (3) anteriorly yellow, posteriorly dark; (4) anteriorly dark, posteriorly yellow.
129. Color of 1st tergit of abdomen: (0) entirely yellow; (1) entirely black or dark brown; (2) dark in 1 to 3 vertical lines; (3) anteriorly yellow, posteriorly dark; (4) ventral laterals dark.

Male terminalia

130. Syntergosternite 7+8 (Figure 117): (0) broad; (1) narrow.
131. Epandrium medial line (dorsal sulcus) (Figure 118): (0) present; (1) absent.
132. Antero-ventral corner of epandrium in posterior view (Figure 119a-b): (0) with a short projection; (1) with a long projection; (2) absent. Riccardi & Amorim (submitted)
133. Size of surstylius (comparing with the size of epandrium) (Figure 120a-b): (0) short; (1) long. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018

134. Elongated setae at the edge of anterior lateral margins of surstylius (Figure 121a-b): (0) present; (1) absent. Riccardi & Amorim (submitted)
135. Elongated setae at lateral margins of surstylius modified to spines (Figure 122): (0) present; (1) absent.
136. Marginals of surstylius in posterior view (Figure 123a-b): (0) straight; (1) indentured. Riccardi & Amorim (submitted)
137. Anterior and posterior lateral margins of surstylius (Figure 124a-d): (0) parallel; (1) convergent; (2) divergent. Mlynarek & Wheeler (2018)
138. Location of cercus on epandrium (Figure 125a-b): (0) placed on proctiger, free; (1) below proctiger, connected with epandrium. Riccardi & Amorim (submitted)
139. Cercus articulation (Figure 126a-b): (0) articulated; (1) fused to epandrium.
140. Length of cercus (Figure 127a-e): (0) almost vestigial, in the middle; (1) almost vestigial, in laterals; (2) small; (3) enlarged, broad; (4) enlarged, narrow. Riccardi & Amorim (submitted), Mlynarek & Wheeler 2018
141. Elongated setae at tip of cercus (Figure 128a-c): (0) absent; (1) present, 1 to 3; (2) present, several. Mlynarek & Wheeler (2018)
142. Cerci (Figure 129a-d): (0) separated from each other; (1) fused basally or until midway to apex; (2) fused entirely or more than midway broadly; (3) fused entirely narrowly (mesolobe). Mlynarek & Wheeler (2018)
143. Proctiger (Figure 130a-b): (0) projected dorsally; (1) almost flat, not visible laterally.
144. Proctiger in posterior view (Figure 131a-c): (0) elongated dorsoventrally; (1) widened laterally; (2) almost as long as wide.
145. Shape of proctiger in lateral margins (posterior view) (Figure 132a-c): (0) concave; (1) almost 90°; (2) almost straight.
146. Ventral margin of proctiger (Figures 132c, 133): (0) concave; (1) straight.
147. Sub-anal plate (under proctiger) (Figure 134a-b): (0) present; (1) absent. Riccardi & Amorim (submitted)
148. Hypandrium (Figure 135): (0) firmly connected to epandrium, articulated outside of epandrium; (1) sclerotized simply, articulated inside.
149. Shape of hypandrium (Figure 136a-b): (0) arms not connected posteriorly; (1) arms connected posteriorly. Riccardi & Amorim (submitted)

150. Phallapodeme length (Figures 136a, 137): (0) long; (1) short. Riccardi & Amorim (submitted)
151. Base of phallapodeme (Figures 137, 138): (0) unbranched basally; (1) branched basally.
152. Phallapodem sclerite (Figure 139a-d): (0) absent; (1) developed only basally (branches are occupied by that); (2) developed only distally (branches are free); (3) developed basally and distally. Riccardi & Amorim (submitted)
153. Length of endophalic process (Figure 140a-b): (0) developed; (1) vestigial.
154. Distiphallus (Figure 141a-b): (0) hairy; (1) bare. Riccardi & Amorim (submitted)
155. Synchrony of S6 (Figure 142a-c): (0) asymmetrical; (1) symmetrical, frontally covers hypandrium; (2) absent. Riccardi & Amorim (submitted)
156. Hypandrium, anterior view (Figure 143a-b): (0) not sclerotized ventrally; (1) sclerotized ventrally, divided it in 2 parts.

Female terminalia

157. Shape of segment 7 (Figure 144): (0) longer than wide; (1) as long as wide; (2) shorter than wide.
158. Shape of segment 8 (Figure 145): (0) three times or more longer than wide; (1) longer or as long as wide; (2) shorter than wide.
159. Sternite 8 (Figure 146a-b): (0) one piece; (1) V-shaped; (2) completely divided longitudinally in two pieces lateral sclerites.
160. Shape of sternite 8 (Figure 146a): (0) flattened at the segment 8; (1) protruding in 2 lobes anteriorly.
161. Cerci coming out: (0) separated distally; (1) close to each other distally.
162. Cerci (Figure 147): (0) not sclerotized; (1) sclerotized.
163. Shape of cerci (Figure 148a-c): (0) elongated, cylindral; (1) short, round; (2) short, triangular.
164. Hypoproct (Figure 149): (0) densely covered with microtrichia; (1) few microtrichia present; (2) entirely bare.
165. Hypoproct setation (Figure 150): (0) aligned at the frontal margin of hypandrium in row(s); (1) spread all over of the disk of hypoproct.
166. Epiproct (Figure 151): (0) with microtrichia; (1) entirely bare of microtrichia.

167. Number of setae on epiproct (Figure 152a-b): (0) 2 in the centre of epiproct disk; (1) 3 in the centre of epiproct disk; (2) numerous and dispersal; (3) 0.

Of the complete list of characters, 101 are binary characters and 66 have three or more character states, in a matrix with 55 oscinelline species of 50 genera, and five rhodesielline species of three genera. The analysis under implied weight with k value = 3 rendered one single maximum parsimonious tree (MPT) with 1984 steps (Figure 2). The Consistency index (C_i) is 0.14 and the Retention index (R_i) 0.42. The analysis under implied weight using the setk.run script ($k = 17.17770$) also provided only one single most parsimonious tree, with 1903 steps and $C_i = 0.15$ and $R_i = 0.44$ (Figure 1).

As briefly discussed above, the use of successive posterior weighting of characters prevents the risk of highly plastic characters to establish nodes in the parts of the tree with less support from mutually congruent characters. The topology chosen as the best approach here, with default option in TNT with $k = 3$, enhances the weight of the features with nested congruence over incongruent characters. Our position is that, more important than exact topology of the trees obtained with the two different k values, the comparison of between the trees helps detecting the rogue terminals and the larger stable clades in the tree.

There was an effort to extend the outgroup sampling within chloropids, rooting at Carnidae, although the character sampling at the level of the outgroups was beyond the scope of this study. Nevertheless, the discussion of the relationships between the subfamilies is relevant. There is a considerable evidence that the Siphonellopsinae is sister to the remaining chloropids. In this sense, the position of the Chloropinae as sister to the remainder of the family in our tree (Figure 2) seems to be due to undersampling of characters. The monophyly of (Rhodesiellinae + Oscinellinae), however, has clear support in the literature (Figures 2, 4, 5).

The monophyly of the Rhodesiellinae, with its tribes Rhodesiellini, Stenoscinini, and Scoliophthalmini, as proposed by Nartshuk (2012), was not recovered here. The results we obtained, however, shed light over the problem of the relationships between the Rhodesiellinae and the Oscinellinae. *Rhodesiella* indeed appears as a clade sister to all Oscinellinae (including the Stenoscinini). *Stenoscinis* and *Psilacrum*, on the other hand, do not fit together with *Rhodesiella* in a clade (Figure 5). We did not have samples of *Scoliphthalmus*, so for the time being we cannot solve the problem of its position.

Stenoscinis belongs in a clade which is sister to all other oscinellines. The curve at the base of M_{1+2} vein of the wing define well a clade with *Rhodesiella* and close by genera (Figures 5, 105). The overall delimitation of Rhodesiellinae in Nartshuk (2012), however, mix apomorphic features shared by Rhodesiellinae s.s. (i.e., Rhodesiellini) and Oscinellinae, and the plesiomorphic condition of features that are apomorphic for the core oscinellines. This helps to produce Rhodesiellinae as a grade at the base of the Oscinellinae.

Stenoscinis in our results fits into a clade together with *Disciphus*, *Anatrichus* and *Rhopalopterum*, which is sister to all remaining oscinellines (Figures 3, 5). The position of this clade in the tree with $k = 3$ differs from the position in the tree obtained from the setk script (Figures 1, 2). The generic composition of the clade, however, does not change, meaning that the clade itself is stable. It is supported by the presence of supercervial setae, an elongated palpus, the presence of purinosity on the anepisternum, the color of the first tarsal segment of the foretibia, and the shape of the female proctiger in posterior view (Figure 5). Hence, we keep the tribal status of Stenoscinini (for the time being with a different generic composition), but transferred back the tribe from the Rhodesiellinae to the Oscinellinae.

The position of *Psilacrum* was particularly puzzling. In none of our analyses it gathered either with *Rhodesiella* or with *Stenoscinis*, as it would first be expected (Figures 2, 8). This either means that the position of *Psilacrum* in the $k = 3$ tree is due to noise or that the position of *Psilacrum* is indeed not in the Rhodesiellinae or in the Stenoscinini, in such a way that non-homologous similarities between *Psilacrum* and *Stenoscinis* would have resulted in their approximation in the classification. We do not have now information at hand to answer this question. A wider study of the rhodesiellines will help to establish a clear picture of the position of the other genera. This includes particularly *Scoliphthalmus*, but also *Javanoscinis*, and the remaining genera associated to *Rhodesiella*.

Andersson's (1977) discussion on the Rhodesiellinae (as a tribe in his system) clearly supports the conclusions of this study at this level. He carefully discussed the features shared by oscinellines and rhodesiellines from a phylogenetic perspective (Andersson 1977, p. 55): "The Oscinellinae genera can be grouped into two groups which I think deserve the rank of tribes, viz. Rhodesiellini, which show many plesiomorphous features such as divergent ocellar setae, hairy eyes, hairy mesopleuron, and Oscinellini, with a higher

number of apomorphic characters.” Kanmiya (1983, p.32) agreed with this division and added some additional features of the male terminalia.

In other words, Andersson (1977) was already able to recognize apomorphic features that join these two main groups, but recognized that there are apomorphies of the core oscinellines which are not present in the Rhodesiellinae s.s., i.e., excluding *Javanoscini*. Later on, Andersson says (p. 56), “The Rhodesiellini undoubtedly belongs to Oscinellinae but is quite distinct from Oscinellini. The plesiomorphous feature, divergent procurved *oc* is present in both Chloropinae and Siphonellopsinae but not in Oscinellini except in the odd genus *Javanoscini*. On the other hand the apomorphous feature, femoral organ is present also in Oscinellini”. This means that he even recognized that there are apomorphic features in *Javanoscini* (what also applies to *Stenoscini*, a genus he did not examine) that do not strictly fit into a clade with *Rhodesiella*. Kanmiya (1983, p. 64) had a species of *Stenoscini* in his study. He included the genera *Stenoscini* and *Psilacrum* (*Oscinoides* s.l.) together with *Javanoscini* into the “Oscinellini”.

The presence of *Anatrichus* and *Disciphus* within the Stenoscinini is confusing. Andersson (1977, p. 66) and Kanmiya (1983) include them in the *Elachiptera* genus group, a position followed by Mlynarek & Wheeler (2012). We hardly would have any doubt about their connection to the Elachipterini, and we understand that possibly decisions concerning character coding may have displaced these two genera. Sabrosky (1980) mentioned that *Rhopalopterum* corresponds to *Lioscinella* by Andersson (1977) and that Nearctic species associated to the genus have been previously placed in *Stenoscini*. Hence, there is a chance that *Rhopalopterum* is either part of this clade with *Stenoscini*, though deserving its generic rank, or is a relatively plesiomorphic genus of core oscinellines.

With the results of this study (Figure 2), both kinds of ranking at this level would work—a single subfamily Oscinellinae, with two main subclades, as in Andersson’s (1977) system, or two sister subfamilies, Rhodesiellinae and Oscinellinae, as in Nartshuk’s (2012) system. We prefer here to keep the subfamily status given to the Rhodesiellinae, with more space for a detailed tribal classification within the oscinellines. The basic difference with Nartshuk’s (2012) system about the Rhodesiellinae is that we transfer back the Stenoscinini to the Oscinellinae, where it fits as a clade sister to the core oscinellines. Mlynarek & Whelees’s (2018) study of the Elachipterini had a sampling of outgroups with eight oscinelline genera, what does not warrant a safe test of the hypothesis of monophyly of the

tribe. They found, within their composition of the Elachipterini, a clade sister to the remaining members of the tribe composed by the genera *Disciphus*, *Allomedeia*, *Alombus*, *Sepsidoscinis* and *Anatrichus*. The other clade has the genera *Goniaspis*, *Ceratobarys*, *Lasiochaeta*, and *Elachiptera*. As mentioned ahead, our results corroborate the position of *Sepsidoscinis* close to *Elachiptera*. It is interesting to note that *Anatrichus* and *Disciphus* come together in the Stenoscinini.

The genera *Goniaspis* and *Monochaetoscinella* in our study (Figures 2, 6) compose a clade which is sister to all remaining oscinellines except the Stenoscinini. This suggests that these two genera are plesiomorphic for a number of important features in the core oscinellines and that they should not be part of the higher clades of the subfamily. Both these genera are unplaced at the tribal level in Nartshuk's (2012) system for the Oscinellinae. Their precise position, however, is not clear and we prefer, for the time being, to keep them *incertae sedis*, in the classification.

The relationships found here between the genera of the core oscinellines are not easy to interpret (Figure 2). One of the reasons is that 14 of the 53 genera included in our analysis were not included by Nartshuk's (2012) in any of the tribes; and 38 of the 66 genera included in her system could not be included in this study. Hence, of the 124 genera of Oscinellinae, only 38 are common to both studies.

A second reason for the complexity of the task is that the diagnoses of some of the tribes in Nartshuk's (2012) system are based on plesiomorphies or homoplasies. To bring together the entire breadth of the oscinellines into a single system is a major effort and a guide for the study of the group. Still, some of the tribes under her delimitation apparently do not correspond to clades. A final reason for the difficulty in interpreting the incongruence is that we are aware that this first approach still does not have the taxon density and density of characters to recover the entire robust clades.

The differences in the list of genera examined by Andersson (1977) and by Nartshuk (2012), with many genera missing in both systems, creates an even more difficult scenario to evaluate the results of this study, in the sense that there is not a common ground between authors in the literature.

In the group that we informally refer to as the core oscinellines (Figure 6), there is a clade including the type-species of *Oscinella*—*Oscinella frit*—that is sister to all oscinellines except *Goniaspis* and *Monochaetoscinella* and the Stenoscinini. The clade includes the

genera *Oscinella*, *Malloewia* and *Lipara*. The generic composition of our Oscinellini, of course, is puzzling—supported by inner vertical setae, the rate of eye comparing with head capsule vertically, the shape of the anterior end of R₂₊₃, the color of the stem of halter and the length of endophallic process. *Lipara* has a broad facial carina (Figure 51a), which is not typical of *Oscinella* s.s. These features are highly homoplastic and may have gathered genera not indeed nor directly related. The *Oscinella* genus group of Andersson (1977) also includes *Tropidoscinis* (not analysed in this study), *Lioscinella* and *Hapleginella*. The Oscinellini of Nartshuk (2012) include *Oscinella* and the genera *Camptoscinella* Sabrosky (removed from the matrix due to amount of missing data), *Conioscinella* Duda, *Oicella* Enderlein (not analysed here), *Oscinimorpha* Lioy, *Neolcella* Cherian (also not analysed), and *Neoscinella* Sabrosky. *Malloewia*, not present in Andersson's (1977) and Kanmiya's (1983) studies, integrates the Incertellini sensu Nartshuk (2012).

This position of *Oscinella* in the tree (Figure 6), however, seems consistent: the diagnosis of the *Oscinella* genus group of Andersson (1977) is largely composed of plesiomorphies, what may explain why the genera gathered in Andersson's (1977) *Oscinella* genus group also have a relatively basal position in the clade corresponding to the core oscinellines. In other words, the genera *Tropidoscinis*, *Hapleginella*, and *Lioscinella* are clearly plesiomorphic for features in higher oscinellines, as in the enlarged Elachipterini clade or in the Siphonellini / Oscinisomatini / Fiebrigellini clade.

Our clade Siphonellini/Oscinisomatini/Fiebrigellini/Tricimbini corresponds to a rather large group including the genera *Calamoncosis*, *Chaetochlorops*, *Epimadiza*, *Eribolus*, *Fiebrigella*, *Hapleginella*, *Heteroscinis*, *Oscinisoma*, *Loxobathmis*, *Polyodaspis*, *Siphonella*, *Siphunculina* and *Tricimba* (Figure 6). This clade is supported by the color of the first antennal flagellomere (which is homoplastic) and the height of the basal radial cell (dorsally projected), which is an apomorphy unique to this group in the tree (Figure 98).

Hapleginella is included by Andersson (1977) and Kanmiya (1983) in the *Oscinella* group, while Nartshuk (2012) includes it in the Botanobiini. This conflict is quite revealing of the doubts about position of the genus. Independently of the question of its precise position, *Hapleginella* is clearly plesiomorphic for modified features in the higher oscinellines, so it is most certainly not a Botanobiini. *Calamoncosis* is placed in the *Lipara* genus group by Andersson (1977) and Kanmiya (1983), and in the Liparaini by Nartshuk

(2012), so its position in the clade with genera of Siphonellini, Oscinisomatini, and Fiebriegellini should be dismissed as due to noise in the analysis.

Most of the other genera in this clade belong to the Fiebriegellini of Nartshuk (2012)—*Chaetochlorops*, *Epimadiza*, *Fiebriegella*, *Heteroscinis*, *Polyodaspis*—, meaning that there is a considerably large overlap between Nartshuk's (2012) delimitation of the tribe and this clade. The clade, however, also includes genera of other tribes, as *Hapleginella* (Botanobiini), *Tricimba* (Tricimbini), *Oscinisoma* (Oscinisomatini), *Calamoncosis* (Liparaini), and *Siphonella* (Siphonellini). Considering the conflicts between the generic composition of the supra-generic taxa in the systems of Andersson (1977) and Nartshuk (2012), and the amount of plesiomorphies and homoplasies in the diagnoses of these groups, it is hard to assess how robust or how weak is our clade.

The *Lipara* group of Andersson (1977) includes *Lipara*, *Calamoncosis* and *Siphonella*, while the *Polyodaspis* genus group of Andersson (1977) includes most of Nartshuk's (2012) genera of Fiebriegellini. Sabrosky (1941, p. 749) already had mentioned that “there is considerable doubt about the relation of *Calamoncosis* to *Gymnopoda* s.l.” (in Nartshuk 2012 synonymized as *Lipara*), which finds support in our results. A separation between *Lipara* and *Calamoncosis* and a connection between *Calamoncosis* and *Siphonella* both find support in the literature.

Andersson (1977, p. 83) specifically mentioned, however, that *Pseudeurina* “differs from the other genera in having a yellow ground color, bare frontal triangle, erect, cruciate *oc* and no tibial organ”. He lists features to justify the inclusion of the genus in the *Lipara* genus group, but this brings some support that *Pseudeurina* in some degree has differences from the core Liparaini. Because *Calamoncosis* and *Siphonella* are clearly plesiomorphic in relation to feature typic of the higher oscinellines, which is also the case of *Lipara*, it would not be out of place admitting that the Liparaini has a diagnosis that brings together non related genera. In this case, *Pseudeurina* would definitely not belong with *Lipara* in a smaller clade with tribal status.

Kanmiya (1983) proposed a *Siphonella* genus group excluding *Lipara*, while Nartshuk (1983) transferred all members of the *Lipara* group to a new genus group, *Siphonella*, but Nartshuk (2012) followed Kanmiya's (1983) position and her Liparaini excludes *Siphonella*.

Tricimba, recovered in our tree as a member of this clade that also has *Siphonella*, *Fiebriegella*, *Oscinisoma*, and some other genera (Figure 2), is one of the large stable

oscinelline clades in our study. *Tricimba* is a cosmopolitan genus, with a large interspecific variation. In his excellent study of *Tricimba* and *Aprometopis*, Ismay (1993, p. 313) compared the tribes of Incertellini and Tricimbini, arguing that the delimitation of these groups in the literature at that time was not accurate. He mentioned “(...) to maintain the distinction between the two tribes requires many cases of apomorphic characters having reverted to the plesiomorphic state.” Ismay (1993) synonymized *Nartshukiella* to *Tricimba*, and *Tricimbomyia* and *Pseudotricimba* were placed in Tricimbini. In Ismay’s (1993) system, *Aphanotrigonum*, *Incertella*, *Meijerella*, *Apallates*, *Biorbitella*, and *Malloewia* compose the Incertellini.

In our tree, *Aphanotrigonum* is not in the Siphonellini / Oscinisomatini / Fiebrigellini / Tricimbini clade (Figure 3), but is rather a rogue genus floating off the Dicraeini / Botanobiini / Elachipterini clade (Figure 3), as also happens with *Apallates*, *Biorbitella* and *Incertella*. Andersson (1977, p. 96) mentions that his *Aphanotrigonum* genus group (that also includes *Tricimba* and *Siphunculina*) shares modified features with the groups *Lipara* and *Polyodaspis*, and species in *Siphunculina* had been part of *Fiebrigella* in the past. *Oscinisoma* is part of the *Eribolus* genus group in Andersson’s (1977) system—both genera belonging to the Oscinisomatini of Nartshuk (2012). Andersson (1977, p. 113) mentions that the *Eribolus* genus group has features of the male terminalia similar to the *Oscinella* genus group, suggesting that there are shared plesiomorphies between these groups. *Meijerella*, that belongs to the *Aphanotrigonum* genus group of Andersson (1977), was removed from the matrix in our study due to missing data.

There are 12 genera and one additional species of *Oscinella* that do not fit either in the Siphonellini / Oscinisomatini / Fiebrigellini / Tricimbini clade (Figure 3), nor in the Elachipterini / Botanobiini / Dicraeini clade (Figure 3). They are rather rogue genera, in the sense that their position vary in the tree (Figures 3, 7) with changes in the k value. The reason is probably that there is not enough character sampling for this area of the tree to bring stability and reliability to clades. In other words, there is some information concerning these genera in terms of shared apomorphies and plesiomorphies, but their position in our tree is not reliable as indication of their precise relationships.

In terms of Nartshuk’s (2012) system, *Speccafrons* belongs to the Siphonellini, *Lasiambia* belongs to the Fiebrigellini, *Lioscinella* and *Hippelates* belong to the Hippelatini, *Oscinella* cf. *flavitibia*, *Conioscinella* and *Oscinimorpha* belong to the Oscinellini, and

Apallates, *Biorbitella*, *Aphanotrigonum*, *Incertella*, *Microcercis* and *Neoscinella* belong to the Incertellini. In a certain way, this suggests that Nartshuk's (2012) concept of Incertellini may indeed correspond to a grade relative to the higher Elachipterini.

It is worth mentioning that *Apallates* and *Biorbitella* compose together a small clade, reinforcing the positions in the literature. This clade is supported by eight characters, including the ground color of frons, the position of arista, the size of the surstylus, the length of the phallapodeme, and the shape of segment 7 in the female terminalia. *Apallates* and *Biorbitella* integrate Ismay's (1993) and Nartshuk's (2012) Incertellini, but neither genera were examined by Andersson (1977). *Speccafrons*, in Andersson's (1977) and Kanmiya's (1983) studies, are placed in the *Siphonella* genus group. Nartshuk (1983) included *Speccafrons* in the Incertellini, while Nartshuk (2012) later transferred the genus back to the Siphonellini. Our tree is not able to provide proper clues for the position of *Speccafrons*. The genera belonging to the Oscinellini, the Fiebrigellini, Hippelatini, and the Siphonellini either may have been incorrectly included in other tribes or may have problems in their coding in our analysis and are consequently displaced in relation to their correct placement—impossible to say at this stage.

Despite the lack of resolution of the tree at this level, one important conclusion can be drawn concerning the Neotropical “group *blanda*” of *Oscinella* of Sabroski & Paganelli (1984), to which *Oscinella* cf. *flavitibia*, studied here, and five other species belongs (Figure 7). Sabroski & Paganelli (1984, p. 28) stated that “[t]his small group of tiny species with linear genae and very large, polished black, convex-sided frontal triangle may deserve generic distinction but there is no available name and for the present it is left in *Oscinella* until adequate material is available for study.” Our results clearly show that the *Oscinella* cf. *flavitibia* falls in a separate part of the oscinelline tree and corroborate Sabroski & Paganelli (1984) original suspicion and indeed a taxon of generic rank should be raised for the species of the Neotropical *blanda* group of *Oscinella*.

There is a larger clade that we informally refer to here as the “higher oscinellines”. It includes *Elachiptera* (type genus of the Elachipterini) and *Sepsidoscinis* (also an Elachipterini), *Gaurax* (type genus of Botanobiini) and *Pseudogaurax* (also a Botanobiini), *Dicraeus* (type genus of Dicraeini), two genera assigned by Nartshuk to the Liparaini (*Pseudeurina* and *Paracalamoncosis*), one genus assigned to the Hippelatini (*Chaethippus*), *Psilacrum* (formally associated to the Rhodesiellinae), and 11 genera with no placement in

Nartshuk's (2012) system (Figure 8). This is an important clade in our analysis and is stable between the tree with $k = 3$ and the setk tree. Five homoplastic features support this clade: extension of the anterior end of the ocellar triangle on the frons, the color of the anepisternum, in most cases entirely yellow with a black mark ventrally, the color of katepisternum, entirely yellow in most species, and the hypoproct setation in female terminalia.

This clade is particularly important as a result of the analysis. On the one hand, it is stable under different analysis parameters. On the other hand, it gathers 21 terminals of 18 genera, 11 of which are not present in Nartshuk's (2012) system. Of the seven genera common in both system (Figure 8), *Elachiptera* and *Sepsidoscinis* fit into the Elachipterini, *Pseudogaurax* and *Gaurax* belong in the Botanobiini, *Chaethippus* belongs in the Hippelatini, and *Pseudeurina* fits into the Liparaini, while *Dicraeus* is the only genus in the Dicraeini.

The generic composition of the Elachipterini in the cladistics analysis of the tribe in Mlynarek & Wheeler's (2018) study was presented above. The character treatment of their analysis is very solid, but the complexity of the systematics of the Oscinellinae, with many potentially paraphyletic tribes, would demand a larger number of outgroups to properly test of the monophyly of the tribe. If we ignore the position of *Chaethippus*, the highest clade of this large group is basically of Elachipterini genera, with the presence of two additional, unplaced genera. Two Botanobiini genera, *Gaurax* and *Pseudogaurax* compose with these Elachipterini genera a more inclusive clade. And *Dicraeus* is sister to an even larger clade that gathers the Elachipterini / Botanobiini genera to two Liparaini genera, *Pseudeurina* and *Paracalamoncosis*, and a number of genera that are unplaced in Nartshuk's (2012) system.

The position of *Dicraeus* as sister to the entire remainder of the clade is not a problem. In Nartshuk's (2012) system it is a separate tribe Dicraeini, so there is no conflict of tribal composition. Nartshuk (1967) mentioned a possible relationships between *Dicraeus* with *Aphanotrigonum* and *Tricimba*. In our results, this would have support only on plesiomorphies. The basic question here is only whether or not the Dicraeini would be sister to the Elachipterini / Botanobiini clade.

The position of *Psilacrum* in our study, in this clade is very surprising. Our understanding is that there is some undetected noise that moved the genus from the Stenoscinini to this clade of core Elachipterini. Old World species of *Psilacrum* were dealt with by Ismay (1986, p. 19), where he states that “(...) *Psilacrum* may be placed in the

Javanoscincis genus group of Andersson (1977) which also contains the widespread genus *Stenoscinis*."

One of the questions at this stage of the discussion, hence, from a phylogenetic perspective, is to which other tribes the Elachipterini, in its delimitation in Nartshuk (2012) and in Mlynarek & Wheeler (2018), is associated, composing a larger clade. In other words, if some of the genera associated to other tribes—Liparaini, Botanobiini, and Hippelatini—could compose a larger monophyletic group with the Elachipterini.

In Mlynarek & Wheeler's (2018) analysis, *Cadrema* was used as an outgroup. Andersson (1977, p. 65) in his discussion of the *Elachiptera* genus group mentioned: "*Cadrema* Walker has all the characteristic of the *Elachiptera* genus group; the habitus is similar, as are the genitalia". Kanmiya (1983, p. 67) created a genus group only for *Cadrema*. He mentions symplesiomorphic characters shared with the Siphonellopsinae. This shows that the position seems equivocal and hardly any feature will technically approach the genus from the siphonellopsines. It could be the case that some of the apomorphic features of *Cadrema* corresponds to secondary losses, but this does not affect the question of its position within the oscinellines. Nartshuk (1983) included *Cadrema* into the Hippelatinae s.l. (though the genus is unplaced in her 2012 system) and Andersson (1977) kept *Cadrema* under the *Elachiptera* genus group. The presence of *Cadrema* in this clade with *Elachiptera*, hence, should not be seen as a surprise. In this context, the presence of *Hippelates* as sister of the Dicraeini / Botanobiini / Elachipterini clade in the $k = 3$ tree (Figure 8) is a corroboration of their position concerning the connection between *Hippelates* with *Elachiptera* and other higher oscinellines.

Pseudogaurax and *Gaurax* belong to the *Gaurax* genus group of Andersson (1977) and to the Botanobiini of Nartshuk (2012) (Figure 8). Andersson (1977, p. 76) indicates that the *Gaurax* genus group "is close to the *Elachipterus* genus group and the similarity of the species of the two groups is sometimes striking." He listed features that combine both groups—upright, cruciate *oc*, usually kidney-shaped or obliquely oval *ant₃*, and densely haired or thickened arista, and well-developed tibial organs". Kanmiya (1983, p. 102) agrees with Andersson's (1977) proposal and noted "this genus group is not distinctly defined because of the lack of the autapomorphic characters". The genera *Gampsocera* and *Cestoplectus*, not examined here, also integrate the *Gaurax* genus group, while these two genera add to *Gaurax* Loew, *Hapleginella* Duda, *Leucochaeta* Becker, *Pselaphia* Becker,

Pseudogaurax Malloch, *Pterogaurax* Duda in Nartshuk's (2012) Botanobiini. It is interesting to note that Andersson (1977) did not keep *Hapleginella*, as mentioned above, together with *Gaurax*, placing the genus in the *Oscinella* genus group (Figure 6). This probably means that the genus has important plesiomorphies concerning features that are modified in the Botanobiini (and closely related tribes in the higher oscinellines). Its placement in our tree, away from the other botanobine genera give some support to Andersson's (1977) position for this *Hapleginella*.

The genera *Medeventor*, *Batrachomyia*, *Opetiophora*, and *Paracalamoncosis* were proposed more recently and were not examined by Andersson (1977) and Nartshuk (2012). Wheeler (2007, p. 48) states that *Medeventor* "appears to be most closely related to the Old World genera *Lipara* Meigen and *Pseudeurina* de Meijere." *Medeventor* and *Pseudeurina* in our $k = 3$ tree (Figure 3, 8) are very close to each other into this Elachipterini/Botanobiini clade. *Lipara*, as was already discuss, is plesiomorphic for the features in this higher oscinelline clade, and does not join *Medeventor*, *Pseudeurina*, and other genera. Indeed, features associating *Medeventor* and *Pseudeurina* to *Elachiptera* seems based on a number of nested features. The fact that species of *Pseudeurina* comes out paraphyletic within this Elachipterini/Botanobiini clade seems to be the result of undersampling of characters at this level. The paraphyly of *Medeventor* in relation to *Pseudeurina*, however, seems reasonable (Figure 8).

There is nearly nothing about *Opetiophora* in the literature, a genus not examined by Andersson (1977) and not included in any tribe by Nartshuk (2012), but the proximity of *Opetiophora* with the Botanobiini/Elachipterini seems obvious. *Batrachomyia* has eleven described species, all from Australia and Papua New Guinea (Evenhuis 2006). It seems reasonable that the genus fit into this clade, but its position as sister of *Opetiophora* within the higher oscinellines may be subject to change as more characters and species are considered.

Paracalamoncosis was described very recently (Riccardi et al., 2018) as a genus of Liparaini based on a new Neotropical species similar to *Calamoncosis*—a genus known from all biogeographical regions except the Neotropics and the Australasian/Oceania. As we discussed above, the delimitation of the the Liparaini in Andersson (1977) and Nartshuk (2012) was not recovered here, *Lipara* falling into a clade with *Oscinella frit*. In our tree, *Calamoncosis* belongs in the clade with *Siphonella* and genera mostly of Fiebrigellini. In this

context, it is hard to assess the question of the position of *Paracalamoncosis*. The tree topology suggests that the Liparaini is not monophyletic and that *Paracalamoncosis* is not related to *Calamoncosis*. It is conceivable that the presence of *Paracalamoncosis* in this larger Elachipterini clade may be due to noise.

Not much is available about the genera *Trachysiphonella* and *Notaulacella*, in such a way that not much can be said about its position in the tree in terms of other opinions on their taxonomic position in the classification. Finally, the position of *Chaethippus*, a genus placed by Nartshuk (2012) in the Hippelatini, is not entirely conflicting with the results here. Its precise position in the tree may be subject to changes within the clade in the future, but there is ground to accept its connection to the clade of the higher oscinellines (Figure 8).

Conclusions and perspectives

This study is the first formal phylogenetic analysis for the Oscinellinae as a whole, based on 50 genera of the subfamily. Limited taxon sampling brings some analytical challenges, not only for the taxon not included in the analysis, but also for the solution of some of the problems of homology, with risk of homoplastic features generating nodes. The number of characters, the use of analytical tools to reduce the influence of incongruent characters over nested characters, the systematic comparison of features across the subfamily, the number of outgroup levels used, and a careful consideration of information in the literature show that the phylogenetic signal obtained in this study is able to bring some phylogenetic order to the group.

Comparison between the trees obtained here under different analytical parameters helped to discern between stable clades and rogue taxa. Even though we do not intend to propose any formal changes to the classification of the subfamily at this stage, the tree has clades stable enough to corroborate comments in the literature about relationships among genera and about conflicting genera within the group. One of the important conclusions in the analysis is about the position of the Oscinellinae relatively to the remaining subfamilies and about the paraphyly of the Rhodesiellinae. The Rhodesiellinae with the delimitation including three tribes is shown here to be paraphyletic in relation to the Oscinellinae. The Stenoscinini, previously assumed to be a rhodesielline, is in a clade sister to all remaining Oscinellinae—informally referred to here as the core oscinellines.

Oscinella frit is considerably plesiomorphic for a number of features seen in other typical clades and has a relatively basal position in the tree. In other words, a clade that includes *Oscinella frit* seems to be sister of the set of core oscinelline genera. A larger, stable clade joins most of the Fiebriegellini to genera previously included in the tribes Siphonellini (*Siphonella*), Tricimbini (*Tricimba* and *Siphunculina*), Oscinisomatini (*Oscinisoma*), Liparaini (*Calamoncosis*), and Botanobiini (*Hapleginella*). It is clear that the Neotropical group *blanda* of *Oscinella* does not fit together with the type-species of the genus, corroborating previous indication in the literature that it needs a taxon of generic rank. A large group of genera that in Nartshuk's (2012) system belong to different tribes have an unstable position in the tree, but do not belong either in the Fiebriegellini / Siphonellini / Tricimbini / Oscinisomatini clade or in the Dicraeini / Botanobiini / Elachipterini clade. These rogue genera belong mostly to

the Incertellini, but there are also genera that belong to the Hippelatini, Oscinellini, and Siphonellini. The diagnoses of these tribes are actually largely based on plesiomorphies and/or homoplastic features. Even not having the relationships between these genera clear, it is not surprising that genera from different tribes do not join the type genera of their respective tribes.

A large, stable clade informally referred to here as the higher oscinellines bring together the Dicraeini (*Dicraeus*) and genera of Botanobiini (*Gaurax*, the type-species of the tribe, and *Pseudogaurax*), Elachipterini (*Elachiptera*), Liparaini (*Pseudeurina*), and Hippelatini (*Chaethippus*). There is a good chance that *Hippelates* would compose a monophyletic group with this clade. Relevant information in the literature suggest that this group of genera indeed share apomorphic features and may compose a large clade in the subfamily.

It is still necessary to add a good number of the 74 genera of Oscinellinae to consider here into an integrated, formal phylogenetic analysis of the group to propose reliable changes in the classification of the subfamily. The results obtained here, however, brings considerable light to the understanding of the relationships in the Oscinellinae, clarifying the position of the Stenoscinini, indicating a relatively plesiomorphic condition of *Oscinella frit*, showing a large clade joining most of the Fiebriegellini to genera of the Siphonellini, Tricimbini, Oscinisomatini, Liparaini, and Botanobiini, and gathering in a higher oscinelline clade genera of the Dicraeini, Botanobiini, Elachipterini, and possibly of the Hippelatini.

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Figures

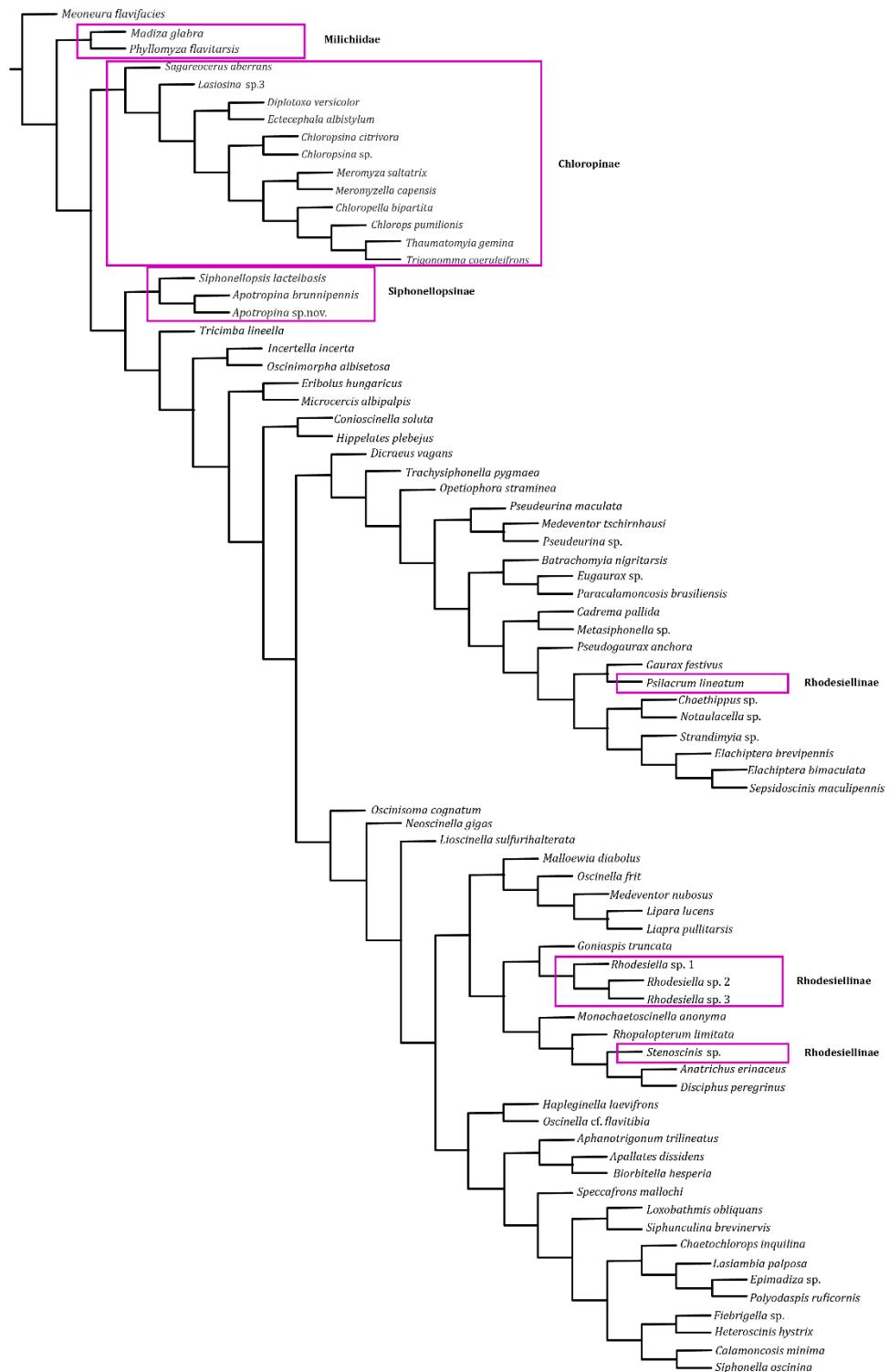


Figure 1. The single maximum parsimonious tree in phylogeny, under implied weighting scheme, setk script = ~ 17, Ci = 0.15, Ri = 0.44. Marked areas, are representing the outgroups, and the position of rhodesielline genera in the obtained phylogeny.

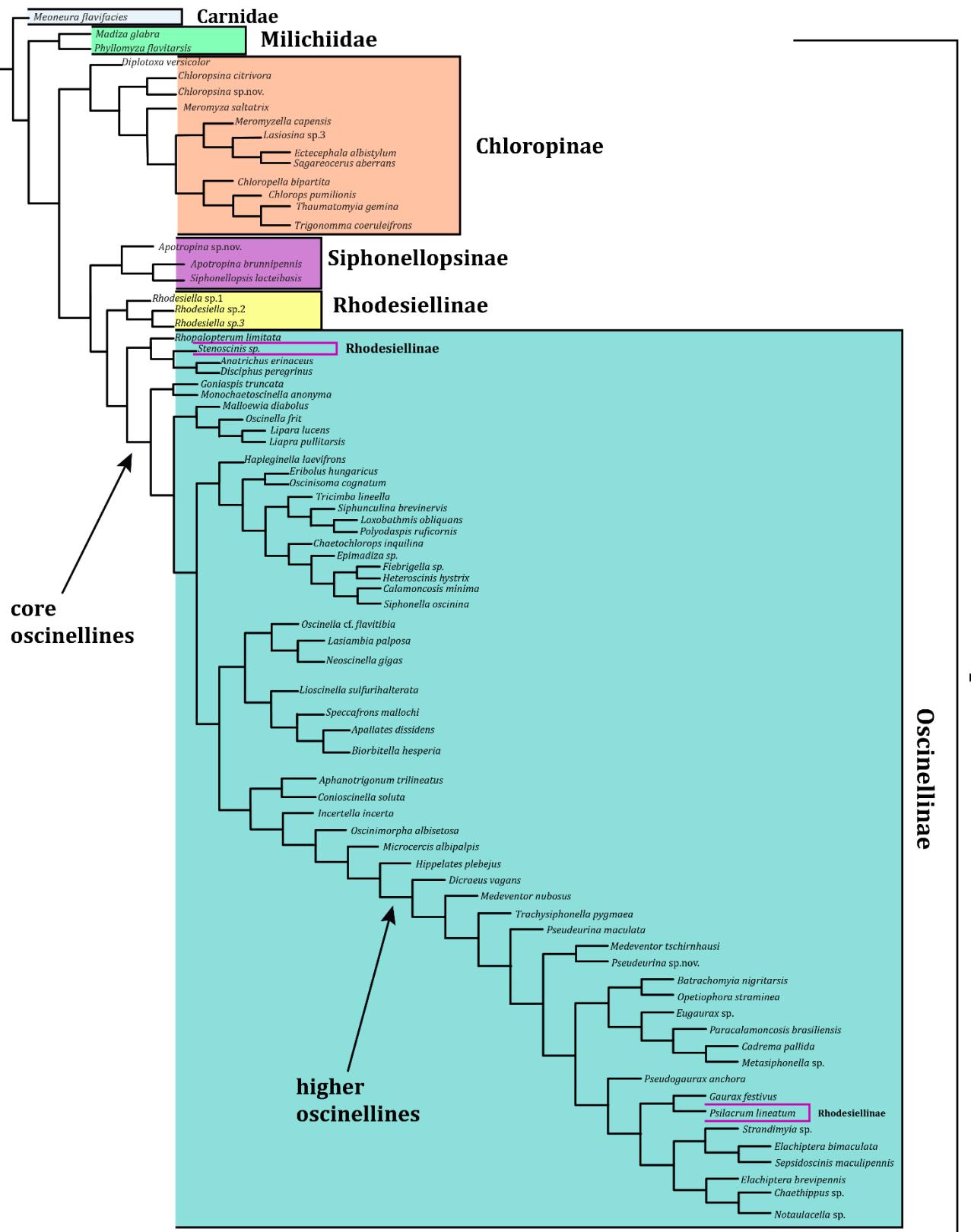


Figure 2. The single maximum parsimonious tree in phylogeny, under implied weighting scheme, $k = 3$, $Ci = 0.14$, $Ri = 0.42$. Marked areas are representing the outgroups and ingroups. The areas indicated with purple represent the position of rhodesielline genera in obtained phylogeny.

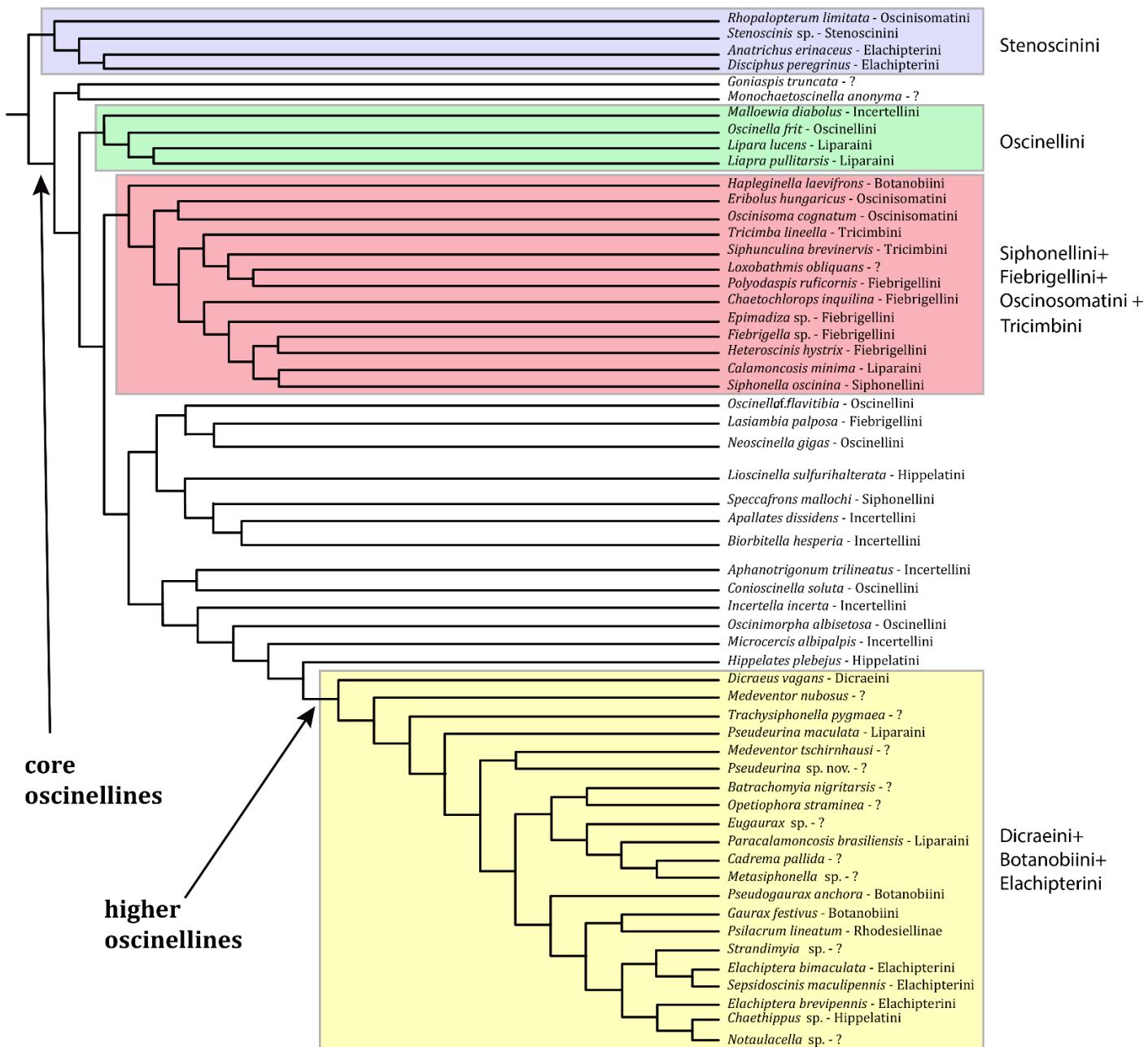


Figure 3. The phylogenetical relationship among the oscinellines (under implied weighting scheme, $k = 3$), with their tribal classifications in the previous literatures, front of each genus (Nartshuk 2012, Riccardi et al. 2018).

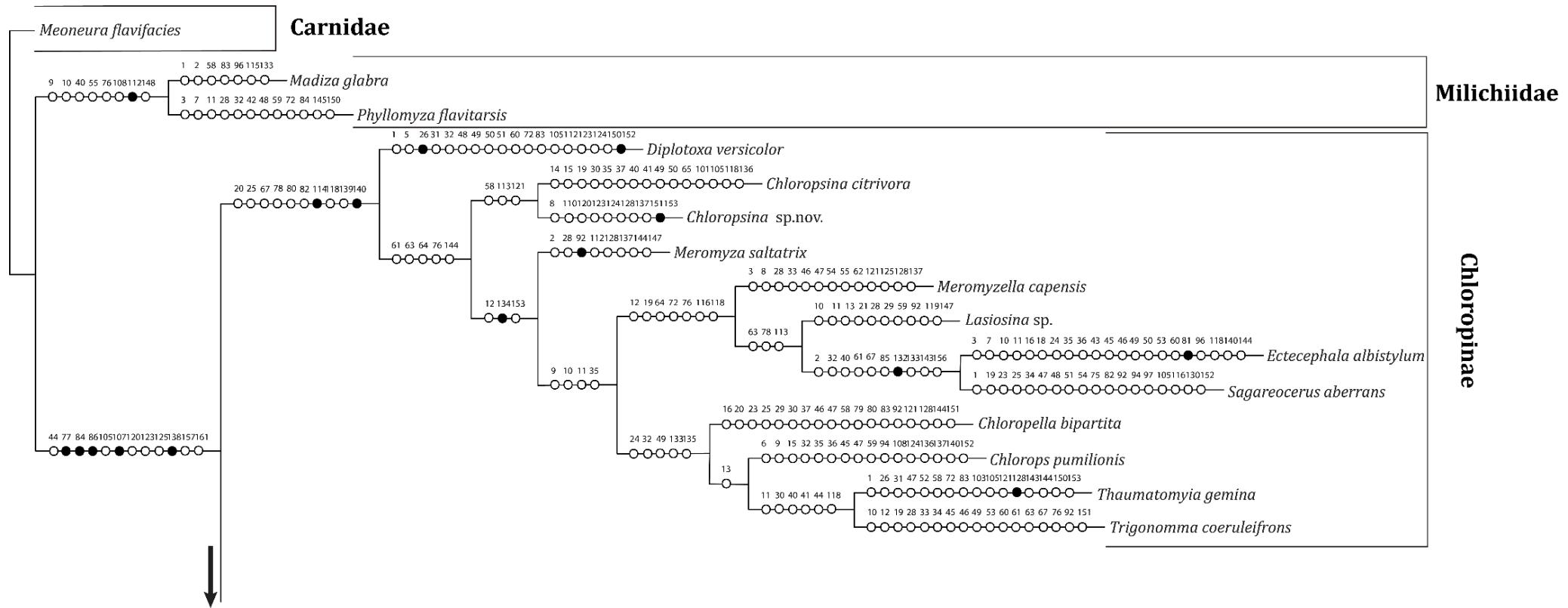


Figure 4. The single maximum parsimonious tree in phylogeny, under implied weighting scheme, $k = 3$, $Ci = 0.14$, $Ri = 0.42$; with unambiguous mapped on branches. White circles, homoplastic synapomorphies; full black circles, non – homoplastic synapomorphies. (Continuing)

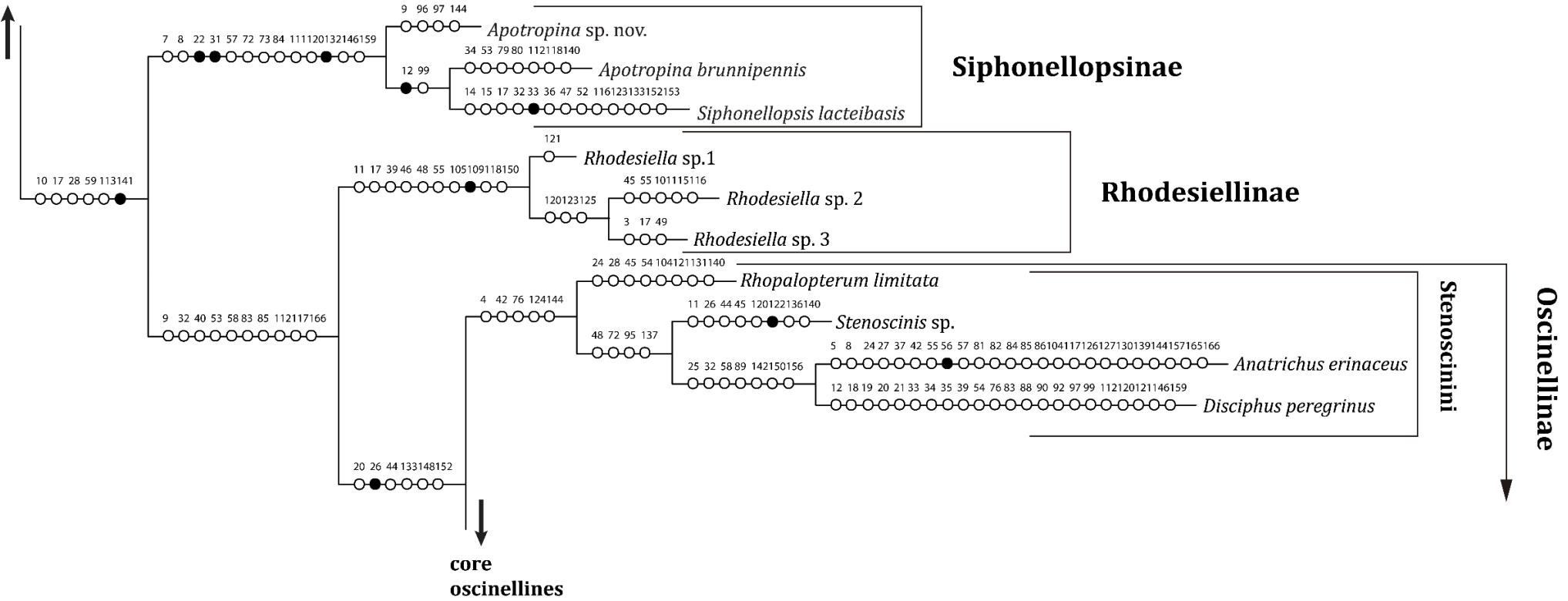


Figure 5. The single maximum parsimonious tree in phylogeny, under implied weighting scheme, $k = 3$, $Ci = 0.14$, $Ri = 0.42$; with unambiguous mapped on branches. White circles, homoplastic synapomorphies; full black circles, non – homoplastic synapomorphies. (Continuing)

Oscinellini

Siphonellini

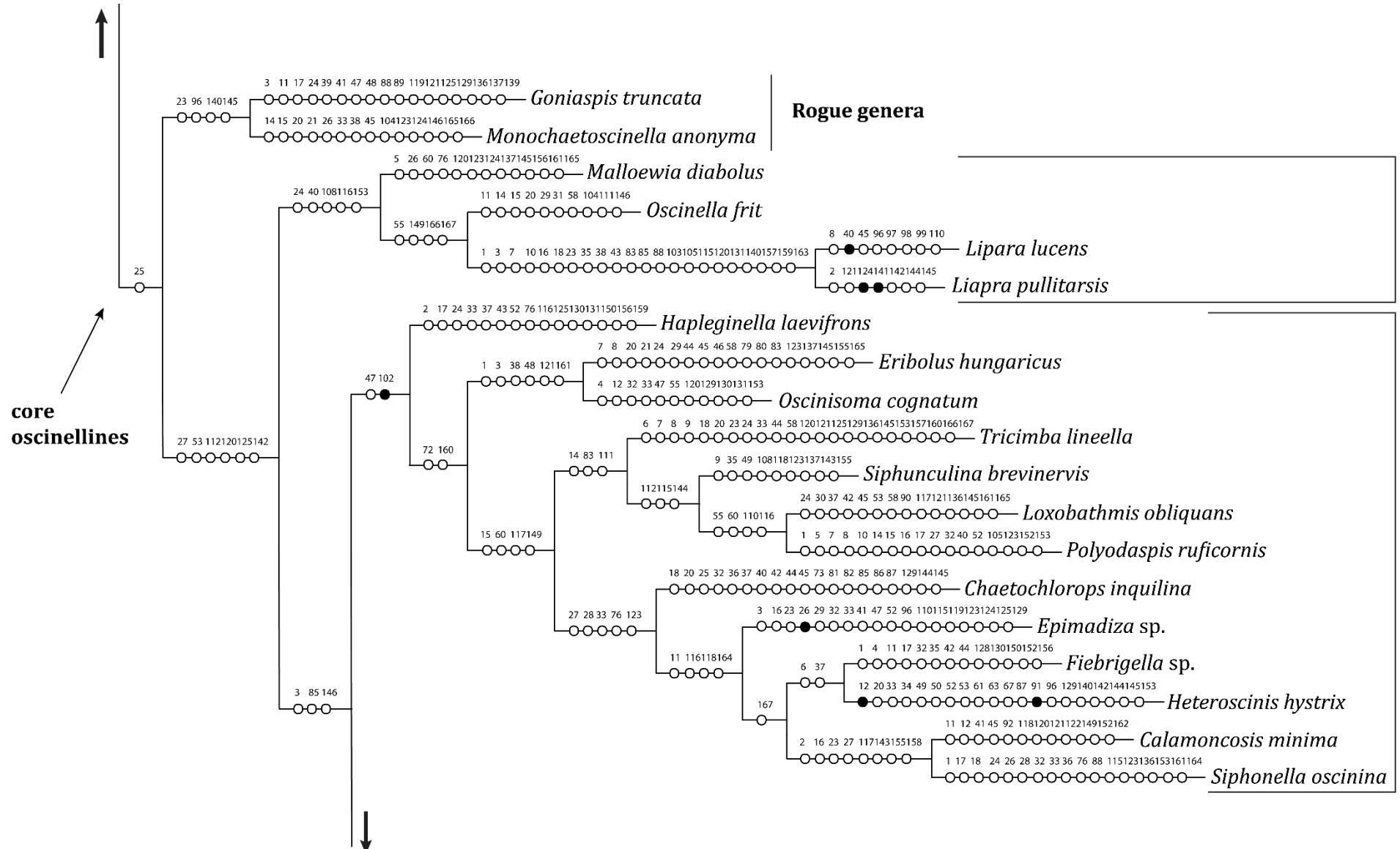
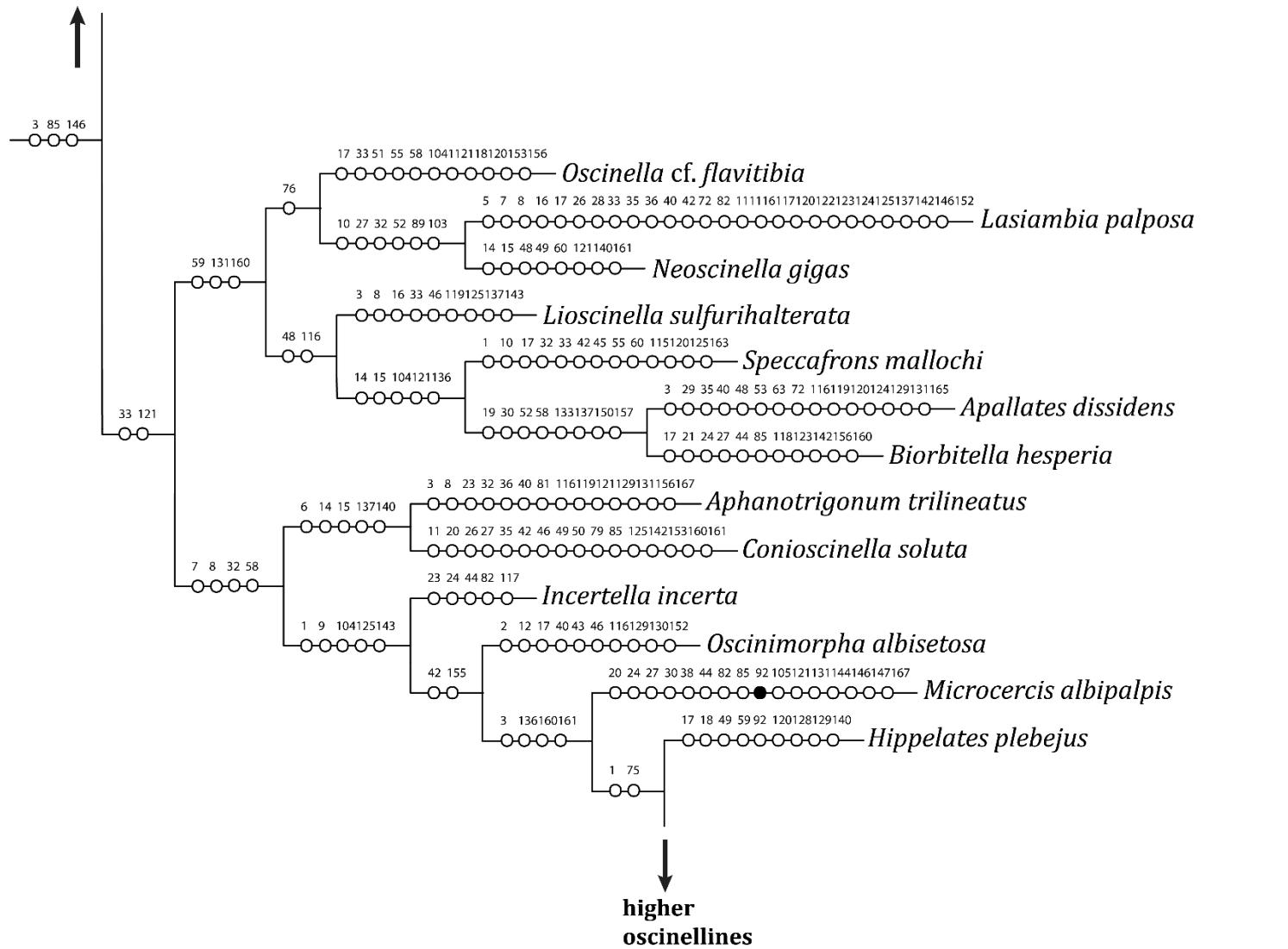


Figure 6. The single maximum parsimonious tree in phylogeny, under implied weighting scheme, $k = 3$, $Ci = 0.14$, $Ri = 0.42$; with unambiguous mapped on branches. White circles, homoplastic synapomorphies; full black circles, non – homoplastic synapomorphies. (Continuing)



Rogue genera

Figure 7. The single maximum parsimonious tree in phylogeny, under implied weighting scheme, $k = 3$, $Ci = 0.14$, $Ri = 0.42$; with unambiguous mapped on branches. White circles, homoplastic synapomorphies; full black circles, non – homoplastic synapomorphies. (Continuing)

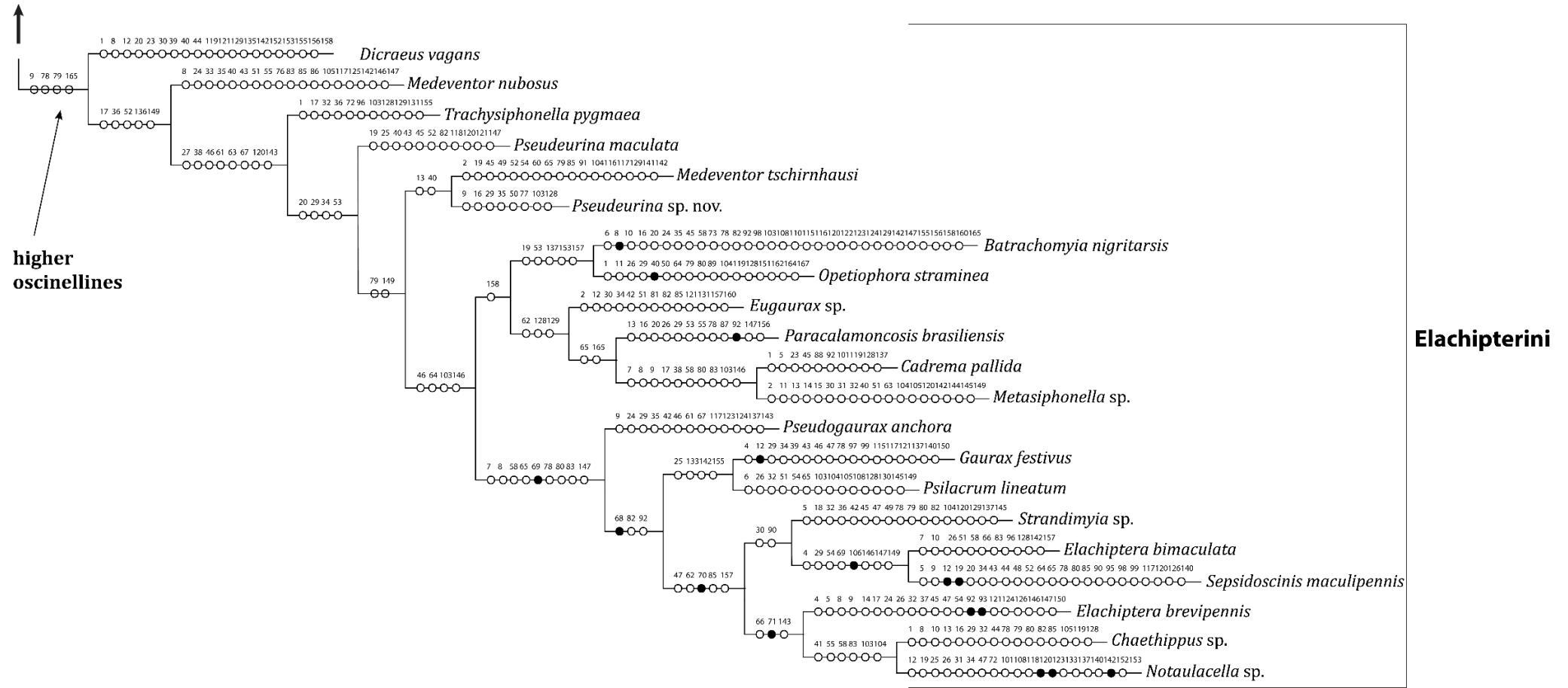


Figure 8. The single maximum parsimonious tree in phylogeny, under implied weighting scheme, $k = 3$, $Ci = 0.14$, $Ri = 0.42$; with unambiguous mapped on branches. White circles, homoplastic synapomorphies; full black circles, non – homoplastic synapomorphie.

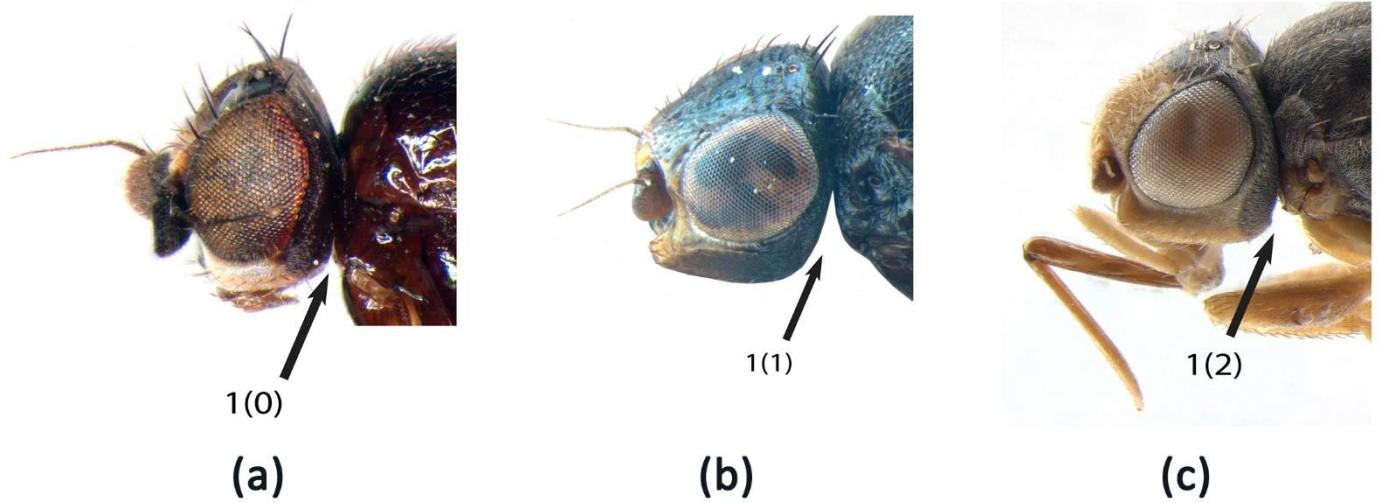


Figure 9a-c. Character 1, connection of head capsule with thorax: a. *Biorbitella Hesperia*, state 0, ventrally; b. *Polyodaspis ruficornis*, state 1, posteriorly; c. *Oscinimorpha albisetosa*, state 2, medially.

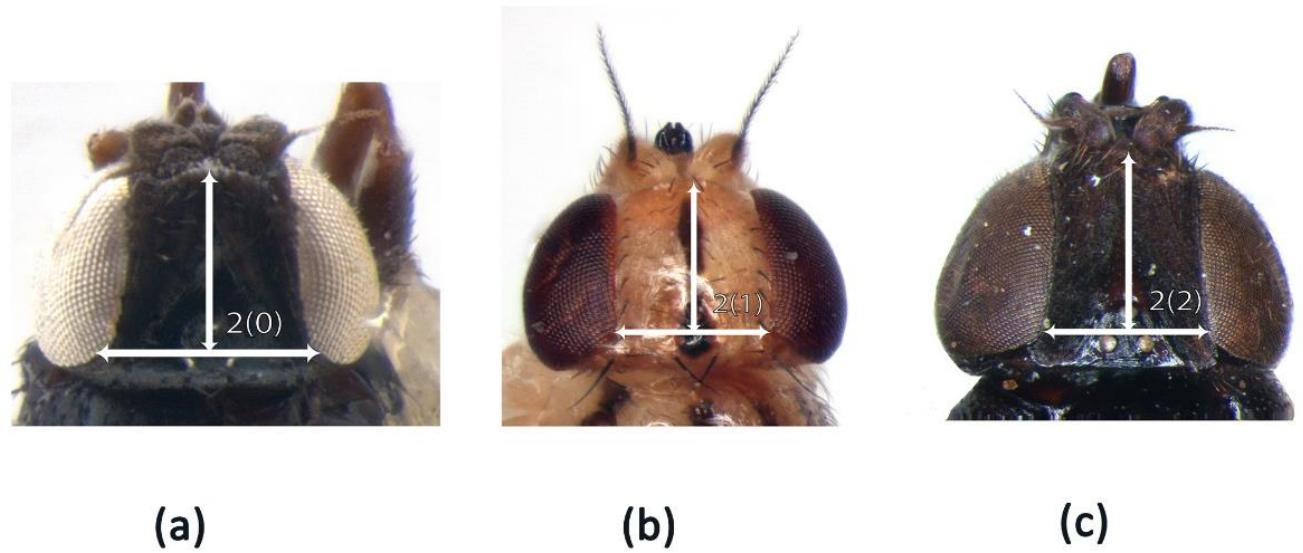


Figure 10a-c. Character 2, frons in dorsal view: a. *Malloewia diabolus*, state 0, wider than long; b. *Metasiphonella* sp., state 1, as wide as long; c. *Siphonella oscinina*, state 2, longer than wide.

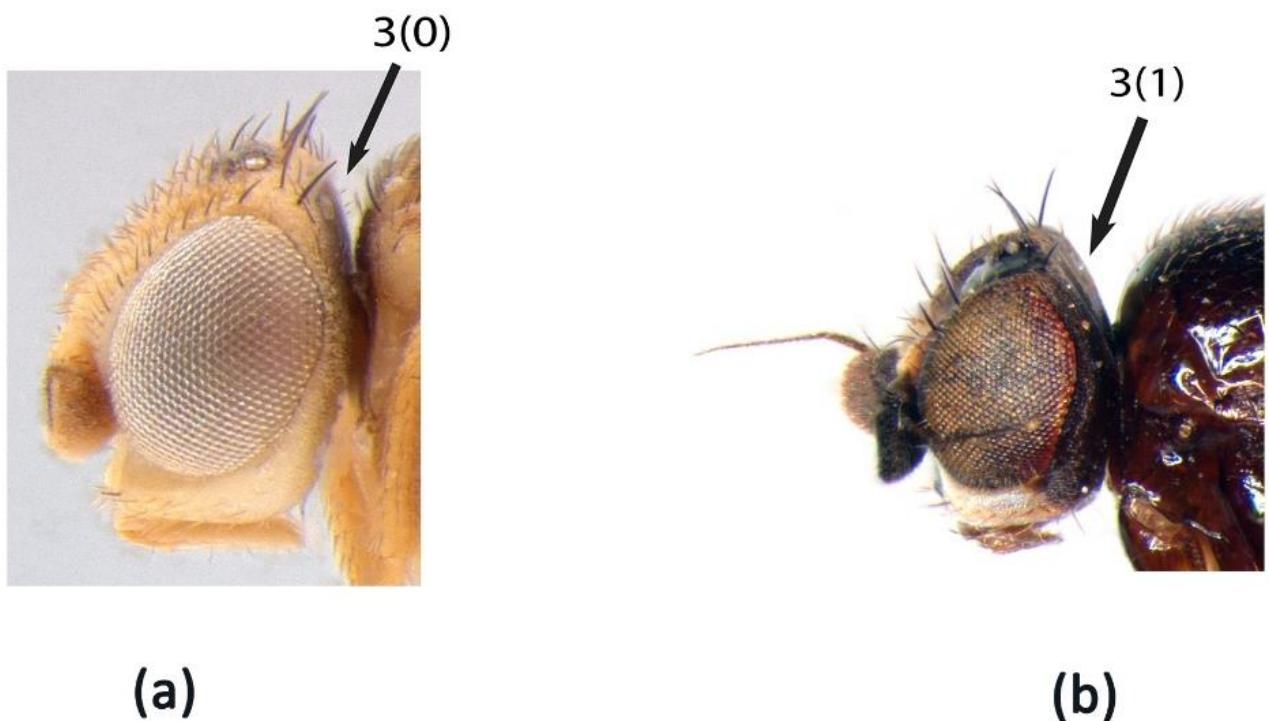


Figure 11a-b. Character 3, occiput: a. *Trachysiphonella pygmaea*, state 0, convex; b. *Biorbitella hesperia*, state 1, straight, angulated with frons.

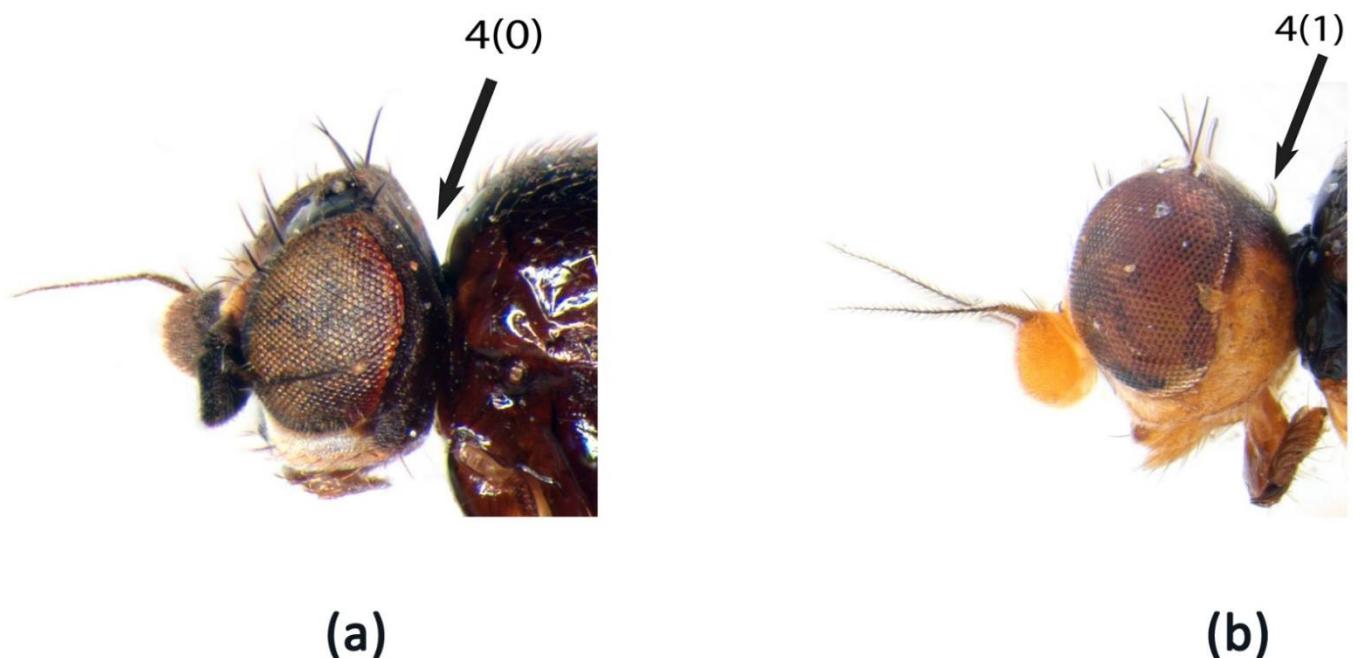


Figure 12a-b. Character 4, occiput with pair of setae, basally (supercervial setae): a. *Biorbitella hesperia*, state 0, absent; b. *Disciphus peregrinus*, state 1, present .

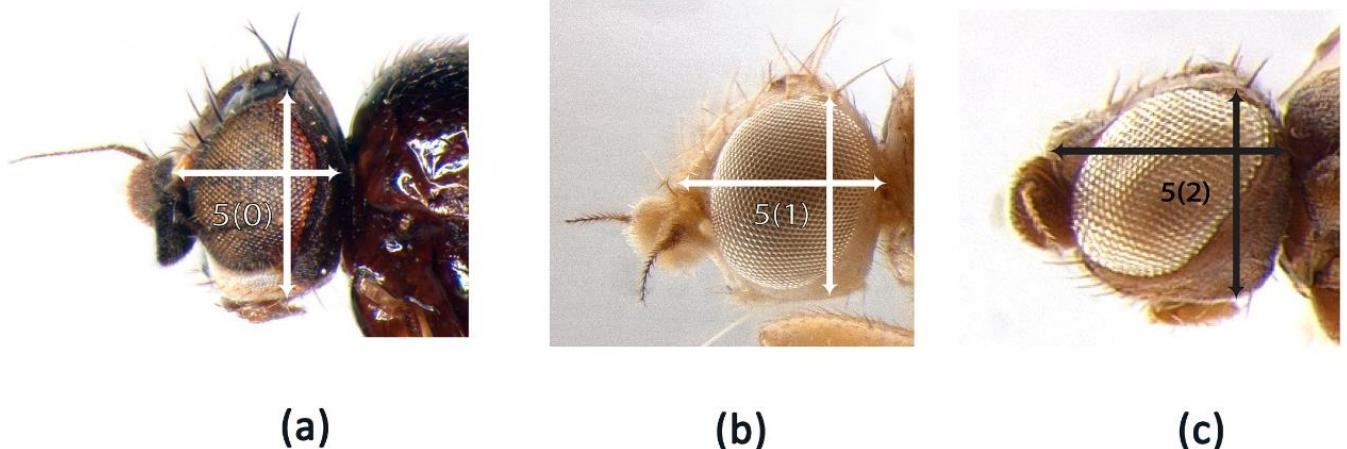


Figure 13a-c. Character 5, head in lateral view: a. *Biorbitella hesperia*, state 0, longer than wide; b. *Cadrema pallida*, state 1, as wide as long; c. *Eribolus hungaricus*, state 2, wider than long.

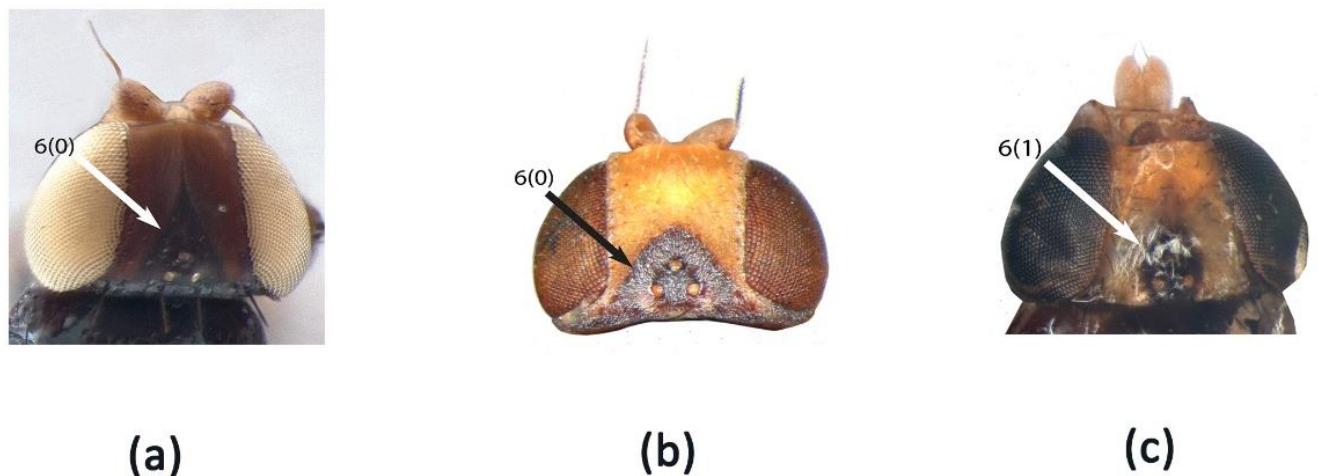


Figure 14a-c. Character 6, ocellar triangle: a. *Epimadiza* sp., state 0, well marked, margins of ocellar triangle conspicuous; b. *Hippelates plebejus*, state 0; c. *Heteroscinis hystrix*, state 1, not well marked, margins not clear or entirely absent.

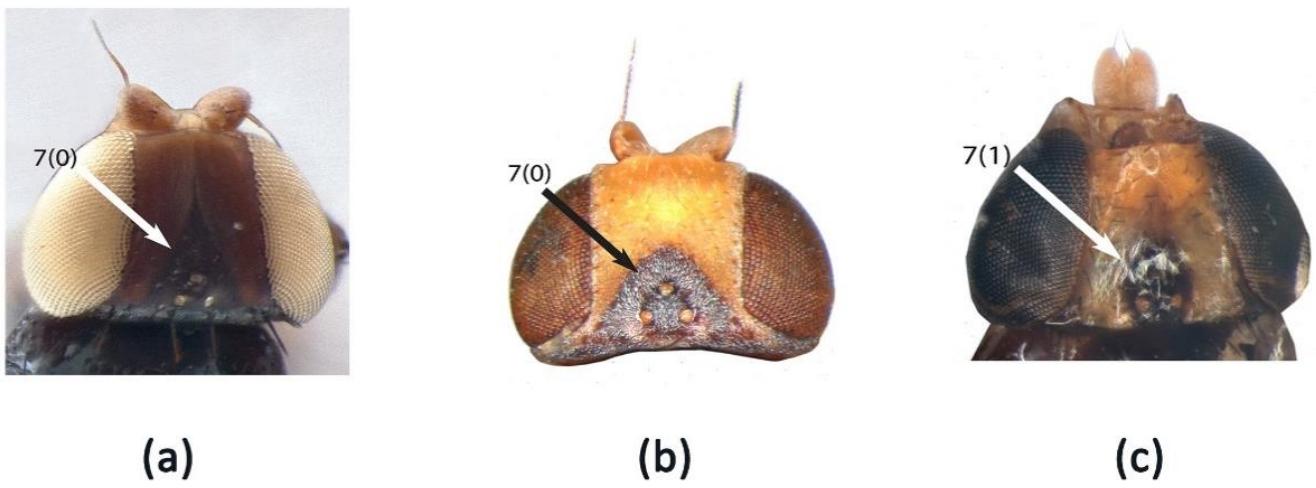


Figure 15a-c. Character 7, texture of ocellar triangle: a. *Epimadiza* sp., state 0, opaque, rugose; b. *Hippelates plebejus*, state 0; c. *Heteroscinis hystrix*, state 1, shinning.

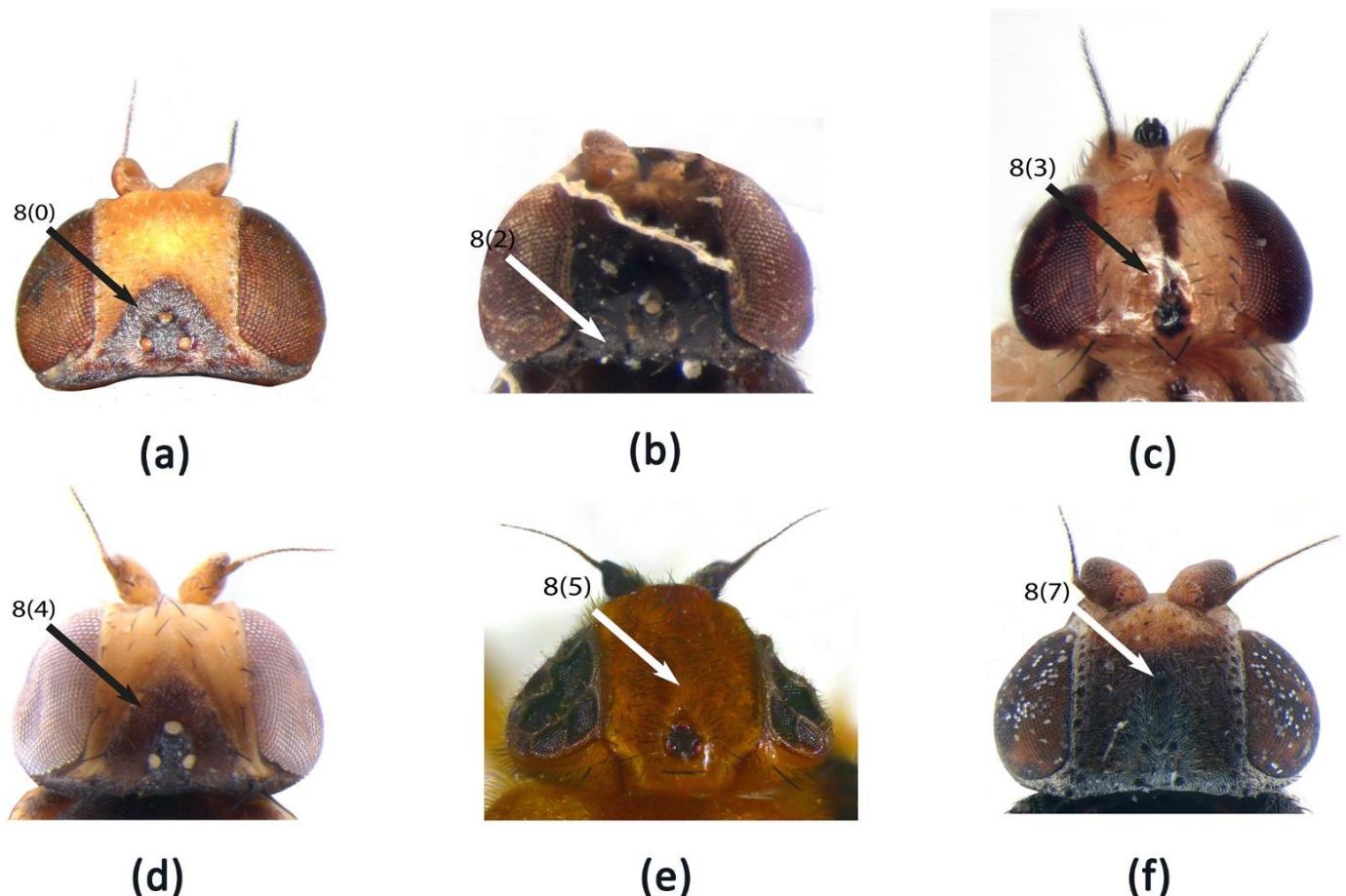


Figure 16a-f. Character 8, pruinosity of ocellar triangle without tubercle: a. *Hippelates plebejus*, state 0, almost entirely pubescent; b. *Lioscinella sulfurihalterata*, state 2, posterior third pubescent; c. *Metasiphonella* sp., state 3, almost bare; d. *Dicraeus vagans*, state 4, anterior two third pubescent; e. *Batrachomyia nigritarsis*, state 5, anterior third pubescent; f. *Aphanotrigonum trilineatus*, state 7, anterior tip of triangle pubescent.

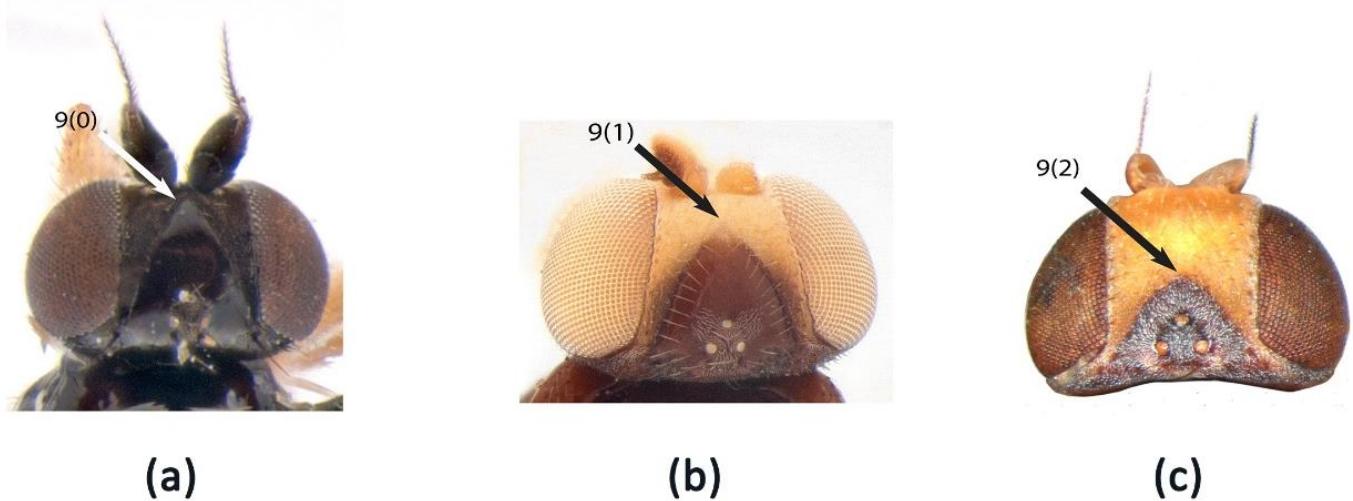


Figure 17a-c. Character 9, anterior end of ocellar triangle: a. *Monochaetoscinella anonyma*, state 0, reaching or almost reaching anterior margin of frons; b. *Oscinisoma cognatum*, state 1, between anterior margin of frons and middle of frons; c. *Hippelates plebejus*, state 2, at most reaches middle of frons.

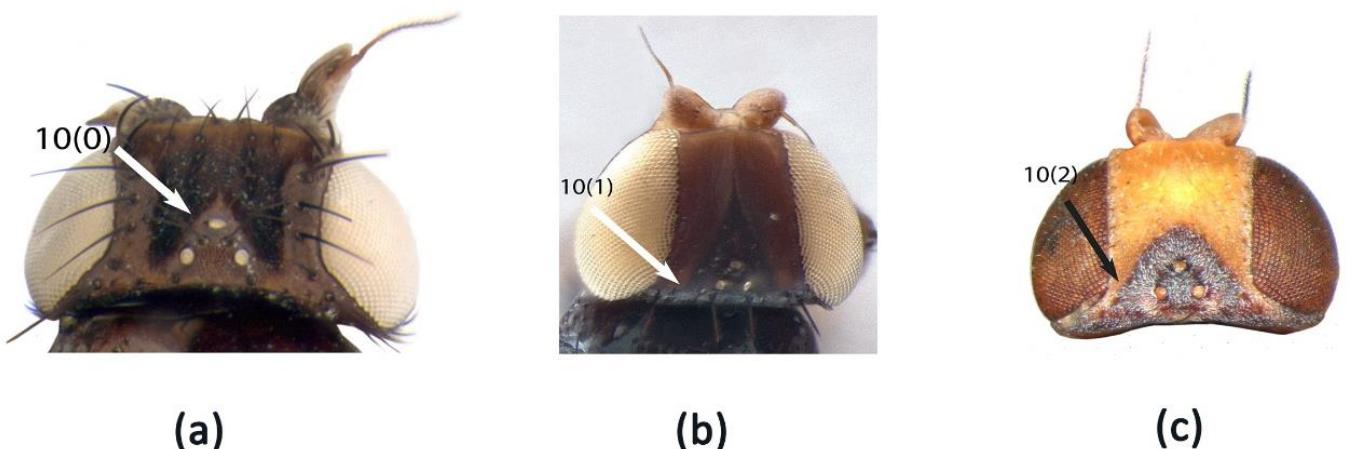


Figure 18a-c. Character 10, ocellar triangle width at posterior margin: a. *Phyllomyza flavitarsis*, state 0, hardly wider than the tubercle itself; b. *Epimadiza* sp., state 1, wider than tubercle, reaching halfway to eye margin; c. *Hippelates plebejus*, state 2, getting close or laterally reaching the eye margins.

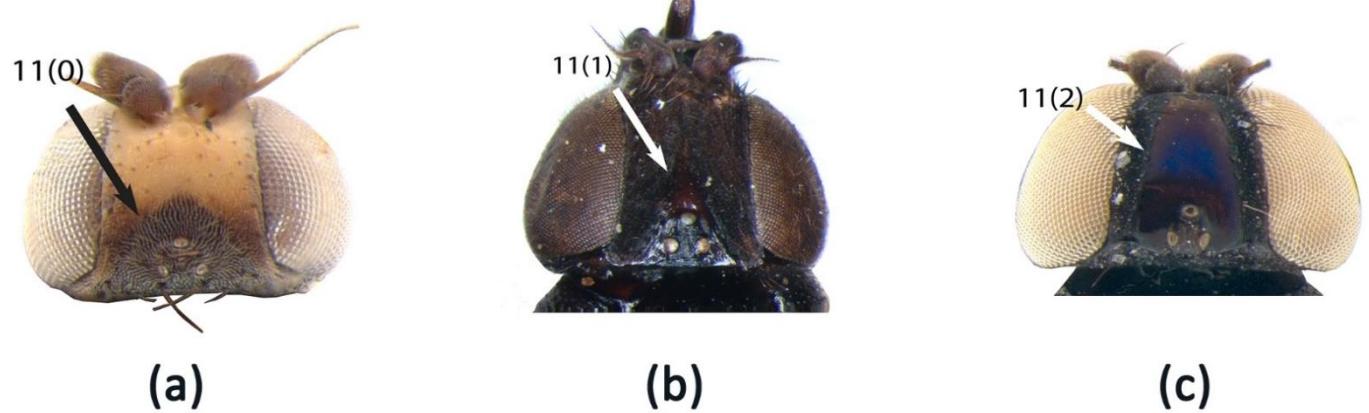


Figure 19a-c. Character 11, lateral margins of ocellar triangle: a. *Microcercis albipalpis*, state 0, convex; b. *Siphonella oscinina*, state 1, concave; c. *Rhodesiella* sp.2, state 2, straight.

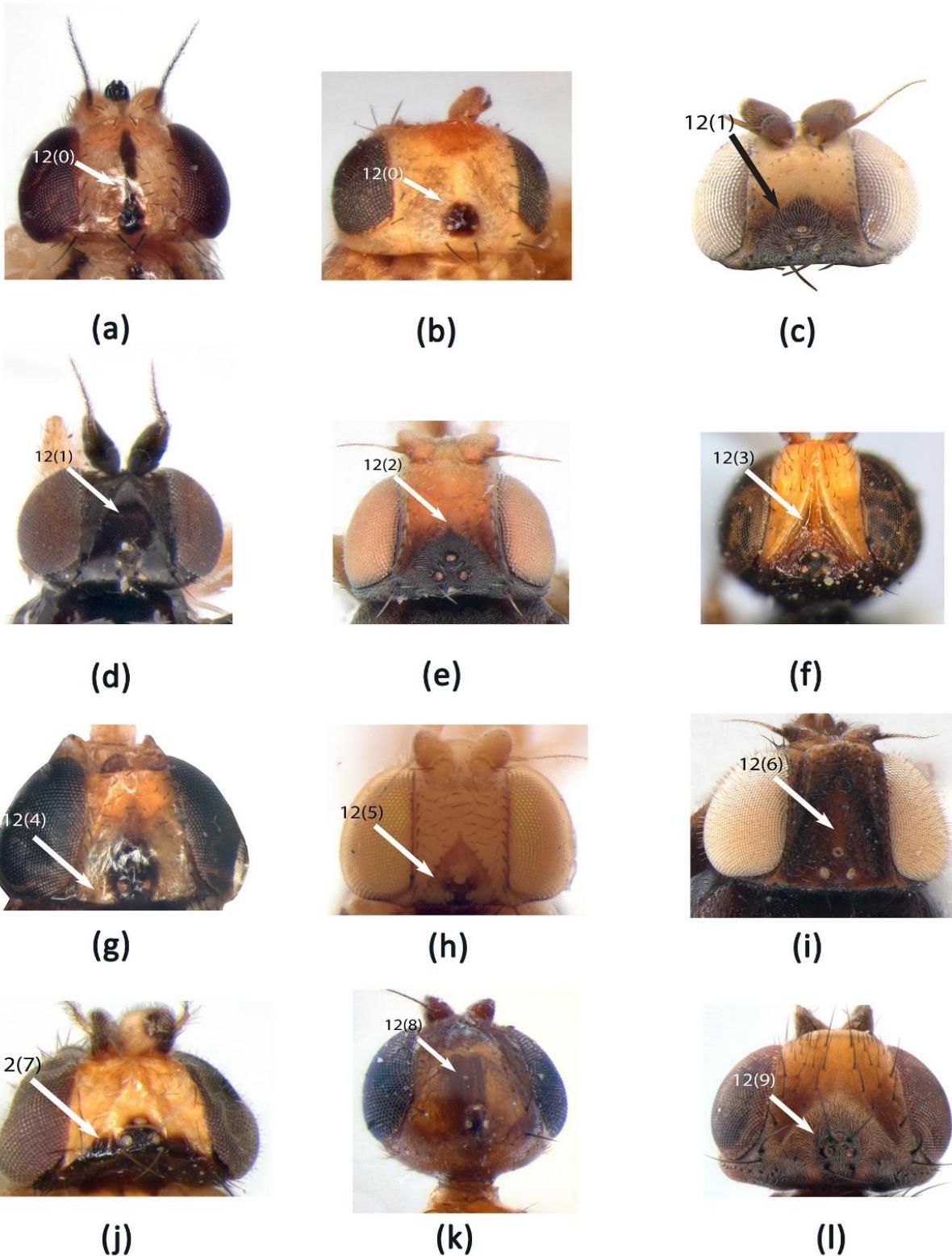


Figure 20a-l. Character 12, color of ocellar triangle: a. *Metasiphonella* sp., state 0, light brown to yellow entirely; b. *Opetiophora straminea*, state 0; c. *Microcercis albipalpis*, state 1, dark brown to black entirely; d. *Monochaetoscinella anonyma*, state 1; e. *Oscinimorpha albisetosa*, state 2, anterior end light, the rest dark; f. *Sagareocerus aberrans*, state 3, anterior half light, posterior half dark; g. *Heteroscinis hystrix*, state 4, posterior end light, the rest dark; h. *Eugaurax* sp., state 5, posterior light, anterior dark; i. *Calamoncosis minima*, state 6, middle (oval or linear) light, around dark; j. *Gaurax festivus*, state 7, posterior end dark, the rest light; k. *Sepsidescinis maculipennis*, state 8, anterior fifth and a median band dark, with dark yellow background; l. *Siphonellopsis lacteibasis*, state 9, dark tubercle with darker lateral areas over lighter background.

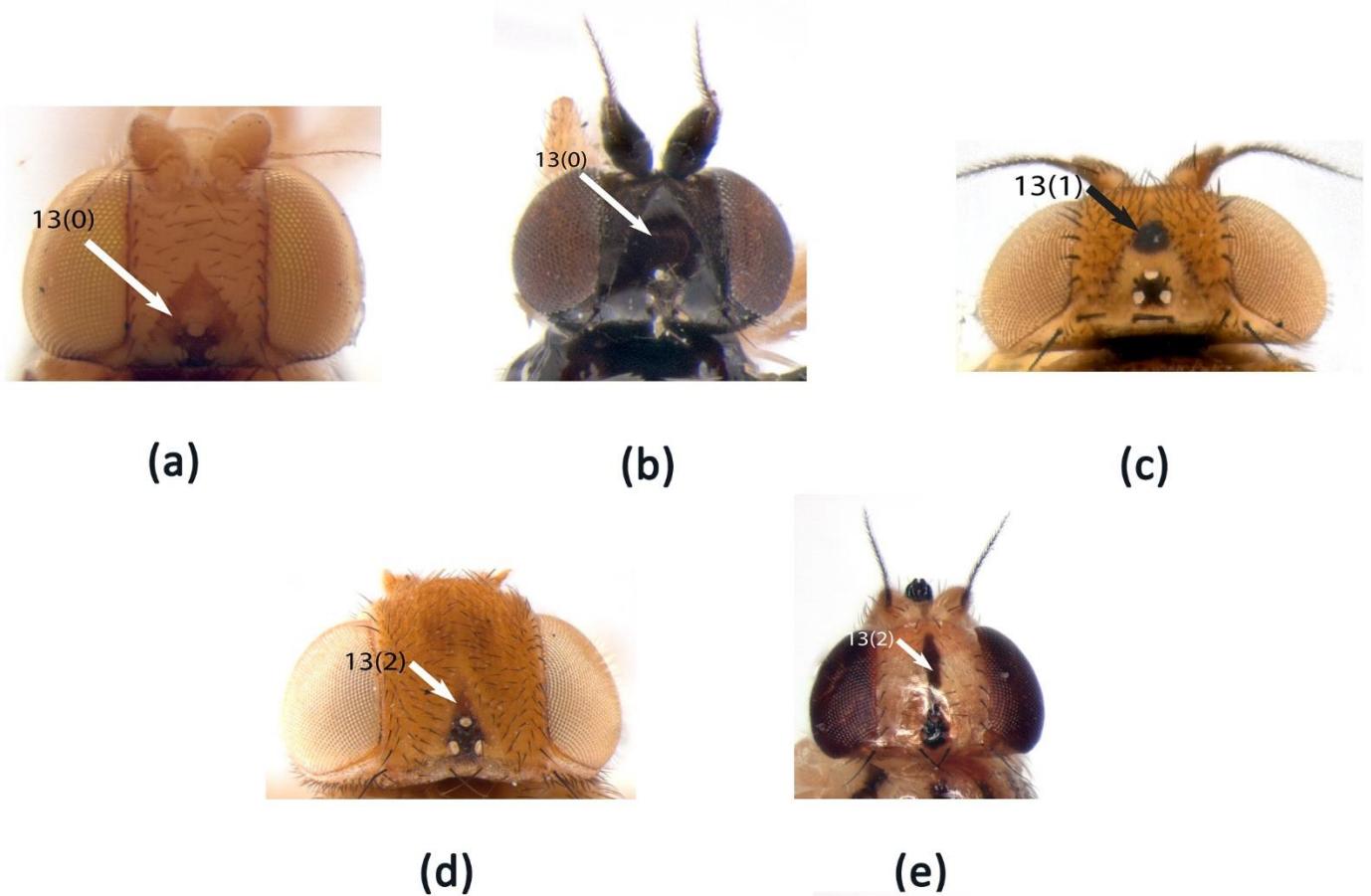


Figure 21a-e. Character 13, ocellar triangle: a. *Eugaurax* sp., state 0, concolor; b. *Monochaetoscinella anonyma*, state 0; c. *Chaethippus* sp., state 1, with spot; d. *Medeventor tschirnhausi*, state 2, with band; e. *Metasiphonella* sp., state 2.



Figure 22a-b. Character 14, posterior ocelli: a. *Medeventor tschirnhausi*, state 0, yellow or light brown; b. *Metasiphonella* sp., state 1, black or dark brown.



Figure 23a-b. Character 15, anterior ocellus: a. *Medeventor tschirnhausi*, state 0, yellow or light brown; b. *Heteroscinis hystrix*, state 1, black or dark brown.

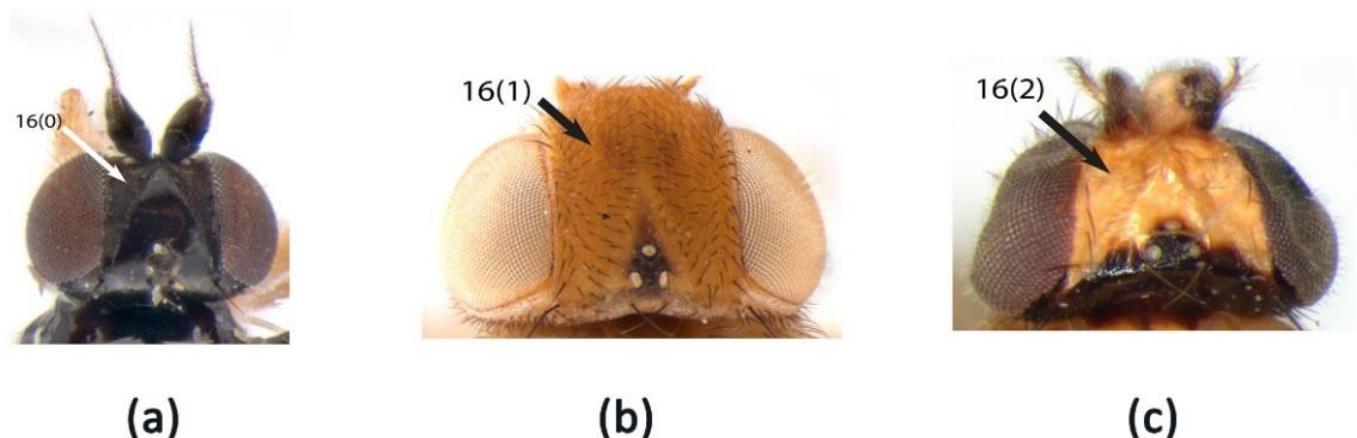


Figure 24a-c. Character 16, density of setation on frons: a. *Monochaetoscincella anonyma*, state 0, bare; b. *Medeventor tschirnhausi*, state 1, dense; c. *Gaurax festivus*, state 2, scattered.

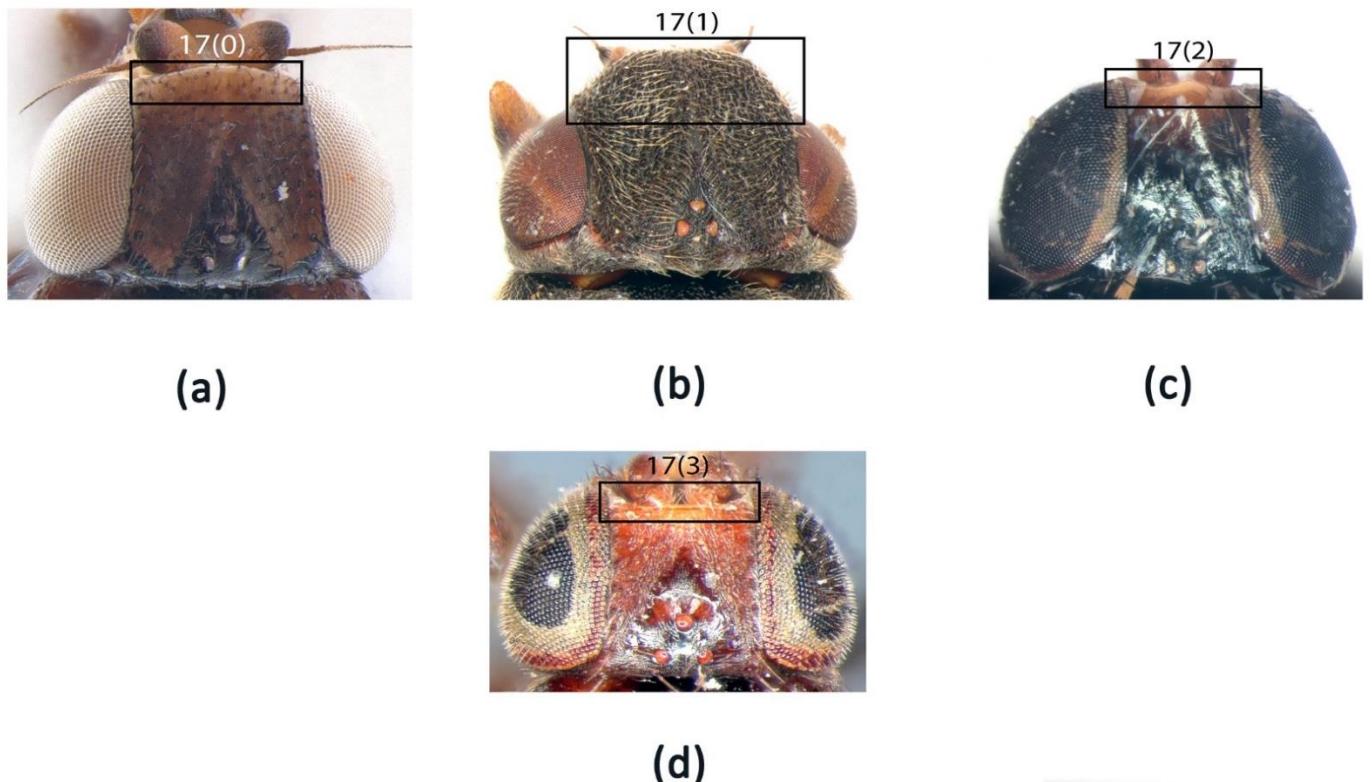


Figure 25a-d. Character 17, anterior margin of frons in dorsal view (in comparison of the level of eyes): a. *Lasiambia palposa*, state 0, straight or slightly projected; b. *Lipara lucens*, state 1, projected moderately beyond the anterior margin of eyes; c. *Fiebrigella* sp., state 2, concave, medially with projection; d. *Speccafrons mallochi*, state 3, concave, medially straight.

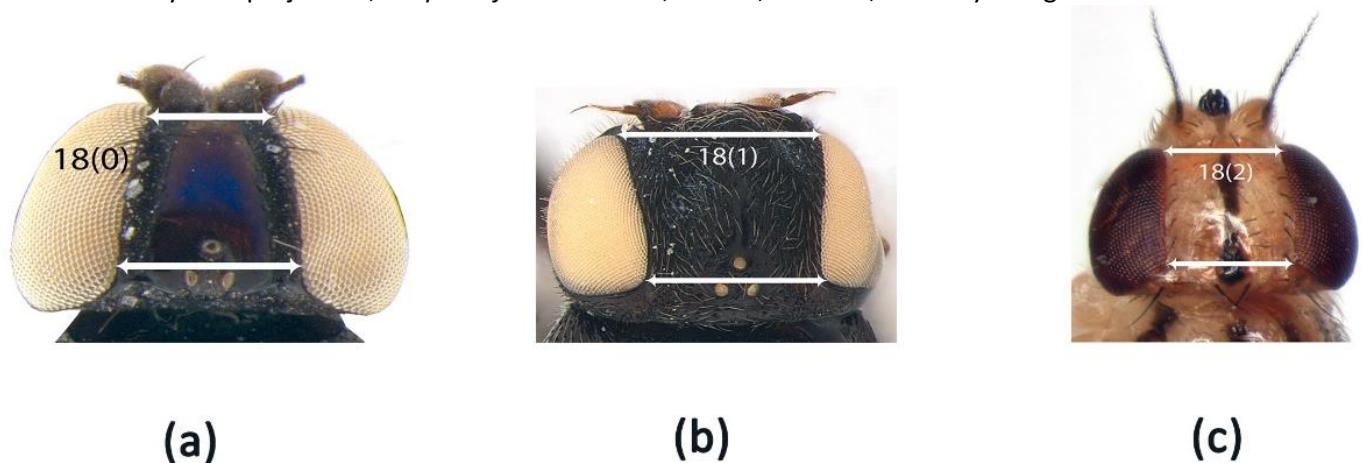
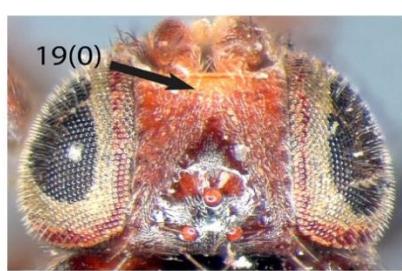


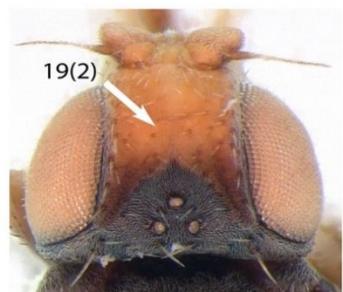
Figure 26a-c. Character 18, lateral margins of frons in dorsal view: a. *Rhodesiella* sp.2, state 0, converging towards anterior margin; b. *Lipara pullitarsis*, state 1, diverging towards anterior margin; c. *Metasiphonella* sp., state 2, almost parallel.



(a)



(b)



(c)



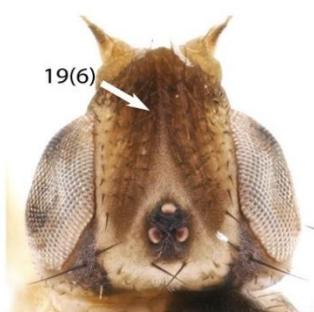
(d)



(e)



(f)



(g)



(h)

Figure 27a-h. Character 19, ground color of frons: a. *Speccafrons mallochi*, state 0, anterior third yellow; b. *Heteroscinis hystrix*, state 1, anterior half yellow; c. *Oscinimorpha albisetosa*, state 2, anterior two third yellow; d. *Metasiphonella* sp., state 3, entirely yellow; e. *Monochaetoscinella anonyma*, state 4, entirely dark; f. *Opetiophora straminea*, state 5, anterior third dark; g. *Pseudeurina maculata* (photography by Barbara Ismay), state 6, anterior two third dark; h. *Sepsidoscinis maculipennis*, state 7, anterior half dark.



(a)

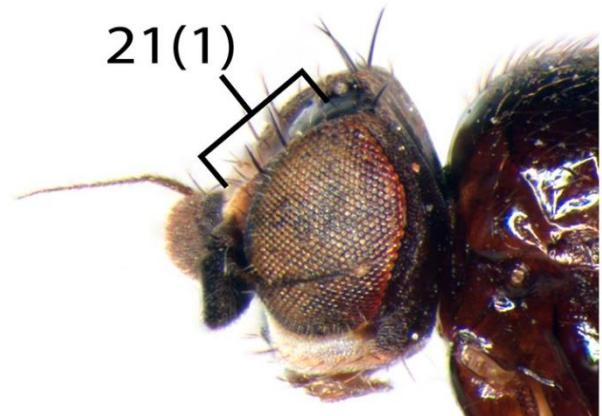


(b)

Figure 28a-b. Character 20, length of orbital setae: a. *Gaurax festivus*, state 0, long; b. *Trachysiphonella pygmaea*, state 1, short.



(a)



(b)

Figure 29a-b. Character 21, comparison of length of orbital setae to each other: a. *Aphanotrigonum trilineatus*, state 0, of same length; b. *Biorbitella Hesperia*, state 1, some clearly longer than others.



(a)



(b)

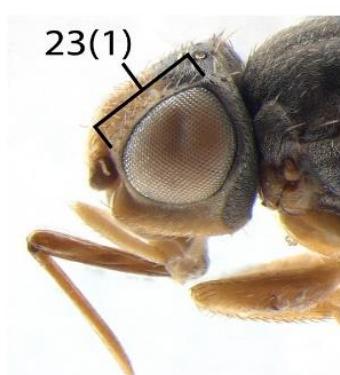


(c)

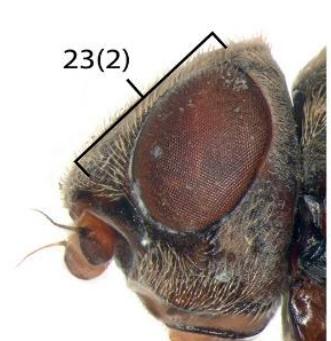
Figure 30a-c. Character 22, direction of orbital setae: a. *Gaurax festivus*, state 0, all reclinate; b. *Siphonellopsis lacteibasis*, state 1, all proclinate; c. *Meoneura flavifacies*, state 2, anterior one proclinate, posterior two reclinate.



(a)



(b)



(c)

Figure 31a-c. Character 23, number of orbital setae: a. *Aphanotrigonum trilineatus*, state 0, less than five; b. *Oscinimorpha albisetosa*, state 1, between five and ten; c. *Lipara lucens*, state 2, more than ten.



Figure 32a-b. Character 24, inner vertical seta: a. *Dicraeus vagans*, state 0, conspicuous and strong; b. *Biorbitella hesperia*, state 1, absent or not distinguishable.



Figure 33a-b. Character 25, length of ocellar setae: a. *Dicraeus vagans*, state 0, shorter than or as long as ocellar tubercle; b. *Rhodesiella* sp.1, state 1, longer than ocellar tubercle.

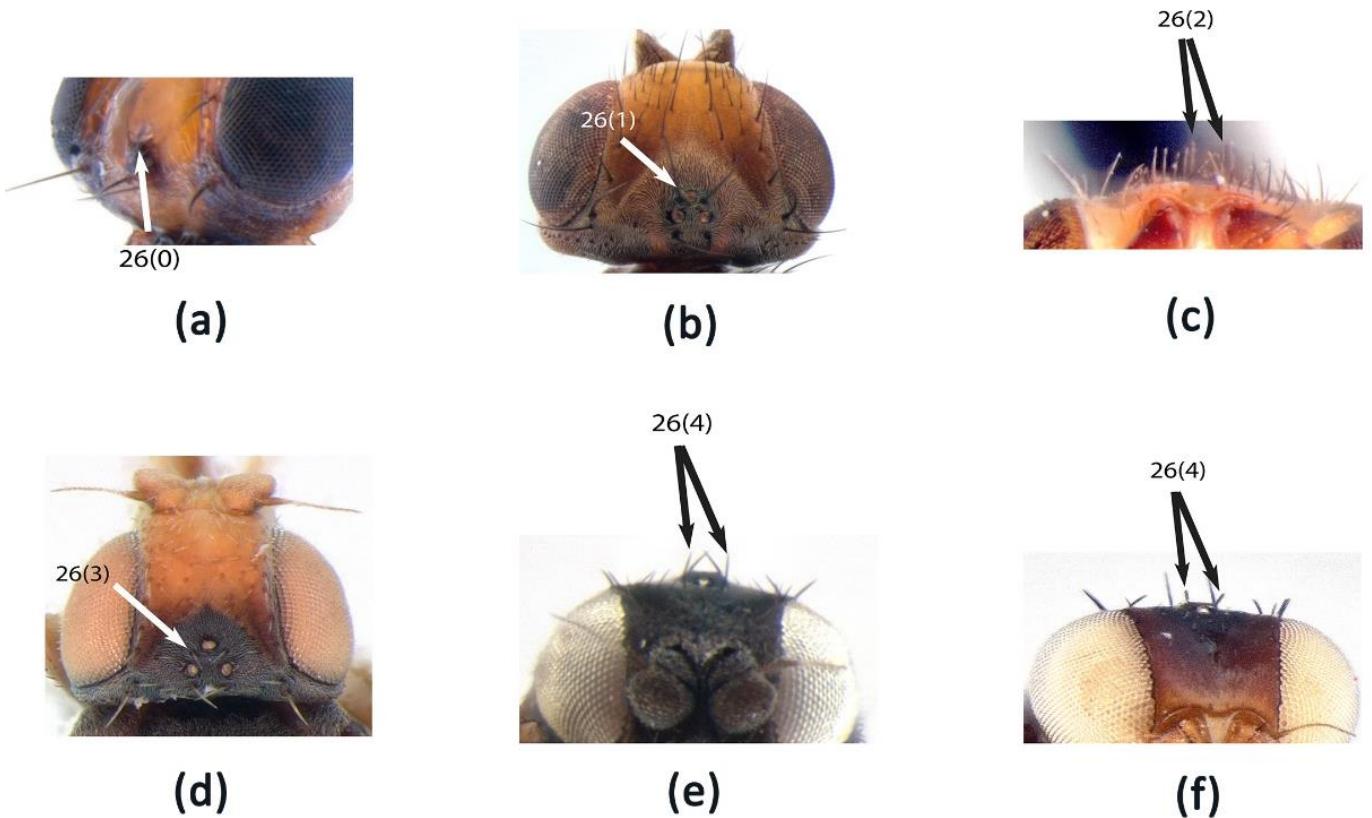


Figure 34a-f. Character 26, direction and orientation of ocellar setae: a. *Elachiptera brevipennis*, state 0, proclinate and convergent; b. *Siphonellopsis lacteibasis*, state 1, proclinate and divergent; c. *Diplotoxa versicolor*, state 2, proclinate and parallel; d. *Oscinimorpha albisetosa*, state 3, reclinate and convergent; e. *Malloewia diabolus*, state 4, reclinate and parallel; f. *Epimadiza* sp., state 4.



Figure 35a-b. Character 27, length of post-ocellar setae: a. *Eribolus hungaricus*, state 0, shorter or as long as the ocellar tubercle; b. *Metasiphonella* sp., state 1, longer than the ocellar tubercle.

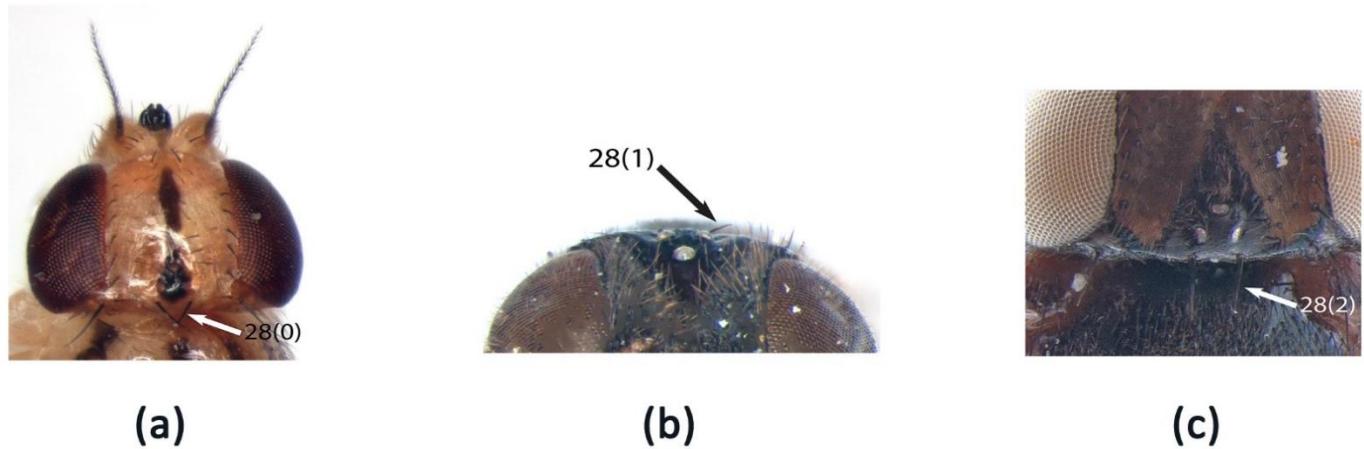


Figure 36a-c. Character 28, orientation of postocellar setae: a. *Metasiphonella* sp., state 0, convergent; b. *Siphonella oscinina*, state 1, divergent; c. *Lasiambia palposa*, state 2, parallel.

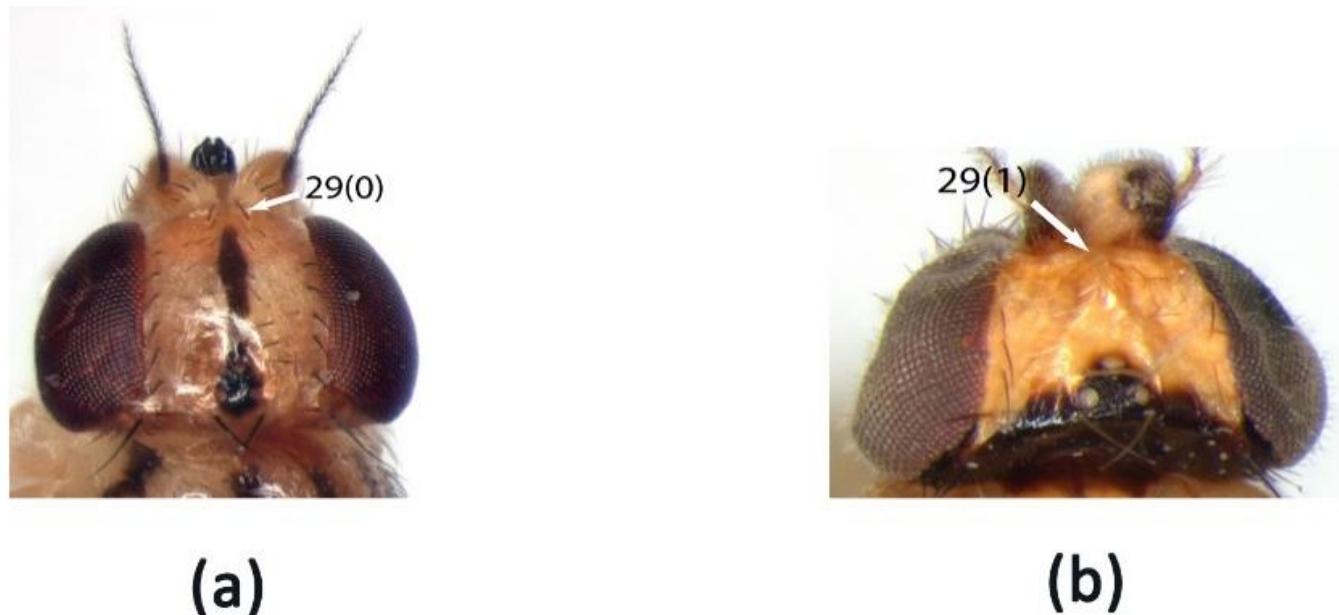


Figure 37a-b. Character 29, anterior interfrontal setae: a. *Metasiphonella* sp., state 0, longer than remaining of interfrontal setae; b. *Gaurax festivus*, state 1, shorter or as long as remaining of interfrontal setae.

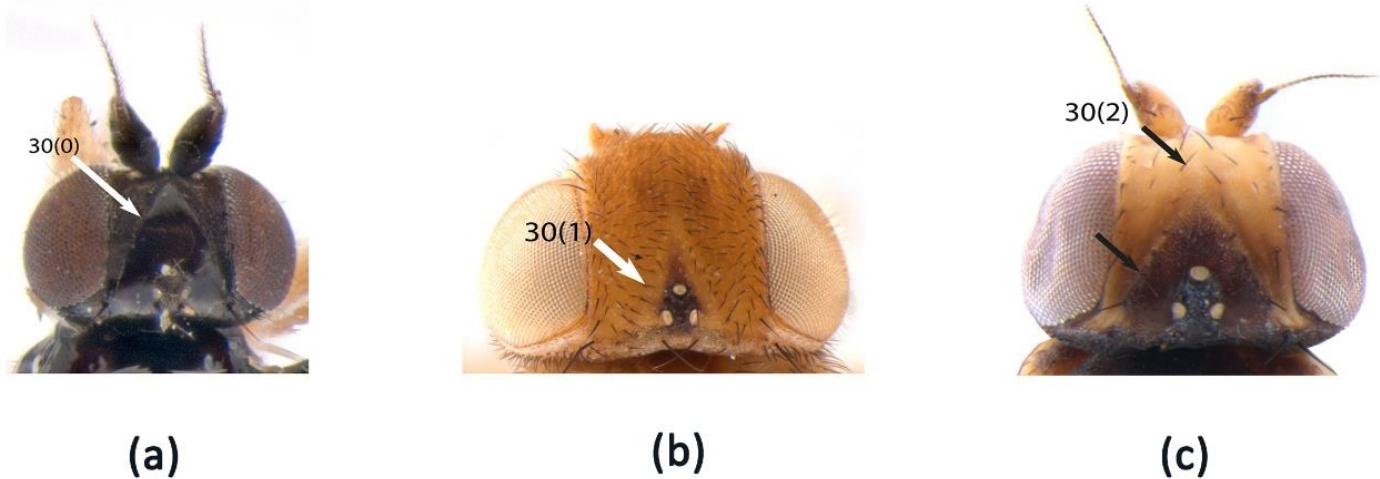


Figure 38a-c. Character 30, interfrontal setae relative to the frontal setae: a. *Monochaetoscincella anonyma*, state 0, absent; b. *Medeventor tschirnhausi*, state 1, present but as long as frontal setae; c. *Dicraeus vagans*, state 2, conspicuous.

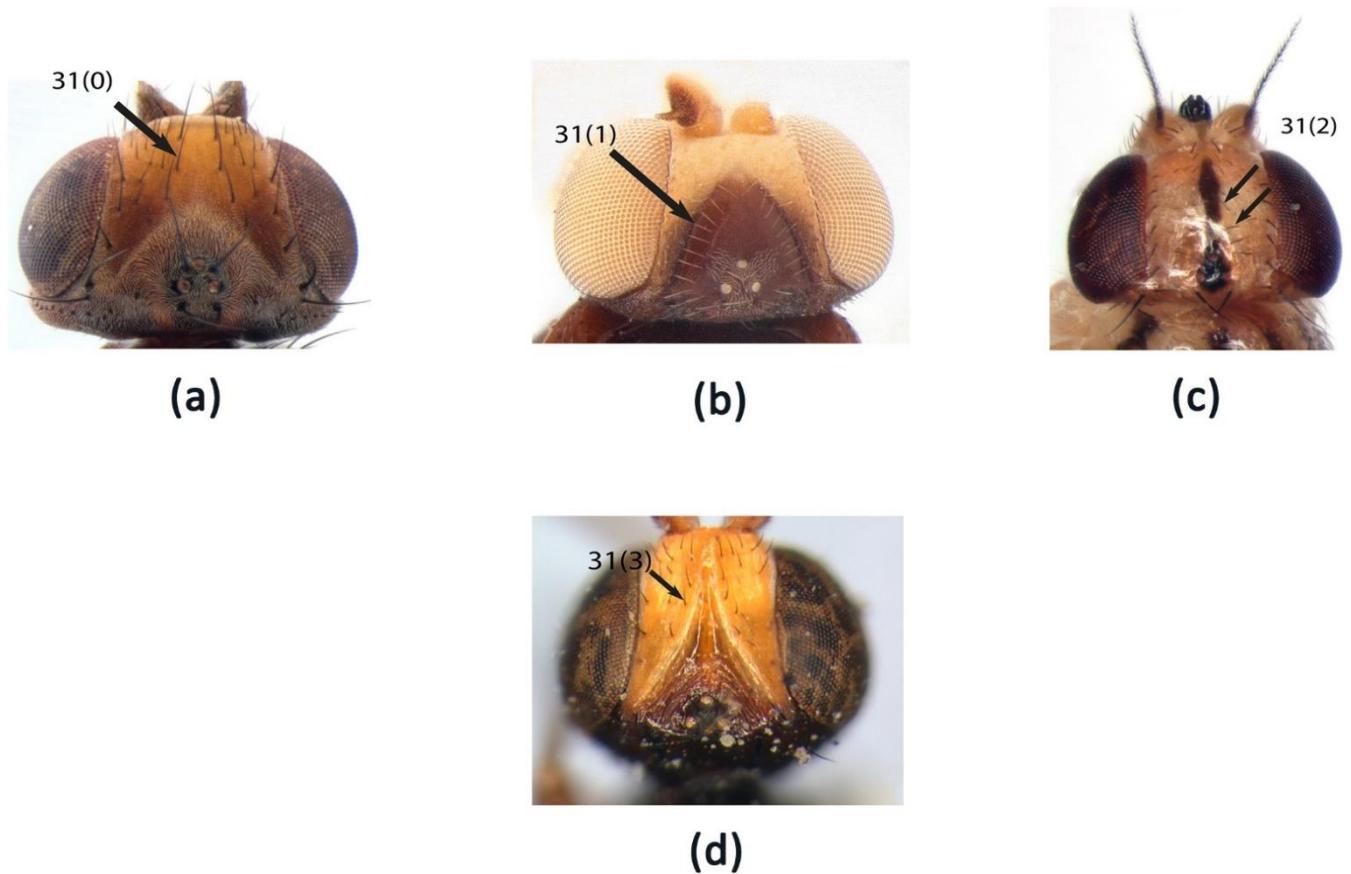


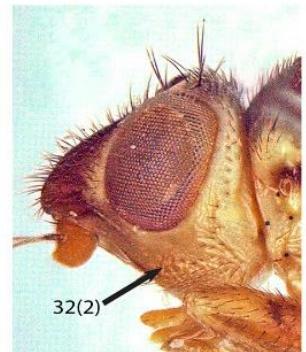
Figure 39a-d. Character 31, direction of interfrontal seta: a. *Siphonellopsis lacteibasis*, state 0, all proclinate; b. *Oscinisoma cognatum*, state 1, all inclinate; c. *Metasiphonella* sp., state 2, anteriorly proclinate and posteriorly inclinate; d. *Sagareocerus aberrans*, state 3, all straight.



(a)

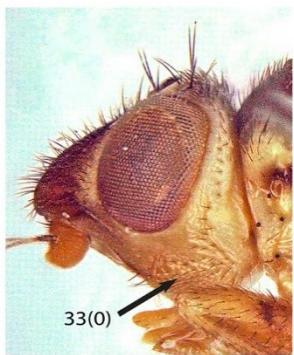


(b)



(c)

Figure 40a-c. Character 32, height of gena relative to the height of first flagellomere of antenna: a. *Biorbitella hesperia*, state 0, shorter; b. *Malloewia diabolus*, state 1, almost as long; c. *Pseudeurina maculata* (photography by Barbara Ismay), state 2, longer.



(a)



(b)



(c)



(d)



(e)



(f)



(g)



(h)

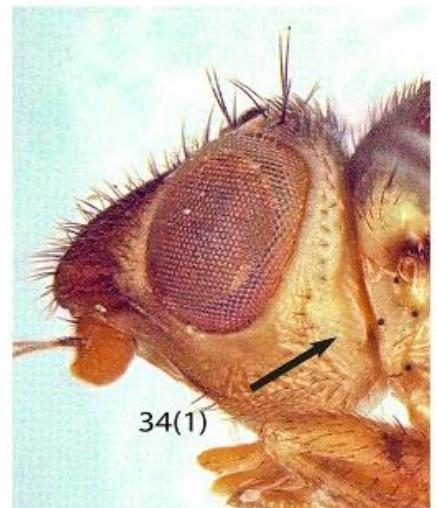


(i)

Figure 41a-i. Character 33, color of gena: a. *Pseudeurina maculata* (photography by Barbara Ismay), state 0, all over yellow or light brown; b. *Oscinisoma cognatum*, state 1, posterior half yellow; c. *Monochaetoscinella anonyma*, state 2, anterior half yellow; d. *Eribolus hungaricus*, state 3, dark color; e. *Polyodaspis ruficornis*, state 4, posterior third yellow; f. *Siphonellopsis lacteibasis*, state 5, anterior third yellow; g. *Trigonomma coeruleifrons* (Photography by Paula Raile Riccardi), state 6, posterior two third yellow; h. *Lasiambia palposa*, state 7, anterior two third yellow; i. *Loxobathmis obliquans*, state 8, all over yellow except anterior tip dark.



(a)



(b)

Figure 42a-b. Character 34, color of postgena: a. *Loxobathmis obliquans*, state 0, black or dark brown; b. *Pseudeurina maculata* (photography by Barbara Ismay), state 1, yellow or light brown.



(a)



(b)

Figure 43a-b. Character 35, vibrissal seta: a. *Loxobathmis obliquans*, state 0, present; b. *Lasiambia palposa*, state 1, absent.

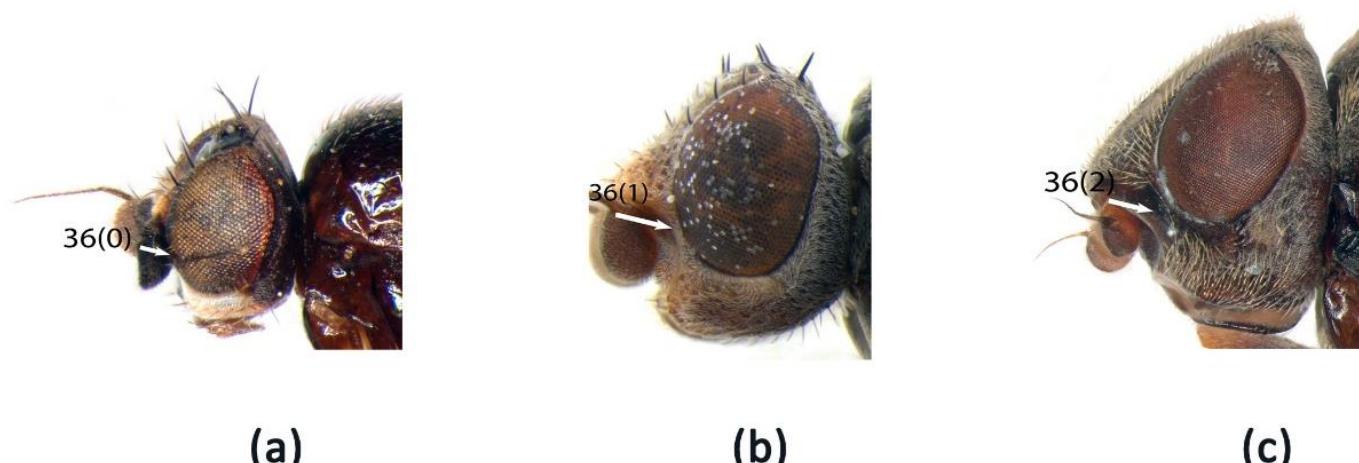
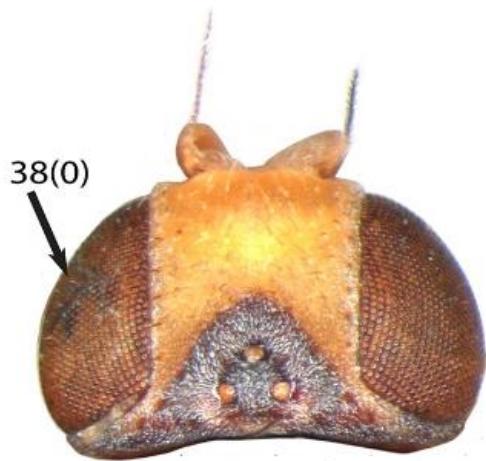


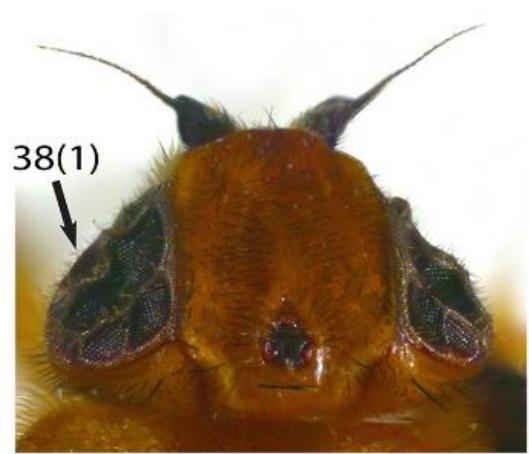
Figure 44a-c. Character 36, parafacialia (related to the broadness of first flagellomere of antenna):
 a. *Biorbitella hesperia*, state 0, absent; b. *Aphanotrigonum trilineatus*, state 1, narrow; c. *Lipara lucens*, state 2, wider.



Figure 45a-b. Character 37, pilosity of eye: a. *Heteroscincis hystrix*, state 0, bare; b. *Batrachomyia nigritarsis*, state 1, hairy.



(a)

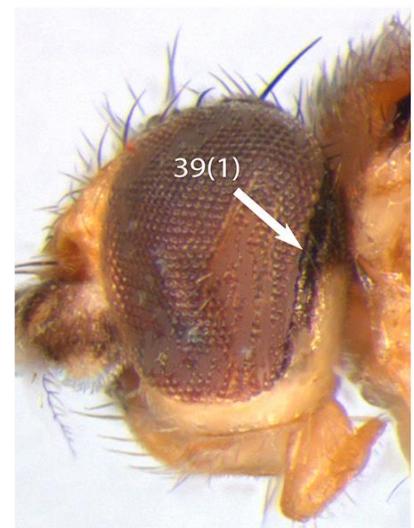


(b)

Figure 46a-b. Character 38, dispersal pilosity of eye: a. *Hippelates plebejus*, state 0, scattered; b. *Batrachomyia nigritarsis*, state 1, dense.



(a)



(b)

Figure 47a-b. Character 39, posterior margin of eye, ¼ ventral: a. *Malloewia diabolus*, state 0, continues; b. *Gaurax festivus*, state 1, with notch.

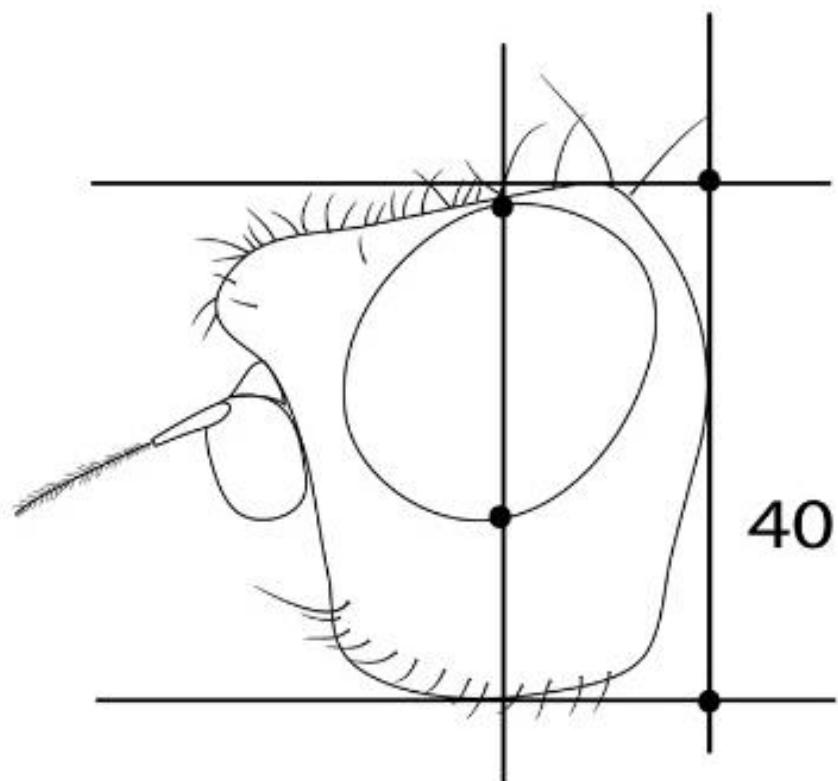


Figure 48: Character 40, rate of eye compared with head capsule vertically in lateral view: Schematic shape.



Figure 49a-b. Character 41, proboscis: a. *Oscinimorpha albisetosa*, state 0, geniculate; b. *Speccafrons mallochi*, state 1, not geniculate.

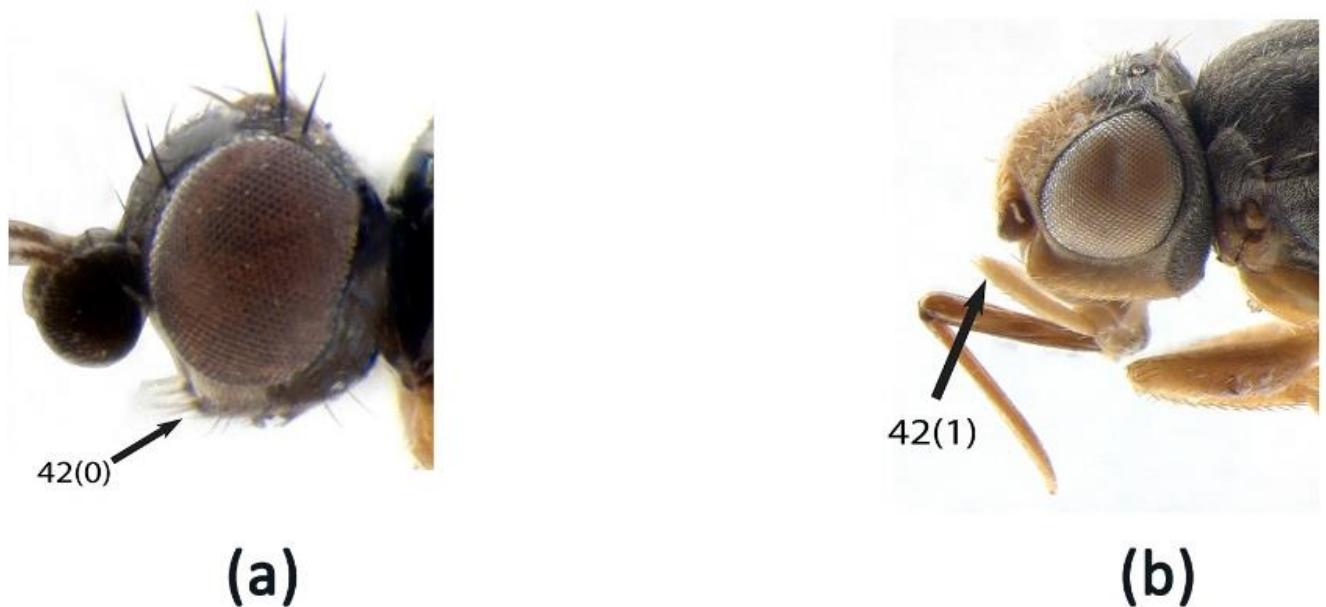


Figure 50a-b. Character 42, length of palpus in comparison with the oral cavity (lower margin of the face): a. *Monochaetoscinella anonyma*, state 0, at most at the margin of oral cavity; b. *Oscinimorpha albisetosa*, state 1, longer than the margin of oral cavity.

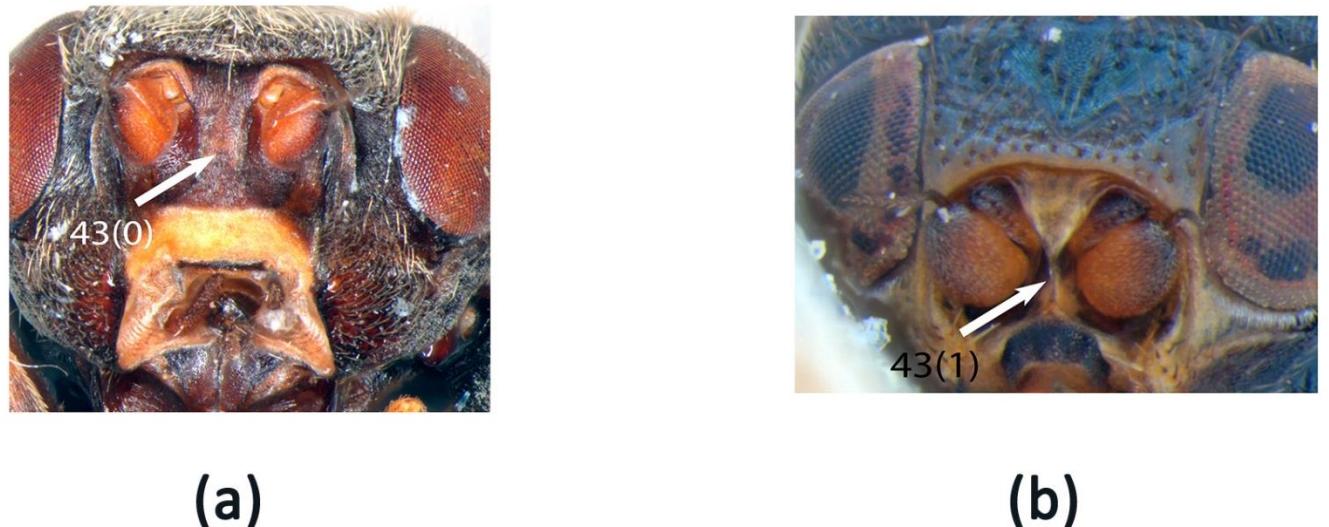
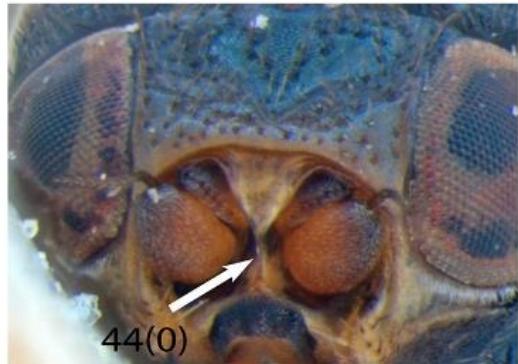
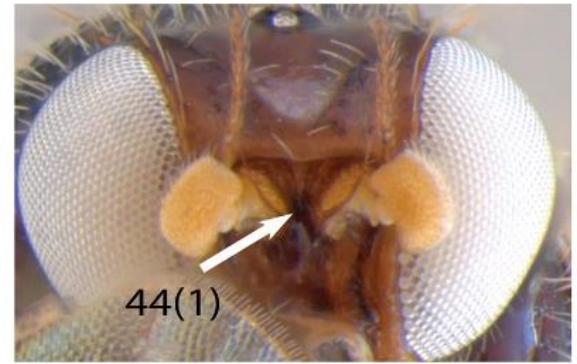


Figure 51a-b. Character 43, shape of facial carina: a. *Lipara lucens*, state 0, wide dorsally and ventrally; b. *Polyodaspis ruficornis*, state 1, narrow ventrally and wide or narrow dorsally.



(a)



(b)

Figure 52a-b. Character 44, facial carina: a. *Polyodaspis ruficornis*, state 0, complete, reaching to the epistomal margin or very close; b. *Rhodesiella* sp.1, state 1, incomplete, extending almost halfway to epistomal margin.

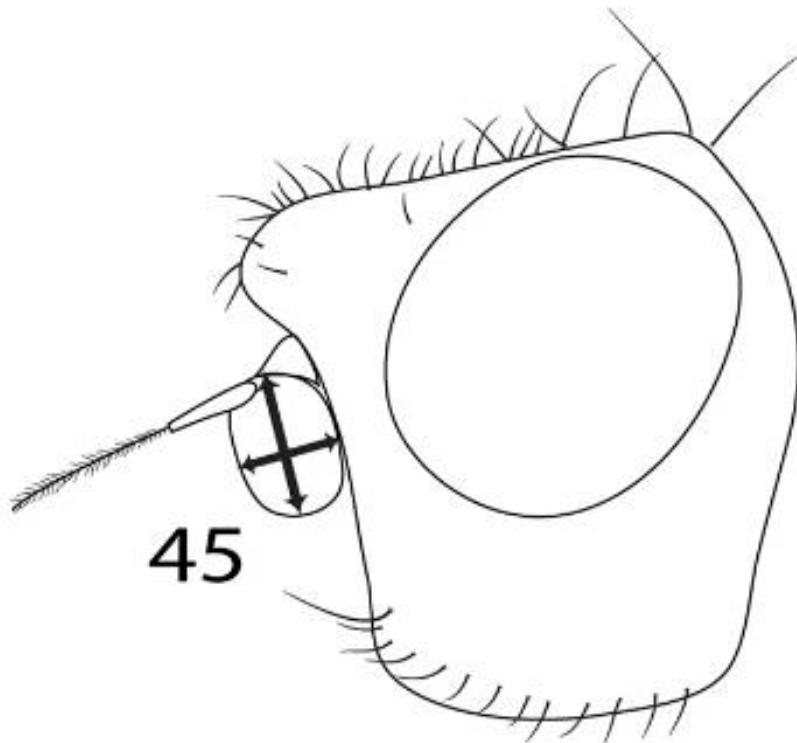
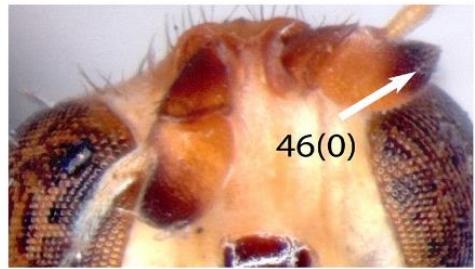
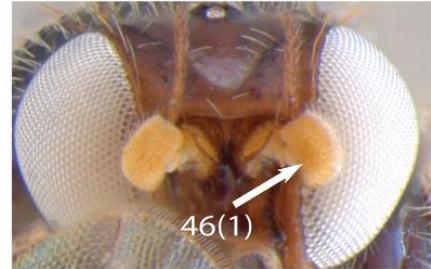


Figure 53: Character 45, rate of first antennal flagellomere (length/wide): Schematic shape.



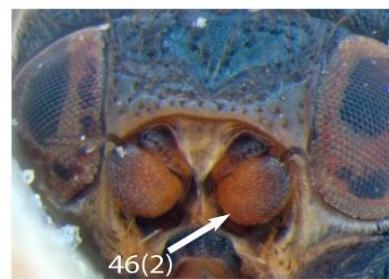
(a)



(b)



(c)



(d)

Figure 54a-d. Character 46, first antennal flagellomere distally: a. *Diplotoxa versicolor*, state 0, one; b. *Rhodesiella* sp.1, state 1, between 1.1 and 1.5; c. *Monochaetoscinella anonyma*, state 2, more than 1.5 ; d. *Polyodaspis ruficornis*, state 2.

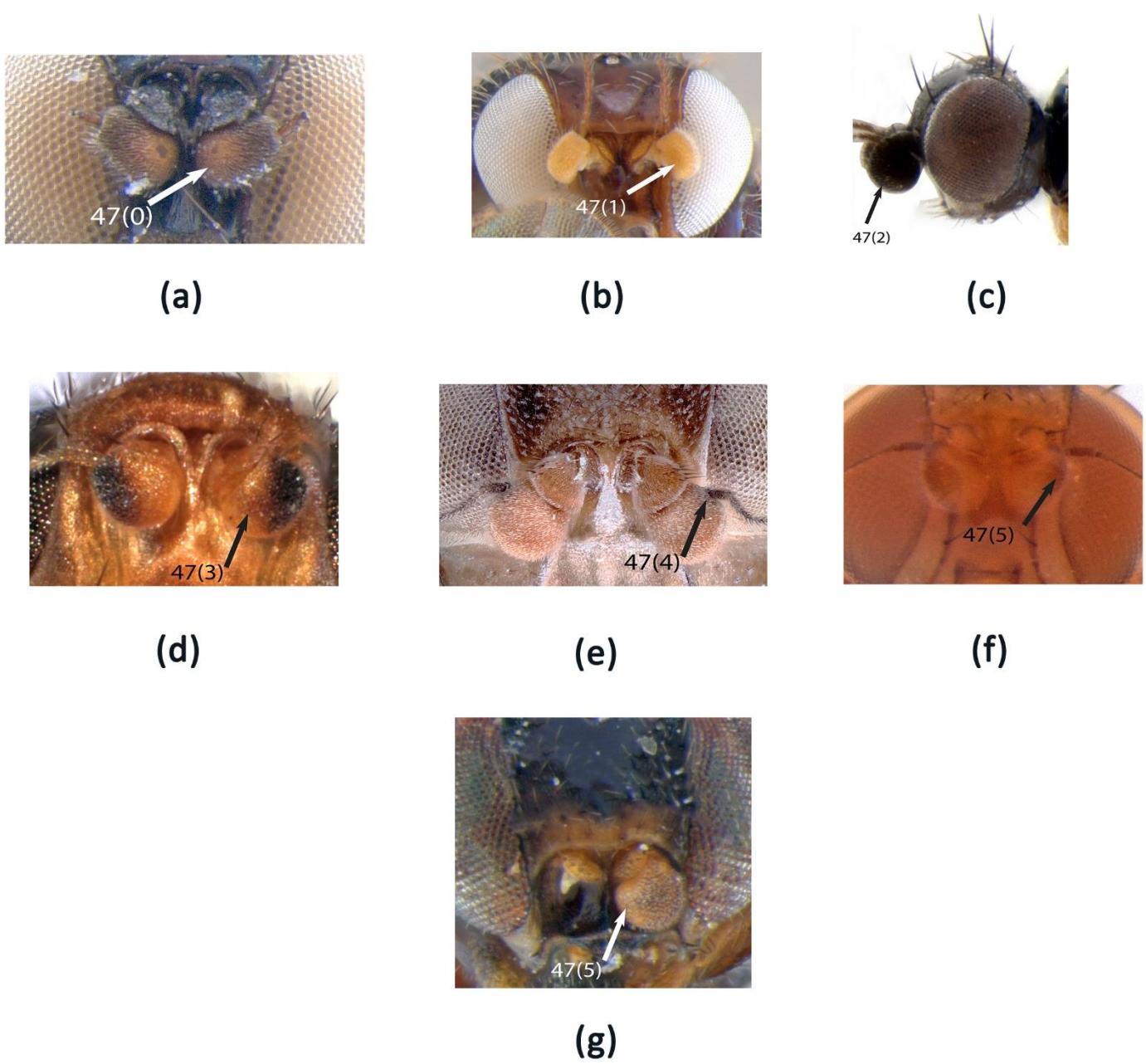
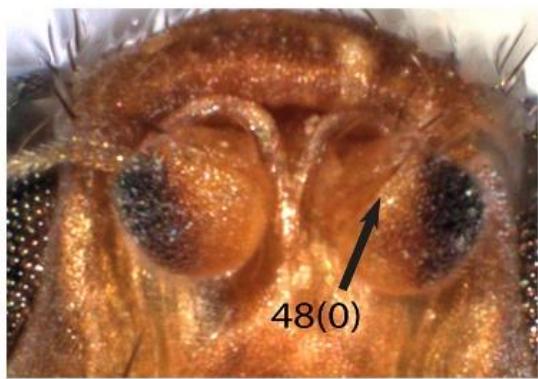
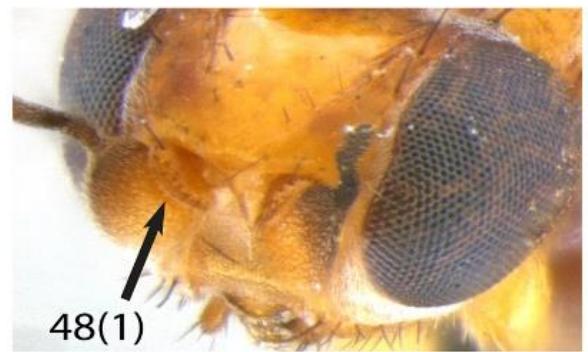


Figure 55a-g. Character 47, color of first antennal flagellomere: a. *Rhodesiella* sp.2, state 0, posterior half yellow or light; b. *Rhodesiella* sp.1, state 1, entirely yellow or light brown; c. *Monochaetoscinella anonyma*, state 2, entirely dark brown or black; d. *Opetiophora straminea*, state 3, posterior two third yellow or light brown; e. *Medeventor nubosus* (Photography by Canadian National Collection Museum), state 4, entirely yellow or light brown except at base of arista; f. *Notaulacella* sp., state 5, yellow or light brown, dark dorsobasally; g. *Lioscinella sulfurihalterata*, state 5.



(a)



(b)

Figure 56a-b. Character 48, posterior end of first antennal flagellomere, in frontal view: a. *Opetiophora straminea*, state 0, straight; b. *Elachiptera brevipennis*, state 1, concave (reniform).



(a)



(b)

Figure 57a-b. Character 49, color of basal segment of arista: a. *Elachiptera brevipennis*, state 0, dark; b. *Opetiophora straminea*, state 1, yellow.

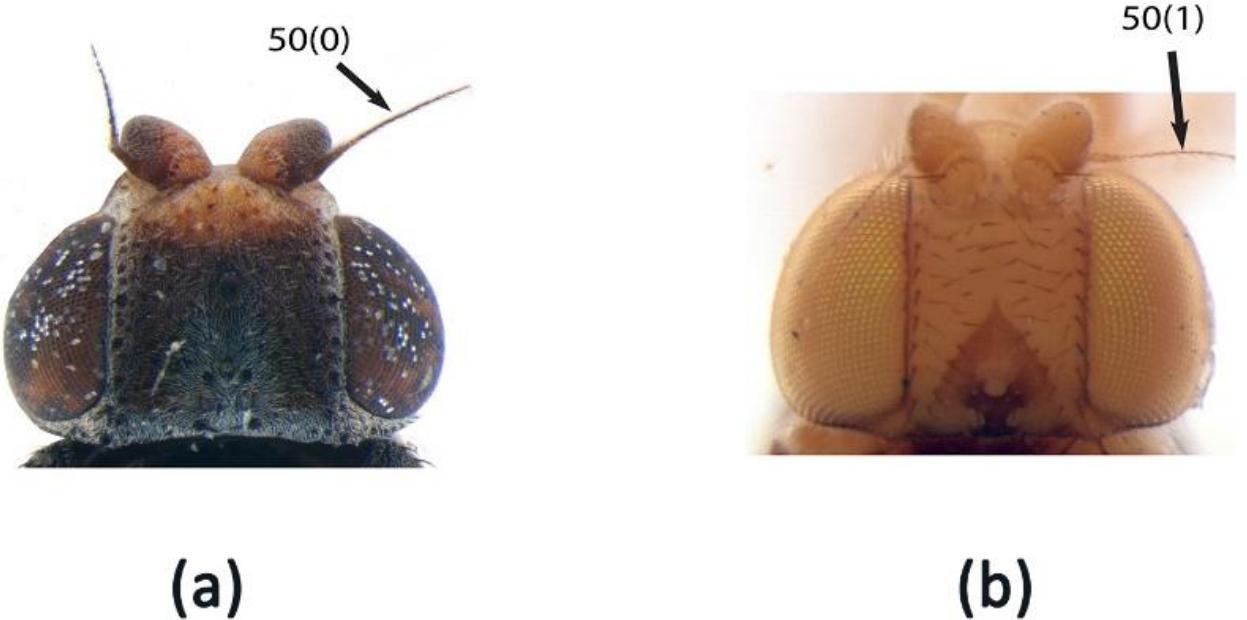


Figure 58a-b. Character 50, color of distal segment of arista: a. *Aphanotrigonum trilineatus*, state 0, dark; b. *Eugaurax* sp., state 1, yellow.

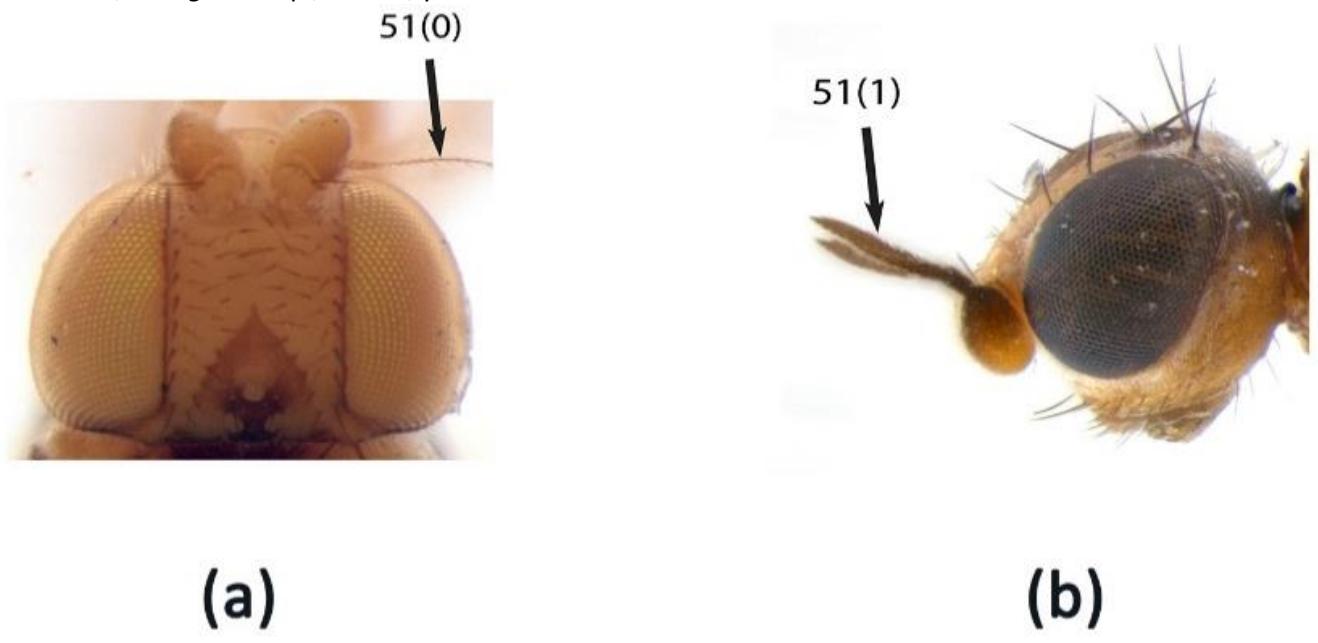
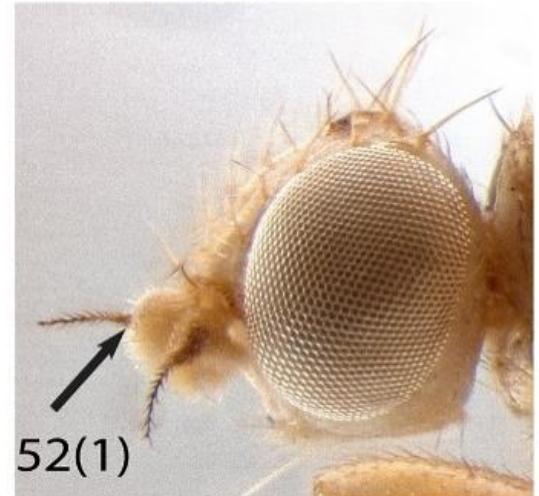


Figure 59a-b. Character 51, width of distal half arista: a. *Eugaurax* sp., state 0, thin; b. *Elachiptera brevipennis*, state 1, thick.

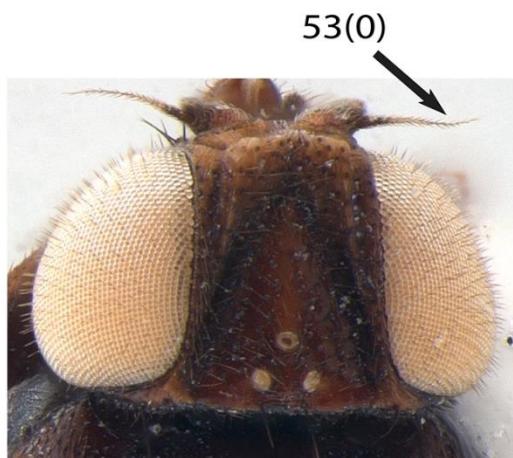


(a)

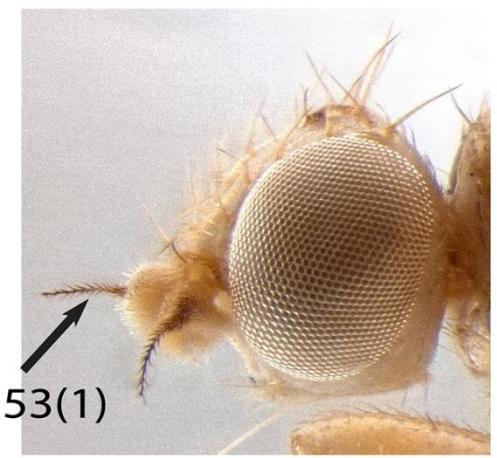


(b)

Figure 60a-b. Character 52, position of arista on first antennal flagellomere: a. *Lipara lucens*, state 0, placed at most equal with arista base; b. *Cadrema pallida*, state 1, more than arista base, at least twice.

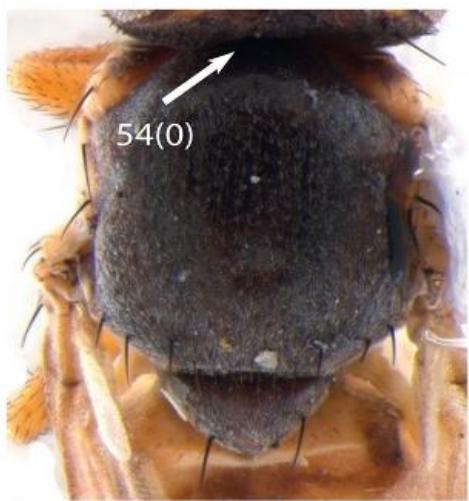


(a)

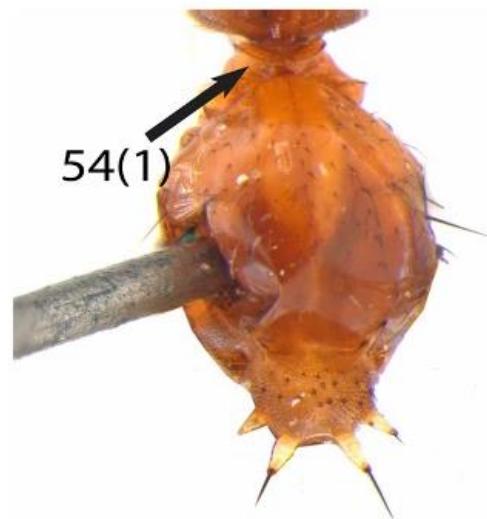


(b)

Figure 61a-b. Character 53, pilosity of entire arista comparing with the stem of arista: a. *Calamoncosis minima*, state 0, short hairs; b. *Cadrema pallida*, state 1, long hairs.



(a)



(b)

Figure 62a-b. Character 54, anterior part of mesonotum: a. *Dicraeus vagans*, state 0, not projected; b. *Sepsidoscinis maculipennis*, state 1, projected (neck form).

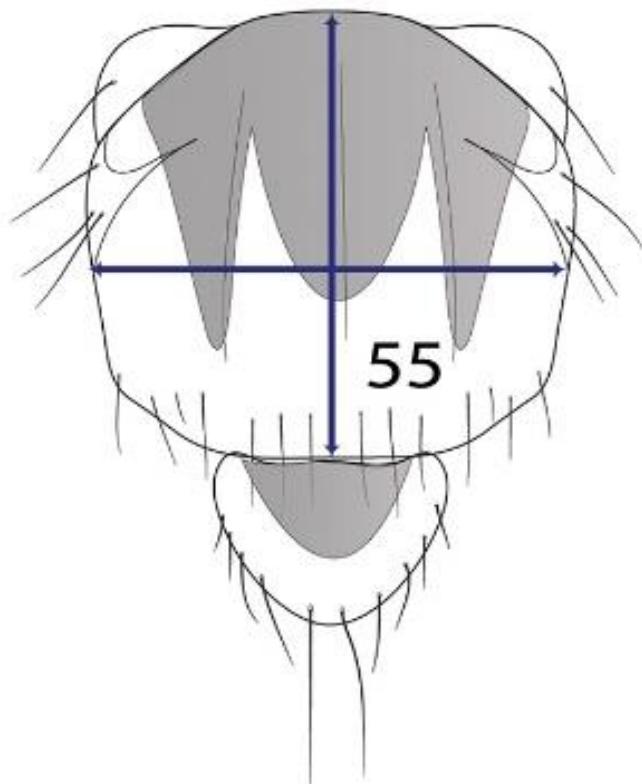
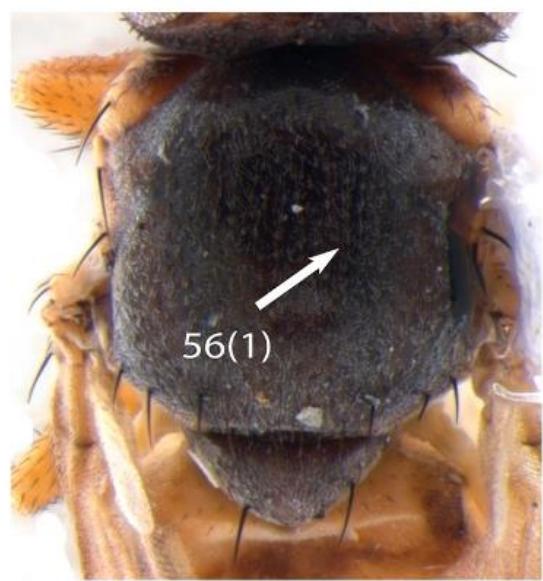


Figure 63: Character 55, length of scutum dorsally (width/length): Schematic shape.



(a)

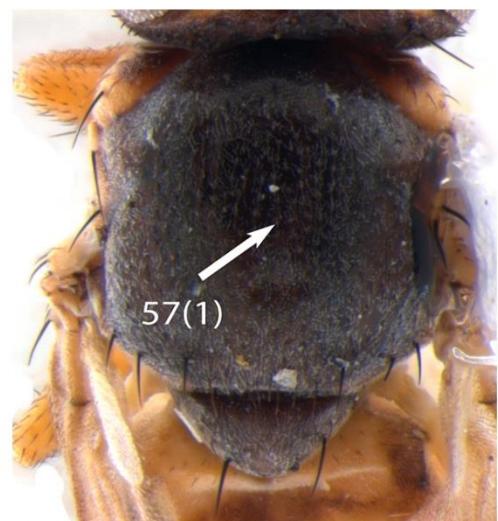


(b)

Figure 64a-b. Character 56, acrostical seta: a. *Anatrichus erinaceus*, state 0, present; b. *Dicraeus vagans*, state 1, absent.

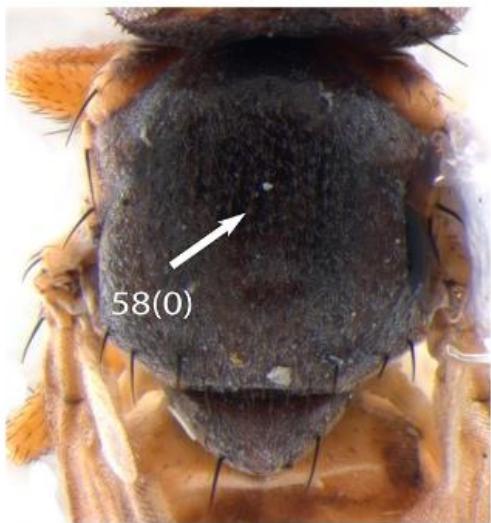


(a)

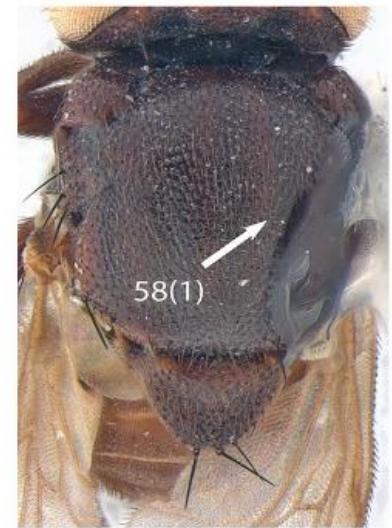


(b)

Figure 65a-b. Character 57, dorsocentral seta: a. *Anatrichus erinaceus*, state 0, present; b. *Dicraeus vagans*, state 1, absent.



(a)

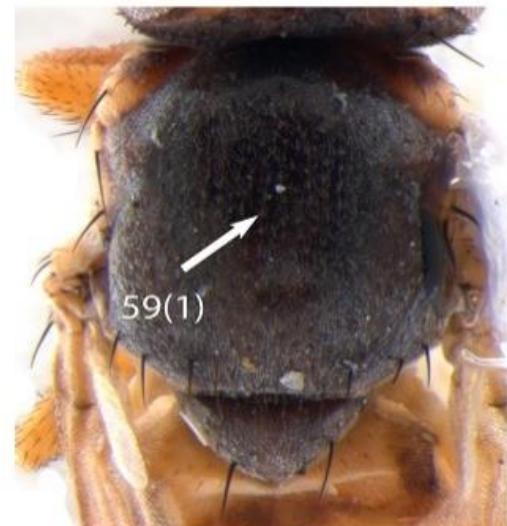


(b)

Figure 66a-b. Character 58, pruinosity all over the scutum: a. *Dicraeus vagans*, state 0, present; b. *Calamoncosis minima*, state 1, absent.

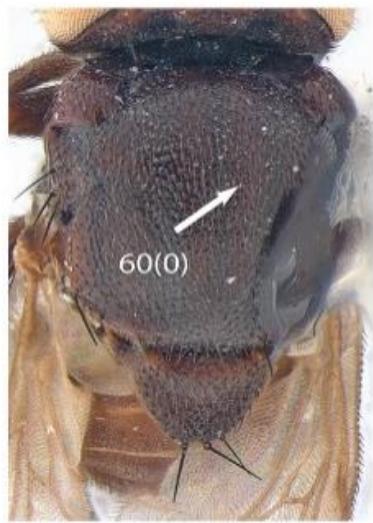


(a)



(b)

Figure 67a-b. Character 59, color of pruinosity on scutum: a. *Apallates dissidens*, state 0, dark brown or black; b. *Dicraeus vagans*, state 1, yellow or whitish.

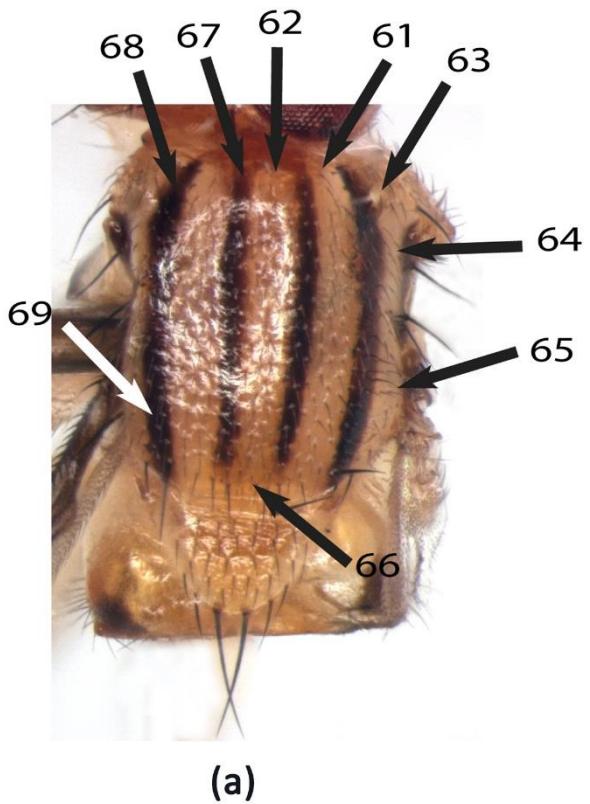


(a)

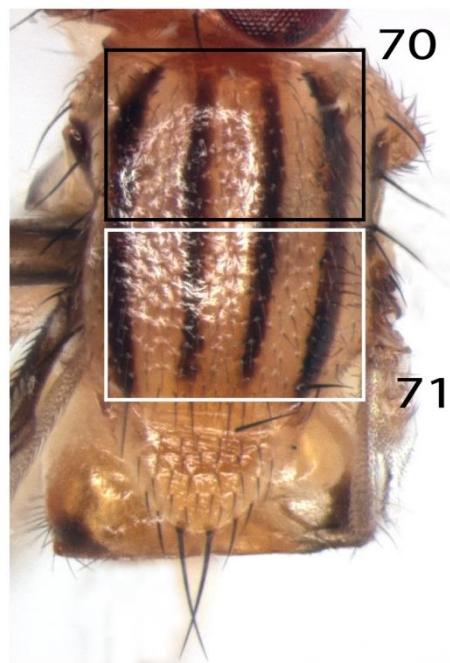


(b)

Figure 68a-b. Character 60, scutum: a. *Calamoncosis minima*, state 0, no longitudinal sulcus; b. *Tricimba lineella*, state 1, with 1-3 longitudinal sulcus.



(a)



(b)

Figure 69a-b. Characters 61-71, areas over the scutum: a,b. *Metasiphonella* sp., C61, area over dc; C62, area over ac; C63, lateral area, dorsal to margin on scutum; C64, lateral most area on scutum; C65, scutum dorsal to wing base; C66, scutum posterior end; C67, scutum area between ac and dc; C68, scutum area, external line to the dorso-lateral to dc; C69, scutum area, external line to the ventro-lateral to dc; C70, scutum anterior half; C71, scutum area posterior half.

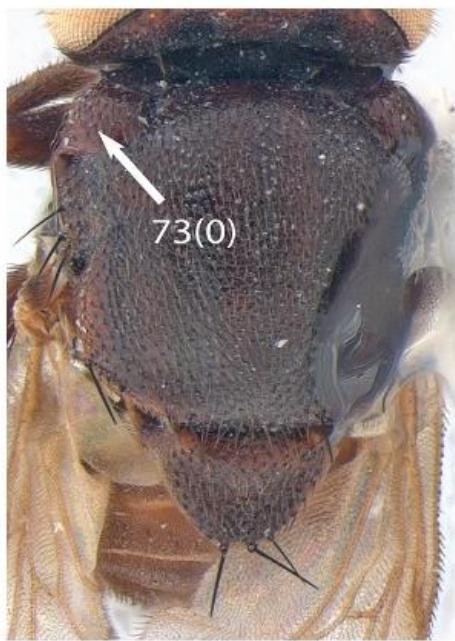


(a)



(b)

Figure 70a-b. Character 72, propleuron: a. *Tricimba lineella*, state 0, well developed; b. *Calamoncosis minima*, state 1, weakly developed.



(a)



(b)

Figure 71a-b. Character 73, postpronotal seta: a. *Calamoncosis minima*, state 0, zero or one; b. *Siphonellopsis lacteibasis*, state 1, two or more.

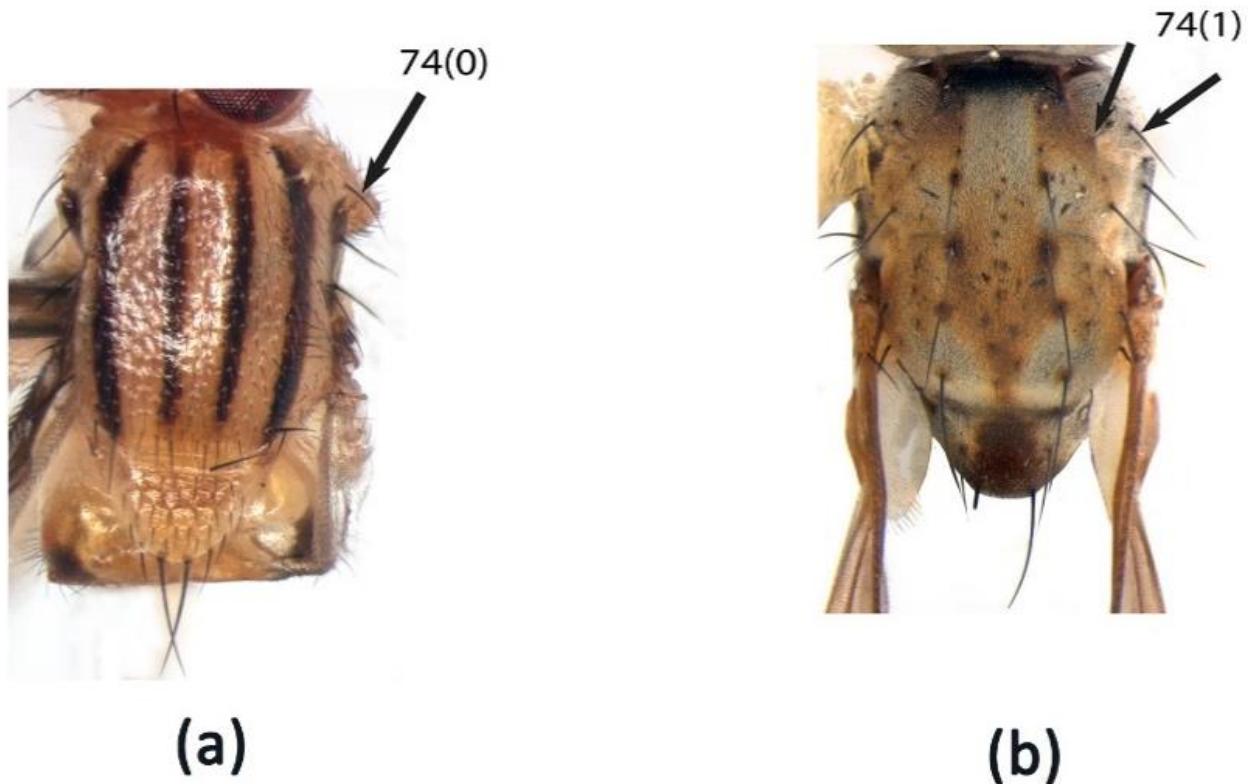
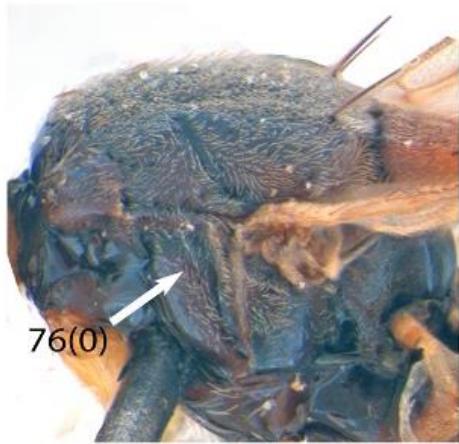


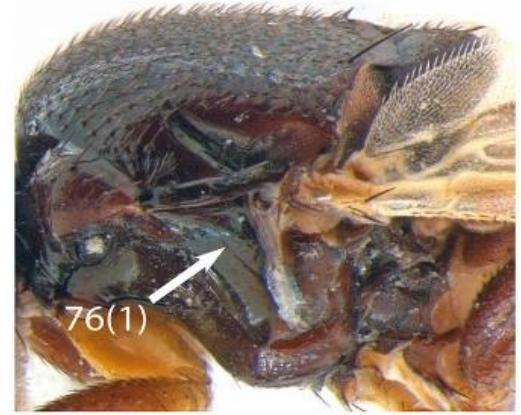
Figure 72a-b. Character 74, postpronotal seta orientation, in case of 2 or more setae: a. *Metasiphonella* sp., state 0, only laterocinate; b. *Siphonellopsis lacteibasis*, state 1, reclinate and laterocinate.



Figure 73a-b. Character 75, postpronotal lobe: a. *Dicraeus vagans*, state 0, mostly yellow; b. *Disciphus peregrinus*, state 1, mostly brown or black.



(a)



(b)

Figure 74a-b. Character 76, anepisternum: a. *Disciphus peregrinus*, state 0, purinosity; b. *Epimadiza* sp., state 1, bare.

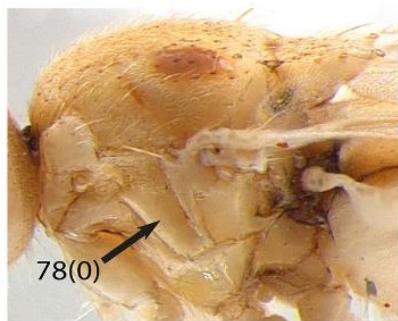


(a)



(b)

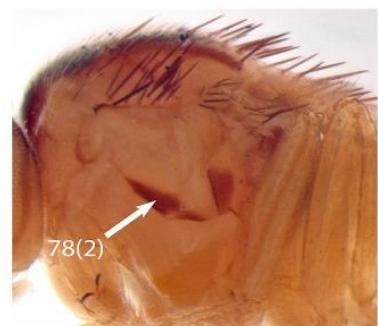
Figure 75a-b. Character 77, anepisternum setaceous: a. *Meoneura flavifacies*, state 0, present; b. *Epimadiza* sp., state 1, absent.



(a)



(b)



(c)

Figure 76a-c. Character 78, anepisternum color: a. *Elachiptera bimaculata*, state 0, entirely yellow(ish); b. *Epimadiza* sp., state 1, entirely brown or black; c. *Eugaurax* sp., state 2, mostly yellow with brown marketing ventrally.



(a)



(b)



(c)

Figure 77a-c. Character 79, katepisternum color: a. *Eugaurax* sp., state 0, entirely yellow(ish); b. *Disciphus peregrinus*, state 1, entirely brown or black; c. *Paracalamoncosis brasiliensis* (Photography by Paula Raile Riccardi), state 2, mostly yellow with brown marketing.

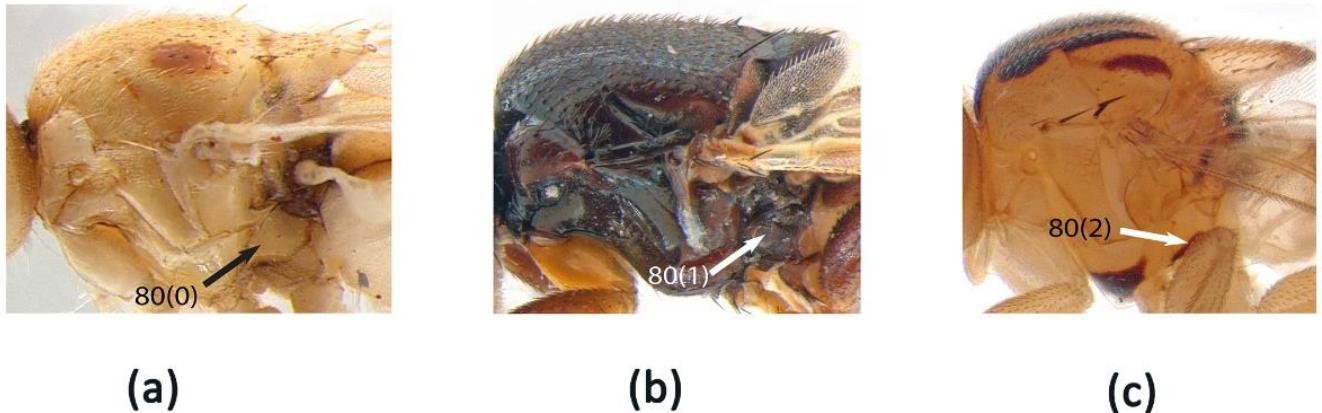


Figure 78a-c. Character 80, meron color: a. *Elachiptera bimaculata*, state 0, yellow or light brown; b. *Epimadiza* sp., state 1, brown or black; c. *Paracalamoncosis brasiliensis* (Photography by Paula Raile Riccardi), state 2, yellow(ish), dark marketing.

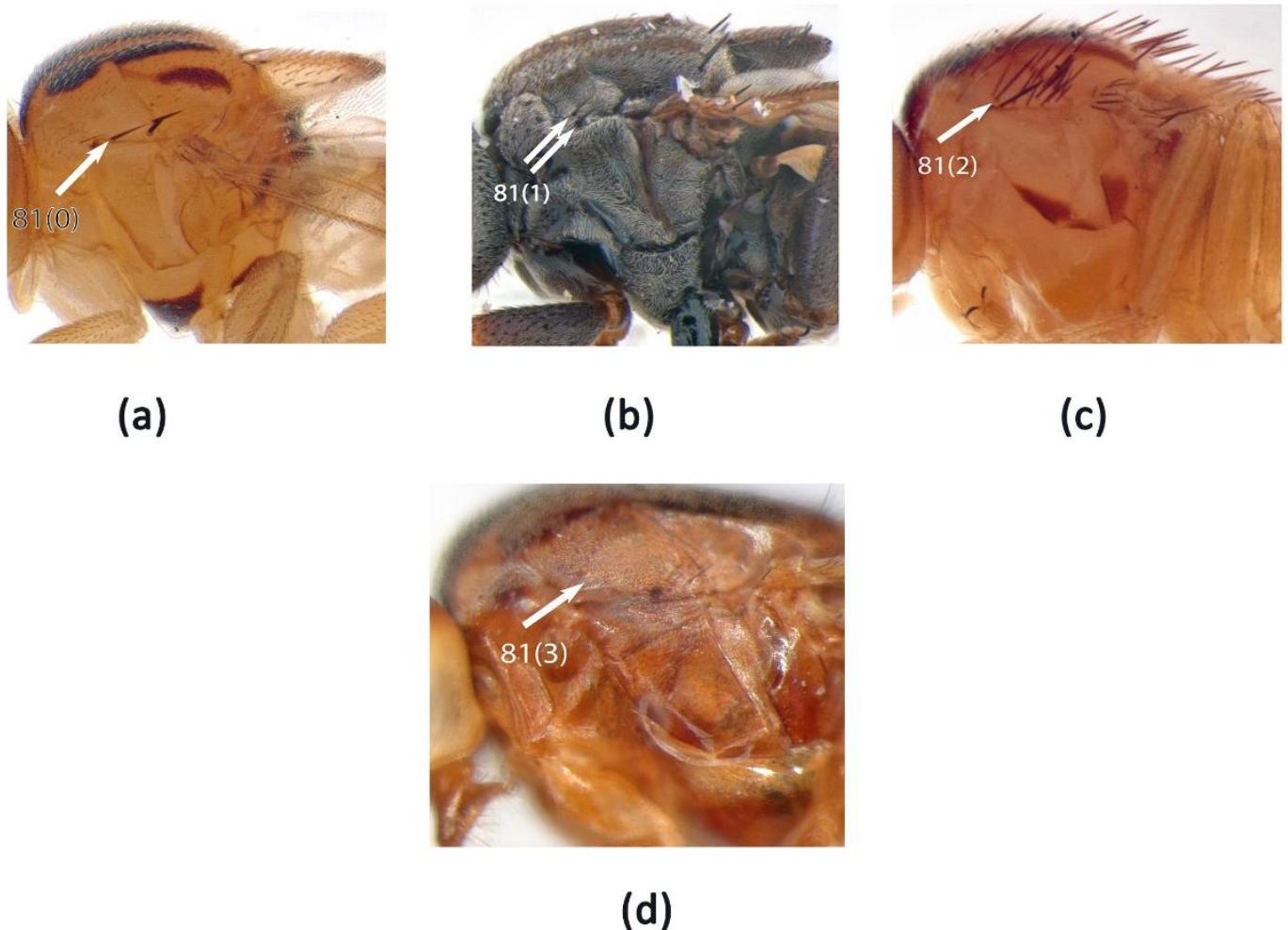


Figure 79a-d. Character 81, number of distinct anterior notopleural setae: a. *Paracalamoncosis brasiliensis* (Photography by Paula Raile Riccardi), state 0, one; b. *Aphanotrigonum trilineatus*, state 1, two; c. *Eugaurax* sp., state 2, more; d. *Ectecephala albistylum* (Photography by Paula Raile Riccardi), state 3, zero.

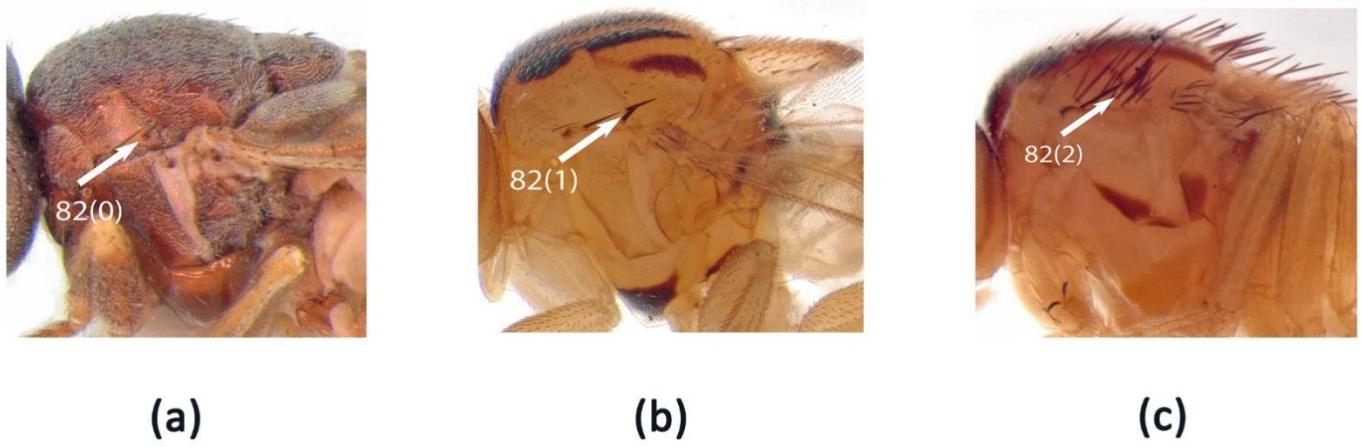


Figure 80a-c. Character 82, number of distinct posterior notopleural setae: a. *Microcercis albipalpis*, state 0, one; b. *Paracalamoncosis brasiliensis* (Photography by Paula Raile Riccardi), state 1, two; c. *Eugaurax* sp., state 2, more.



Figure 81a–b. Character 83, purinosity on postpronotal lobe: a. *Disciphus peregrinus*, state 0, present; b. *Epimadiza* sp., state 1, absent.

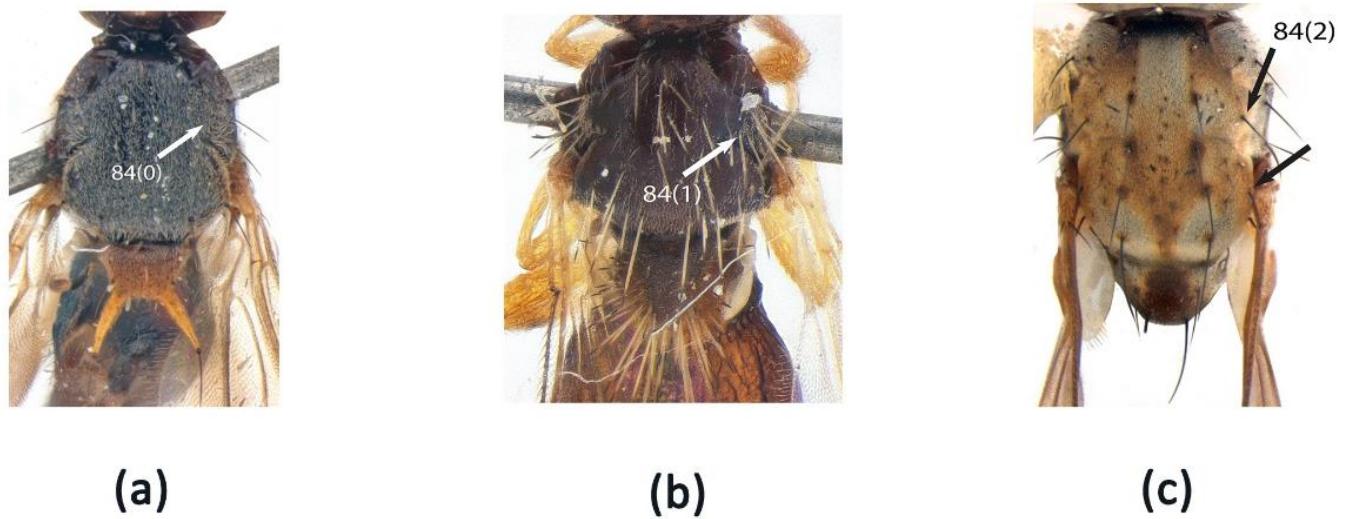


Figure 82a-c. Character 84, numbers of supraalars: a. *Disciphus peregrinus*, state 0, zero; b. *Anatrichus erinaceus*, state 1, one; c. *Siphonellopsis lacteibasis*, state 2, two.

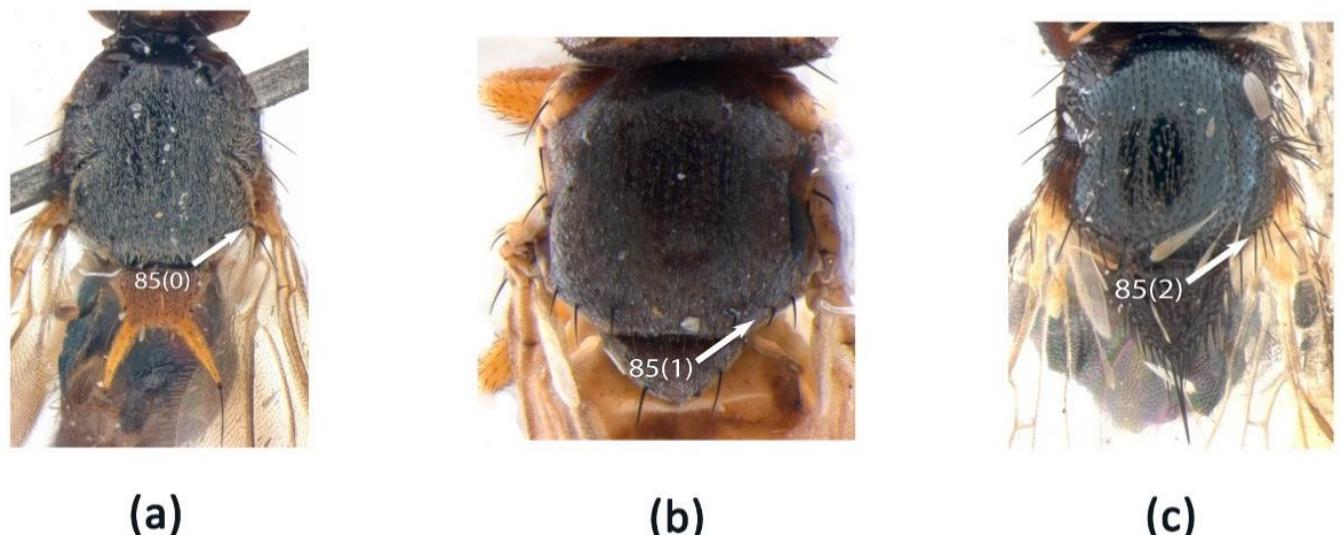
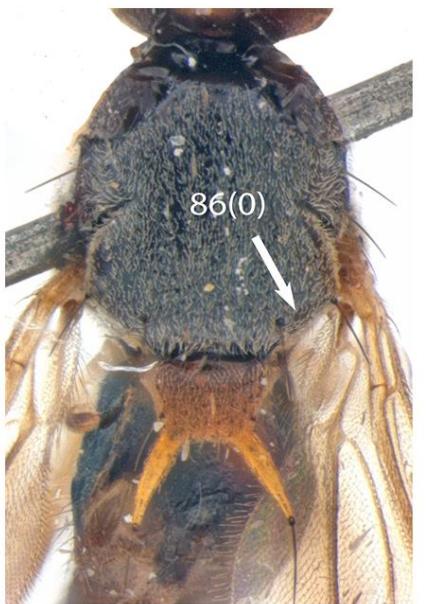
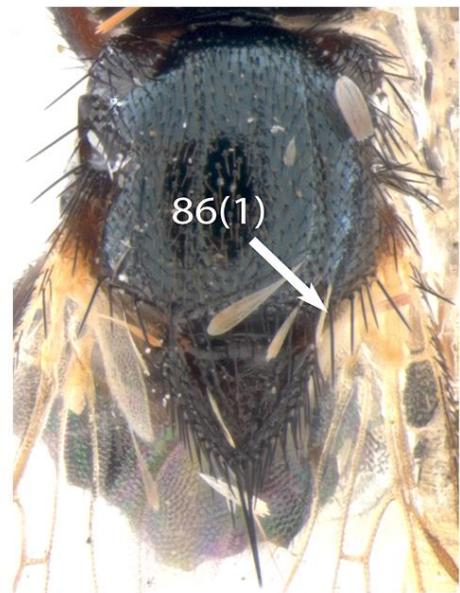


Figure 83a-c. Character 85, numbers of postalars: a. *Disciphus peregrinus*, state 0, one; b. *Dicraeus vagans*, state 1, two; c. *Chaetochlorops inquilina*, state 2, more.



(a)



(b)

Figure 84a-b. Character 86, intrapostalar: a. *Disciphus peregrinus*, state 0, absent; b. *Chaetochlorops inquilina*, state 1, present.



(a)



(b)



(c)

Figure 85a-c. Character 87, length of scutellum: a. *Paracalamoncosis brasiliensis* (Photography by Paula Raile Riccardi), state 0, longer than wide; b. *Calamoncosis minima*, state 1, wider than long; c. *Elachiptera brevipennis*, state 2, almost as long as wide.



(a)

(b)

Figure 86a-b. Character 88, tip of scutellum in dorsal view: a. *Apallates dissidens*, state 0, apically rounded or slightly pointed; b. *Disciphus peregrinus*, state 1, apically straight (flattened).



(a)

(b)

Figure 87a-b. Character 89, laterals of scutellum in dorsal view: a. *Elachiptera brevipennis*, state 0, convex; b. *Disciphus peregrinus*, state 1, straight.

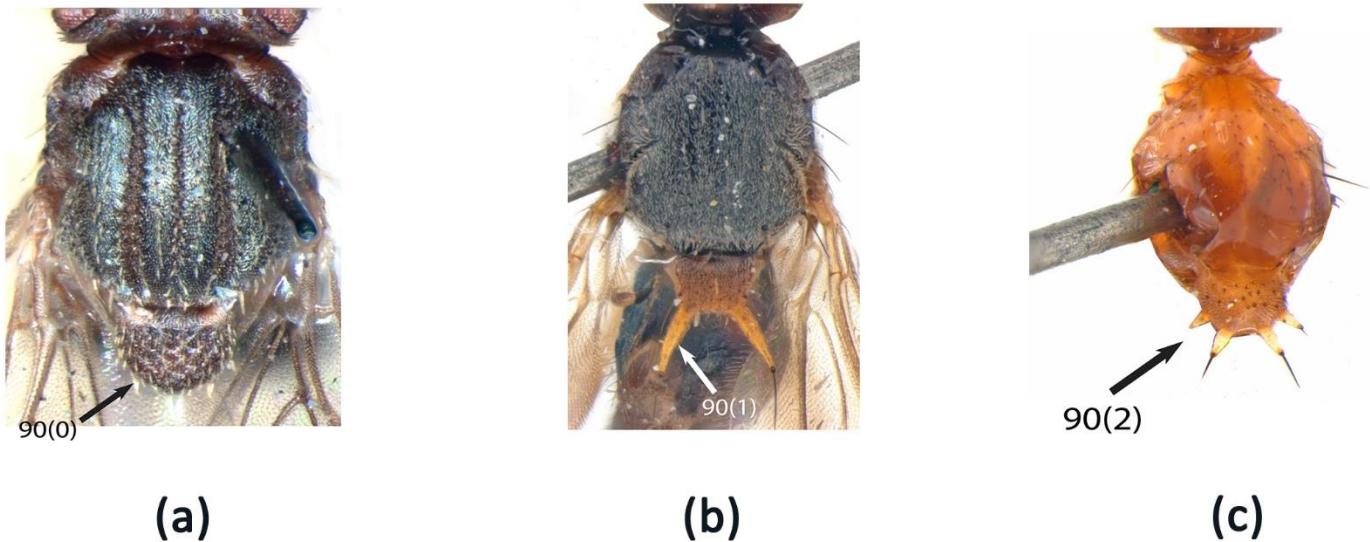


Figure 88a-c. Character 90, scutellar finger-like tubercles: a. *Tricimba lineella*, state 0, absent; b. *Disciphus peregrinus*, state 1, present, only apicals; c. *Sepsidoscinis maculipennis*, state 2, present, apicals and subapicals.

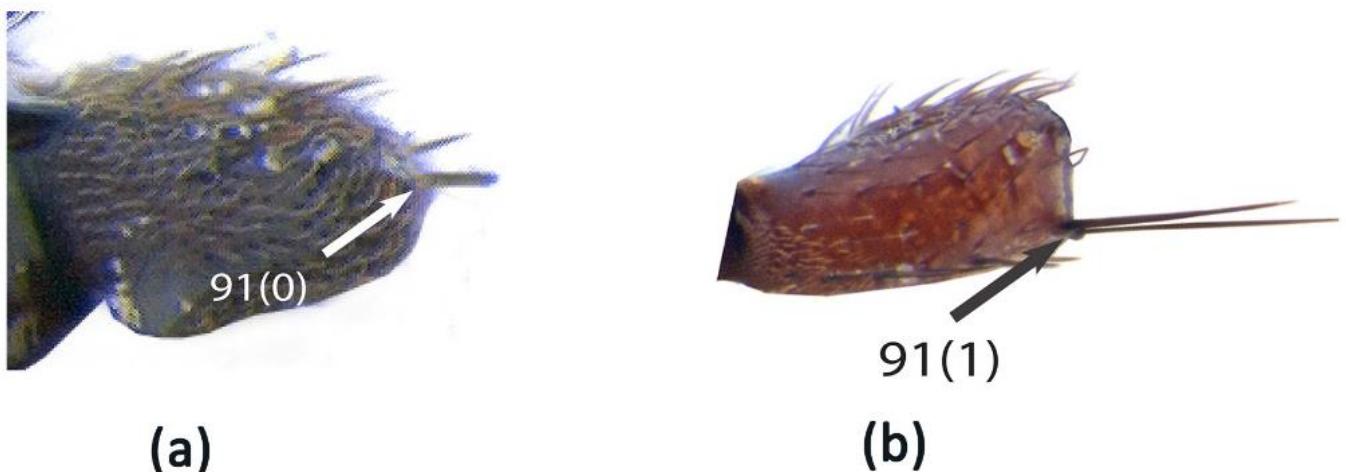


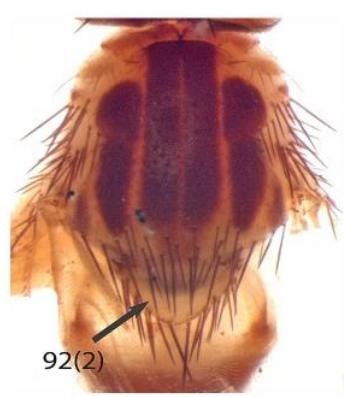
Figure 89a-b. Character 91, scutellar large setae position: a. *Hapleginella laevifrons*, state 0, marginal; b. *Heteroscinis hystrix*, state 1, ventral.



(a)



(b)



(c)



(d)

Figure 90a-d. Character 92, scutellum color: a. *Dicraeus vagans*, state 0, entirely dark brown or black; b. *Elachiptera bimaculata*, state 1, entirely yellow or light brown; c. *Eugaurax* sp., state 2, apically and laterally yellow or brown; d. *Calamoncosis minima*, state 5, basally yellow or brown.

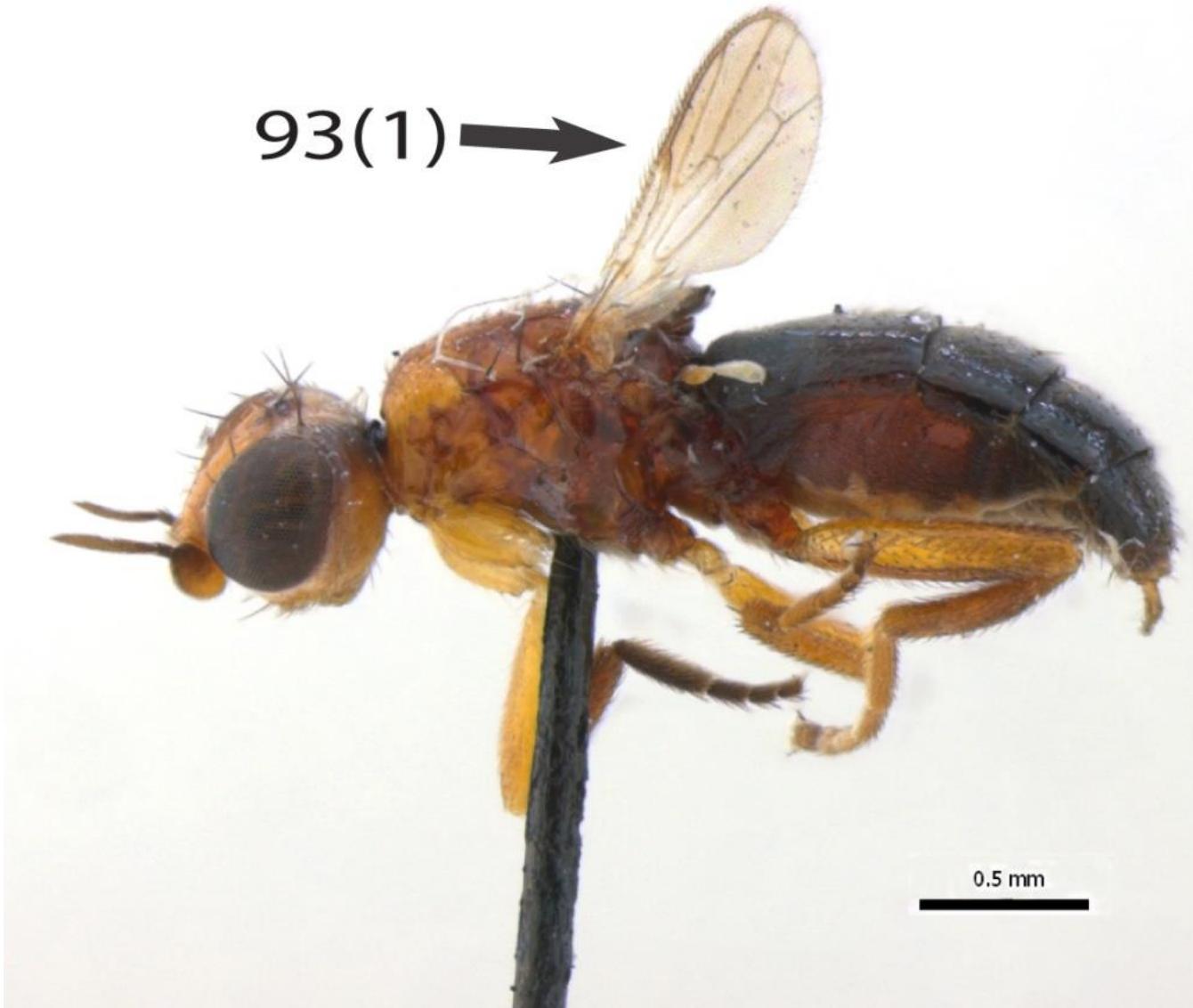


Figure 91: Character 93, wing length compared to abdomen length: *Elachiptera brevipennis*, state 1, shorter.

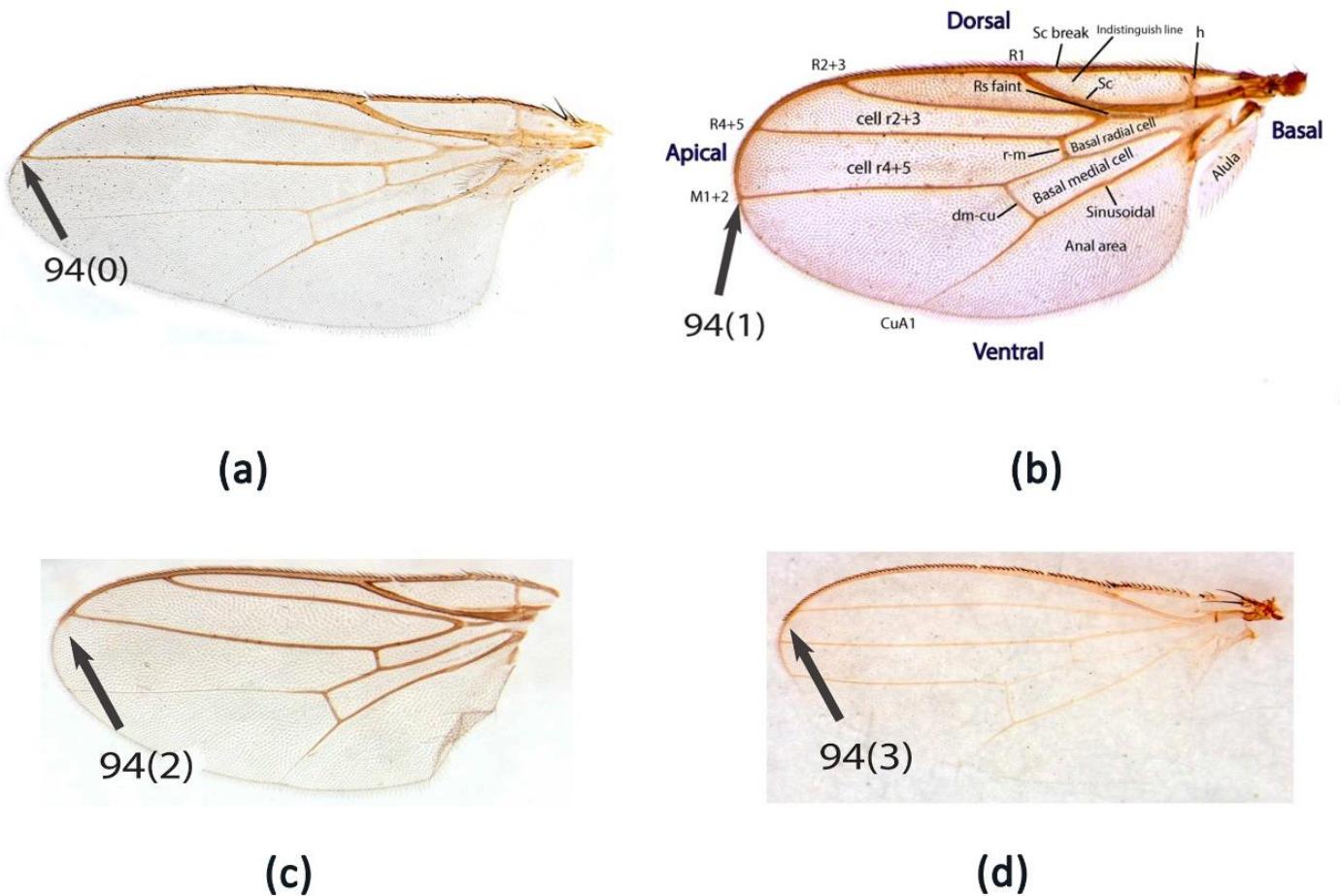


Figure 92a-d. Character 94, costal: a. *Chlorops pumilionis* (Photography by Paula Raile Riccardi), state 0, ending at R₄₊₅; b. *Siphonella oscinina* (with areas of the wing), state 1, ending at M₁₊₂; c. *Hapleginella laevifrons*, state 2, ending between R₄₊₅ and M₁₊₂; d. *Heteroscinis hystrix*, state 3, ending before R₄₊₅.

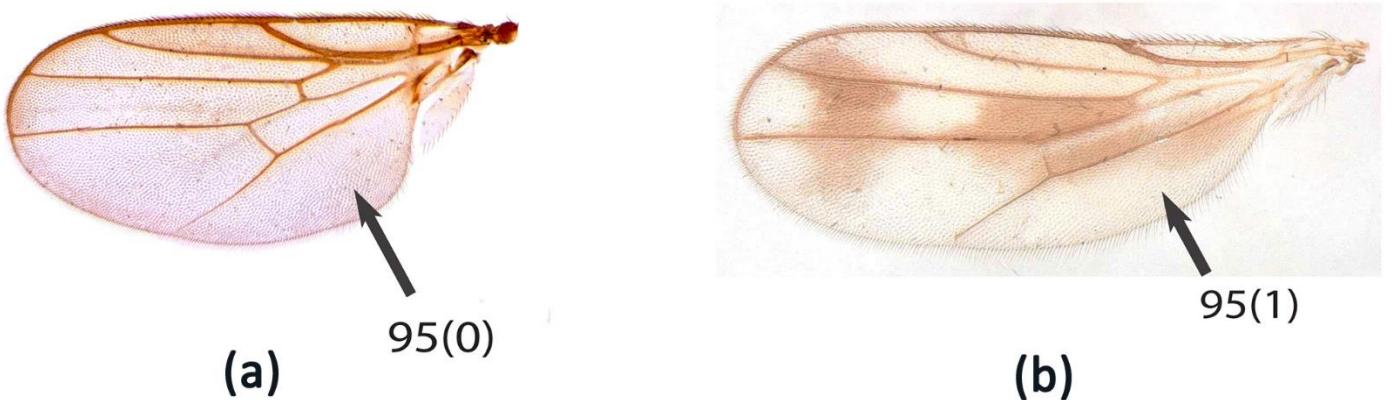


Figure 93a-b. Character 95, anal lobe: a. *Siphonella oscinina*, state 0, present; b. *Disciphushystrinus*, state 1, absent.

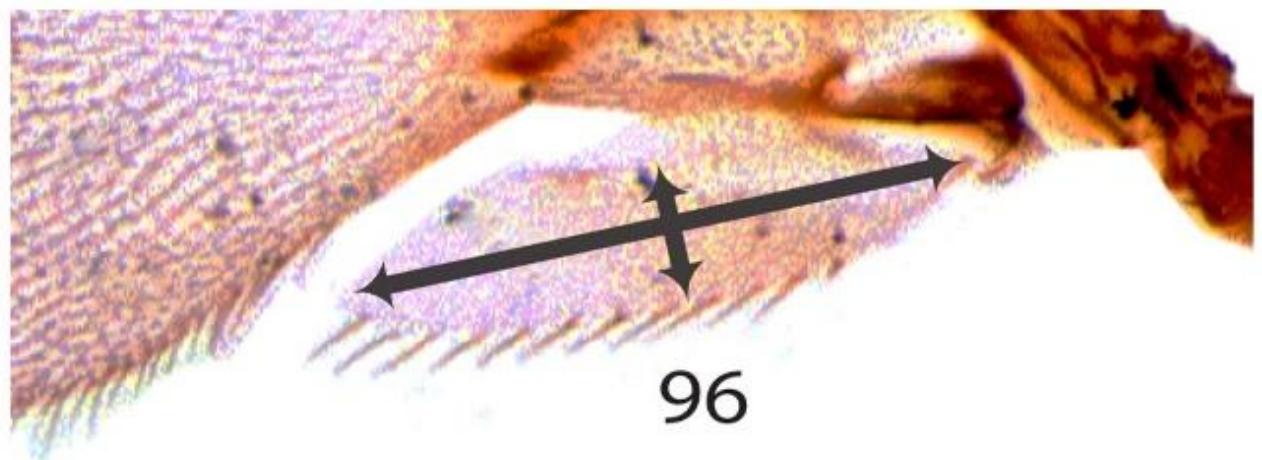


Figure 94: Character 96, alula (length/width): *Siphonella oscinina*.

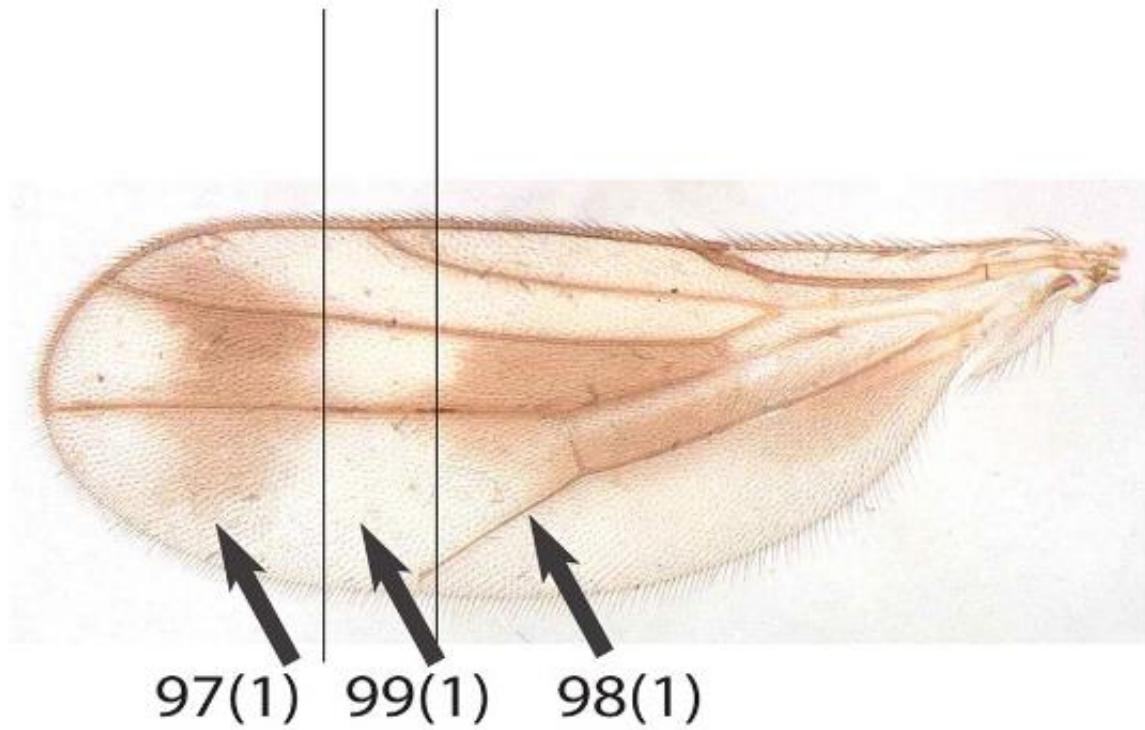


Figure 95: Characters 97-98; C97, pattern on the wing, apically; C98, pattern on the wing, basally; C99, pattern on the wing, medially: *Disciphus peregrinus*, C97, state 1, marked; C98, state 1, marked; C99, state 1, marked.

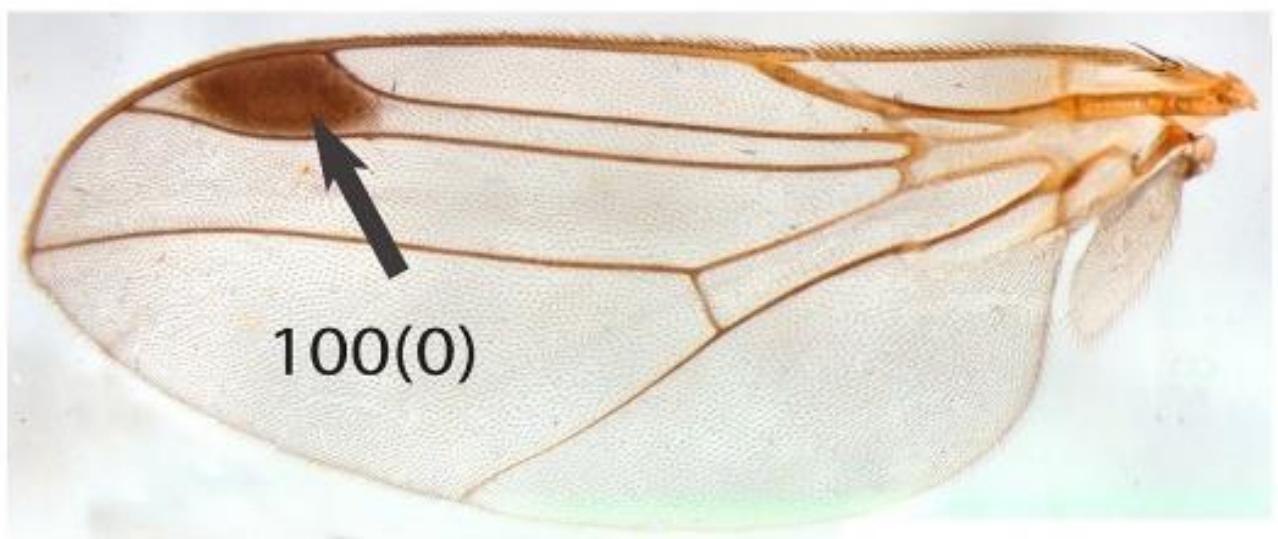


Figure 96: Character 100, shape of pattern on the wing: *Daltastoma unipunctatum*, state 0, restricted between veins.



Figure 97a-b. Character 101, basal radial cell relating to the basal medial cell: a. *Notaulacella* sp., state 0, reaches before medium of basal medial cell; b. *Siphonella oscinina*, state 1, at least at the medium of basal medial cell.

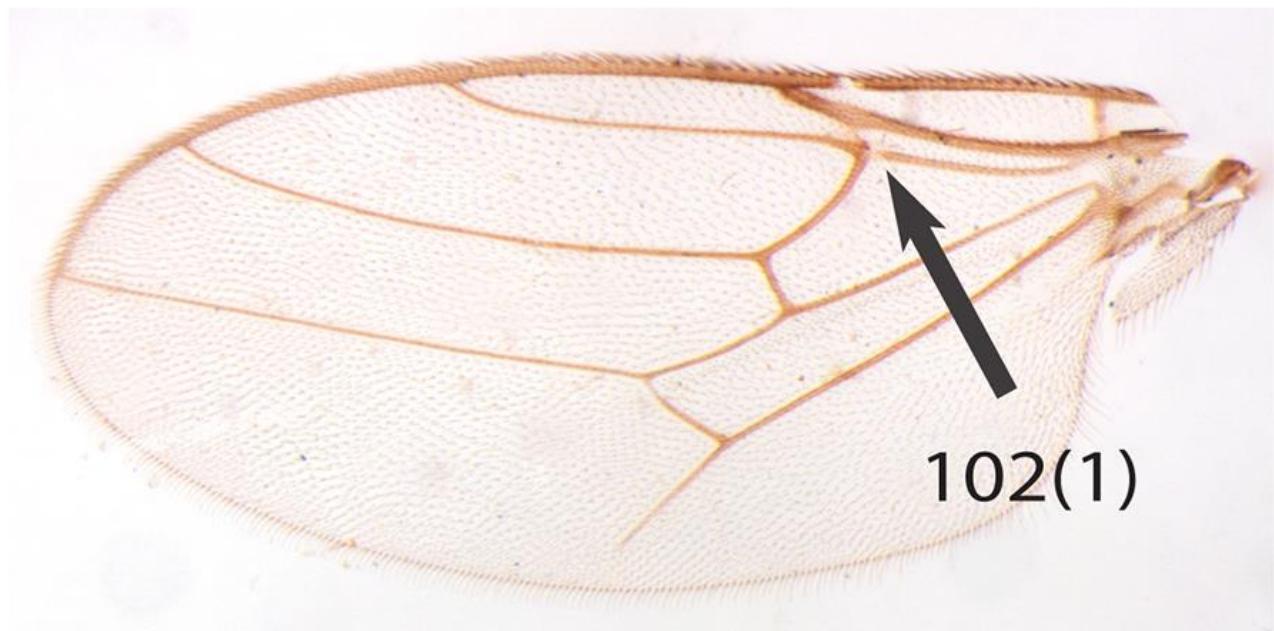
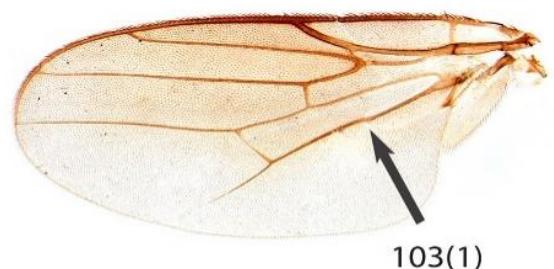


Figure 98: Character 102, height of basal radial cell: *Loxobathmis obliquans*, state 1, projecting dorsally.

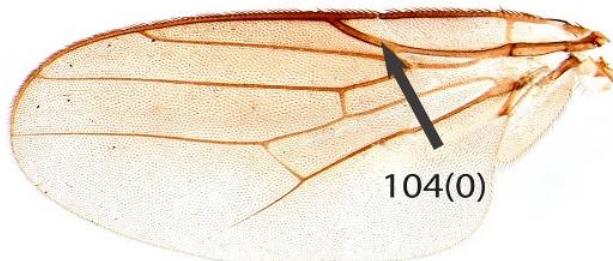


(a)

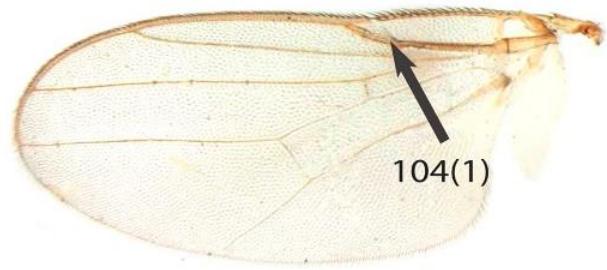


(b)

Figure 99a-b. Character 103, sinusoidal of CuA1 (flexure part): a. *Loxobathmis obliquans*, state 0, absent (straight or slightly inward); b. *Lasimambia palposa*, state 1, present (notably inward).

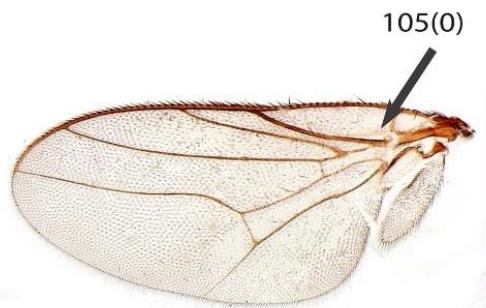


(a)

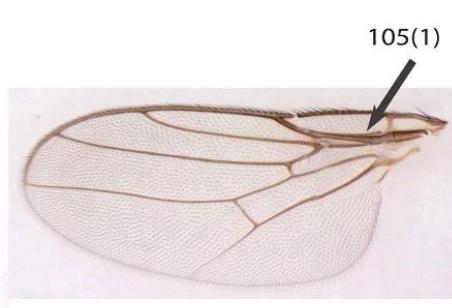


(b)

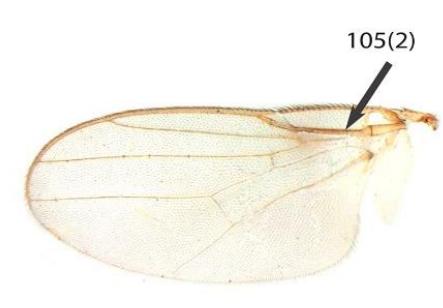
Figure 100a-b. Character 104, R₁: a. *Lasiambia palposa*, state 0, slightly distally; b. *Hippelates plebejus*, state 1, with a short bump.



(a)

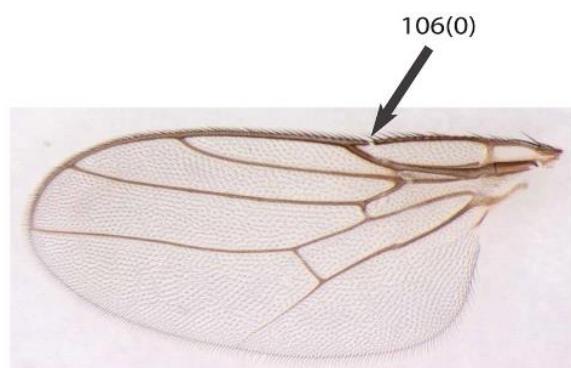


(b)

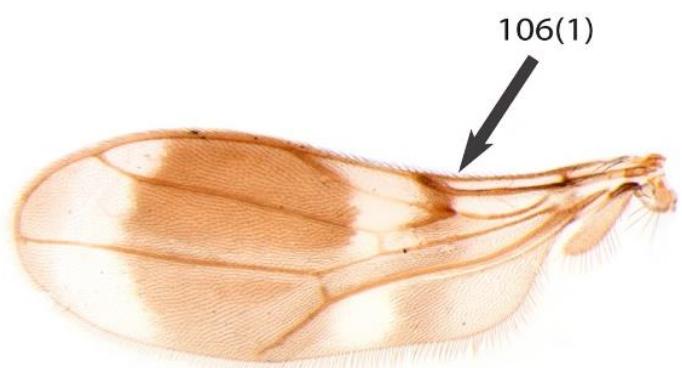


(c)

Figure 101a-c. Character 105, Sc: a. *Rhodesiella* sp.2, state 0, almost entirely independent from R₁; b. *Metasiphonella* sp., state 1, distinct from R₁ basally; c. *Hippelates plebejus*, state 2, entirely indistinctive.



(a)



(b)

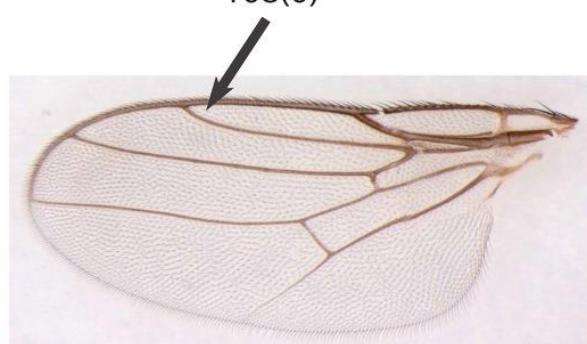
Figure 102a-b. Character 106, costal break on Sc part: a. *Metasiphonella* sp., state 0, present; b. *Sepsidoscinius maculipennis*, state 1, absent.

107(0)



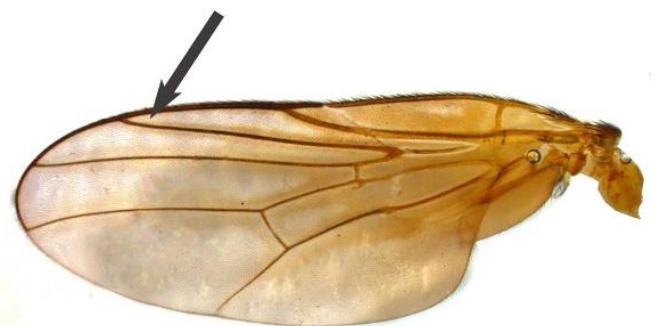
Figure 103: Character 107, costal break on humeral part of wing: *Madiza glabra*, state 0, present.

108(0)



(a)

108(1)



(b)

Figure 104a-b. Character 108, shape of anterior end of R_{2+3} : a. *Metasiphonella* sp., state 0, curved to the C; b. *Batrachomyia nigritarsis*, state 1, about straight to the C.

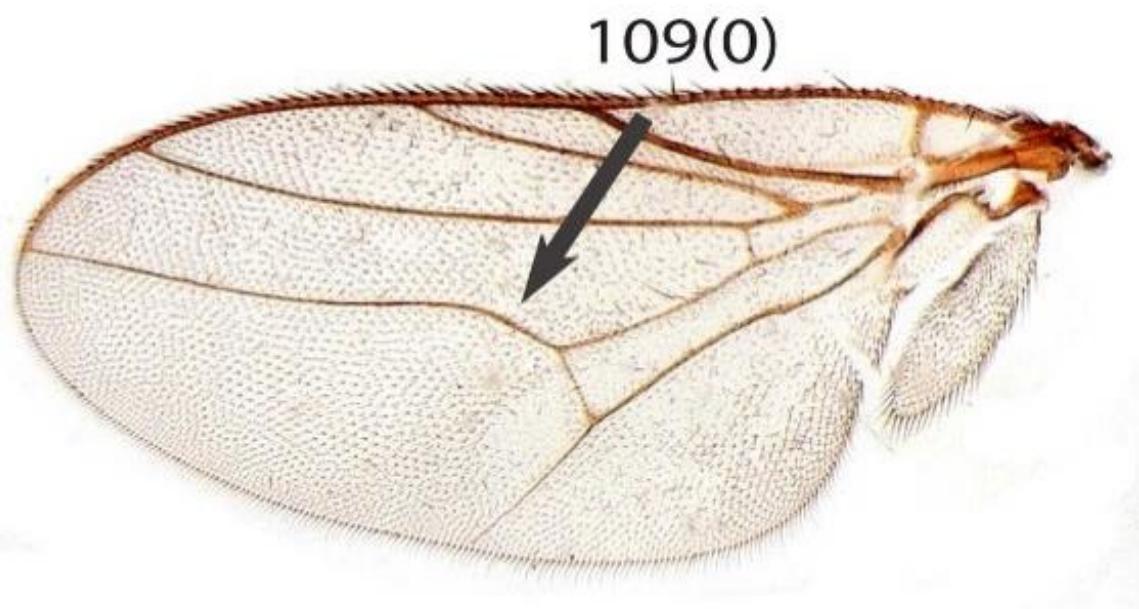


Figure 105: Character 109, shape of basal half of M_{1+2} : *Rhodesiella* sp.2, state 0, convex anteriorly.

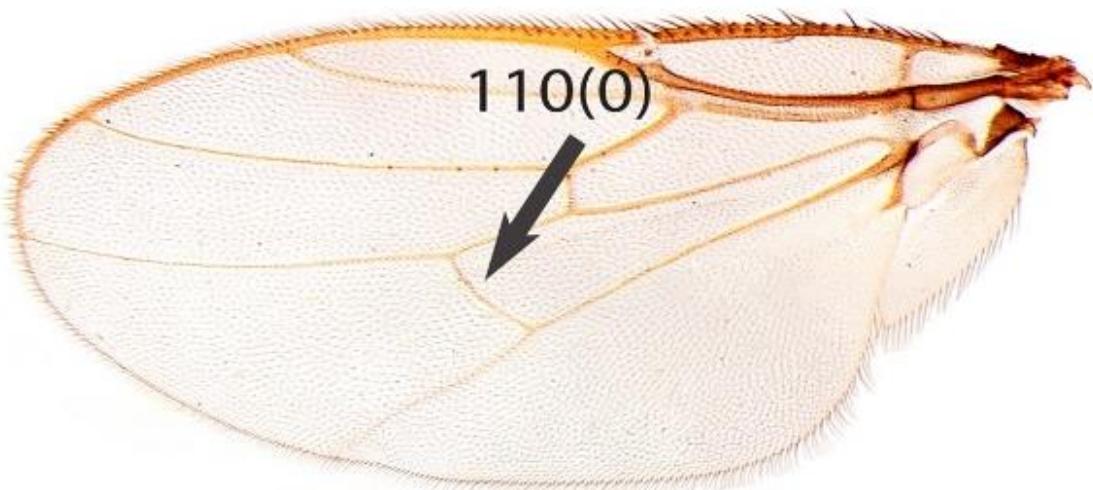


Figure 106: Character 110, shape of dm-cu: *Polyodaspis ruficornis*, state 0, convex.



Figure 107a-b. Character 111, position of dm-cu in relation to CuA_1 : a. *Lasiambia palposa*, state 0, more than 100° ; b. *Rhodesiella* sp.2, state 1, about 90° or less.

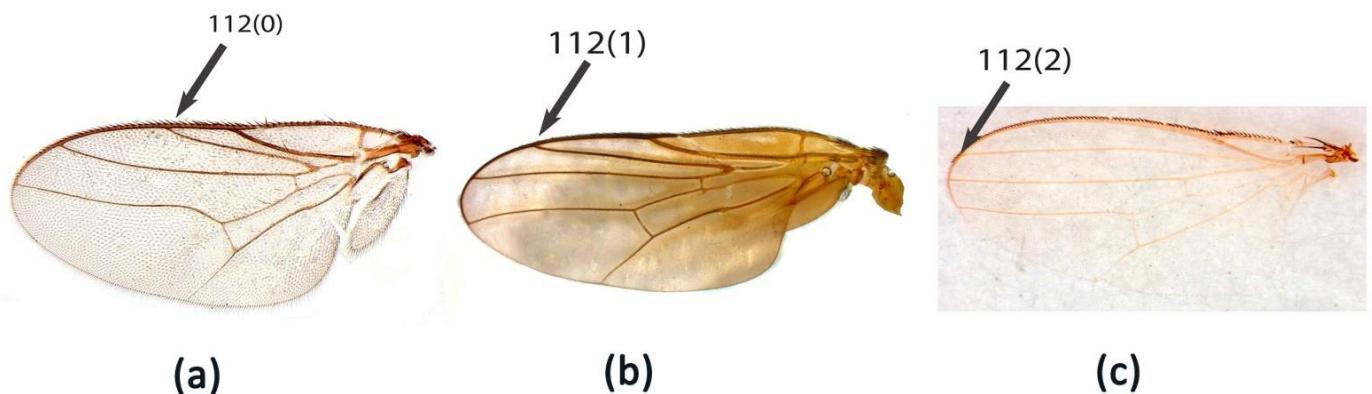


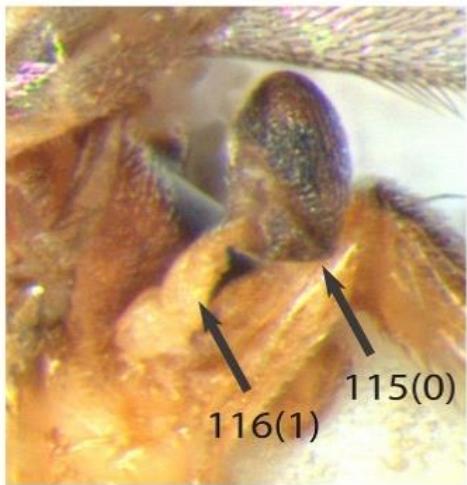
Figure 108a-c. Character 112, C2: a. *Rhodesiella* sp.2, state 0, at most reaches to the middle of the wing; b. *Batrachomyia nigritarsis*, state 1, between middle and tip of the wing; c. *Madiza glabra*, state 2, at the tip of the wing.



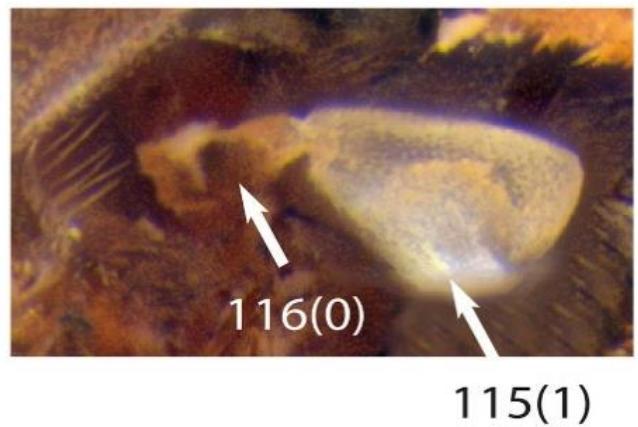
Figure 109a-b. Character 113, C4: a. *Thaumatomyia gemina*, state 0, ending below of apical margin of the wing; b. *Metasiphonella* sp., state 1, ending at the apical margin of the wing.



Figure 110a-b. Character 114, M_{1+2} thickness: a. *Metasiphonella* sp., state 0, as thick as R_{4+5} ; b. *Thaumatomyia gemina*, state 1, thinner than R_{4+5} .

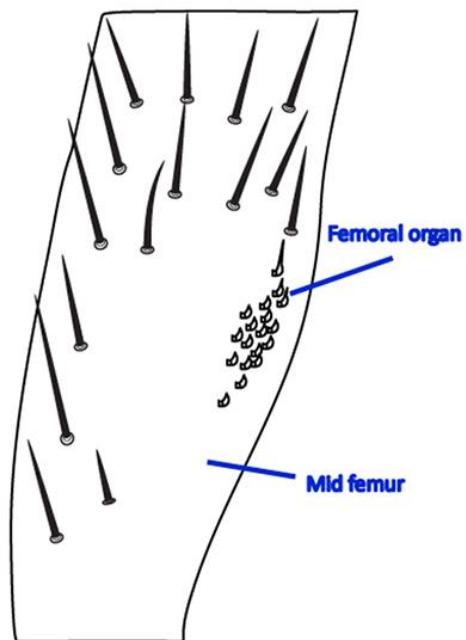


(a)



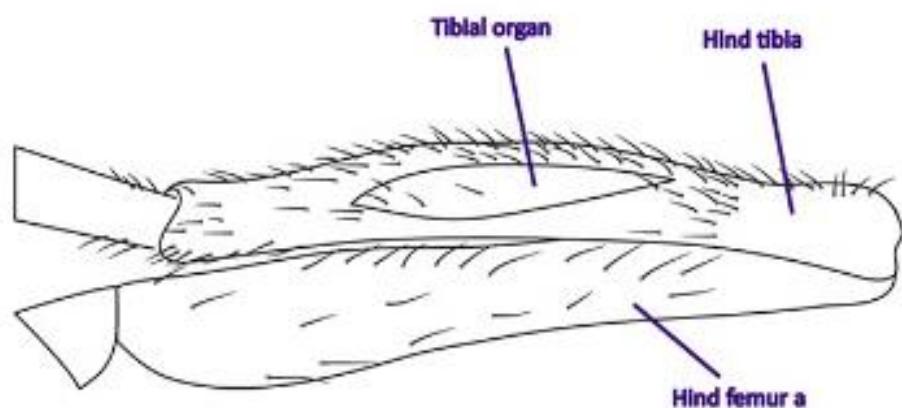
(b)

Figure 111a-b. Character 115-116; C115, halter color (knob); C116, halter color (stem): a. *Pseudogaurax anchora*, C115, state 0, black or dark brown; C116, state 1, yellow-ish or light brown; b. *Heteroscinis hystrix*, C115, state 1, yellow-ish or light brown; C116, state 0, black or dark brown.



117

Figure 112: Character 117, male mid femoral organ: Schematic shape.



118

Figure 113: Character 118, tibial organ: Schematic shape.

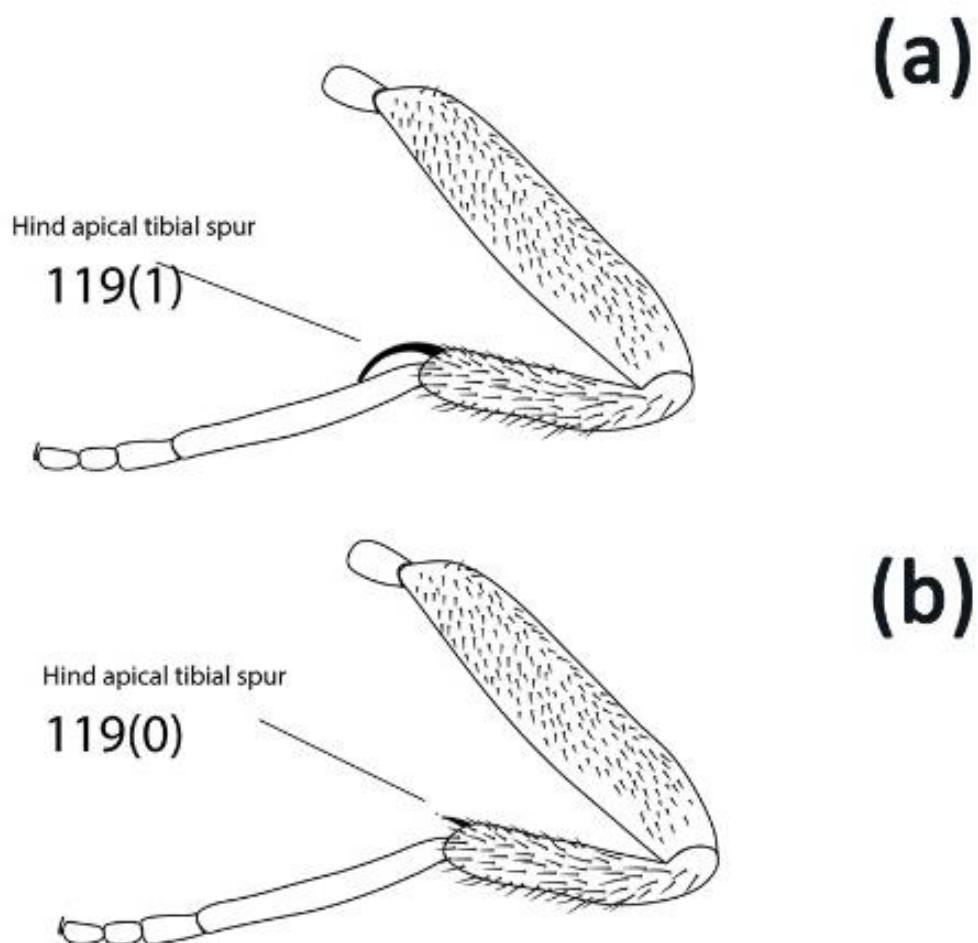


Figure 114a-b. Character 119, hind tibial spur: Schematic shape, a. state 1, clearly longer; b. state 0, shorter or slightly longer than hind tibia diameter.

126(1)



Figure 115: Character 126, abdominal tergites: *Anatrichus erinaceus*, state 1, syntergites 1+2 expanded comparing with other tergites.

127(2)

127(1)



(a)



(b)

Figure 116a-b. Character 127, sclerotization of tergite: a. *Elachiptera brevipennis*, state 1, syntergites 1+2 firmly sclerotized; b. *Anatrichus erinaceus*, state 2, syntergites 1+2 and tergite 3 firmly sclerotized.

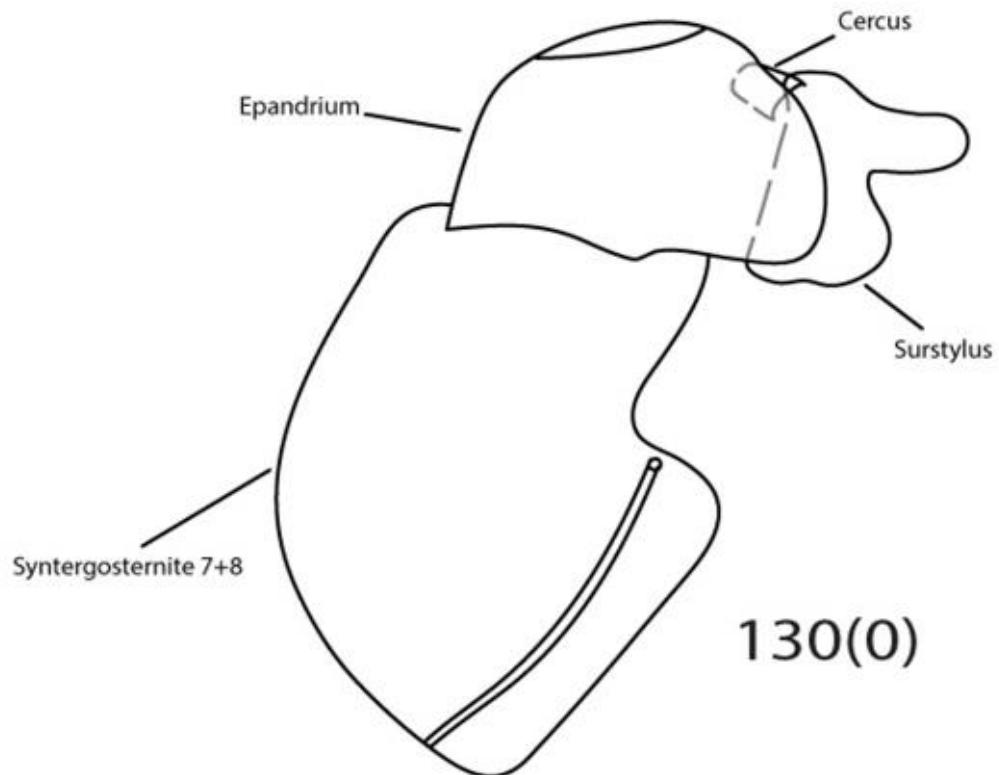


Figure 117: Character 130, syntergosternite 7+8: *Dicraeus vagans*, state 0, broad.

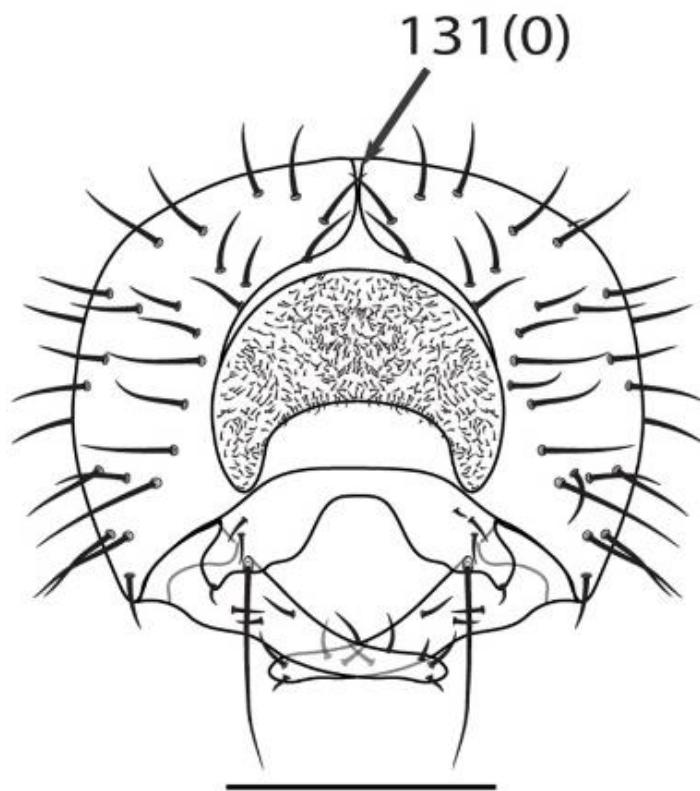
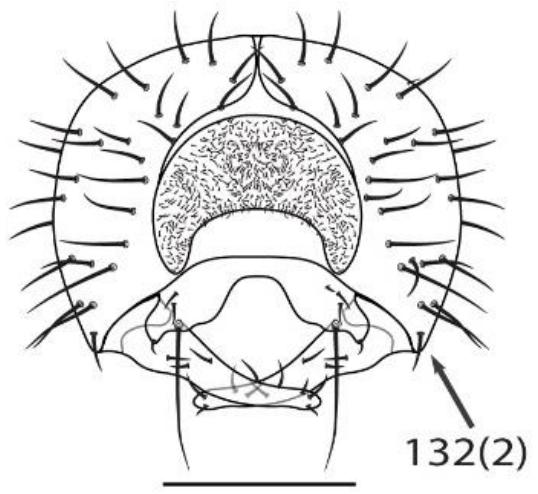


Figure 118: Character 131, epandrium medial line (dorsal sulcus): *Elachiptera brevipennis*, state 0, present.

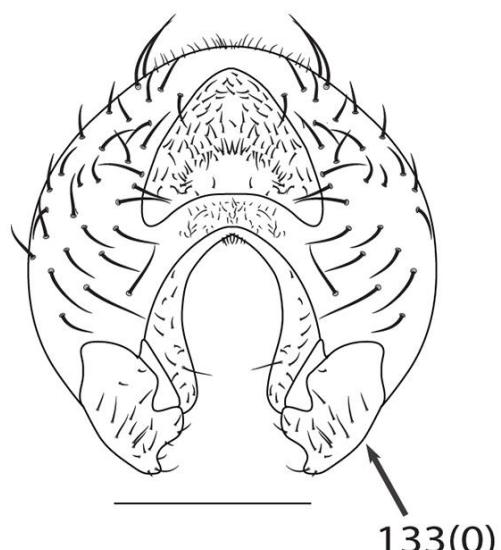


(a)

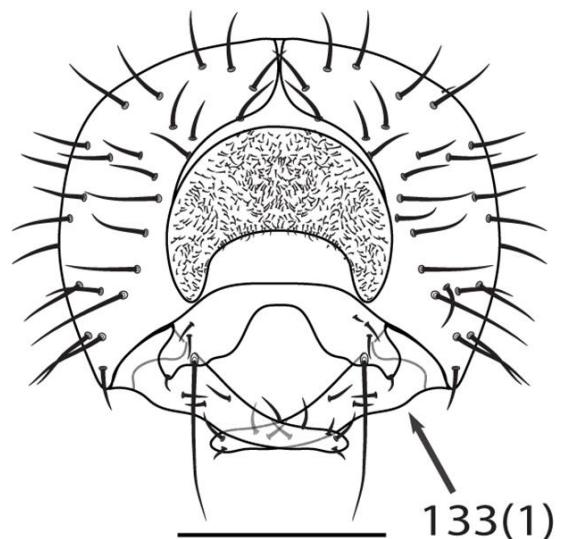


(b)

Figure 119a-b. Character 132, antero-ventral corner of epandrium in posterior view: a. *Apotropina* sp. nov., state 1, with a long projection; b. *Elachiptera brevipennis*, state 2, absent.



(a)



(b)

Figure 120a-b. Character 133, size of surstyli (comparing with the size of epandrium): a. *Apallates dissidens*, state 0, short; b. *Elachiptera brevipennis*, state 1, long.

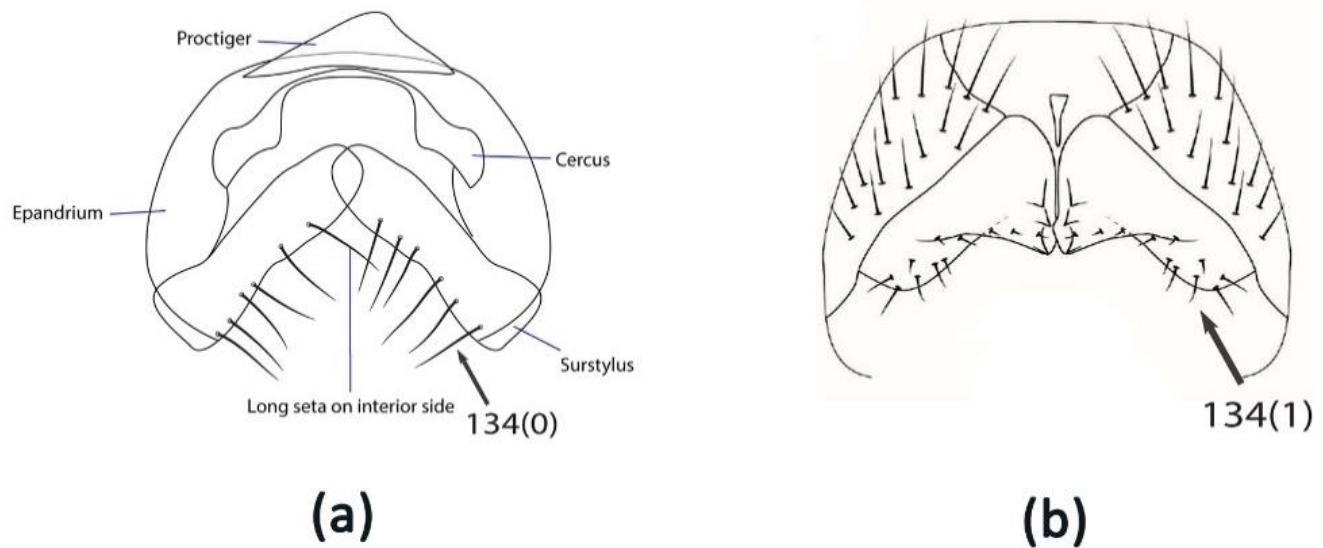


Figure 121a-b. Character 134, elongated setae at the edge of anterior lateral margins of surstylus:
a. *Disciphus peregrinus*, state 0, present; b. *Thaumatomyia gemina* (Riccardi 2016, modified), state 1, absent.

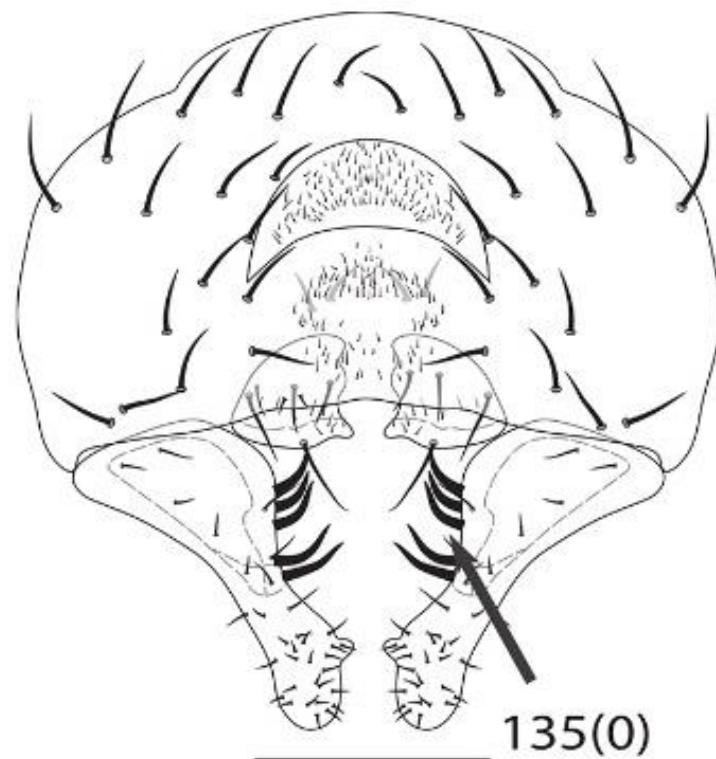
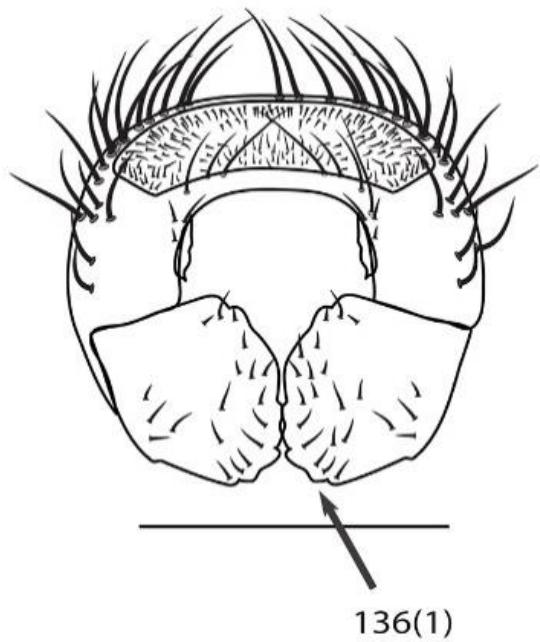
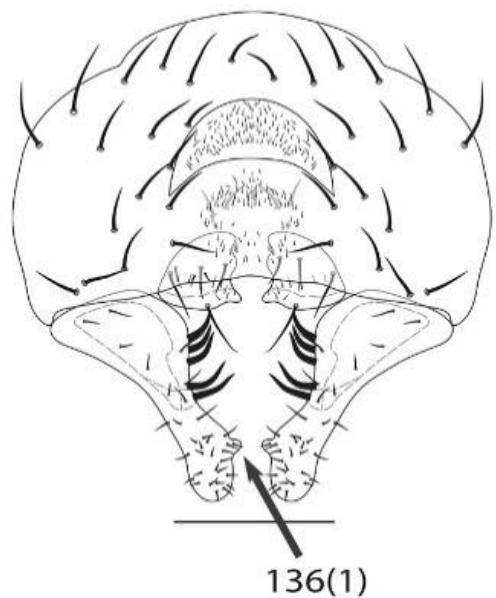


Figure 122: Character 135, elongated setae at lateral margins of surstylus modified to spines:
Dicraeus vagans, state 0, present.



(a)

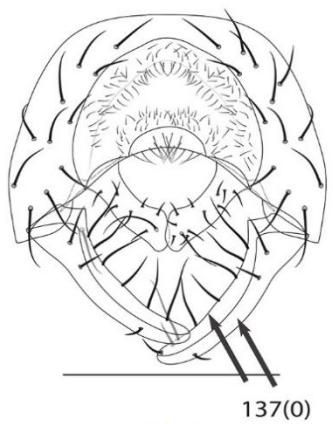


(b)

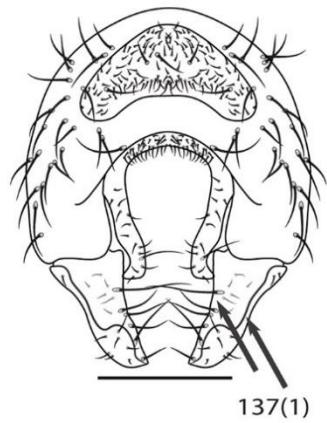
Figure 123a-b. Character 136, marginals of surstyli in posterior view: a. *Biorbitella hesperia*, state 1, indented; b. *Dicraeus vagans*, state 1.



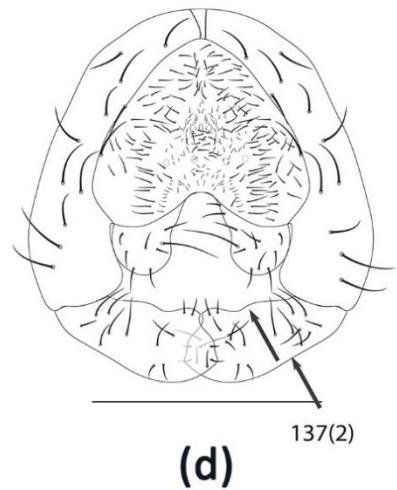
(a)



(b)



(c)



(d)

Figure 124a-d. Character 137, anterior and posterior lateral margins of surstyli: a. *Calamoncosis minima*, state 0, parallel; b. *Conioscinella solute*, state 0; c. *Hippelates plebejus*, state 1, convergent; d. *Microcercis albipalpis*, state 2, divergent.

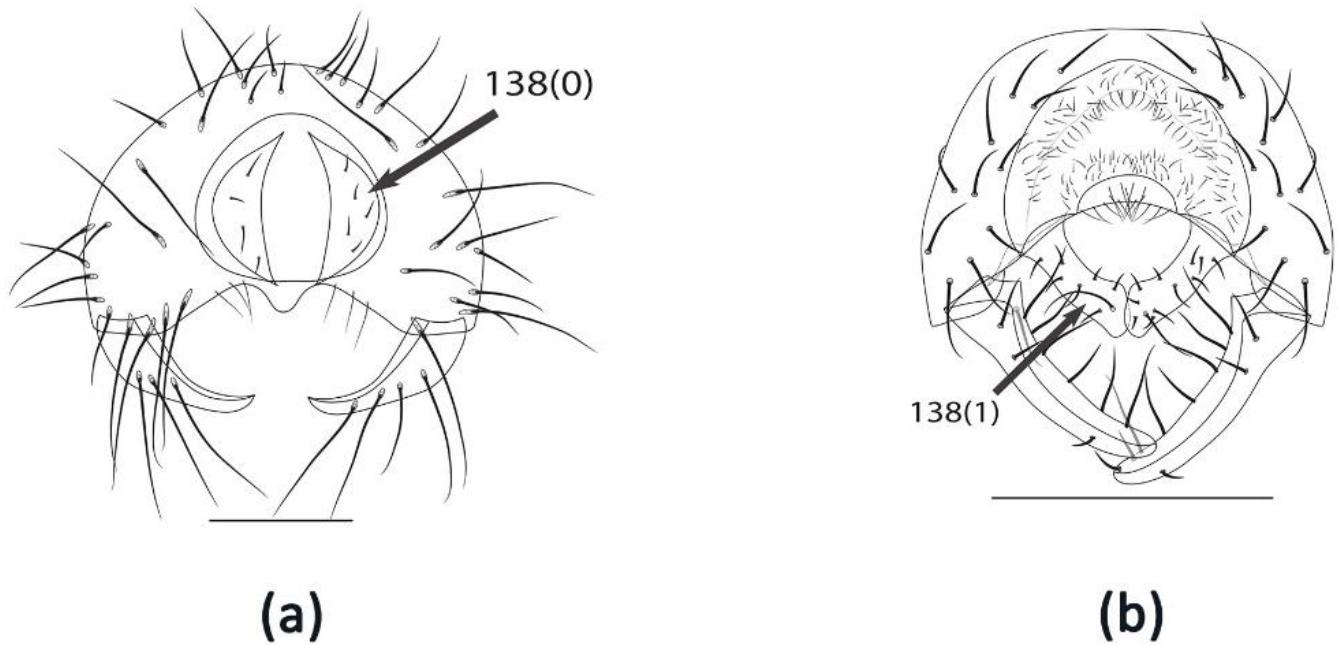


Figure 125a-b. Character 138, location of cercus on epandrium: a. *Meoneura flavifacies* (Drawn by Paula Raile Riccardi), state 0, placed on proctiger, free; b. *Conioscinella solute*, state 1, bellow proctiger, connected with epandrium.

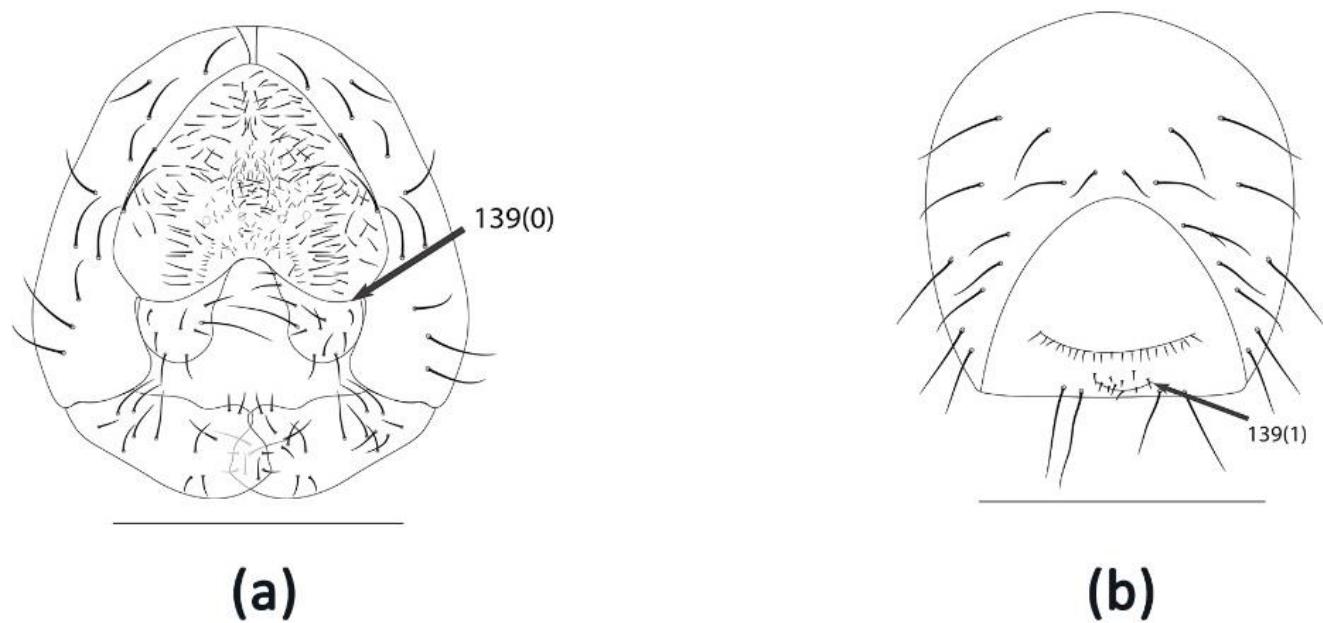


Figure 126a-b. Character 139, cercus articulation: a. *Microcercis albipalpis*, state 0, articulated; b. *Chloropella bipartita* (Drawn by Paula Raile Riccardi), state 1, fused to epandrium.

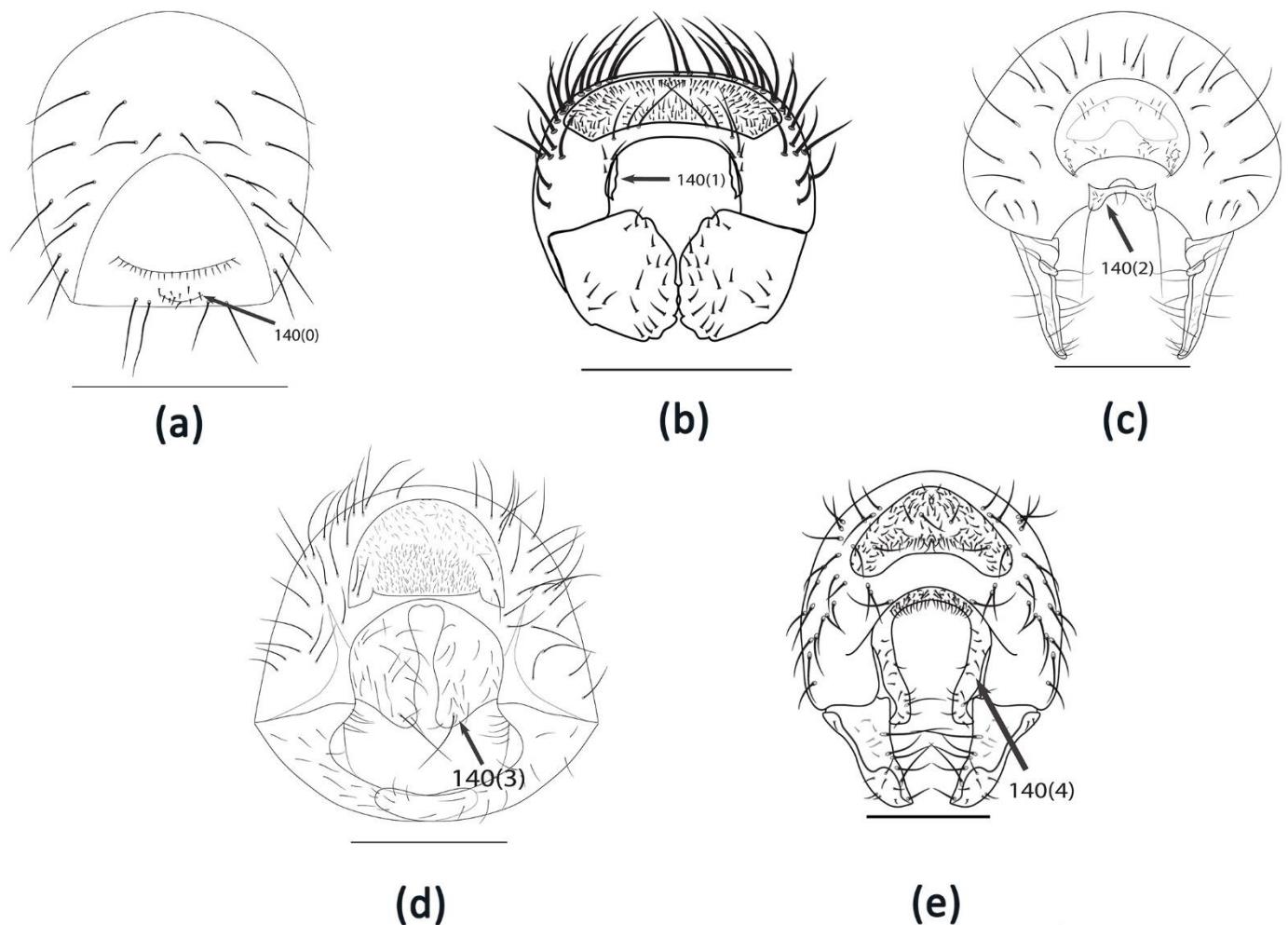


Figure 127a-e. Character 140, length of cercus: a. *Chloropella bipartita* (Drawn by Paula Raile Riccardi), state 0, almost vestigial, in the middle; b. *Biorbitella hesperia*, state 1, almost vestigial, in laterals; c. *Sepsidoscinis maculipennis*, state 2, small; d. *Oscinella frit*, state 3, enlarged, broad; e. *Hippelates plebejus*, state 4, enlarged, narrow.

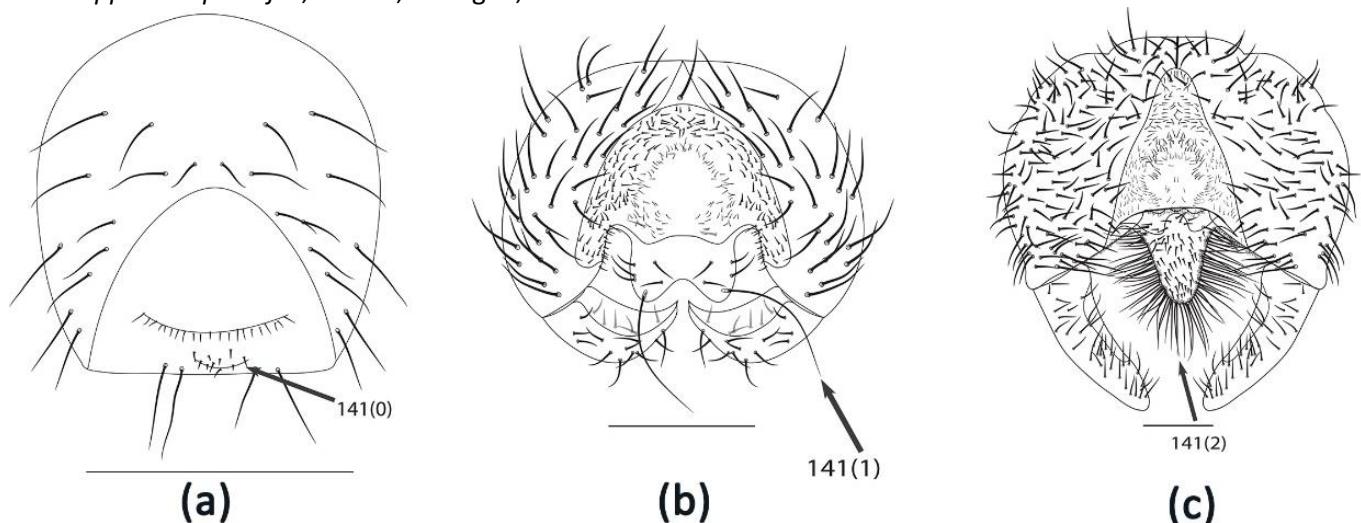
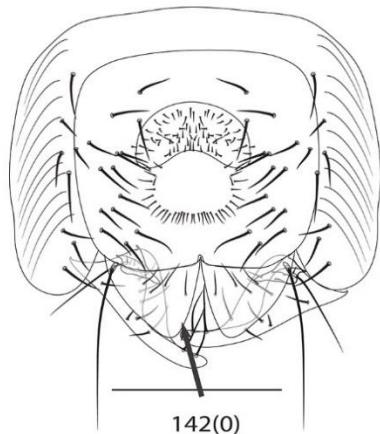


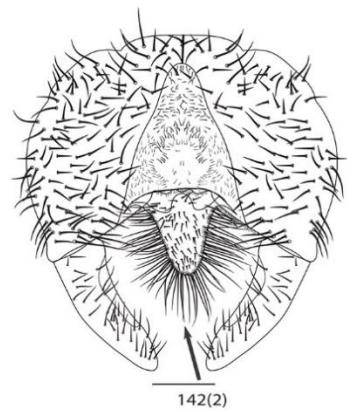
Figure 128a-c. Character 141, elongated setae at tip of cercus: a. *Chloropella bipartita* (Drawn by Paula Raile Riccardi), state 0, absent; b. *Calamoncosis minima*, state 1, present, 1 to 3; c. *Lipara pullitarsis*, state 2, present, several.



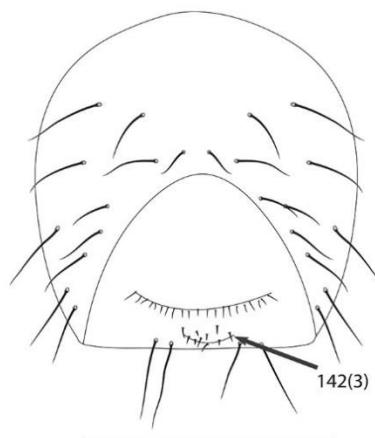
(a)



(b)



(c)



(d)

Figure 129a-d. Character 142, cerci: a. *Elachiptera bimaculata*, state 0, separated from each other; b. *Oscinella frit*, state 1, fused basally or until midway to apex; c. *Lipara pullitarsis*, state 2, fused entirely or more than midway broadly; d. *Chloropella bipartita* (Drawn by Paula Raile Riccardi), state 3, fused entirely narrowly (mesolobe).

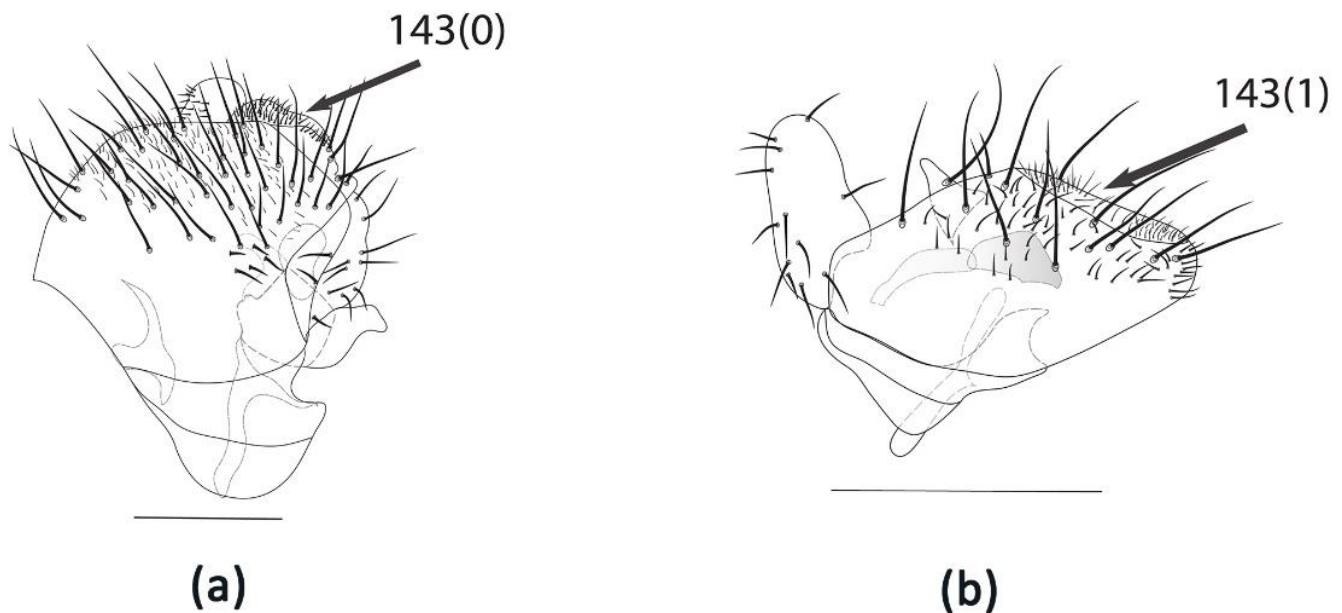


Figure 130a-b. Character 143, proctiger: a. *Calamoncosis minima*, state 0, projected dorsally; b. *Conioscinella soluta*, state 1, almost flat, not visible laterally.

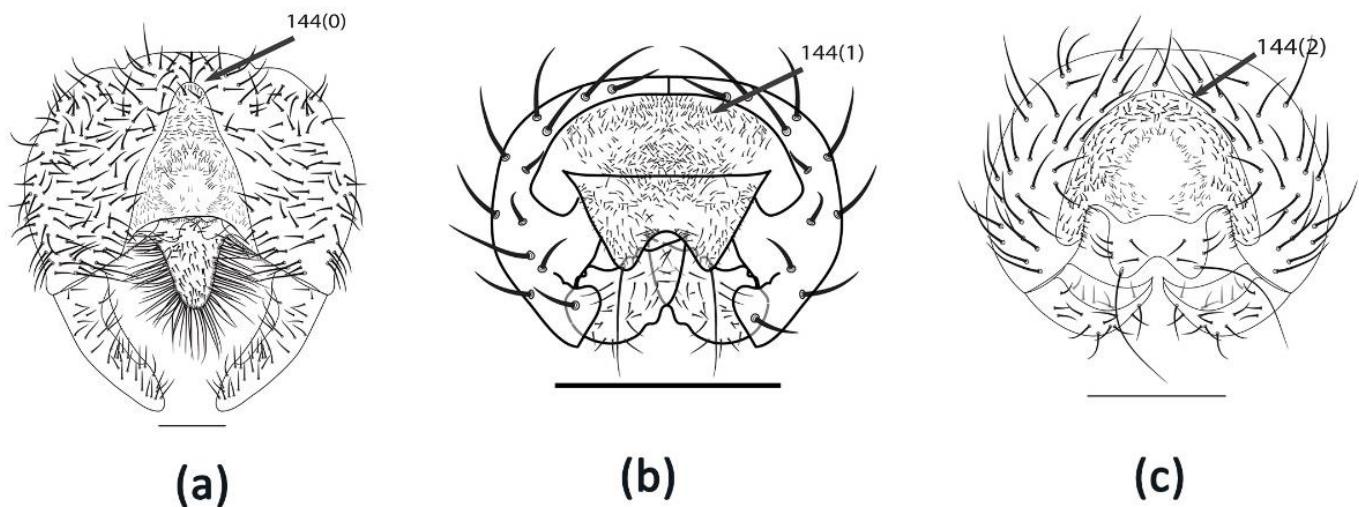
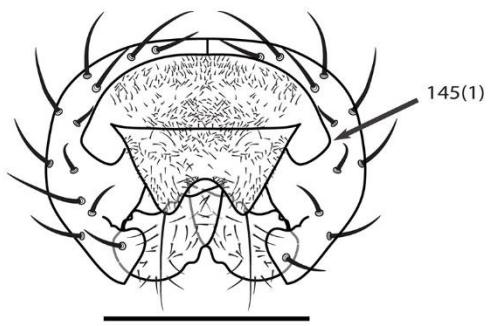


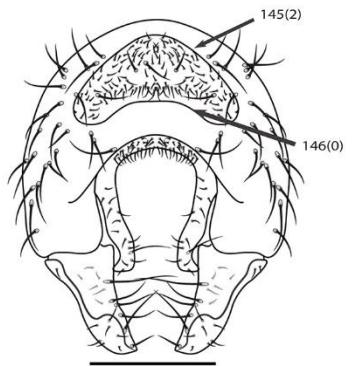
Figure 131a-c. Character 144, proctiger in posterior view: a. *Lipara pullitarsis*, state 0, elongated dorsoventrally; b. *Loxobathmis obliquans*, state 1, widened laterally; c. *Calamoncosis minima*, state 2, almost as long as wide.



(a)



(b)



(c)

Figure 132a-c. Characters 145-146; C145, shape of proctiger in lateral margins (posterior view); C146, ventral margin of proctiger: a. *Calamoncosis minima*, C145, state 0, concave; b. *Loxobathmis obliquans*, C145, state 1, almost 90°; c. *Hippelates plebejus*, C145, state 2, almost straight; C146, state 0, concave.

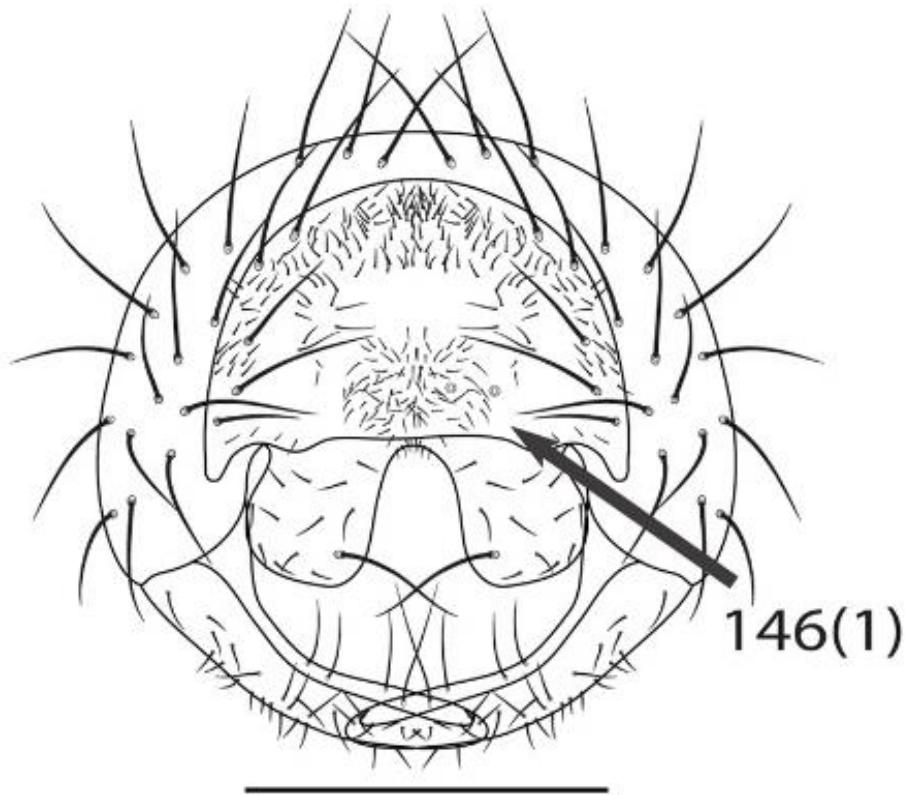
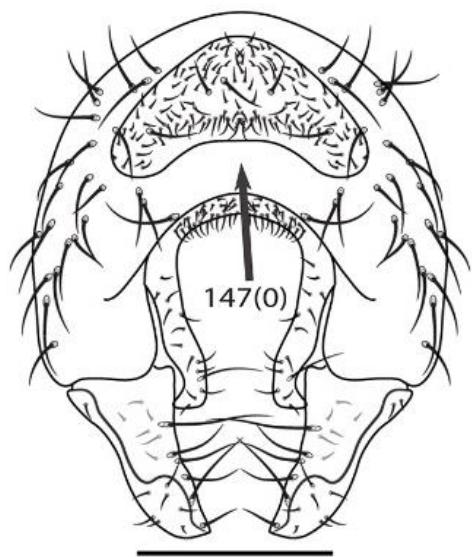
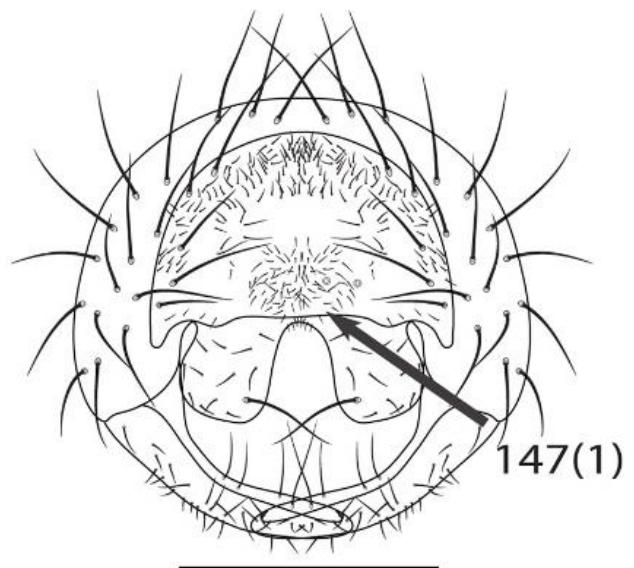


Figure 133: Character 146, ventral margin of proctiger: *Pseudogaurax anchora*, state 1, straight.



(a)



(b)

Figure 134a-b. Character 147, sub-anal plate (under proctiger): a. *Hippelates plebejus*, state 0, present; b. *Pseudogaurax anchora*, state 1, absent.

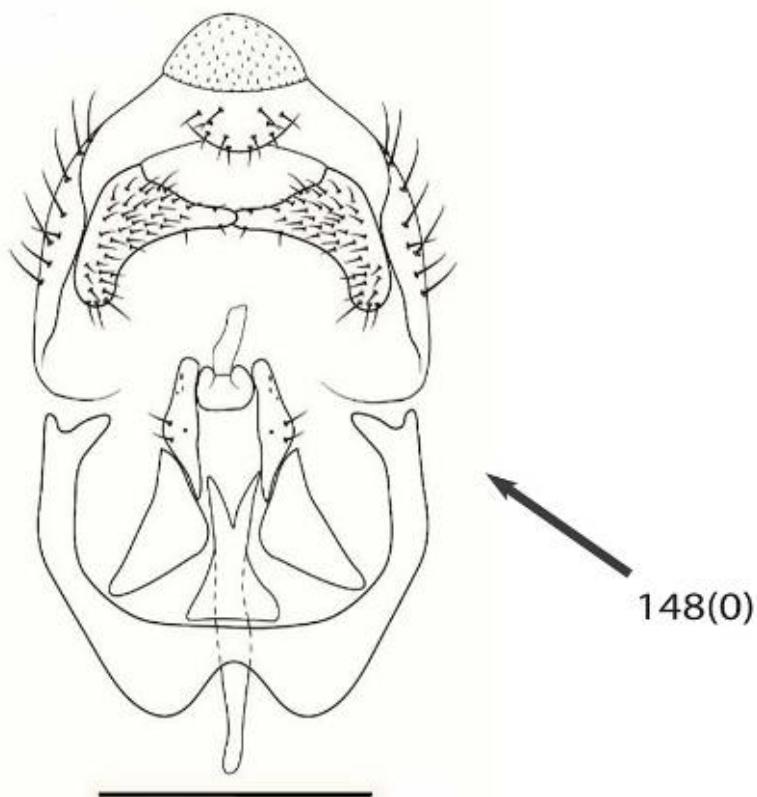


Figure 135: Character 148, hypandrium: *Chloropella bipartita* (Riccardi 2016), state 0, firmly connected to epandrium, articulated outside of epandrium.

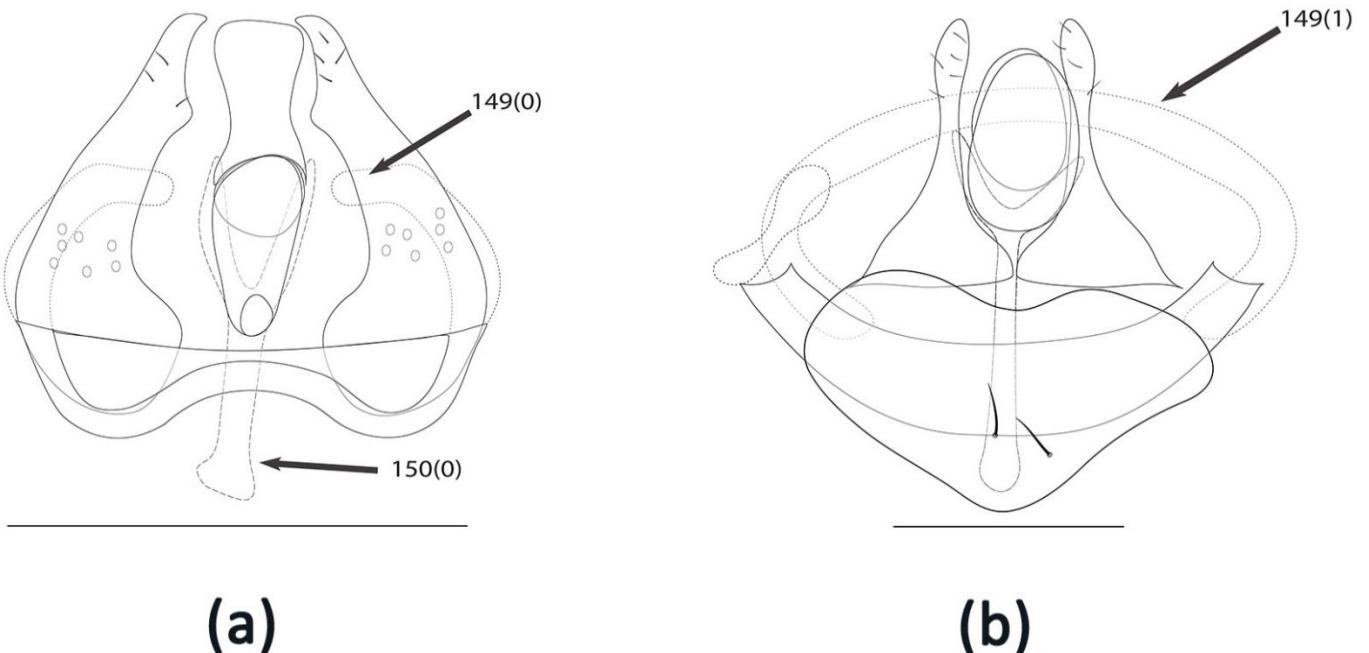


Figure 136a-b. Character 149-150; C149, shape of hypandrium; C150, phallapodeme length: a. *Tricimba lineella*, C149, state 0, arms not connected posteriorly; C150, state 0, long; b. *Pseudogaurax anchora*, C149, state 1, arms connected posteriorly.

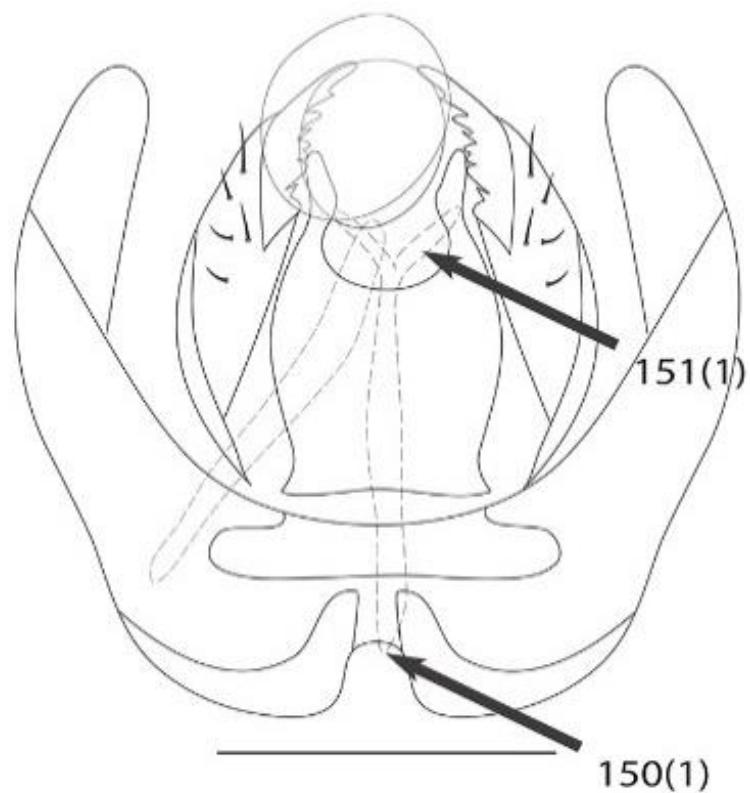


Figure 137: Character 150-151; C150, phallapodeme length and shape of base of phallapodeme; C151, base of phallapodeme: *Fiebrigella* sp., C150, state 1, short; C151, state 1, branched basally.

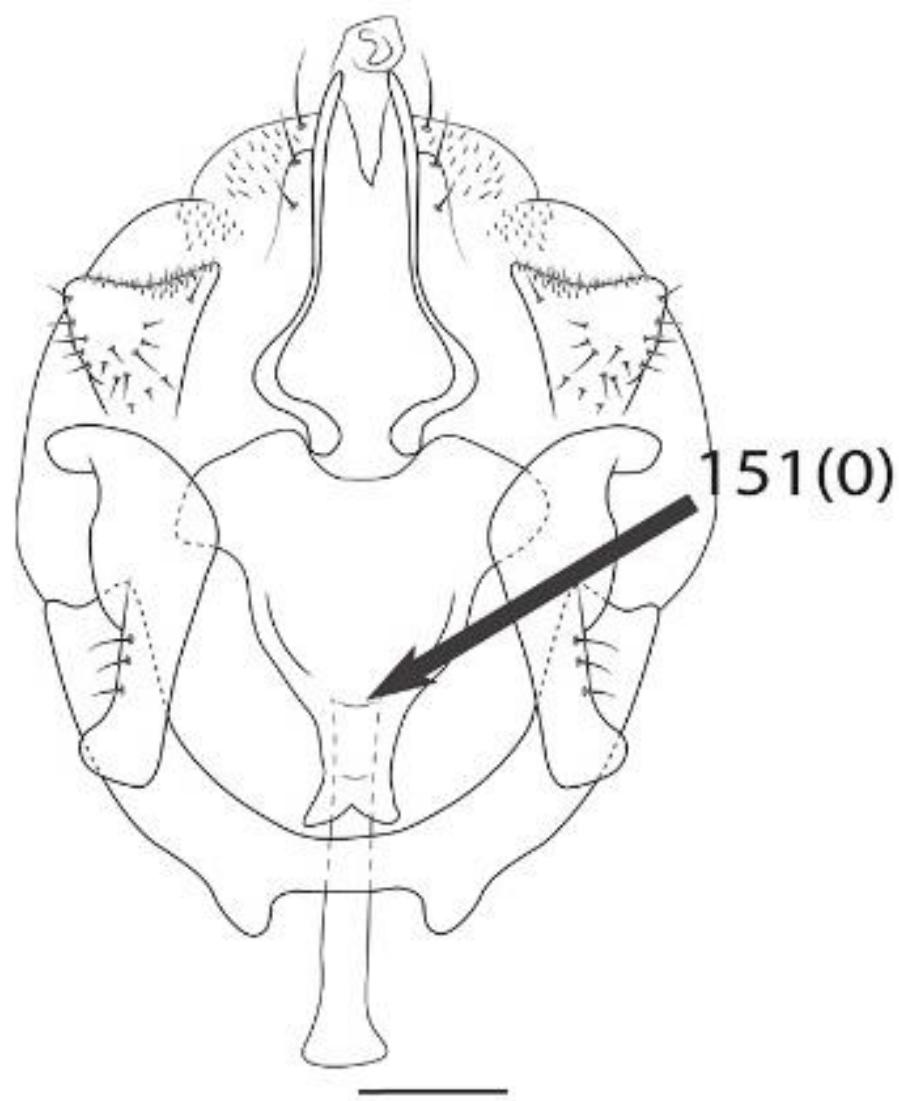


Figure 138: Character 151, base of phallapodeme: *Meromyza saltatrix* (Riccardi 2016), state 0, unbranched basally.

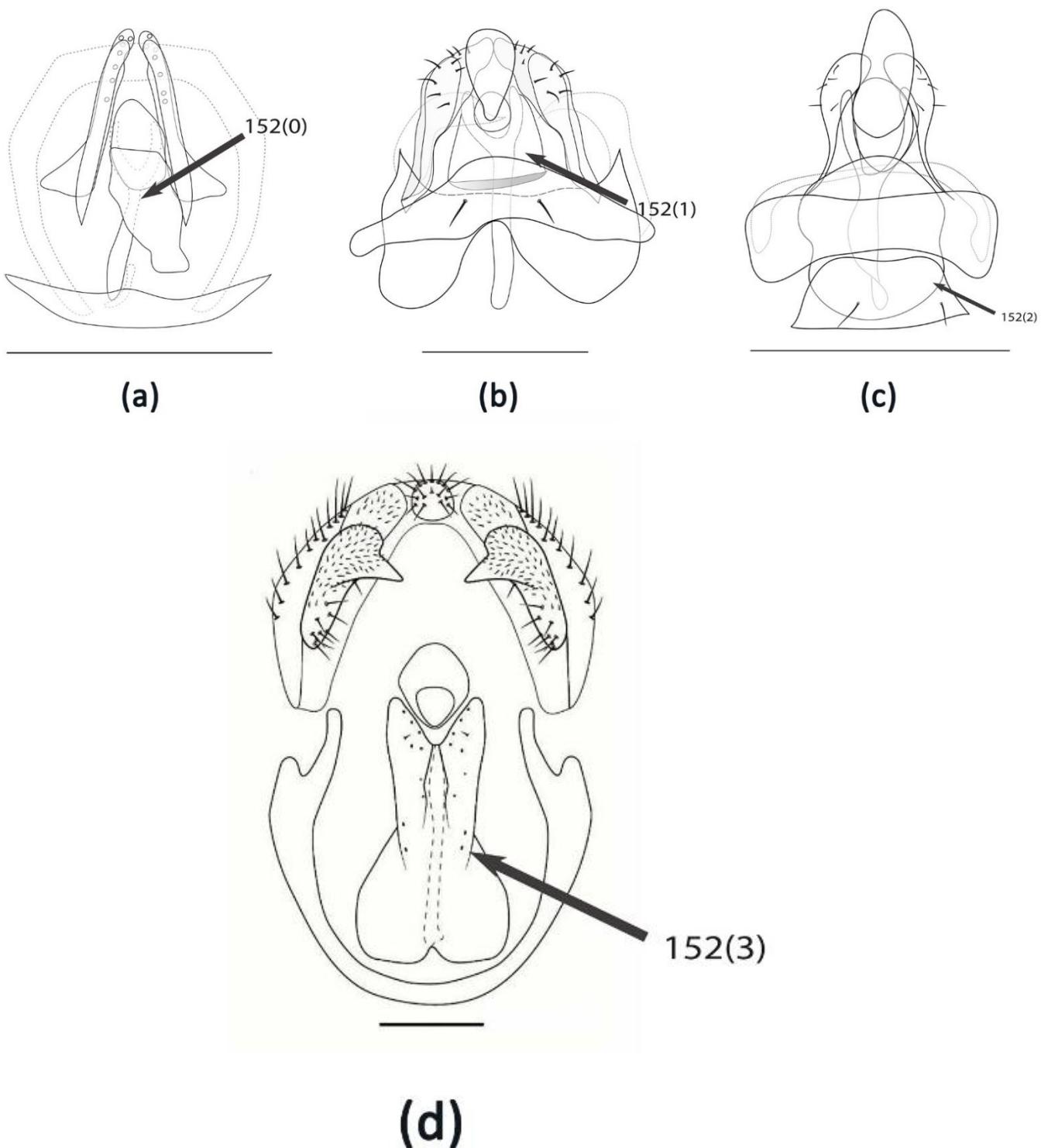
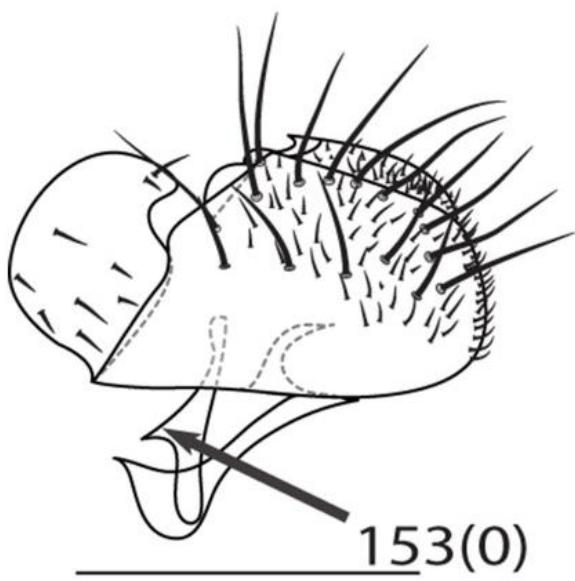
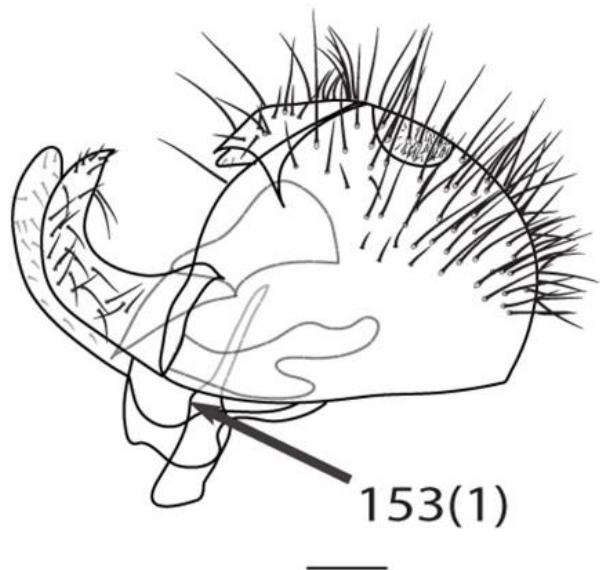


Figure 139a-d. Character 152, phallapodem sclerite: a. *Apallates dissidens*, state 0, absent; b. *Calamoncosis minima*, state 1, developed only basally (branches are occupied by that); c. *Notaulacella* sp., state 2, developed only distally (branches are free); d. *Diplotoxa versicolor* (Riccardi 2016), state 3, developed basally and distally.

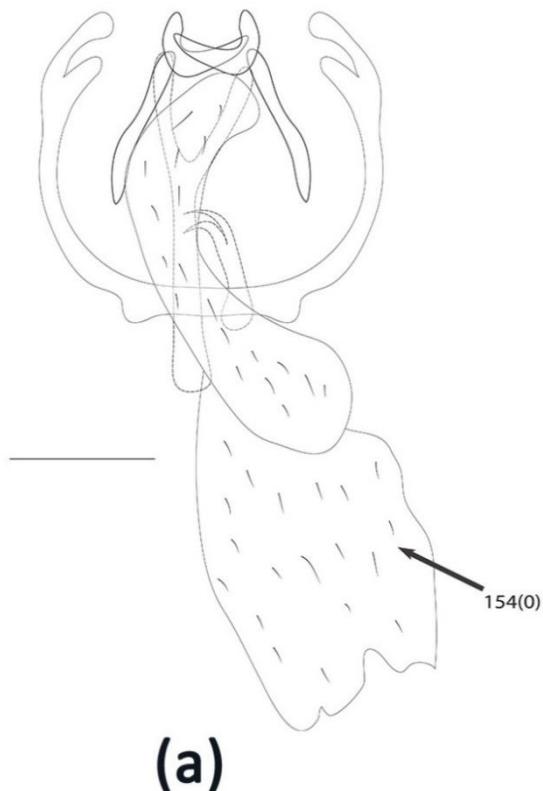


(a)

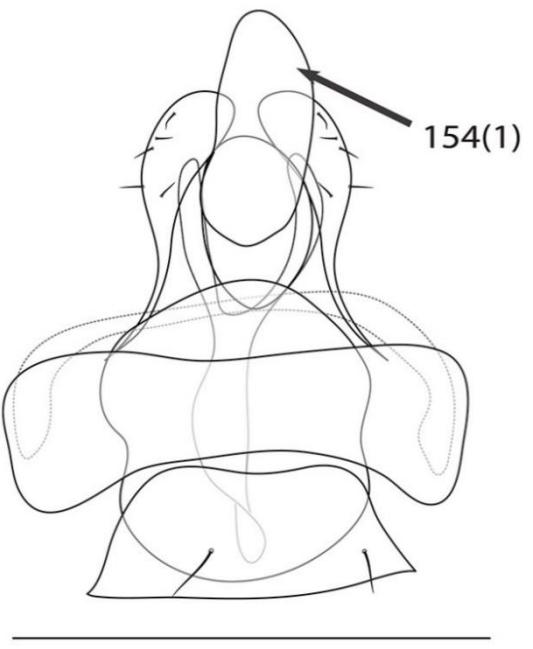


(b)

Figure 140a-b. Character 153, length of endophalic process: a. *Biorbitella hesperia*, state 0, developed; b. *Batrachomyia nigritarsis*, state 1, vestigial.



(a)



(b)

Figure 141a-b. Character 154, distiphallus: a. *Meoneura flavifacies* (Drawn by Paula Raile Riccardi), state 0, hairy; b. *Notaulacella* sp., state 1, bare.

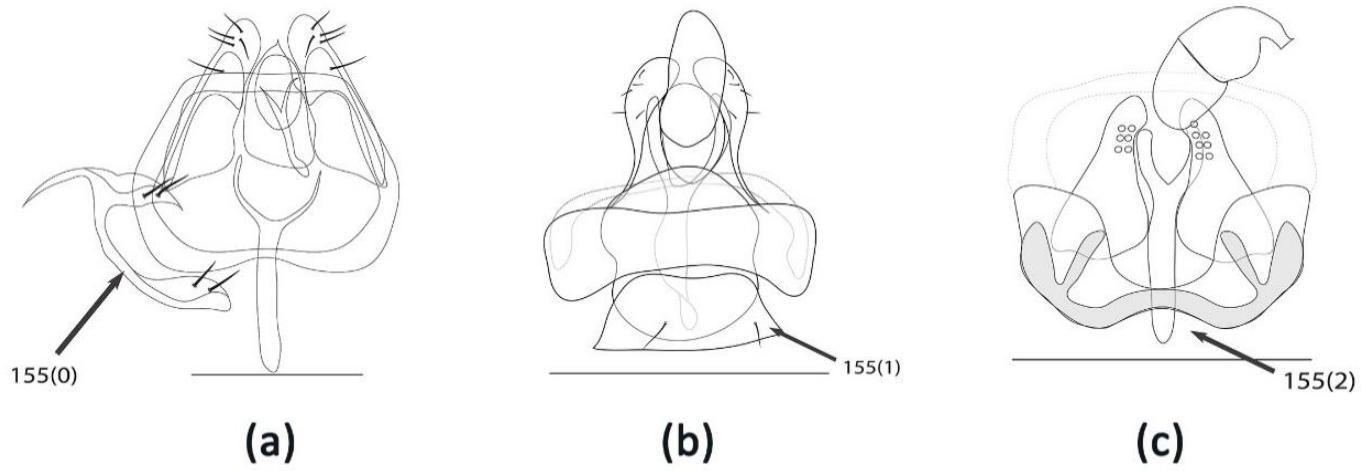


Figure 142a-c. Character 155, synchrony of S6: a. *Siphonellopsis lacteibasis*, state 0, asymmetrical; b. *Notaulacella* sp., state 1, symmetrical, frontally covers hypandrium; c. *Malloewia diabolus*, state 2, absent.

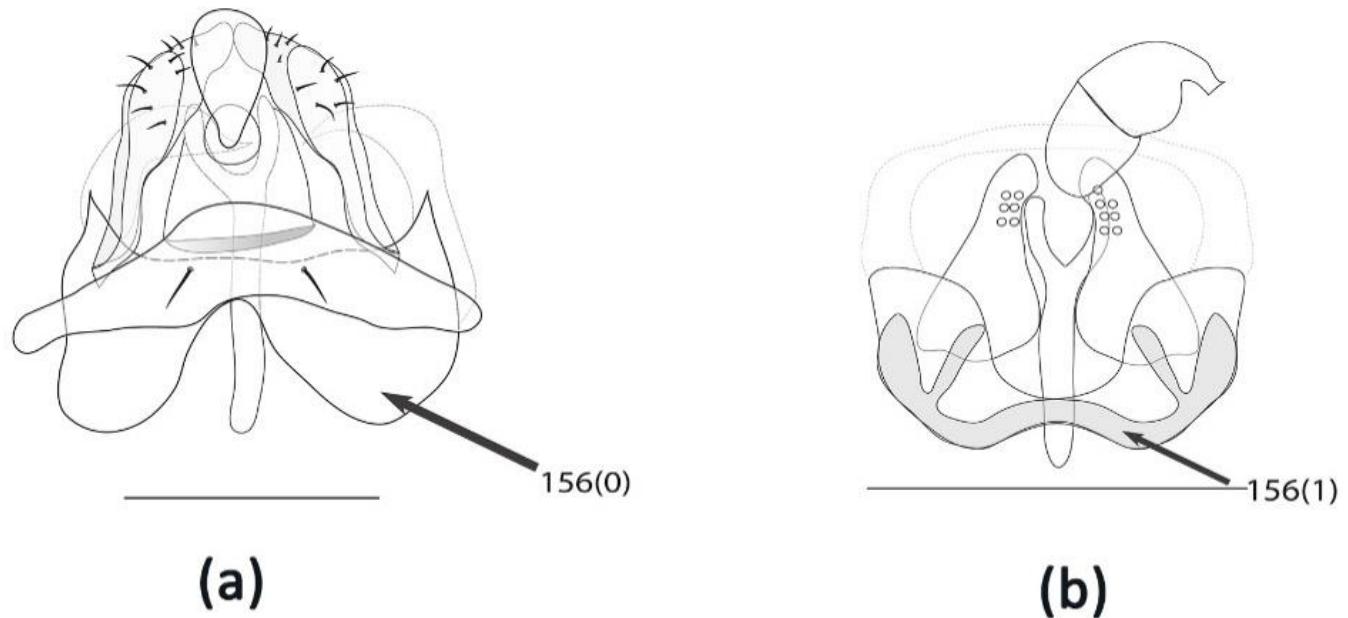


Figure 143a-b. Character 156, hypandrium, anterior view: a. *Calamoncosis minima*, state 0, not sclerotized ventrally; b. *Malloewia diabolus*, state 1, sclerotized ventrally, divided it in 2 parts.

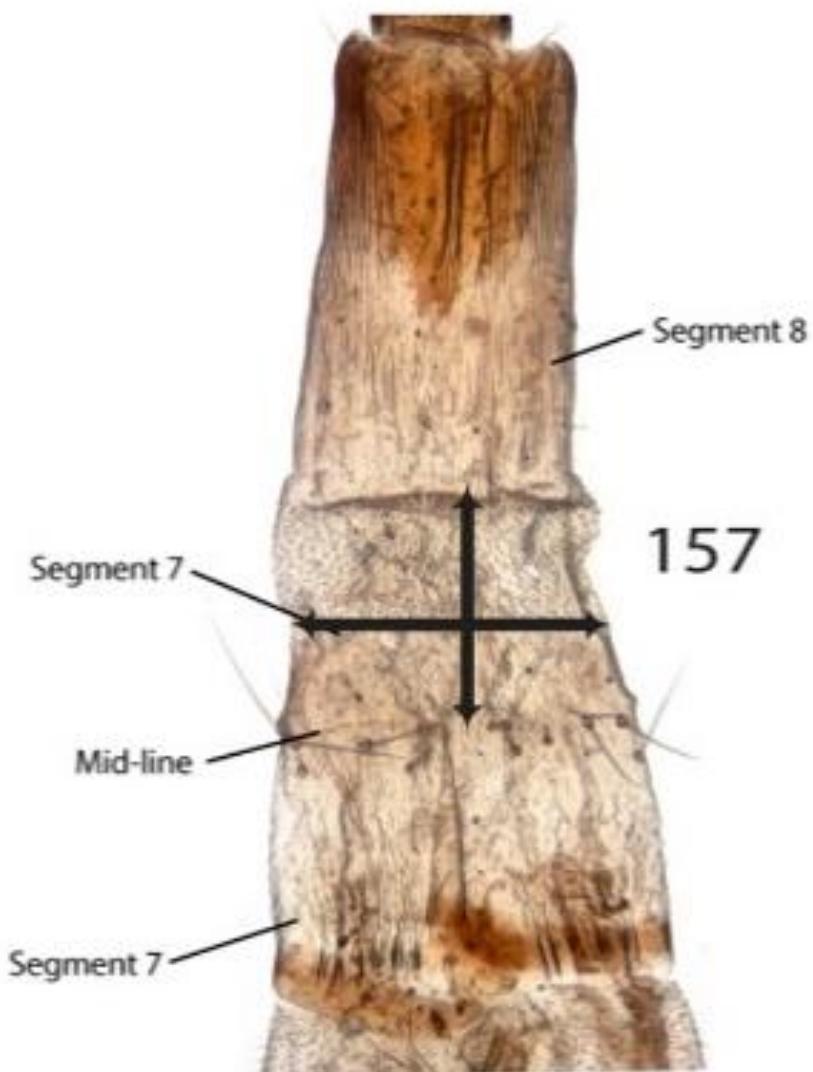


Figure 144: Character 157, shape of segment 7: *Anatrichus erinaceus*.

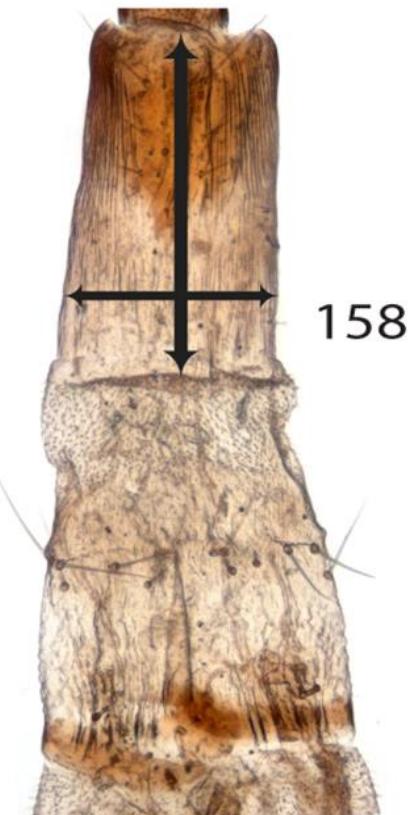


Figure 145: Character 158, shape of segment 8: *Anatrichus erinaceus*.

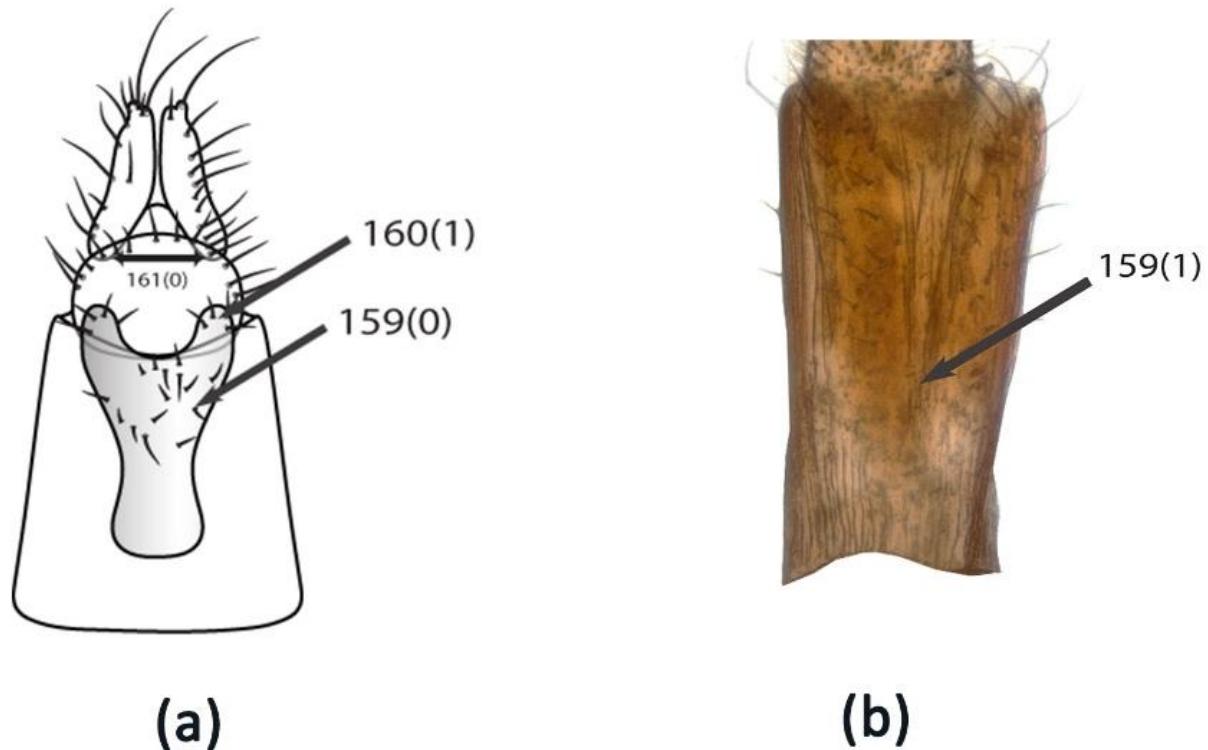


Figure 146a-b. Characters 159-160; C159, sternite 8; C160, shape of sternite 8: a. Schematic shape, C159, state 0, one piece; C160, state 1, protruding in 2 lobes anteriorly; b. *Disciphus peregrinus*, C159, state 1, V-shaped.

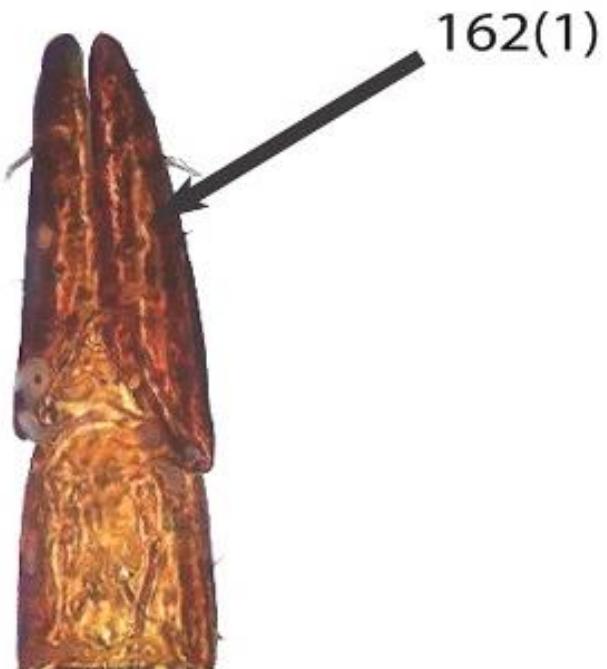


Figure 147: Character 162, cerci: *Opetiophora straminea*, state 1, sclerotized.

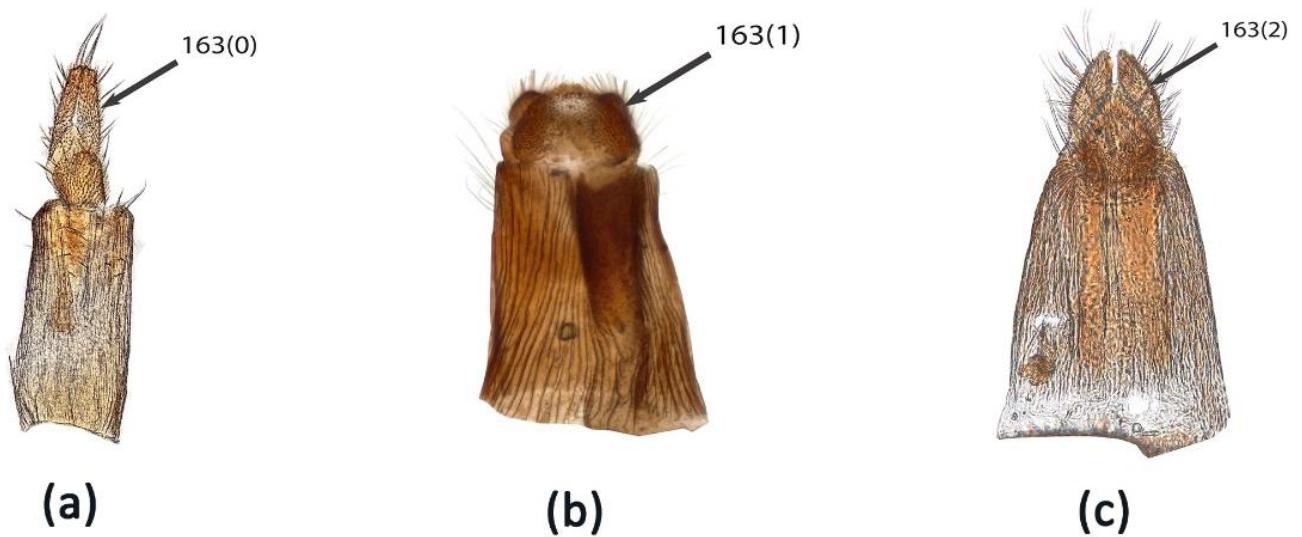


Figure 148a-c. Character 163, shape of cerci: a. *Oscinimorpha albisetosa*, state 0, elongated, cylindral; b. *Lipara lucens*, state 1, short, round; c. *Speccafrons mallochi*, state 2, short, triangular.

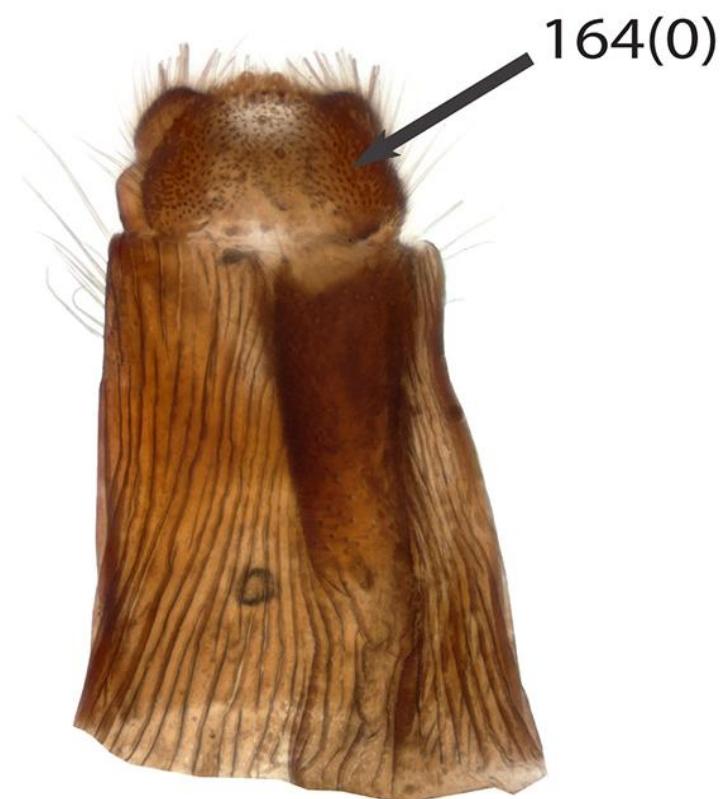


Figure 149: Character 164, hypoproct: *Lipara lucens*, state 0, densely covered with microtrichia.

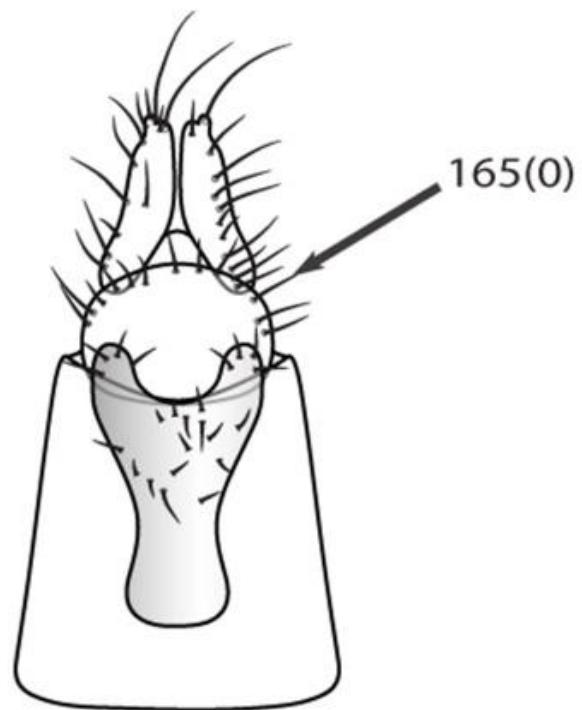


Figure 150: Character 165, hypoproct setation: Schematic shape, state 0, aligned at the frontal margin of hypandrium in row(s).



Figure 151: Character 166, epiproct: *Lipara lucens*, state 0, with microtrichia.



Figure 152a-b. Character 167, number of setae on epiproct: a. *Psilacrum lineatum* (Riccardi & Ismay 2017), state 0, two in the centre of epiproct disk; b. *Lipara lucens*, state 2, numerous and dispersal.

Table

Table 1: Morphological data matrix. ?, missing data; -, inapplicable characters

Appendix

Appendix I. Placement of the genera of Oscinellinae and Rhodesiellinae into tribes or genus groups in different papers.

Genus	Andersson 1977	Kanmiya 1983	Nartshuk 1983	Nartshuk 2012	Mlynarek & Wheeler 2018
<i>Acanthopeltastes</i> Enderlein, 1911	Unplaced	Unplaced	Unplaced	Fiebrigellini	Unplaced
<i>Agrophaspidium</i> Wheeler & Mlynarek, 2008	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Allomedeia</i> Mlynarek & Wheeler, 2010	Unplaced	Unplaced	Unplaced	Unplaced	Elachipterini
<i>Alombus</i> Becker, 1914	Unplaced	Unplaced	Elachipterini	Elachipterini	Elachipterini
<i>Amnonella</i> Cherian, 1992	Unplaced	Unplaced	Unplaced	Rhodesiellini	Unplaced
<i>Anacampτoneurum</i> Becker, 1903	Unplaced	<i>Polyodaspis</i> (Oscinellini s.l.)	Fiebrigellini	Unplaced	Unplaced
<i>Anatrichus</i> Loew, 1860	<i>Elachiptera</i> (Oscinellini s.l.)	<i>Elachiptera</i> (Oscinellini s.l.)	Elachipterini	Elachipterini	Elachipterini
<i>Anomoeoceros</i> Lamb, 1918	<i>Lipara</i> (Oscinellini s.l.)	<i>Lipara</i> (Oscinellini s.l.)	Siphonellini	Liparaini	Unplaced
<i>Apallates</i> Sabrosky, 1980	Unplaced	Unplaced	Incertellini	Incertellini	Unplaced
<i>Aphanotrigonella</i> Nartshuk, 1964	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Unplaced	Tricimbini	Tricimbini	Unplaced
<i>Aphanotrigonum</i> Duda, 1932	<i>Aphanotrigonum</i> (Oscinellini s.l.)	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Incertellini	Incertellini	Unplaced
<i>Aprometopis</i> Becker, 1910	<i>Aphanotrigonum</i> (Oscinellini s.l.)	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Unplaced	Tricimbini	Unplaced
<i>Apterosepsis</i> Richards, 1962	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Arcuator</i> Sabrosky, 1985	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Aulacogaurax</i> Becker & Meijere, 1913	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Batrachomyia</i> Krefft, 1864	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Benjaminella</i> Malloch, 1925	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Bharathella</i> Cherian, 1990	Unplaced	Unplaced	Unplaced	Rhodesiellini	Unplaced
<i>Biorbitella</i> Sabrosky, 1980	Unplaced	Unplaced	Incertellini	Incertellini	Unplaced
<i>Cadrema</i> Walker, 1859	<i>Elachiptera</i> (Oscinellini s.l.)	<i>Cadrema</i> (Oscinellini s.l.)	Hippelatinae s.l.	Unplaced	Unplaced
<i>Calamoncosis</i> Enderlein, 1911	<i>Lipara</i> (Oscinellini s.l.)	<i>Lipara</i> (Oscinellini s.l.)	Siphonellini	Liparaini	Unplaced

<i>Camptopeltes</i> Wheeler & Mlynarek, 2010	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Camptoscinella</i> Sabrosky, 1951	Unplaced	Unplaced	Oscinellini	Oscinellini	Unplaced
<i>Cauloscincis</i> Yang & Yang, 1991	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Caviceps</i> Malloch, 1924	Unplaced	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Unplaced	Unplaced	Unplaced
<i>Cestoplectus</i> Lamb, 1918	<i>Gaurax</i> (Oscinellini s.l.)	<i>Gaurax</i> (Oscinellini s.l.)	Unplaced	Botanobiini	Unplaced
<i>Chaethippus</i> Duda, 1930	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Chaetochlorops</i> Malloch, 1914	Unplaced	<i>Polyodaspis</i> (Oscinellini s.l.)	Fiebrigellini	Fiebrigellini	Unplaced
<i>Conioscinella</i> Duda, 1929	<i>Aphanotrigonum</i> (Oscinellini s.l.)	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Oscinellini	Oscinellini	Unplaced
<i>Coryphisoptron</i> Enderlein, 1911	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Cyrtomomyia</i> Becker, 1913	Unplaced	Unplaced	Elachipterini	Elachipterini	Elachipterini (Synonymized)
<i>Dactylothreya</i> Meijere, 1910	Rhodesiellini s.l.	Rhodesiellini s.l.	Rhodesiellini	Rhodesiellini	Unplaced
<i>Dasyopa</i> Malloch, 1918	Unplaced	Unplaced	Siphonellini	Liparaini	Unplaced
<i>Deltastoma</i> Malloch, 1924	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Dicraeus</i> Loew, 1873	<i>Dicraeus</i> (Oscinellini s.l.)	<i>Dicraeus</i> (Oscinellini s.l.)	Dicraeini	Dicraeini	Unplaced
<i>Disciphus</i> Becker, 1911	<i>Elachiptera</i> (Oscinellini s.l.)	<i>Elachiptera</i> (Oscinellini s.l.)	Elachipterini	Elachipterini	Elachipterini
<i>Discogastrella</i> Enderlein, 1911	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Dysartia</i> Sabrosky, 1991	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Elachiptera</i> Macquart, 1835	<i>Elachiptera</i> (Oscinellini s.l.)	<i>Elachiptera</i> (Oscinellini s.l.)	Elachipterini	Elachipterini	Elachipterini
<i>Elaphaspis</i> Bezzi, 1912	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Enderleiniella</i> Becker, 1912	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Epimadiza</i> Becker, 1910	Unplaced	<i>Polyodaspis</i> (Oscinellini s.l.)	Fiebrigellini	Fiebrigellini	Unplaced
<i>Eribolus</i> Becker, 1910	<i>Eribolus</i> (Oscinellini s.l.)	Unplaced	Oscinisomatini	Oscinisomatini	Unplaced
<i>Eugaurax</i> Malloch, 1913	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Euthyridium</i> Frey, 1923	Rhodesiellini s.l.	Rhodesiellini s.l.	Rhodesiellini	Rhodesiellini	Unplaced

<i>Fiebrigella</i> Duda, 1921	<i>Polyodaspis</i> (Oscinellini s.l.)	<i>Polyodaspis</i> (Oscinellini s.l.)	Fiebrigellini	Fiebrigellini	Unplaced
<i>Gampsocera</i> Schiner, 1862	<i>Gaurax</i> (Oscinellini s.l.)	<i>Gaurax</i> (Oscinellini s.l.)	Botanobiini	Botanobiini	Unplaced
<i>Gaurax</i> Loew, 1863	<i>Gaurax</i> (Oscinellini s.l.)	<i>Gaurax</i> (Oscinellini s.l.)	Botanobiini	Botanobiini	Unplaced
<i>Goniaspis</i> Duda, 1930	Unplaced	Unplaced	Unplaced	Unplaced	Elachipterini
<i>Hapleginella</i> Duda, 1933	<i>Oscinella</i> (Oscinellini s.l.)	<i>Oscinella</i> (Oscinellini s.l.)	Botanobiini	Botanobiini	Unplaced
<i>Heteroscinis</i> Lamb, 1918	Unplaced	Unplaced	Unplaced	Fiebrigellini	Unplaced
<i>Heteroscinoides</i> Cherian, 1989	Unplaced	Unplaced	Fiebrigellini	Fiebrigellini	Unplaced
<i>Hippelates</i> Loew, 1863	Unplaced	Unplaced	Hippelatinae s.l.	Unplaced	Unplaced
<i>Incertella</i> Sabrosky, 1980	Unplaced	<i>Oscinella</i> (Oscinellini s.l.)??	Incertellini	Incertellini	Unplaced
<i>Indometopis</i> Cherian, 1989	Unplaced	Unplaced	Unplaced	Tricimbini	Unplaced
<i>Indonella</i> Cherian in Cherian & Shinimol, 2008	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Indophthalmus</i> Cherian, 2002	Unplaced	Unplaced	Unplaced	Rhodesiellini	Unplaced
<i>Javanoscinis</i> Andersson, 1977	<i>Javanoscinis</i> (Oscinellini s.l.)	Unplaced (Oscinellini s.l.)	Stenoscinini	Stenoscinini	Unplaced
<i>Kurumemyia</i> Kanmiya, 1983	Unplaced	<i>Siphonella</i> (Oscinellini s.l.)	Unplaced	Siphonellini	Unplaced
<i>Kwarea</i> Sabrosky, 1954	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Lasiambia</i> Anonymous	<i>Polyodaspis</i> (Oscinellini s.l.)	<i>Polyodaspis</i> (Oscinellini s.l.)	Fiebrigellini	Fiebrigellini	Unplaced
<i>Lasiochaeta</i> Corti, 1909	Unplaced	Unplaced	Unplaced	Elachipterini	Elachipterini (Synonymized)
<i>Leucochaeta</i> Becker, 1913	Unplaced	Unplaced	Botanobiini	Botanobiini	Unplaced
<i>Liohippelates</i> Duda 1929	Unplaced	Unplaced	Hippelatinae s.l.	Unplaced	Unplaced
<i>Lioscinella</i> Duda 1929	<i>Oscinella</i> (Oscinellini s.l.)	<i>Oscinella</i> (Oscinellini s.l.)??	Hippelatinae s.l.	Unplaced	Unplaced
<i>Lipara</i> Meigen, 1830	<i>Lipara</i> (Oscinellini s.l.)	<i>Lipara</i> (Oscinellini s.l.)	Siphonellini	Liparaini	Unplaced
<i>Loxobathmis</i> Enderlein, 1911	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Malloewia</i> Sabrosky, 1980	Unplaced	Unplaced	Incertellini	Incertellini	Unplaced
<i>Medeventor</i> Wheeler, 2007	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced

<i>Meijerella</i> Sabrosky, 1976	Unplaced	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Unplaced	Incertellini	Unplaced
<i>Melanochaetomyia</i> Cherian, 2002	Unplaced	Unplaced	Unplaced	Elachipterini	Unplaced
<i>Merobates</i> Duda, 1934	Unplaced	Unplaced	Rhodesiellini	Unplaced	Unplaced
<i>Merodonta</i> Malloch, 1940	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Metasiphonella</i> Duda, 1930	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Microcercis</i> Beschovski, 1978	Unplaced	Unplaced	Unplaced	Incertellini	Unplaced
<i>Mimosepsis</i> Sabrosky, 1951	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Monochaetoscinella</i> Duda, 1930	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Neolcella</i> Cherian, 1996	Unplaced	Unplaced	Unplaced	Oscinellini	Unplaced
<i>Neorhodesiella</i> Cherian, 2002	Unplaced	Unplaced	Unplaced	Rhodesiellini	Unplaced
<i>Neoscinella</i> Sabrosky, 1980	Unplaced	Unplaced	Unplaced	Oscinellini	Unplaced
<i>Nomba</i> Walker, 1860	Rhodesiellini s.l.	Rhodesiellini s.l.	Unplaced	Rhodesiellini	Unplaced
<i>Notaulacella</i> Enderlein, 1911	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Olcella</i> Enderlein, 1911	Unplaced	Unplaced	Oscinellini	Oscinellini	Unplaced
<i>Onychaspidium</i> Enderlein, 1911	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Opetiophora</i> Loew, 1872	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Oscinella</i> Becker, 1909	<i>Oscinella</i> (Oscinellini s.l.)	<i>Oscinella</i> (Oscinellini s.l.)	Oscinellini	Oscinellini	Unplaced
<i>Oscinicita</i> Wheeler, 2007	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Oscinimorpha</i> Lioy, 1864	<i>Aphanotrigonum</i> (Oscinellini s.l.)	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Oscinellini	Oscinellini	Unplaced
<i>Oscinisoma</i> Lioy, 1864	<i>Eribolus</i> (Oscinellini s.l.)	Unplaced	Oscinisomatini	Oscinisomatini	Unplaced
<i>Paraapallates</i> Cherian in Cherian & Tilak, 2008	Unplaced	Unplaced	Unplaced	Incertellini	Unplaced
<i>Paracalamoncosis</i> Riccardi & Bazyar, 2018*	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Parameijerella</i> Cherian, 1991	Unplaced	Unplaced	Unplaced	Incertellini	Unplaced
<i>Parasiphonella</i> Enderlein, 1913	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced

<i>Platyina</i> Malloch, 1927	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Polyodaspis</i> Duda, 1933	<i>Polyodaspis</i> (Oscinellini s.l.)	<i>Polyodaspis</i> (Oscinellini s.l.)	Fiebrigellini	Fiebrigellini	Unplaced
<i>Pselaphia</i> Becker, 1911	Unplaced?	Unplaced	Botanobiini	Botanobiini	Unplaced
<i>Pseudeurina</i> Meijere, 1904	<i>Lipara</i> (Oscinellini s.l.)	<i>Lipara</i> (Oscinellini s.l.)	Siphonellini	Liparaini	Unplaced
<i>Pseudogampsocera</i> Sabrosky, 1964	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Pseudogaurax</i> Malloch, 1915	<i>Gaurax</i> (Oscinellini s.l.)	<i>Gaurax</i> (Oscinellini s.l.)	Botanobiini	Botanobiini	Unplaced
<i>Pseudonomba</i> Cherian, 1989	Unplaced	Unplaced	Unplaced	Rhodesiellini	Unplaced
<i>Pseudotricimba</i> Ismay, 1993	Unplaced	Unplaced	Unplaced	Tricimbini	Unplaced
<i>Psilacrum</i> Becker, 1912	Unplaced	Unplaced	Stenoscinini	Stenoscinini	Unplaced
<i>Pterogaurax</i> Duda, 1930	Unplaced	Unplaced	Unplaced	Botanobiini	Unplaced
<i>Rhodesiella</i> Adams, 1905	Rhodesiellini s.l.	Rhodesiellini s.l.	Rhodesiellini	Rhodesiellini	Unplaced
<i>Rhopalopterum</i> Duda, 1929	Unplaced	Unplaced	Oscinisomatini	Oscinisomatini	Unplaced
<i>Sabroskyina</i> Beschovski, 1987	Unplaced	Unplaced	Unplaced	Oscinisomatini	Unplaced
<i>Sacatonia</i> Sabrosky, 1967	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Scoliophthalmus</i> Becker, 1903	Rhodesiellini s.l.	Rhodesiellini s.l.	Scoliophthalmini	Scoliophthalmini	Unplaced
<i>Sepsidoscinis</i> Hendel, 1914	<i>Elachiptera</i> (Oscinellini s.l.)	<i>Myrmecosepsis</i> s.l.	Elachipterini	Elachipterini	Elachipterini
<i>Siphonella</i> Macquart, 1835	<i>Lipara</i> (Oscinellini s.l.)	<i>Siphonella</i> (Oscinellini s.l.)	Siphonellini	Siphonellini	Unplaced
<i>Siphonellomyia</i> Seguy, 1934	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Siphunculina</i> Rondani, 1856	<i>Aphanotrigonum</i> (Oscinellini s.l.)	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Tricimbini	Tricimbini	Unplaced
<i>Speccafrons</i> Sabrosky, 1980	Unplaced	<i>Siphonella</i> (Oscinellini s.l.)	Incertellini	Siphonellini	Unplaced
<i>Stenoscinis</i> Malloch, 1918	Unplaced	Unplaced (Oscinellini s.l.)	Stenoscinini	Stenoscinini	Unplaced
<i>Strandimyia</i> Duda, 1930	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Tachinoceros</i> Meijere, 1921	Rhodesiellini s.l.	Rhodesiellini s.l.	Rhodesiellini	Rhodesiellini	Unplaced
<i>Thyridula</i> Becker, 1911	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced

<i>Togeciphus</i> Nishijima, 1955	Unplaced	<i>Elachiptera</i> (Oscinellini s.l.)	Elachipterini	Elachipterini	Elachipterini (Synonymized)
<i>Trachysiphonella</i> Enderlein, 1936	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Unplaced	Unplaced	Unplaced	Unplaced
<i>Tricimba</i> Lioy, 1864	<i>Aphanotrigonum</i> (Oscinellini s.l.)	<i>Aphanotrigonum</i> (Oscinellini s.l.)	Tricimbini	Tricimbini	Unplaced
<i>Tricimbomyia</i> Cherian, 1989	Unplaced	Unplaced	Unplaced	Tricimbini	Unplaced
<i>Tropidoscinis</i> Enderlein, 1911	<i>Oscinella</i> (Oscinellini s.l.)	<i>Oscinella</i> (Oscinellini s.l.)	Unplaced	Unplaced	Unplaced
<i>Tylopterna</i> Bezzi, 1916	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced
<i>Vanchium</i> Cherian, 1999	Unplaced	Unplaced	Unplaced	Unplaced	Unplaced

Appendix II. List and distribution of the genera of Oscinellinae of the world. Caption: NEO, Neotropical; NEA, Nearctic; PAL, Palaearctic; AFR, Afrotropical; ORI, Oriental; AUS, Australian. The * indicates the place of the type-species of each genus. Green background indicates the distribution of the genus.

	Genus	NEO	NEA	PAL	AFR	ORI	AUS
1	<i>Acanthopeltastes</i> Enderlein, 1911	*					
2	<i>Agrophaspidium</i> Wheeler & Mlynarek, 2008	*					
3	<i>Allomedeia</i> Mlynarek & Wheeler, 2010				*		
4	<i>Alombus</i> Becker, 1914				*		
5	<i>Amnonella</i> Cherian, 1992					*	
6	<i>Anacampτoneurum</i> Becker, 1903			*			
7	<i>Anatrichus</i> Loew, 1860				*		
8	<i>Anomoeoceros</i> Lamb, 1918				*		
9	<i>Apallates</i> Sabrosky, 1980		*				
10	<i>Aphanotrigonella</i> Nartshuk, 1964			*			
11	<i>Aphanotrigonum</i> Duda, 1932			*			
12	<i>Aprometopis</i> Becker, 1910				*		
13	<i>Apterosepsis</i> Richards, 1962				*		
14	<i>Arcuator</i> Sabrosky, 1985				*		
15	<i>Aulacogaurax</i> Becker & Meijere, 1913					*	
16	<i>Batrachomyia</i> Krefft, 1864						*
17	<i>Benjaminella</i> Malloch, 1925						*
18	<i>Bharathella</i> Cherian, 1990					*	
19	<i>Biorbitella</i> Sabrosky, 1980		*				
20	<i>Cadrema</i> Walker, 1859					*	
21	<i>Calamoncosis</i> Enderlein, 1911			*			
22	<i>Camptopeltes</i> Wheeler & Mlynarek, 2010	*					
23	<i>Camptoscinella</i> Sabrosky, 1951				*		
24	<i>Cauloscincis</i> Yang & Yang, 1991					*	
25	<i>Caviceps</i> Malloch, 1924						*
26	<i>Cestoplectus</i> Lamb, 1918					*	
27	<i>Chaethippus</i> Duda, 1930	*					
28	<i>Chaetochlorops</i> Malloch, 1914		*				
29	<i>Conioscinella</i> Duda, 1929	*					
30	<i>Coryphisopteron</i> Enderlein, 1911	*					
31	<i>Cyrtomomyia</i> Becker, 1913				*		
32	<i>Dactylothryea</i> Meijere, 1910					*	
33	<i>Dasyopa</i> Malloch, 1918		*				
34	<i>Deltastoma</i> Malloch, 1924						*
35	<i>Dicraeus</i> Loew, 1873			*			
36	<i>Disciphus</i> Becker, 1911					*	
37	<i>Discogastrella</i> Enderlein, 1911	*					
38	<i>Dysartia</i> Sabrosky, 1991		*				
39	<i>Elachiptera</i> Macquart, 1835			*			
40	<i>Elaphaspis</i> Bezzı, 1912				*		
41	<i>Enderleiniella</i> Becker, 1912	*					
42	<i>Epimadiza</i> Becker, 1910				*		
43	<i>Eribolus</i> Becker, 1910			*			
44	<i>Eugaurax</i> Malloch, 1913		*				
45	<i>Euthyridium</i> Frey, 1923					*	
46	<i>Fiebrigella</i> Duda, 1921	*					
47	<i>Gampsocera</i> Schiner, 1862						*

	Genus	NEO	NEA	PAL	AFR	ORI	AUS
48	<i>Gaurax</i> Loew, 1863		*				
49	<i>Goniaspis</i> Duda, 1930	*					
50	<i>Hapleginella</i> Duda, 1933			*			
51	<i>Heteroscinis</i> Lamb, 1918				*		
52	<i>Heteroscinoides</i> Cherian, 1989					*	
53	<i>Hippelates</i> Loew, 1863		*				
54	<i>Incertella</i> Sabrosky, 1980		*				
55	<i>Indometopis</i> Cherian, 1989					*	
56	<i>Indonella</i> Cherian in Cherian & Shinimol, 2008					*	
57	<i>Indophthalmus</i> Cherian, 2002					*	
58	<i>Javanoscinis</i> Andersson, 1977					*	
59	<i>Kurumemyia</i> Kanmiya, 1983			*			
60	<i>Kwarea</i> Sabrosky, 1954				*		
61	<i>Lasiambia</i> Anonymous			*			
62	<i>Lasiochaeta</i> Corti, 1909			*			
63	<i>Leucochaeta</i> Becker, 1913			*			
64	<i>Liohippelates</i> Duda, 1929		*				
65	<i>Lioscinella</i> Duda, 1929	*					
66	<i>Lipara</i> Meigen, 1830			*			
67	<i>Loxobathmis</i> Enderlein, 1911	*					
68	<i>Malloewia</i> Sabrosky, 1980		*				
69	<i>Medeventor</i> Wheeler, 2007	*					
70	<i>Meijerella</i> Sabrosky, 1976					*	
71	<i>Melanochaetomyia</i> Cherian, 2002					*	
72	<i>Merobates</i> Duda, 1934					*	
73	<i>Merodontia</i> Malloch, 1940						*
74	<i>Metasiphonella</i> Duda, 1930	*					
75	<i>Microcercis</i> Beschovski, 1978			*			
76	<i>Mimosepsis</i> Sabrosky, 1951				*		
77	<i>Monochaetoscinella</i> Duda, 1930	*					
78	<i>Neolcella</i> Cherian, 1996					*	
79	<i>Neorrhodesiella</i> Cherian, 2002					*	
80	<i>Neoscinella</i> Sabrosky, 1980		*				
81	<i>Nomba</i> Walker, 1860					*	
82	<i>Notaulacella</i> Enderlein, 1911	*					
83	<i>Olcella</i> Enderlein, 1911	*					
84	<i>Onychaspidium</i> Enderlein, 1911	*					
85	<i>Opetiophora</i> Loew, 1872		*				
86	<i>Oscinella</i> Becker, 1909			*			
87	<i>Oscinicita</i> Wheeler, 2007	*					
88	<i>Oscinimorpha</i> Lioy, 1864			*			
89	<i>Oscinisoma</i> Lioy, 1864			*			
90	<i>Paraapallates</i> Cherian in Cherian & Tilak, 2008					*	
91	<i>Paracalamoncosis</i> Riccardi & Bazyar, 2018	*					
92	<i>Parameijerella</i> Cherian, 1991					*	
93	<i>Parasiphonella</i> Enderlein, 1913	*					
94	<i>Platyina</i> Malloch, 1927						*
95	<i>Polydodaspis</i> Duda, 1933			*			
96	<i>Pselaphia</i> Becker, 1911				*		
97	<i>Pseudeurina</i> Meijere, 1904					*	
98	<i>Pseudogampsocera</i> Sabrosky, 1964				*		

	Genus	NEO	NEA	PAL	AFR	ORI	AUS
99	<i>Pseudogaurax</i> Malloch, 1915		*				
100	<i>Pseudonomba</i> Cherian, 1989					*	
101	<i>Pseudotricimba</i> Ismay, 1993						*
102	<i>Psilacrum</i> Becker, 1912				*		
103	<i>Pterogaurax</i> Duda, 1930	*					
104	<i>Rhodesiella</i> Adams, 1905				*		
105	<i>Rhopalopterum</i> Duda, 1929	*					
106	<i>Sabroskyina</i> Beschovski, 1987			*			
107	<i>Sacatonia</i> Sabrosky, 1967		*				
108	<i>Scoliophthalmus</i> Becker, 1903			*			
109	<i>Sepsidoscinis</i> Hendel, 1914					*	
110	<i>Siphonella</i> Macquart, 1835			*			
111	<i>Siphonellomyia</i> Seguy, 1934	*					
112	<i>Siphunculina</i> Rondani, 1856			*			
113	<i>Speccafrons</i> Sabrosky, 1980		*				
114	<i>Stenoscinis</i> Malloch, 1918		*				
115	<i>Strandimyia</i> Duda, 1930	*					
116	<i>Tachinoceros</i> Meijere, 1921					*	
117	<i>Thyridula</i> Becker, 1911						*
118	<i>Togeciphus</i> Nishijima, 1955					*	
119	<i>Trachysiphonella</i> Enderlein, 1936			*			
120	<i>Tricimba</i> Lioy, 1864			*			
121	<i>Tricimbomyia</i> Cherian, 1989					*	
122	<i>Tropidoscinis</i> Enderlein, 1911	*					
123	<i>Tylopterna</i> Bezzi, 1916					*	
124	<i>Vanchium</i> Cherian, 1999					*	

Appendix III. List of species examined in this study, with label details. * = type-species of the genus; **= material examined only by photo. For institutional abbreviations, see above. m, male; f, female.

Carnidae

Meoneura flavifacies Collin 1930, 1♀ 1♂

- Sweden, Lapland, N68.20°/E18.52°, Pan trap, M.V. Tschirnhaus coll., 13-17.xii.1991 (MVTPC)

Milichiidae

*Madiza glabra** Fallén, 1820, 1♂

- Morocco, Marrakech, Imlil S'Asni, C.F. Kassebeer coll., 26.iv.1994 (MVTPC)

Phyllomyza flavitarsis (Meigen 1830), 1♂

- Germany, Eifel mountains, Kreis Daun, Malaise trap, K. Colln & T. Pompé colls., 1.i-31.xii.1991 (MVTPC)

Chloropidae (Siphonellopsinae)

Apotropina brunnipennis (de Meijere 1913), 1♂

- Australia, Taree, Lorien Wildlife Refugee, S31°45'04"/E152°32'03", Malaise trap, G. & B. Williams colls., 14-31.xii.2011 (NSW)

Apotropina sp. nov. Hendel 1907, 1♀ 1♂

- Australia, Queensland, Carnarvon National Park, M.V. Tschirnhaus coll., 10.x.2002 (MVTPC)

Siphonellopsis lacteibasis Strobl 1906, 1♀ 1♂

- Australia, Royal National Park, Aanol G. Daniels coll., 10.iv.1971 (QM)
- Australia, Newnes Tonnel, Aanol G. Daniels coll., 10.iv.1971 (QM)

Chloropidae (Chloropinae)

*Chloropella bipartita** malloch 1925, 1♂

- Australia, EUA, Near Eccleston, K.A. Spencer coll., 13.xii.1962 (NSW)

*Chlorops pumilionis** (Bjerkander 1778), 1♂

- Austria, Linz, Bruno Wahl coll., ? (USNM)

Chloropsina citrivora (Sabrosky 1976), 1♂

- USA, Hawaii, Maunawili, Bait trap, P. Gow coll., 1.xi.1951 (USNM)

Chloropsina sp.3 nov. Becker 1911, 1♂

- Australia, M.V. Tschirnhaus coll., ? (MVTPC)

*Diplotoxa versicolor** (Loew 1863), 1♂

- Canada, Saskatoon, Kennet M. King coll., 18.vi.1925 (MZUSP)

*Ectecephala albistylum** Macquart 1851, 1♂

- El Salvador, Santiago de Maria, G.F. & S. Hevel colls., 29.viii.1972 (MZUSP)

Lasiosina sp.3 Becker 1910, 1♂

- USA, Arizona, S. Fork, Cave Creek Coch Co., G. R. Balmer coll., 20.viii.1965 (CDFA)

***Meromyza saltatrix** (Linnaeus 1761), 1♂**

- Austria, Obergurgl, Tirol 1950m, J.R. Vockeroth coll., 13.viii.1953 (MZUSP)

***Meromyzella capensis** Loew 1860, 1♀**

- Nigeria, Zaria, J.C. Deeming coll., 16.v.1970 (MZUSP)

***Sagareocerus aberrans** (Schiner, 1868), 1♂**

- Colombia, Venadillo, Malaise trap, M. Revelo coll., 3.ix.1959 (MZUSP)

***Thaumatomyia gemina* (Becker 1912), 1♂**

- Brazil, PR, Chapecó, S27°07'11.74''/W52°32'20.22'', M. Savaris & S. Lampert colls., 1-31.xii.2012 (MZUSP)

***Trigonomma coeruleifrons* (Becker 1912), 1♂**

- Brazil, SP, Gália, Sweeping, ?, 3.ix.2010 (MZUSP)

Chloropidae (Rhodesiellinae)

***Psilacrum lineatum* Riccardi & Ismay 2017, 1♀ 1♂**

- Brazil, RS, Camaquã, S31.12159°/W51.79237°, Malaise trap, F.D. Kirst & R.F. Krüger coll., 25.xi.2011 (MZUSP)

***Rhodesiella* sp.1 Adams 1905, 1♀**

- Germany, Rhein near Krefeld, Malaise trap, M.V. Tschirnhaus coll., v.1990 (MVTPC)

***Rhodesiella* sp.2 Adams 1905, 1♂**

- Cameroon, Yaoundé, Malaise trap, Sevilor Kekeumou coll., 14-31.v.2010 (JFPC)

***Rhodesiella* sp.3 Adams 1905, 1♂**

- Ivory Coast, S. Hilger & C.F. Kassebeer colls., 13.i-24.ii.1998 (MZUSP)

***Stenoscinis* sp. Malloch 1918, 1♂**

- Brazil, RJ, Nova Friburgo (Mury), S22°24'41''/W42°31'13'', Malaise trap, Amorim & eq. colls. 20-23. ix. 2015 (DMEL)

Chloropidae (Oscinellinae)

***Anatrichus erinaceus** Loew 1860, 2♀**

- Sumatra, Fort de Kock, E. Jacobson coll., 1925 (ZMHU)

***Apallates dissidens** (Tucker 1908), 2♀ 1♂**

- Bahamas, Grand Bahama Island, W. E. Steiner, M. J. & R. Molineaux colls., 24.v.1987 (USNM)
- Maryland, Calvert Co. Chesapeake Beach, Sweeping, Jos. J. Anderson coll., 7.vi.1981 (USNM)
- USA, Florida, ? coll., 6.iii.1930 (USNM)

***Aphanotrigonum trilineatus** (Meigen 1830), 1♀ 1♂**

- Poland, Nimptsch Schles, Duda coll., 26.iv.1912 (ZMHU)

***Batrachomyia nigritarsis** Skuse 1889, 1♀ 1♂**

- Australia, From Frog Royal Park, D.K. McAlpine, D.S. Kent & B. Day colls., 30.vi.1980 (NSW)

***Biorbitella hesperia** (Sabrosky 1940), 1♀ 1♂**

- USA, Antioch, Dickson coll., 18.x.1936 (USNM)
- USA, Victorville, San Berna, R. Schuster & G. A. Marsh colls., 2.v.1953 (USNM)

***Cadrema pallida* (de Meijere 1904), 1♀ 1♂**

- Madagascar, N14°38'/E50°12'. M.V Tschirnhaus coll., 6.vi. 2006 (MVTPC)

***Calamoncosis minima* (Strobl 1893), 1♀ 1♂**

- Germany, emerged from *Lipara lucens* galls, Kiel-Wellsee coll., 15.iv.1976 (MVTPC)

***Chaethippus* sp. Duda 1930, 1♀**

- Peru, Madre de Dios, S13.14°/W69.61°, Malaise trap, B.Brown & G.Kung 23-25.vii.2001 (MZUSP)

***Chaetochlorops inquilina** Coquillett (orig. des.). Ref. Sabrosky 1950c (key, biol.), 1♀ 1♂**

- USA, Falls Church Va, N!, JJDeGryse. coll., 10-19.viii.? (USNM)
- USA, Glassboro, N. J., W.F. Rapp, Jr. coll., 20.viii.1943, (NHM)

***Conioscinella soluta** (Becker 1912), 1♀ 3♂**

- Costa Rica, Farm La Caja., S. José coll., 12.vi-20.vii.1924 (ZMHU)
- Brazil, Nova Teutônia, B27°11'/L52°23', Fritz Plaumann museum coll., 1.iv.1937 (NHMUK)
(*Conioscinella soluta* var. *rufoscutellata*)

***Deltastoma unipunctatum* Malloch 1924, 1♀**

- Australia, Lorien Wildlife Refuge, 3 km N. Lansdowne, G.Williams coll., 3.xi.1991 (NSW)

***Dicraeus vagans* Meigen 1838, 1♀ 1♂**

- Germany, Neumorscheu, Halberg, N51°03'/E90°36', M.V. Tschirnhaus coll., 16.vi.2007 (MVTPC)

***Disciphus peregrinus** Becker 1911, 1♀ 1♂**

- Sumatra, SumatraZool, E. Jacobson coll., 1925 (ZMHU)

***Elachiptera bimaculata* (Loew 1845), 1♀ 1♂**

- Iran, Fars, Jahrom, Malaise trap, Z. Bazyar coll., 2010 (ZBPC)

***Elachiptera brevipennis** (Meigen 1830), 1♀ 1♂**

- Poland, Laband, Os. L. Duda coll., 2.ix.1935 (ZMHU)
- Poland, Nimptsch, Schles. & Duda colls., 01.v.1951 (AMHU)

***Epimadiza* sp. Becker 1910, 1♀**

- Kenya, Kakamega Forest, Kramer et al. colls., 2.v.1929 (MVTPC)

***Eribolus hungaricus* Becker 1910, 1♀ 1♂**

- Germany, Danish border, M.V. Tschirnhaus coll., 12.vi.1968 (MVTPC)

***Eugaurax* sp. Malloch 1913, 1♂**

- Nicaragua, Jinotega, Penas Blancas, N13.17°/W35.38°, Maes & B. Hernandez colls., 25.vii.1997 (MZUSP)

***Fiebrigella* sp. Duda 1921, 1♂**

- Brazil, MA, Bom Jardim REBIO-RES, Armadilha Suspensa, F. Limeira-de-Oliveira, J.T.Camara & J.O.A. Silva colls., 17-27. i.2010 (INPA)

***Gaurax festivus** Loew 1863, 1♂**

- Maryland, Maryland Bethesda, McPhail Trap, G.C. Steyskal coll., 1.vii.1978 (USNM)

***Goniaspis truncata* (Malloch 1913), 1♀**

- Mexico, Tepec, R. & K. Dreisbach coll., 7.v.1956 (USNM)

***Hapleginella laevifrons** (Loew 1858), 1♀ 1♂**

- Austria, Tyrol. Oetz., J. Abraham & J.C. Deeming Colls., 14-19.vi.1964 (NHM)
- Azerbaijan, Zabrat, D. Duda coll., 16.vi.1931 (ZMHU)

***Heteroscinis hystrix* Seguy, 1957, 1♀ 1♂**

- Sierra Leone, extract from rotting coffee berries, E. Hargreaves coll., 17.x.1936 (NHM)
- Nigeria, C.I.E. coll., 5-v-1983 (NHM)

***Hippelates plebejus** Loew 1863, 1♀ 1♂**

- USA, Gatlinburg. Tenn, Sweeping, R.H. Whittaker coll., 29.v.1947 (USNM)
- USA, Ithaca N.Y., R.C.Shannon coll., 5.ix.1922 (USNM)

***Incertella incerta** (Becker 1912), 2♀ 1♂**

- Canada, Ungva Bay, J.F. McAlpine coll., 29.vii.1954 (USNM)
- USA, Union Cty. Tn., G.I. Reeves coll., ? (USNM)
- Canada, Treesbank, Man, N. Criddle coll., 7.ix.1915 (USNM)

***Lasiambia palposa* (Fallén 1820), 1♀ 1♂**

- Italy, N46°37'/E10°35', Ziegler et al. colls., ? (MVTPC)

***Lioscinella sulfurihalterata** (Enderlein 1911), 1♀**

- Paraguay, San Bernadino, K.Fiebrig coll., 3.ii.? (ZMHU)

***Lipara lucens** Meigen 1830, 2♀**

- Germany, Berlin, Lichtwardt coll., 3.vi.1911 (ZMHU)

***Lipara pullitarsis* Doskocil & Chvála 1971, 1♀ 1♂**

- Germany, Bielefeld, extract from *Phragmites*, Doskocil & Chvala colls., 1977 (MVTPC)

***Loxobathmis obliquans** Enderlein 1911, 1♀ 1♂**

- USA, San Mateo, Pablo Schild coll., ? (ZMHU)

***Malloewia diabolus** (Becker 1912), 1♀ 1♂**

- USA, Redding Calif., B. Wade coll., 11. iv.1955 (USNM)

Medeventor nubosus** Wheeler 2007, 1♂ *

- Costa Rica, Puntarenas, Light trap, B.J.Sinclair coll., 22-27.ii.1991 (CNC)

***Medeventor tschirnhausi* Bazyar & Silva 2018, 1♀ 1♂**

- Brazil, MT, Parque Nacional, Chapada dos Guimarães, S15°24'21.8''/W55°50'07.5'', Malaise trap, Lams & Nihei colls., 27.viii-11.ix.2011 (MZUSP)

***Metasiphonella* sp. Duda 1930, 1♂**

- Brazil, SP, Ribeirão Preto, S21°09'54''/W47°50'56'', Sweeping, P. Riccardi coll., 20.xi.2016 (MZUSP)

***Microcercis albipalpis* (Meigen 1830), 1♀ 1♂**

- Germany, Hessen : Neumorschen, M.V. Tschirnhaus coll., 16.vi.2007 (MVTPC)

***Monochaetoscincella anonyma** (Williston 1896), 1♀ 1♂**

- USA, Hawaii, near shore, G. Steyskal coll., 6.vi.1968 (USNM)

***Neoscincella gigas** (Sabrosky 1940), 1♀**

- USA, Iowa, Gould Warren coll., 5.vi.1935 (USNM)

***Notaulacella* sp. Enderlein, 1911, 1♂**

- Nicaragua, Masaya Las Flores, UV trap, Lecocq & Cantamessa colls., vi.1993 (DMEL)

***Opetiophora straminea** Loew 1872, 1♀ 1♂**

- USA, Moab, Utab, G.F.Knowlton coll., 3. viii.1942 (USNM)

***Oscinella frit** (Linnaeus 1758), 1♀ 1♂**

- USA, Hagerstown, Md, Reared from wheat, PRMyers coll., 13.x.1914 (USNM)
- USA, Middleburg Pa, Reared from wheat, PRMyers coll., 5.xi.1919 (USNM)

***Oscinella cf. flavitibia* (Duda 1933), 1♂**

- Brazil, Sta. Rita, Sweeping, Amorim & Falaschi colls., 30.xi.2008 (DMEL)

***Oscinimorpha albisetosa* (Duda 1932), 1♀ 1♂**

- Germany, Island Mellum North Sea, Pan trap, V. Haeseler coll., 8.vi.1985 (MVTPC)

***Oscinisoma cognatum* (Meigen 1830), 1♀ 1♂**

- Germany, Kiel, Extract from *Glyceria maxima*, H. Meyer coll., 26.vi.1983 (MVTPC)

***Paracalamoncosis brasiliensis** Riccardi & Bazyar 2018, 1♂**

- Brazil, MT, Porto Murtinho, S21°41'52.0"/ W57°45'57.1", Malaise trap, Lamas, Nihei & eq. col., 1.vii–15.viii.2012 (MZUSP)

***Polydaspis ruficornis** (Macquart, 1835), 1♀ 1♂**

- Greece, Samothrace, Guichard & Harvey coll., 17.viii. 1962 (NHM)
- France, Abzac (chaseute), K.A. Spencer coll., xi.1989 (NHM)

***Pseudeurina maculata** de Meijere 1904, 1♂**

- Malaysia, Malaysia Johore, 15K NE Kata, J.W. Ismay coll., 28.x.1983 (JIPC)

***Pseudeurina* sp. nov., 1♀ 1♂**

- Brazil, SP, Salesópolis, S23°39.06'/W45°53.53', Sweeping, P.R. Riccardi coll., 20.xi.2016 (DMEL)

***Pseudogaurax anchora** (Loew 1866), 1♀ 1♂**

- USA, Falls Church, Reared from *Philosamia*, A.B.Gurney coll., x.1950 (USNM)
- USA, Lexington, Hatched from Bagworm, KY, Monte Johnson coll., 16.v.1992 (USNM)

***Rhopalopterum limitata** (Becker 1912), 1♀ 2♂**

- Costa Rica, San Mateo CR, Pablo Schild coll., ? (USNM)
- Colombia, Cundinamarca, E.I.Schlinger & E.S.Ross colls., 9.iii.1955 (USNM)
- Costa Rica, K.A. Spencer coll., 25.i.1982 (NHM)

***Sepsidoscinis maculipennis** Hendel 1914, 1♀ 1♂**

- Sumatra, Fort de Kock, E. Jacobson coll., 1923 (ZMHU)

***Siphonella oscinina** (Fallén 1820), 2♀ 1♂**

- USA, Woods Hole, A.H.Sturtevant coll., ix.1970 (USNM)
- USA, Shannon Camp, C. Beegle coll., 15.viii.1967 (USNM)
- Norway, Aurland, M.W. Joyce coll., 3.ix.1958 (NHM)

***Siphunculina brevinervis** Rondani 1856, 1♀ 1♂**

- Poland, Nimptsch, Schles Duda coll., 8.ix.1910 (ZMHU)
- Austria, Rauden, O.S.I. Duda coll., 2.viii.1932 (ZMHU)

***Speccafrons mallochi** Sabrosky 1938, 1♀ 1♂**

- USA, Washington DC, From bird nest, RC SHANNON coll. 2.ii.1913 (USNM)

***Strandimyia* sp. Duda 1930, 1♂**

- Brazil, Nova Teulonia, B27°11'/L52°23', Fritz Plaumann Museum coll., x.1970 (MZUSP)

***Trachysiphonella pygmaea* (Meigen 1838), 1♀ 1♂**

- Germany, Niederbeisheim, N51°03'/E9°31', M.V. Tschirnhaus coll., 16.vi.2007 (MVTPC)

***Tricimba lineella** (Fallén 1820), 1♀ 1♂**

- Germany, Oldenburg, Schildhorn coll., v.1998 (USNM)
- UK, Bristol, E.A. Fonseca coll., 15.ix.1978 (NHM)