Male terminalia of Cercopidae (Hemiptera, Cicadomorpha): towards a consensus terminology

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The study of male genital appendages is often necessary to identify a species and to characterise the higher systematics ranks for the Cercopidae, a large family of Hemiptera. Therefore, many authors have used them in their work but without any clear consensus on the terms used for each part constituting the male terminalia. A standardised terminology is important for the quality of a taxonomic description but even more essential when we want to compare species and establish a primary homology between states of character and their use in the frame of phylogenetic analysis. The use of a consensus terminology should ensure that we are all observing, speaking and describing the same genital appendage and comparing homologous characters. In order to propose a consensus terminology, we have reviewed all the major works on the anatomy of terminalia for the family since the first description using those characters in 1922. We proposed the use of consensual terms, listed with their definitions. In addition we studied a diversified panel of male specimens, chosen in order to represent as many Cercopidae tribes as possible. We categorised five different groups of Cercopidae according to their male terminalia structures. This opens the reflection on the evolutionary patterns for these structures.

The Cercopidae constitutes a diverse family found around the world, with 1540 species described and distributed in 176 genera. They are xylem-feeders feeding on a large range of plants. Adults are found above ground, feeding on different parts of the plants, while some of the nymphs sap suck on roots. The terminologies used to describe the different body parts of species in taxonomy can differ greatly depending on the group, authors and over time. The lack of accurate and precise terminology makes it impossible to compare characters rigorously. It is a problem not only for an accurate identification but for building a phylogenetic analysis and using characters for which primary homology should be evaluated and stated prior to comparing data described for the compared species. In 1970, Tuxen made a glossary referencing all the terms used through the different studies of the genitalia of insects with their definition. Nevertheless, discrepancy between the terminology and the specific organ applies, and remains in most groups, Cercopidae are no exception. Singh-Pruthi mentioned in his works on Rhynchota, that the works of several authorities proving the importance of genitalia in classification, show that in the absence of a detailed morphological account there has been a great multiplicity of terms and a considerable amount of confusion in their application.

The conservatism in the body shape and the convergence in the colouration patterns observed within the Cercopidae family make the identification to the generic or specific level challenging. When working on South American Cercopidae, Fennah in 1968 stated that female and male genital characters can be used for grouping species since they can be considered the least likely to have been influenced by parallel evolution. Male terminalia structures can also be diagnostic for species identifications, but in the majority of the old taxonomic literature, illustration and/or description of such diagnostic features is lacking, making the identifications more complicated. However the use of genitalia characters is not new for this group but as predicted by Singh-Pruthi in 1925, and shown by Fennah, the male genitalia play a decisive role in the discrimination of the species. Therefore it is a necessary tool in every taxonomic work on Cercopidae. Numerous works on the morphology of Hemipteran genitalia have been done through the years. Some tried to homogenize the terminology but no consensus has been reached yet and many different terms remain, used by authors and producing literature that can be tricky. In this work, focusing on the Cercopidae, we propose to review the terminologies and to standardise it for the different pieces constituting the male terminalia.
Cercopidae systematics
Suborder Cicadomorpha Evans, 1946
Superfamily Cercopoidea Leach, 1815
Family Cercopidae Leach, 1815

Type species: Cercopis sanguinolenta (Scopoli, 1763)

In 1961, the family Cercopidae was classically divided into two subfamilies: Cercopinae Leach, 1815 and Callitettixinae Metcalf 1961. In 1968, Fennah was working on Cercopidae from the New World and grouped them according to the structures of male and female genitalia. He suggested subdividing the family into two subfamilies, the Tomaspidinae containing all the New World genera and the Cercopinae dedicated to the Old World genera. He ignored the Callitettixinae because he was working on the New World taxa. According to Fennah, the Tomaspidinae generally present a metatibiae bearing two lateral spines, the male subgenital plates appear as an extension of the pygofer without any separation or groove and the first female valvulae bear some basal processes. In 2001, Hamilton described a new family from the American tropics, the Epipygidae and suggested including the Aphrophoridae as a subfamily in the Cercopidae. Cryan and Svenson in 2010 presented the first phylogenetic molecular investigation on the Cercopoidea, which suggests that four of the five described families, Cercopidae, Clastopteridae, Madaerotidae and Eppygidae are monophyletic, the latest being nested within the Aphrophoridae. According to the selection of genera present in the phylogeny, a monophyletic lineage for the New World can be observed and designated as subfamily Ischnorhininae (sensu Carvalho & Webb 2005). Paladini et al. in 2015 follow Cryan & Svenson and propose to subdivide the subfamily in three tribes: Ischnorhinini, Neanini and Tomaspidini. In 2018, Paladini et al. indicate a need to revise the genera included in the Tomaspidini and Ischnorhinini since those tribes do not remain monophyletic in their molecular analyses. According to Liang and Webb (2002), the current Old World classification of Cercopidae, together with many generic concepts, is based on the work of Lallemand, using the number of spines on the hind tibia, and characters of the head, pronotum and fore wings. The Cercopidae is composed of numerous tribes and a series of incertae sedis genera. The monophyly of this subfamily was never tested. Liang and Webb revised the Rhinaulicinae from southern Asia. It is the latest morphological work done at a tribal level for the Cercopidae. Cryan and Svenson point out that the taxonomic sample included in their phylogeny did not allow a comprehensive examination of Old World tribal structure, but some trends are emerging and suggest that their generic constituency needs to be examined in greater detail. If the construction of a molecular phylogeny for the Old World genera is needed in order to better understand their relationships, and the study of morphological structures should not be neglected. In order to be able to compare those structures we have to be sure that we compare the same structures. Male terminalia are no exception.

Results and discussion on the general morphology of male terminalia (Fig. 1). In 1910, Jacoby valued the inclusion of the male terminalia description and their illustration, through the description of a series of new species of Cercopidae. This practice is now widespread among the authors and became a necessity in the description of each taxon. In the meantime, this generated numerous terminologies. For the Hemiptera different scientists made some attempt to homogenise the vocabulary used in this group, such as Crampton 1922, Singh-Pruthi 1925, Snodgrass 1935, Kramer 1950, and Marks 1951. As presented in Table 1, no consensus has been reached yet. The absence of standardisation in the terminologies can lead to misidentification, confusion in identification keys or homology recognition, difficulty in the communication between scientists, and inefficiency in scientific results (Bourgoin et al. 2015). If for some terms, such as pygofer, subgenital plates and aedeagus a consensus seems to have emerged, others are still described under different names. Finally, other structures were mentioned recently since their presence was observed only in few taxa. This is the case for the lateral and intermediate plates, respectively mentioned by Liang and Webb and Soulier-Pernis and Le Cesne. We propose here a consensual terminology regarding the practices of authors in this domain (Table 1).

Terminalia. We group under this term the pygofer and the structures it bears plus the anal tube.

Pygofer (Fig. 1A). Here we consider it as being the ninth abdominal segment. However certain authors introduce some subtlety. Singh-Pruthi refers to the pygofers as the large and conspicuous lateral regions of the ninth abdominal segment. Crampton refers to the ninth sternite when he uses the term hypantrum. In the Cercopidae, it is a ring-like structure composed of the tergite and sternite, excluding the subgenital plates appearing as an appendage of it.

Anal tube (Fig. 1A). It corresponds to the tenth and eleventh segments. The sclerites of the tenth and eleventh segments are separated by inter-segmental membrane) and terminate in an elongated spoon-shaped process under the anus, the anal style as described by Singh-Pruthi.

Subgenital plates (Fig. 1A). They are a pair of plates arising from the posterior ventral margin of the pygofer as referred to by Hamilton and Morales. Singh-Pruthi refers to them as a pair of well-developed appendages of the ninth sternite. They can be flexible but are never provided by muscles. In some groups, these appendages have developed in continuity with the pygofer and are fused to it. Some intermediate cases can be observed as well. The three alternatives can be observed for the Cercopidae.

Parameres (Fig. 1A,B). Crampton calls them Styles, gonostyli or gonopods and mentions their connections with the base of the aedeagus by what he calls a connective. Singh-Pruthi lists the terms claspers, laterals or
genital styles as synonyms. Snodgrass calls them harpagones and describes them as a paired structure articulated to some part of the ninth segment. Individually provided with muscles, they arise from the floor of the genital chamber and are connected to the sclerites of the phallobase via the connectives. These appendages are generally placed on each side of the aedeagus.

*Aedeagus (Fig. 1A,B,D).* It is a median tubular structure equally chitinised. Some authors call the aedeagus plus the phallobase, the penis, or phallus. When the theca of the phallobase is developed and completely or

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**Figure 1.** Schematic representation for the morphology of male terminalia. (A) Lateral view of a male terminalia. (B) Antero-posterior view of the parameres, basal plates and aedeagus. (C) Internal view of the right side of the Terminalia, showing the subgenital plate, the sterno-lateral plate and the intermediate plate in between. (D) Lateral view of the Aedeagus and phallobase.
Table 1. Terminologies used by different authors since Crampton, 1922 to designate different parts of the male terminalia.

| Proposed terminology | Pygofer | Anal tube | Subgenital plates | Intermediate plates | Sterno-lateral plates | Parameres | Phallobase | Aedeagus |
|----------------------|---------|-----------|-------------------|---------------------|-----------------------|-----------|------------|----------|
| Crampton, 1922 | Ninth sternite or Hypandrium | – | Hypovalvae, Hypan- drial valves | – | – | Styl., Gonostyli, Gonopods | – | Aedeagus |
| Singh-Pruthi, 1925 | Pygofer | – | Sub-genital plates | – | – | Parameres | Perandrium | Aedeagus |
| Snodgrass, 1935 | – | – | – | – | – | Harpagones | Phallobase | Aedeagus |
| Lallemand, 1949 | IXth segment | Anal tube | Genital plates | – | – | Styles | – | Penis |
| Kramer, 1950 | IXth segment | Anal tube | Subgenital plates | – | – | Parameres | Basal plates | Aedeagus |
| Marks, 1951 | IXth sternum | Anal tube | – | – | – | Gonoforceps | Basal plates | Aedeagus |
| Fennah, 1968 | Pygofer | Anal segment | Subgenital plates | – | – | Genital styles | – | Aedeagus |
| Hamilton and Morales, 1992 | Pygofer | Anal tube | Subgenital plates | – | – | Styles | Phallobase | Aedeagus |
| Yang and Chang, 2000 | IXth segment | IX–X segments | Genital plates | – | – | Genital styles | Phallobase | Aedeagus |
| Liang and Webb, 2002 | Pygofer | Anal tube | Subgenital plates | – | – | Lateral plates | Styles | – | Aedeagus |
| Liang, 2003 | Pygofer | Anal tube | Subgenital plates | – | – | Basal plates | Genital styles | – | Aedeagus |
| Carvalho and Webb, 2005 | Pygofer | – | Subgenital plates | – | – | Parameres | Connective | Aedeagus |
| Soulier-Perkins and Kunz, 2012 | Pygofer | Anal tube | Subgenital plates | – | – | Lateral plates | Parameres | – | Aedeagus |
| Liang et al. 2012 | Pygofer | Anal tube | Subgenital plates | – | – | Lateral plates | Genital styles | – | Aedeagus |
| Paladini et al. 2015 | Pygofer | Anal tube | Subgenital plates | – | – | Parameres | – | Aedeagus |
| Soulier-Perkins and Le Cesne, 2016 | Pygofer | Anal tube | Subgenital plates | Intermediate plates | Lateral plates | Parameres | – | Aedeagus |

Phallobase (Fig. 1A,B,D). As defined by Tuxen⁴, it is the whole structure supporting the aedeagus. For the Cercopidae it is reduced to a small ring at the base of the aedeagus. It is composed of the basal plates (BsP), nested in the genital chamber, extending toward the parameres and the thickened segmental membrane of the IXth segment covering them. Tuxen also mentions the connective as being a sclerotized structure belonging to the phallobase and connecting it to the styles and mentions that for the Auchenorrhyncha, it is a synonym for basal plate. It is Snodgrass in 1935⁴⁴, who describes the phallobase for the first time as being the proximal part of the phallus highly variable in its development, sometimes a large structure supporting the aedeagus, often produced in a thecal fold of sheath about the aedeagus, sometimes represented only by basal phallic sclerites in the wall of the wall of the aedeagus. Since then, in descriptive works, the sclerified basal parts, extending toward the parameres took different names. Yang and Chang in 2000⁷,⁷⁷, call it basal part phallobase, when Carvalho and Webb⁶⁷ call it connective.

Sterno-lateral plates (Fig. 1C). They are a pair of plates present only in some genera of Cercopidae. First described by Liang and Webb⁷⁷, they seem to have the same origin as the subgenital plates, they arise from the ninth sternite and are generally flexible but are not provided with muscles. They are located above the subgenital plates, on the pygofer margin.

Intermediate plates (IR, Fig. 1C). These structures are paired like the subgenital and lateral plates. They were observed first in 2016 by Soulier-Perkins and Le Cesne⁶⁴ and illustrated as well in Crispolon et al. 2019⁷⁷. When present, the intermediate plate links the subgenital plate to the lateral plate and often takes the shape of a small bridge.

All five families of Cercopoidea possess male genitalia with the same basic parts even if in the literature we encounter different terminologies. Using common terms to all of them should be an achievable goal. The terminology problems increase when we compare these structures to those described in other groups within the Auchenorrhyncha. The term pygofer is used in all the other families of Cercopoidea⁴⁸–⁴⁹, as well as in Cicadellidae⁵⁵,⁶⁶ and Membracidae⁵⁷–⁵⁹ but pygofer does not cover quite the same structures. In Membracoidea
only the tergite is considered the pygofer. The sternite, which may be fused or articulated to the tergite, is called
the valve, and the subgenital plates, which also may be either fused or articulated to the valve (IXth sternite) are
usually not considered part of the pygofer. In the Fulgoromorpha the term pygofer includes tergite and sternite,16,21
and there is no question about the subgenital plates that are absent in this group. In the Cercopoidea, because the
tergite is fused to the sternite, it seems logical to call this ring-like structure pygofer and consider the subgenital
plates separately, like for the Membracoidea. Those subgenital plates are a pair of plates arising from the IXth
sternite for all the cercopoid,38–44, Cicadellidae45,46, and Membracidae47–50. The term lateral plate is used for the
Cercopidae for the first time by Liang and Webb3 then Soulier-Perkins and Kunz23. These plates are present in
some tribes of the Old World Cercopidae, they arise like the subgenital plates from the IXth sternite. However, the
term lateral plate is also used for the Membracoidea47–50 and designates a synapomorphic character for this group
and this distinctly delimited structure, either entirely or distally free or entirely fused to the pygofer, originating
from the IXth tergite. So, if in both groups we consider that the lateral plates arise from the pygofer, they are not
of the same origin, and are not of homologous structures. For these reasons, we suggest changing the term lateral
plate to sterno-lateral plate for the Cercopidae in order to emphasise their different origin. The appendages on
each side of the aedeagus are generally named parameres in Cercopidae6,12,15,22,23 and Machaerotidae42 when
the term style is preferred for the Aphrophoridae39–43, Clastopteridae42,44, Epipygidae38 and Membracoidea46–50.
Even though the term style is used for the Fulgoromorpha the term gonostyle is widely used as well51,53. Authors
generally describe the aedeagus as the median tubular part bearing the ejaculatory duct. To refer to the sclerotized
part the term theca is sometimes used, for instance for the Clastopteridae by Hamilton42 or aedeagal shaft for
the Cercopidae.5,22. At the base of the aedeagus, the reduced phallobase is essentially represented by a thickened
membrane of the IXth segment and the basal plates, which support the ejaculatory duct and connect the phallic
structure to the parameres. This structure is not always drawn and named in taxonomic works, but when it is
represented it can be called connective5,22,55 or just labelled as phallobase32,37,42. For some Fulgoromorpha such as
the Tropiduchidae, Bourgoin and Huang51 describe the phallobase sensu lato as being a synonym of the perian-
drum and what they describe as phallobase sensu stricto (sensus Fennah 1945)54 is a development of this structure
folding around the aedeagus in an external sclerified phalotheca and an internal membranous endotheca. This
phallobase sensu stricto can be considered absent in the Cercopidae. They described what remains as a
thickening of the diaphragm which corresponds to what we called thickened segmental membrane of the IXth
segment. Bourgoin and Huang also describe precisely what they call the connective sensu lato an internal
composite structure. The first part is composed at the base by a small pregenital invagination of the diaphragm
called the ventral support, followed by the body of the connective, which runs in the general cavity and finishes
in a gutter shape structure. This first part is the connective sensu stricto and it is topped by the second part, the
tectiform structure. In between these two parts the ejaculatory duct goes through and rest in the gutter-shaped
part. The tectiform structure does not exist in the Cercopoidea and the fulgoromorphan’ connective is difficult
to synomrise with the term connective used for the Cercopidae. In both cases the described structures link
the parameres to the base of the phallus and support the ejaculatory duct but are not quite of the same origin.

Focusing on the Cercopidae, and according to the definitions provided above and the observations done on
specimens selected to illustrate the cercopid diversity, we observe different degree of fusion of the subgenital
plates to the pygofer, the presence or absence of sterno-lateral plates and when those plates are present another
pair of plates can sometimes be observed as well, the intermediate plates.

Fennah in his work of 1968 pointed out the importance of the genital characters to study the Cercopidae and
considered them as not being influenced by parallel evolution. Without discussing the higher rank of the
family, Fennah is the first to mention the different configuration of the male terminalia and that it could reflect
the phylogenetic relationship of family. He expressed it by dividing the Cercopidae in two subfamilies but did not
deepen it. His hypothesis was recovered by a first phylogeny of the Cercopidae of the World33, where the new
world cercopids derived from the Old Word. They suggested that the genital characters reflect the same evolution.
As such, a complete fusion of the subgenital plates with the pygofer is a derived state compared to a partially fused
or distinctly separated subgenital plates to the pygofer. The presence of sterno-lateral plates is only observed in
some genera found in the Old world and could be a derived state and a synapomorphy within a monophyletic
lineage. The appearance of intermediate plates linking the sterno-lateral plate to the subgenital plate could be a
step further within the evolution of this character, but those hypotheses remain mere speculation for now since
the phylogeny of the whole Cercopidae family is not yet available. The optimisation of these patterns should be
done when it becomes possible to test them. It has to be pointed at as well that when the subgenital plates are
partially or completely fused to the pygofer, no sterno-lateral plates can be observed.

For now, as a practical tool, but without any intention to describe different states of evolution, we propose to
group the male terminalia of Cercopidae in five categories (Table 2). As illustration for the group 1, we can
take the type-species, Cercopis sanguinolenta for which the subgenital plates are clearly distinct from the pygofer
and do not possess any other plates, neither a sterno-lateral nor an intermediate plate (Fig. 2A,B). The group 2
includes all the New World cercopids observed. It is characterised by the fusion between the subgenital plates
and the pygofer, the subgenital plates appear as an elongation of the sternite IX without any distinction from it
(Fig. 2C,D). Those terminalia do not possess any additional plates. The group 3 possess subgenital plates partly
fused to the pygofer, however a fold is visible, on each side, a groove is running down but does not reach the
ventral part (Fig. 2E,F). If the pygofer is generally shaped as a uniform sclerotized ring, in this third group, a
ventral narrow antero-posterior membranous band can be observed. The group 4 presents some subgenital
plates clearly distinct from the pygofer, some extra structures can be observed, above the subgenital plates.
Those structures are the sterno-lateral plates (Fig. 2G,H). A groove individualises them from the pygofer. The group
5, similar to group 4, possess a pair of subgenital plates distinct from the pygofer, a pair of sterno-lateral plates
and a pair of intermediate plates that are, small sclerotised plates, shaped as a bridge and linking the subgenital
plate to the sterno-lateral plate (Fig. 2I,J).
| Subfamilies       | Tribes          | Species                        | Biogeographic regions | Subgenital fused to the pygofer | Sterno-lateral plates present | Intermediate plates present | Terminalia group |
|-------------------|-----------------|--------------------------------|-----------------------|---------------------------------|-------------------------------|-----------------------------|------------------|
| Calitettixinae    | Calitettixini   | Abdalma producta (Walker, 1851) | Oriental              | No                              | Yes                           | No                          | 4                |
|                   |                 | Callitettix versicolor (Fabricius, 1794) | Oriental              | No                              | Yes                           | No                          | 4                |
|                   | Considiini      | Considia nitidula (Breddin, 1902) | Oriental              | No                              | No                            | No                          | 3                |
|                   |                 | Cercopini                       | Cercopsis sanguinoleta (Scopoli, 1763) | Palearctic                     | No                            | No                          | 1                |
|                   |                 | Hemitricephora haglundi (Schooteden, 1901) | Afrotrropical         | No                              | No                            | No                          | 1                |
|                   |                 | Cosmoscarina herosa (Jacobi, 1921) | Oriental              | Only partially                  | No                            | No                          | 3                |
|                   |                 | Ectomnnotum bivittatum (Le Peletier de Saint-Fargeau & Serville, 1825) | Oriental              | Only partially                  | No                            | No                          | 3                |
|                   |                 | Euryaulacini                    | Euryaulax carnea (Fabricius, 1775) | Oceanic                         | No                            | Yes                         | 5                |
|                   |                 | Leptataspis discolor (Boisduval, 1835) | Oriental & Oceanic     | Only partially                  | No                            | No                          | 3                |
|                   | Locridini       | Locris vicina (Signoret, 1860)  | Afrotropical           | No                              | No                            | No                          | 1                |
|                   |                 | Apthius albonigerus Le Cesne & Soulier-Perkins | Oceanic              | No                              | Yes                           | Yes                         | 5                |
|                   |                 | Eoscarta borealis (Distant, 1878) | Oriental & Oceanic     | No                              | Yes                           | No                          | 4                |
|                   |                 | Miniscartea obesuripennis Schmidt, 1920 | Oriental              | No                              | Yes                           | Yes                         | 5                |
|                   |                 | Paramiscartia brunnea (Lallemand, 1920) | Afrotropical           | No                              | Yes                           | No                          | 4                |
|                   |                 | Poecilotrepa mangkas Crispollon & Yap, 2019 | Oriental              | No                              | Yes                           | Yes                         | 5                |
|                   |                 | Poecilotrepa minutia Lallemand, 1922 | Oriental              | No                              | Yes                           | Yes                         | 5                |
|                   |                 | Wiwi mei Soulier-Perkins & Le Cesne, 2016 | Oceanic              | No                              | Yes                           | Yes                         | 5                |
|                   | Trichoscartini  | Trichoscarta roborea (Distant, 1900) | Oriental              | Only partially                  | No                            | No                          | 3                |
|                   | Suracartini     | Opistharsostethus demonstratus (Distant, 1900) | Oriental              | Only partially                  | No                            | No                          | 3                |
|                   |                 | Simiridia viridans (Guérin-Méneville, 1834) | Oriental              | Only partially                  | No                            | No                          | 3                |
|                   |                 | Suracarta basinotata (Butler, 1874) | Oriental              | Only partially                  | No                            | No                          | 3                |
| Ischnorhininae    | Ischnorhinini   | Laccogrypota valida (Distant, 1909) | Neotropic             | Yes                             | No                            | No                          | 2                |
|                   | Neanini         | Zusta raviella (Lallemand, 1924) | Neotropic             | Yes                             | No                            | No                          | 2                |
|                   | Tomaspini       | Aeneolamia contigua (Walker, 1851) | Neotropic             | Yes                             | No                            | No                          | 2                |
|                   |                 | Huataina inca (Guérin-Méneville, 1844) | Neotropic             | Yes                             | No                            | No                          | 2                |
|                   |                 | Paeahantascomenis bella (Walker, 1851) | Neotropic             | Yes                             | No                            | No                          | 2                |
|                   |                 | Prosapia simulans (Walker, 1858) | Neotropic             | Yes                             | No                            | No                          | 2                |
| Incertae sedis    | Phymatostetha sp. | Neotropic                     | Yes                    | No                              | No                            | No                          | 1                |
|                   | Pogonosceliella madagasarcensis Schmidt, 1910 | Afrotrropical         | No                              | No                            | No                          | No                          | 1                |
|                   | Radioscarta sp. | Neotropic                     | Only partially        | No                              | No                            | No                          | 3                |

Table 2. Species studied with the subfamily, tribe, biogeographical region and terminalia group to which they belong.
Figure 2. Different morphological configurations observed for the male terminalia. (A) *Considia nitidula* (Breddin, 1902), (B) *Cercops sanguinolenta* (Scopoli, 1763), (C) *Pachacanthocnemis bella* (Walker, 1851), (D) *Prosapia simulans* (Walker, 1858), (E) *Cosmoscarta herossa* Jacobi 1921, (F) *Radioscarta* sp. (G) *Eoscarta borealis* (Distant, 1878) (H) *Callitetix versicolor* (Fabricius, 1794), (I) *Aufidus albonigrus* Le Cesne & Souliers 2021 J. *Wawi mehi* Soulier-Perkins & Cesne 2016.
Material and method

Preparation. The abdomen of each specimen examined was cut off and cleared for 20 min in warm (80 °C) 10% KOH. Dissections and cleaning of genital structures were performed in distilled water. If needed, a few drops of blue paragon for dying the ectodermic genital ducts were added for a few minutes. Final observations were done in glycerine using a Leica microscope (MZ16).

Abbreviations. IRScNB: Royal Belgian Institute of Natural Sciences.
MNHN: National Museum of Natural History, Paris.
NHM: British Museum, London.
MNHN-UPLEB: Museum of Natural History, University of the Philippines Los Baños, Philippines.

Material examined. Abidama producta (Walker, 1851) 55: 1 male, [Avril-Juin], [Museum Paris; Tonkin Central, Region de Tuyen-Quan et de Dong-Chau; A. Weiss, 1901], [Museum Paris; MNHN(EH) 24755].
Aeneolamia contigua (Walker, 1851) 55: 1 male, [Museum Paris; Venezuela Llanos; F. Grey, 33–96], [Museum Paris; MNHN(EH) 24756].
Aufidus albomarginus Le Cesne & Soulier-Perkins, 2021 56: 1 male, [Holotype], [Papua New Guinea, Madang province, Wanang 180 m, S5° 13’ 40” E145° 04’ 47”], [Museum Paris, PL camp, 27-XI-2012, A. Soulier-Perkins rec.], [MNHN(EH)240457].
Callitettix versicolor (Fabricius, 1794) 57: 1 male, [Vietnam, Kien Giang, Hon Chong, Kien Luong, Nui Bai Voi hospital-cave, 10°13.358’N 104°36.588’E], [Museum Paris; 4-VI-2008; calcareous hill, 17 m; A. Soulier-Perkins rec.], [Callitettix versicolor (Fabricius, 1794); M. Le Cesne det. 2019], [Museum Paris; MNHN(EH) 24656].
Cercopsis sanguinolenta (Scopoli, 1763) 58: 1 male, [44° 57’ 0–03° N, 5° 44’ 0–10° E; La Motte d’Aveillans, Isère, France; 25.V.12, coll. by O. Béthoux], [sanguinolenta Scopoli, 1763; Cercopis sanguinolenta det. by O. Béthoux, 2012], [IWC OB 1046], [Cercopsis sanguinolenta (Scopoli, 1763); A. Soulier-Perkins det. 2017], [Museum Paris; MNHN(EH) 24542].
Considia nitidula (Breddin, 1902) 59: 1 male, [Museum Paris; Perak.Coll. Nouahlhier 1898], [$], [Considia nitidula (Breddin, 1902); M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24737].
Cosmoscarta herossa Jacobi, 1921 60: 1 male, [Tonkin; Cho-Ganh; L. Duport], [Collection E. Fleutiaux], [Cosmoscarta herossa Jacobi, 1921; M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24658].
Ectomnonotum bivittatum (Le Peletier de Saint-Fargeau & Serville, 1825) 61: 1 male, [Museum Paris; M° du Ht Song-Chai; Rabier 258–95], [Ectomnonotum bivittatum var. flavisfascium Walk.], [Museum Paris; MNHN(EH) 24645].
Eoscarta borealis (Distant, 1878) 61: 1 male, [Museum Paris; Tonkin, reg. de HOA-BINH; A DE COOMAN, 1926], [Eoscarta borealis Distant, 1878; M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24660].
Euryaulax carnifex (Fabricius, 1775) 62: 1 male, [Australie; Chilagoe GPS300; 11/12-III-1997; Th. Bourgoin rec.], [Museum Paris; piège lumineux; Th. Bourgoin rec.], [Euryaulax carnifex (Fabricius, 1775); M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24753].
Hemitrechophora haglundi (Schouteden, 1901) 63: 1 male, [La Maboké; Rep. Centrafric.; V.1966; Michel Bouillard], [Museum Paris], [Hemitrechophora haglundi (Schouteden, 1901); M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24648].
Huaina inca (Guérin-Méneville, 1844) 64: 1 male, [Mexique, Malinalco; Mexico; 24-X-1977; D. Pluot Rec.], [Huaina inca (Guérin-Méneville, 1844); M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24624].
Leptataspis discolor (Boisduval, 1835) 65: 1 male, [Museum Paris; I. Waigeoe; coll. Noahlhier, 1898], [Leptataspis discolor (Boisduval, 1835); M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24650].
Laccogrypota valida (Distant, 1900) 66: 1 male, [18/08/2009; Pocaré; Nouragues; Guyanne; piege vitres], [Laccogrypota valida (Distant, 1900); M. Le Cesne det. 2009], [Museum Paris; MNHN(EH) 24662].
Locris vicina (Signoret, 1860) 67: 1 male, [20/III/2006; 633 m; parc de Zombitse, hospital-cave, 22° 40.460’S 44° 51.633’E], [Museum Paris; Madagascar 2006; reg. Atsimo-andrefana, A; Soulier-Perkins rec.], [Locris vicina (Signoret, 1860); A. Soulier-Perkins det. 2007], [Museum Paris; MNHN(EH) 24659].
Mioscarta obscuripennis Schmidt, 1920 68: 1 male, [Philippines, Negros; volcan Canlaon, forêt; N 10°25’ 31” E 123°05’43”], [Museum Paris; piège lumineux; 1098 m asl; 30-X-2010; A. Soulier-Perkins rec.], [Museum Paris; MNHN(EH) 24661].
Opistharsostethus demonstratus (Distant, 1909) 69: 1 male, [Indonesia, Borneo; West Kalimantan prov.; Mount Bawang; 1400 m], [Opistharsostethus demonstratus (Distant, 1909); M. Le Cesne det. 2009], [Museum Paris; MNHN(EH) 24691].
Pachacanthocnemis bella (Walker, 1851) 55: 1 male, [Museum Paris, EQUATEUR LOCA (Ex. Coll. A. DAVID, R. OBERTHUR 1903)], [Pachacanthocnemis bella (Walker, 1851); M. Le Cesne det. 2020], [Museum Paris; MNHN(EH) 24847].
Paramioscarta brunnea (Lallemand, 1920) 70: 1 male, [22/III/2006; Anjâ, réserve village; forêt, 1000 m; 21° 51.120’S 46° 50.773’E], [Museum Paris; Madagascar 2006; reg. Haute Matsiatra; A. Soulier-Perkins rec.], [Paramioscarta brunnea (Lallemand, 1920); M. Le Cesne det. 2019], [Museum Paris; MNHN(EH) 24657].
Phymatostetha sp.: 1 male, [Forestry P.I.; 100 m; IV-28–58; P. P. Bandong], [Phymatostetha sp.; 1 male, [Forestry P.I.; 100 m; IV-28–58; P. P. Bandong], [UPLBMNH; HEM-04214], [MNHN-UPLEB].
Poeckloterpa mangkas Crisapolon & Yap 2019: 1 male Holotype, [Philippines; Negros; volcan Canlaon, forêt; N 10°25’ 31” E 123°05’40”], [Poeckloterpa mangkas Crisapolon & Yap 2019; 1 male Holotype], [Museum Paris; piège lumineux; 1098 m asl; 29-X-2010; A. Soulier-Perkins rec.], [Museum Paris; MNHN(EH) 23642].
Poeckloterpa minuta Lallemand 1922: Male paratype, [Mt. Makiling; Luzon, Baker], [Lallemand Coll. B.M.1955-832], [Paratype]. (NHM).
Pogonorhinella madagascariensis Schmidt, 191022: 1 male, [Madagascar; province of Toamasina; Andasibe, 1049 m; S18° 53.410′ E48° 23.881′], [Museum Paris; forêt humide, brède piste nickel; 05-XI-2011; A. Soulier-Perkins Rec.], [Pogonorhinella madagascariensis Schmidt, 1910; M. Le Cesne det. 2019], [Museum Paris, MNHN(EH) 2419].

Prosapia simulans (Walker, 1858)23: 1 male, [Mexiq], [Museum Paris, Coll. G. Fallou 259-95] [Tomaspis simulans Walker] [Prosapia simulans (Walker, 1858), M. Le Cesne det. 2016], [Museum Paris; MNHN(EH) 24848].

Radioscarta sp.]: 1 male, [Coll. I.R.Sc.N.B.; Singapore Nee Soon Mal Trap 2; Station 25091; 27-IV-05; swamp forest; Leg P. Grootaert]. (IRScNB).

Simeliria viridans (Guérin-Méneville, 1834)24: 1 male, [Museum Paris; Java, Tjibogo, Preanger (J B Ledru); R. Oberthur, 1898].

Suracarta basinotata (Butler, 1874)25: 1 male, [Suracarta sp ?; Michel Bouabdell 19.], [90-24], [Suracarta tricolor var bainonata (Butl.); det. A.P. Liang ’90], [Museum Paris; MNHN(EH) 24694].

Trichoscarta roborea (Distant, 1900)26: 1 male, [Museum Paris; Borneo; R. Oberthur, 1898], [Museum Paris; MNHN(EH) 24754].

Wawi mehi Soulier-Perkins & Le Cesne, 201627: Male holotype, [Papoua-New-Guinea; Mt Wilhelm; 2073 m; S5° 45′ E145° 11′ 10″], [Museum Paris; Malaise trap; 27-X-2012], [Museum Paris; MNHN(EH) 22754], [Wawi mehi Soulier-Perkins & Le Cesne, 2016; A. Soulier-Perkins det. 2016].

Zuata ravidella (Lallemand, 1924)28: 1 male, [Museum Paris; Bolivia; Coll. Noualhier, 1898], [Museum Paris; MNHN(EH) 24693].

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All authors worked on the specimens studied, on the writing of the manuscript text and reviewed it. The figures were done by M.L.C. and A.S.

**Competing interests**
The authors declare no competing interests.

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