

Cladistic analysis of *Zethus* Fabricius, 1804 (Hymenoptera, Vespidae): a new subgeneric classification

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Academic editor: Michael Ohl | Received 10 March 2021 | Accepted 1 April 2021 | Published 29 April 2021

<http://zoobank.org/47FBD08B-B6AE-4004-A25F-CB7F3FB8D13F>

Citation: Lopes RB, Carpenter JM, Noll FB (2021) Cladistic analysis of *Zethus* Fabricius, 1804 (Hymenoptera, Vespidae): a new subgeneric classification. *Journal of Hymenoptera Research* 82: 253–283. <https://doi.org/10.3897/jhr.82.65760>

Abstract

Zethus is the largest genus in Vespidae with over 270 species. It is currently divided into four subgenera: *Z. (Zethus)*, *Z. (Zethoides)*, *Z. (Zethusculus)* and *Z. (Madecazethus)*. While the last three are restricted to certain biogeographic areas, the first is spread through western and eastern hemispheres. Studies have shown possible phylogenetic incongruence regarding this current division and even raised the possibility of paraphyly in the genus. To evaluate this classification, morphological parsimony analyses under implied weights was carried out, examining external morphology and male genitalia. Analyses showed paraphyly of the genus under various “k” values and paraphyly of two subgenera. *Ischnocoelia* and *Ctenochilus* are lowered to subgenera of *Zethus*. *Zethus (Madecazethus)* is no longer restricted to Malagasy species and now includes those of the African continent as well. *Zethus (Zethastrum)* **subg. nov.** is defined for Oriental representatives. *Z. (Zethus)* is subdivided into three subgenera: *Z. (Zethus)*, *Z. (Didymogastra)* and *Z. (Wettsteinia)*. *Zethus (Zethusculus)* and *Z. (Zethoides)* are monophyletic and hold their status as subgenera. Three species-groups are *Incertae sedis*: *Z. albopictus*, *Z. pallidus* and *Z. spinosus*.

Keywords

Phylogeny, taxonomy, paraphyly, sensitivity analysis, Zethini

Introduction

Zethus is the most species diverse genus in Vespidae and represents 279 out of the 363 species of Zethini, a group of Eumeninae whose status as tribe or subfamily is still in debate (Carpenter 1982; Pickett and Carpenter 2010; Hines et al. 2007; Hermes et al. 2014; Bank et al. 2017; Piekarski et al. 2018). The genus' distribution is mainly Gondwanian excluding the Australian region (Stange 1979). Still, a few species may reach into the Nearctic (Bohart and Stange 1965) or into Palearctic region in areas bordering the Afrotropical (Giordani Soika 1979) or the Oriental Regions (Tan et al. 2018).

The genus is currently divided into four subgenera: *Z. (Zethus)* Fabricius, 1804; *Z. (Zethusculus)* de Saussure, 1855; *Z. (Zethoides)* Fox, 1899; and *Z. (Madecazethus)* Giordani Soika, 1979. While the last subgenus is restricted to Madagascar and the second and third to the Neotropics and parts of the Nearctic, the nominotypical subgenus has species in the New World as well as the Old.

The problematic history of subgeneric divisions in *Zethus*, from de Saussure (1852, 1855, 1875) to Bohart and Stange (1965), has been summarized by Lopes and Noll (2018), whose study revealed possible incongruences in the current classification, where some subgenera, and even the genus *Zethus* itself, may be unnatural groups as they are currently construed. Their study, although focused on *Z. (Zethoides)*, which was retrieved as monophyletic, revealed the following features that discord with the current taxonomy: *Zethus* is paraphyletic in relation to *Ctenochilus*; *Z. (Zethusculus)* is paraphyletic in relation to the remaining *Zethus* (contradicted by Golfetti et al. (2020), who recovered the monophyly of this subgenus); and *Z. (Zethus)* is paraphyletic in relation to *Z. (Madecazethus)* and *Z. (Zethoides)*. Although obtaining these results, the authors refrained from making taxonomic changes since the taxon sampling in these groups was poor. Carpenter and Cumming (1985) had already noted not only the possibility of *Ctenochilus* being a derived lineage of *Zethus*, but also *Ischnocoelia* since these genera are diagnosed based mainly on characters of the palpi. The first genus presents modifications on the labial palpi, with reduced segmentation and dense long pilosity, while the second presents only the reduced segmentation, but of both maxillary and labial palpi. Further, Lopes and Noll (2018) speculated that *Z. (Zethus)* may actually be a number of different lineages that might deserve their own subgeneric status.

Thus, taking such inconsistencies into account, a phylogenetic analysis of *Zethus* was carried out, attempting to verify the validity of the genus as a natural group as well as of its subgenera and to propose taxonomic changes according to the results.

Methods

Taxon sampling

A total of 48 representatives of *Zethus* species were examined (Table 1). Since the genus has subdivisions of species-groups, which are comprised of morphologically similar

Table 1. Number of valid species and the corresponding amount examined of each subgenus of *Zethus* according to biogeographic region.

Subgenus	Biogeographic region	Number of valid species	Number of terminals
<i>Z. (Zethus)</i>	Mainly Neotropical	162	19
<i>Z. (Zethus)</i>	Mainly Afrotropical	15	7
<i>Z. (Zethus)</i>	Mainly Oriental	29	9
<i>Z. (Zethusculus)</i>	Mainly Neotropical	27	3
<i>Z. (Zethoides)</i>	Mainly Neotropical	43	7
<i>Z. (Madecazethus)</i>	Malagasy	2	2
TOTAL		279	48

species (Bohart and Stange 1965), the sampling targeted having one species of each of these groups in the case of the Neotropical representatives. Oriental and African *Zethus* were sampled as widely as possible and the Neotropical *Z. discoelioides* group had two species sampled due to its high diversity and large number of acknowledged undescribed species (Bohart and Stange 1965).

No representatives from the Neotropical *Z. stangei* and *Z. magretti* groups nor from the Oriental *Z. trimaculatus* group were examined.

Additionally, 24 terminals were used as outgroups representing twelve other Zethini genera. *Ischnocoelia* and *Ctenochilus* were sampled as widely as possible, the former by nine species and the later by all five species, while the remaining genera were represented by a single species. The two genera were better represented due to the possibility of being placed within *Zethus*. *Protodiscoelius merula* was used for rooting the tree.

The following institutions provided material for this study:

AMS	Australian Museum, Sydney, Australia;
ANIC	Australian National Insect Collection, Canberra, Australia;
ANMH	American Museum of Natural History, New York, USA;
FSCA	Florida State Collection of Arthropods, Gainesville, US;
HYMSJRP	Coleção de Hymenoptera, Depto. de Zoologia e Botânica, Instituto de Biociências, Letras e Ciências Exatas, Universidade Estadual Paulista “Júlio de Mesquita Filho”, São José do Rio Preto, Brazil;
OLML	Oberösterreichisches Landesmuseum, Linz, Austria;
MMML	Municipal Museum, Mariánské Lázně, Czech Republic;
MNHN	Muséum National d’Histoire Naturelle, Paris, France;
MPEG	Museu Paraense Emílio Goeldi, Belém, Brazil;
MSNVE	Museo Civico di Storia Naturale di Venezia, Venice, Italy;
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil;
NBCN	Naturalis Biodiversity Center, Leiden, Netherlands;
NHM	Natural History Museum, London, England;
RPSP	Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil;
UCD	University of California, Davis-Bohart Museum of Entomology, Davis, USA;

USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA;
CCT-UFGM	Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil;
VAST	Vietnam Academy of Science and Technology, Cau Giay Hanoi, Vietnam;
ZMHB	Zoologisches Museum und der Humboldt-Universität zu Berlin, Berlin, Germany;
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

Obtained material had their identification checked by RBL by using identification keys in Bohart and Stange (1965) for New World specimens and Giordani Soika (1958, 1969, 1979) for Oriental, Australian and Afrotropical specimens respectively. Any specimen belonging to a species described after these studies were compared to its original description.

Character circumscription

The analysis was based on morphological characters from both external morphology and male genitalia. For the examination of the latter, insects were relaxed (when pinned) for extraction of the genital capsule, which was submitted to one of the following processes for dissolution of soft tissues and clarification: a) immersion in 10% KOH solution for approximately 24 hours, followed by neutralization of the base with 10% acetic acid solution, rinsed and stored in glycerin; b) immersion in lactophenol heated in a Thermolyne HP-A1G18B hot plate in the 200 potency for approximately five minutes and, after cooling down, stored in glycerin.

The structures were examined through a Leica Stereoscope Microscope MZ16 and pictures taken with a MZ16 Leica Stereoscope with an attached DFC295 camera. Pictures were taken with the Leica Application Suite software and image stacking performed with Combine ZP or Helicon Focus.

Phylogenetic analysis

Following circumscription, characters were coded and inserted into a matrix using the Winclada software (Nixon 2015) and exported for TNT (Goloboff et al. 2016).

An implied weighting (Goloboff 1993) scheme was carried in order to down-weight homoplastic characters and the script “setk” by Salvador Arias (based on one of the equations in Goloboff et al. 2008) was used to determine a reference value of k . The determination of the constant k has been controversial as to what value should be used and no objective method has yet been set for this matter. For this reason, a series of values were tested based on the provided reference by the script in order to test nodal stability (Giribet 2003) across different concavities of weights through a sensitivity analysis (Wheeler 1995). The script suggested $k=14.067383$ and from this point, seven

k values of whole numbers below and seven above the reference were taken ($8 \leq k \leq 21$; $k \in \mathbb{Z}$), as well as the minimum value of 1 and an extremely high value of 500.

New technology search algorithms were used with the default settings, except for the following differences: Maximum trees held in memory: 10000; random seed 0; number of hits 100; Ratchet 200 iterations, with up-down perturbation 15; Drift 20 iterations; tree fusing 10 rounds.

After the search was complete, the resulting tree was opened in Winclada and exported for editing in Adobe Illustrator CS5.

Support was calculated through symmetric resampling (Goloboff et al. 2003) with 10,000 replications.

Terminology follows Carpenter and Garcete-Barrett (2002), Bohart and Stange (1965), Bitsch (2012), Lopes and Noll (2014) and Lopes and Noll (2018). The following abbreviations were used: T, for tergum and S, for sternum.

Results and discussion

A total of 168 characters were circumscribed, 32 being from the head, 69 the mesosoma, 46 the metasoma and 21 from the male genitalia (the character list is provided in Suppl. material 1, while the matrix is provided in the Suppl material 4 in “.tnt” format – both available in OSF, under <https://doi.org/10.17605/OSF.IO/FJV32>). Characters based on previous studies (Garcete-Barrett 2014; Hermes et al. 2014; Lopes and Noll 2018) were indicated as such in Suppl. material 1.

The script suggested a $k = 14.067383$, for which only one tree was recovered (Fig. 1), which shows *Zethus* as paraphyletic in relation to *Ctenochilus* and *Ischnocoelia*. The first was shown previously by Lopes and Noll (2018), who refrained from making taxonomic changes due to poor sampling and both cases were suspected by Carpenter and Cumming (1985). In this manner, both genera should be synonymized under *Zethus*. The clade comprised of *Zethus*, *Ischnocoelia* and *Ctenochilus* (herein recognized as *Zethus*), is supported by two homoplastic synapomorphies: the presence of a posterior proepisternal lamella (Fig. 2A) and developed stem of T2 (Fig. 2B). The only tested k value that did not recover this clade was $k = 1$, probably due the strong weighting function, which discards homoplasies.

Out of the four subgenera of *Zethus*, only *Z.* (*Zethoides*) and *Z.* (*Zethusculus*) were recovered as monophyletic, while *Z.* (*Zethus*) and *Z.* (*Madecazethus*) were recovered as paraphyletic, what agrees in part with the results of Lopes and Noll (2018). Taxonomic changes proposed herein are based on these results. The genus has a long history of synonyms and subgeneric divisions and if a representative of a lineage deserving of its own subgenus was once affiliated to one of these names, the group or synonym is attributed a new status.

First, although *Z.* (*Zethus*) is indeed paraphyletic in relation to *Z.* (*Madecazethus*), it is regarding only the African representatives of the nominotypical subgenus (dark blue, Fig. 1), diverging from Lopes and Noll (2018) where the Malagasy subgenus is more

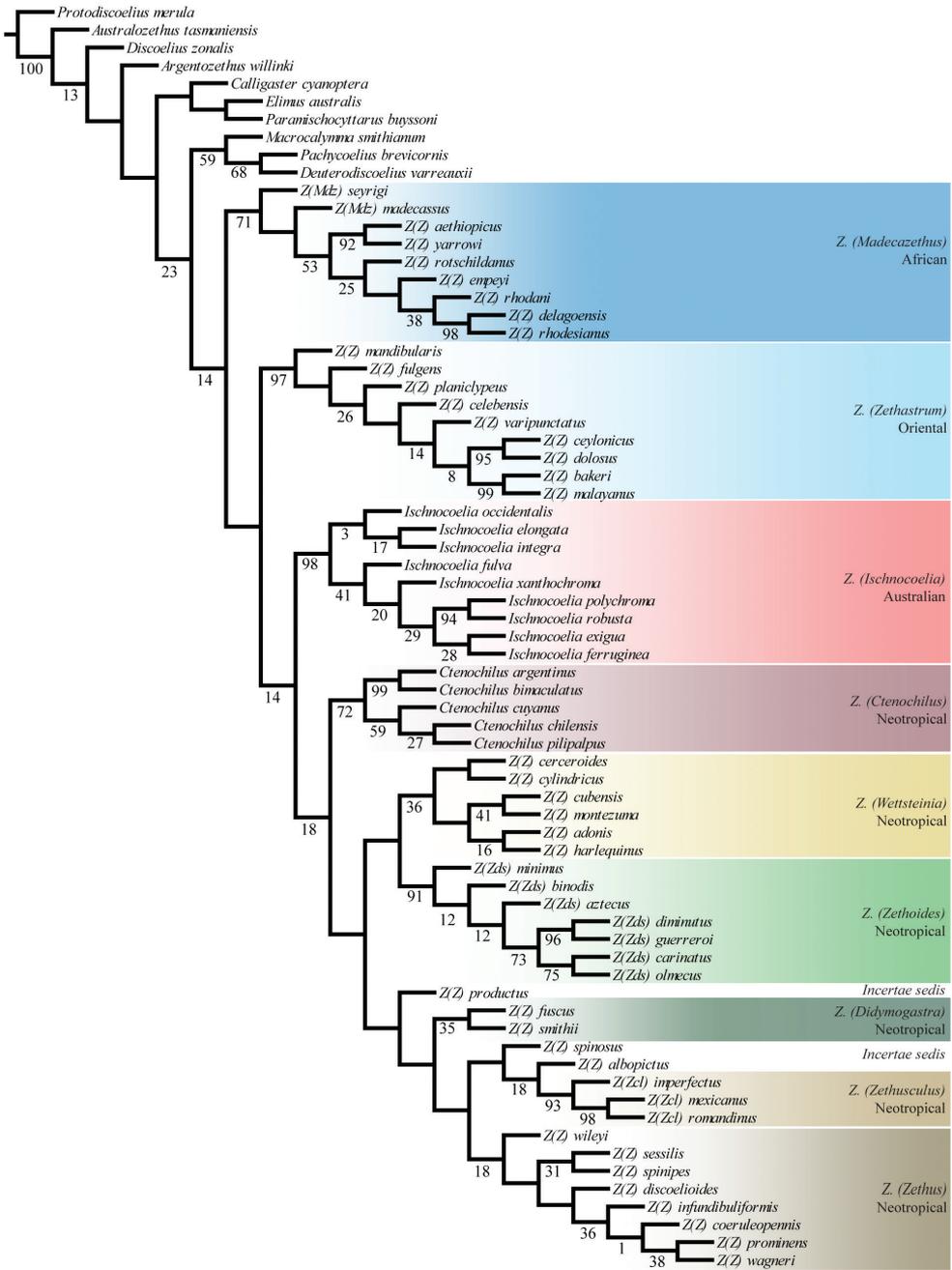


Figure 1. Most parsimonious tree for subgeneric relationships of *Zethus* recovered from New Technology Searches using Implied Weights with $k = 14.067383$. Numbers below nodes indicate GC values of Symetric Resampling. Terminals labeled in current classification. *Z. (Z)* = *Z. (Zethus)*; *Z. (Zds)* = *Z. (Zethoides)*; *Z (Zcl)* = *Z. (Zethusculus)*. Shaded clades indicate newly proposed classification.

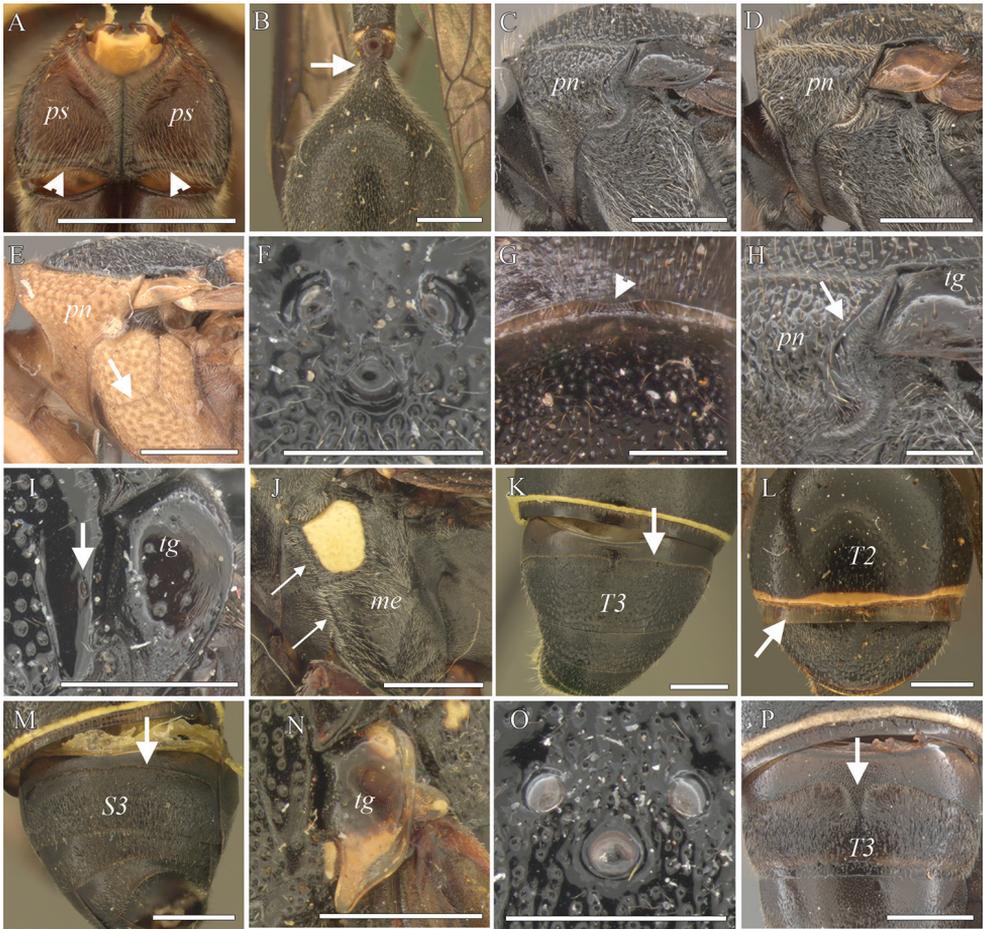


Figure 2. Synapomorphies supporting *Zethus* and relationships between its lineages **A** proepisternum of *Z. spinipes*, ventral view; arrowheads indicate lamellae **B** second metasomal tergum of *Z. yarrowi*, dorsal view; arrow indicates stem **C** pronotum of *Z. rodhaini*, lateral view **D** pronotum of *Z. planicypeus*, lateral view **E** pronotum of *Z. robustus*, lateral view; arrow indicates dorsal suture **F** ocelli of *Z. mandibularis* **G** pronotal carina of *Z. smithii*, postero-dorsal view; arrowhead indicates notch **H** latero-posterior region of the pronotum of *Z. rodhaini*; arrow indicates pre-tegular carina **I** lateral portion of mesoscutum of *Z. spinipes*; arrow indicates discoid puncture **J** mesepisternum of *Z. jurinei*; arrows indicate dorsal (upper arrow) and mid (lower arrow) sections of epicnemial carina **K** third metasomal tergum of *Z. fraternus*; arrow indicates gradulus **L** second metasomal tergum of *Z. aztecus*; arrow indicates lamella. **M** third metasomal sternum of *Z. fraternus*; arrow indicates gradulus **N** tegula of *Z. aztecus* **O** ocelli of *Z. spinipes* **P** third metasomal tergum of *Z. spinipes*; arrow indicates interruption of gradulus. Scale bars: 1.0 mm.

closely related to some Neotropical lineages, while *Z. (Zethusculus)* occupies a more basal position on the tree topology. Also, vice-versa occurs, as *Z. (Madecazethus)* is paraphyletic in relation to *Zethus*, but only the African representatives. Thus, the Malagasy and African representatives belong to the earliest (extant) lineage of *Zethus*, and due to

the relationship between them, this group, in its entirety, shall be included in *Z.* (*Madecazethus*). This lineage shares with most of the other zethines the laterally straight pronotal carina (Fig. 2C), while most other *Zethus* present some sinuosity (Fig. 2D, E).

The redefined *Zethus* (*Madecazethus*) (dark blue, Fig. 1) is sister group to the remaining *Zethus*. This larger clade including Oriental and Neotropical representatives of the genus along with *Ischnocoelia* and *Ctenochilus* is supported by the narrower disposition of the ocelli, forming an equilateral triangle (Fig. 2F), the presence of the aforementioned sinuosity of the lateral portion of the pronotal carina (Fig. 2D, E) and wider gonocoxite.

The second robust lineage found in *Zethus* is that of the Oriental species (light blue, Fig. 1). Although no terminal from the *Z. trimaculatus* group was examined, the similarity of the species, based on literature (Giordani Soika 1958, 1995), reveal them to belong to this lineage. No genus group name was ever used to refer to this group, and thus, a new subgenus is proposed, *Z. (Zethastrum)*.

The following lineage is the clade where the former genus *Ischnocoelia* is placed (light red, Fig. 1), and it is sister group to the Neotropical clade (tones of dark red, yellow, green and brown, Fig. 1). Four characters set this relationship: the pronotal carina dorsally lamellar with a medial notch (Fig. 2G) and with its lateral portion strongly sinuous (Fig. 2E) and the T1 strongly constricted apically. The presence of the dorsal suture in the mesepisternum (Fig. 2E) with only few reversions and is potentially a synapomorphy but its optimization is ambiguous due to outgroup sampling. Still, *Ischnocoelia* is well supported and will be lowered to subgenus. Following recommendation of the International Code of Zoological Nomenclature for species-group names, an adaptation of the gender of the specific epithets will also have to be done and for the same reason.

All Neotropical species of *Zethus*, along with *Ctenochilus*, belong to one single clade (although there are representatives from the Nearctic, these are more derived and the stem lineages, therefore the origin of the group, Neotropical), supported by six homoplastic conditions: presence of a pretegular carina, which is incomplete (Fig. 2H); discoid puncture, when present, beveled with the rest of the mesoscutum (Fig. 2I); epicnemial carina with developed dorsal portion (Fig. 2J); T1 expansion of medium length; presence of gradulus on T3 (Fig. 2K); and gonostylus glabrous.

In summary, *Zethus* presents now a complete Gondwanian distribution, in a manner that the lineages are related as African + (Oriental + (Australian + Neotropical)). This finding would suggest that the *Zethus* lineage probably already existed around 160 million years ago, with its lineages following the same separation sequence as Gondwana. However, Perrard et al. (2017) state that the major groups of Vespidae originated in the early Cretaceous (approx. 100 mya), using, among others, an Eumenine fossil of 89.6 million-years-old that calibrated the divergence of *Zethus-Odynerus* to that date. The fossil *Symmorphus senex*, used in calibration, belongs to a genus that is not among the stem lineage in Eumenine (Piekariski et al. 2018), meaning that Zethini, and therefore probably *Zethus*, could have derived much earlier and follow the vicariance pattern described above.

On the other hand, should we take into account the dating provided by Perrard et al. (2017), *Zethus*, a derived group, would have evolved later than 89 mya. In this sense, this would be a case of pseudocongruence, where the distribution pattern of species does not reflect the geographical history, despite appearances. Amorim et al. (2018) refer to this as a pseudogondwanian distribution, and explains as faunal exchange between Laurasia and Africa, the Nearctic and Neotropics and Oriental and Australasia Regions followed by the extinction of the representatives from the Holarctic. Since both hypotheses seem viable, more studies have to be carried out in order to come to a conclusion for the earlier biogeography of *Zethus* lineages.

Although there is poor support to properly establish a relationship between some Neotropical lineages, these lineages themselves are recovered at least moderately supported. The first identified lineage to diverge is *Ctenochilus*, the second genus to be included in *Zethus* (Fig. 1). All five species are included in the clade and will be placed in the subgenus *Z. (Ctenochilus)*. This subgenus is sister group to a clade containing all the Neotropical *Zethus*, which is supported by three homoplasies: short galea; developed lamella of T2 (Fig. 2L) and presence of gradulus in S3 (Fig. 2M).

The Neotropical *Zethus* clade reveals further paraphyly in the nominotypical subgenus, as *Z. (Zethoides)* and *Z. (Zethusculus)* are nested in this clade but derived from different points in the topology. The first clade to appear among the Neotropical group, which consists of two well defined lineages, is supported by the absence of the transverse interantennal carina and the outer margin of the tegula raised in its entirety (Fig. 2N). The first group is the already established *Z. (Zethoides)*, whose monophyly had been recovered by Lopes and Noll (2018) and therefore, will maintain its status as subgenus.

Sister group to *Z. (Zethoides)* is a clade that consists of representatives from six species-groups: *Z. cubensis*, *Z. heydeni* (represented by *Z. cerceroides*), *Z. montezuma*, *Z. sichelianus* (represented by *Z. cylindricus*), *Z. strigosus* (represented by *Z. adonis*) and *Z. sulcatus* (represented by *Z. harlequinus*) groups (Fig. 1). Dalla Torre (1904) described *Wettsteinia sicheliana* (= *Z. sichelianus*) and *W. brasiliensis* (= *Z. adonis*), but Brèthes (1906) rejected it as a distinct genus from *Zethus*. Since this was a distinct name for an assemblage that included representatives from two species-groups that are in the clade, the name will be carried to subgenus as *Z. (Wettsteinia)*.

The second large clade of Neotropical *Zethus* consists of the remaining *Z. (Zethusculus)* and *Z. (Zethus)* and is supported by a wider disposition of the ocelli as an isosceles triangle (Fig. 2O), the absence of the apical propodeal lamella and the gradulus of T3 medially interrupted (Fig. 2P). Only three robust lineages can be identified within it (*Z. (Didymogastra)*, *Z. (Zethusculus)* and *Z. (Zethus)*-see below) and there are some assemblages that lack strong support to establish a subgenus. Therefore, three species-groups will be dealt with as *Incertae sedis*: *Z. pallidus* (represented by *Z. productus*), *Z. spinosus* and *Z. albopictus* groups. The latter has controversial group taxonomy as it was once assigned to the *Z. cubensis* group only to be relocated into a group of its own (Stange, 2003). While there is moderate support for *Z. albopictus* + *Z. (Zethusculus)*, only the male has been examined. A closer inspection of the female is desired and if

more characters appear to corroborate this relationship, the inclusion of *Z. albopictus* in *Z. (Zethusculus)* could be supported.

The clade comprised of *Z. fuscus* and *Z. smithii* defines another new subgenus, which belongs to the *Z. fuscus* and *Z. hilarianus* species-groups, respectively. Perty (1833) described the genus *Didymogastra*. De Saussure (1855, 1875) later used the name as division of *Zethus* to allocate species which had an elongated stem of T2 and Dalla Torre (1892) later raised the status to subgenus. Since the name has been long since used, and the analysis supports this lineage as a subgenus, its status should be revised.

Despite *Z. (Zethusculus)* being recovered as paraphyletic by Lopes and Noll (2018), this subgenus was recovered here as monophyletic and with high support (Fig. 1). New characters now help support the monophyly of the subgenus, with lesser emphasis given to the aspect of sutures and grooves in the mesopleura and wider sampling of other genera of Zethini. Thus, *Z. (Zethusculus)* will keep its status as subgenus.

Finally, the last clade which consists of representatives from seven species-groups: *Z. chalybeus* (represented by *Z. wagneri*), *Z. coeruleopennis*, *Z. discoelioides*, *Z. infundibuliformis*, *Z. prominens*, *Z. spinipes* and *Z. wileyi* groups. The latter is a novelty, as upon the description of this monotypic group, Lopes et al. (2017) regarded it as being closely related to *Z. hilarianus* group and thus, would be expected to be part of *Z. (Didymogastra)*. Since this large assemblage includes the type species of the genus, *Z. coeruleopennis*, the species in this clade will be kept in the subgenus *Z. (Zethus)*. Although not examined, according to descriptions (Bohart and Stange 1965; Porter 2008; Carpenter 2011), *Z. magretti*, *Z. stangei* and *Z. josefi* fit best this subgenus.

The topology described above presented high nodal stability, except for the extreme values of 1 and 500 for *k* (the topologies for each *k* value can be seen in Suppl. material 2 – available in OSF, under <https://doi.org/10.17605/OSF.IO/FJV32>) used in the sensibility analysis, relationships and subgenera (Fig. 3).

***Zethus* Fabricius, 1804**

Zethus Fabricius, 1804: 282 (genus). Giordani Soika 1958: 75 (revision of Oriental species). Bohart and Stange 1965 (subgenera, revision new world species). Giordani Soika 1979: 20 (revision African species). Carpenter 1986: 88 (cat.). Vecht and Carpenter 1990: 60 (cat.). Carpenter et al. 2010 (cat. African species).

Type species: *Zethus coeruleopennis* (Fabricius, 1798) (= *Vespa coeruleopennis* Fabricius, 1798).

Lethus Say, 1837: 387 (misspelling).

Heros de Saussure, 1856: 115 (division of *Zethus*).

Euzethus Dalla Torre, 1904: 14 (name for division I of *Zethus* in de Saussure 1852).

Type species: *Vespa coeruleopennis* (Fabricius, 1798).

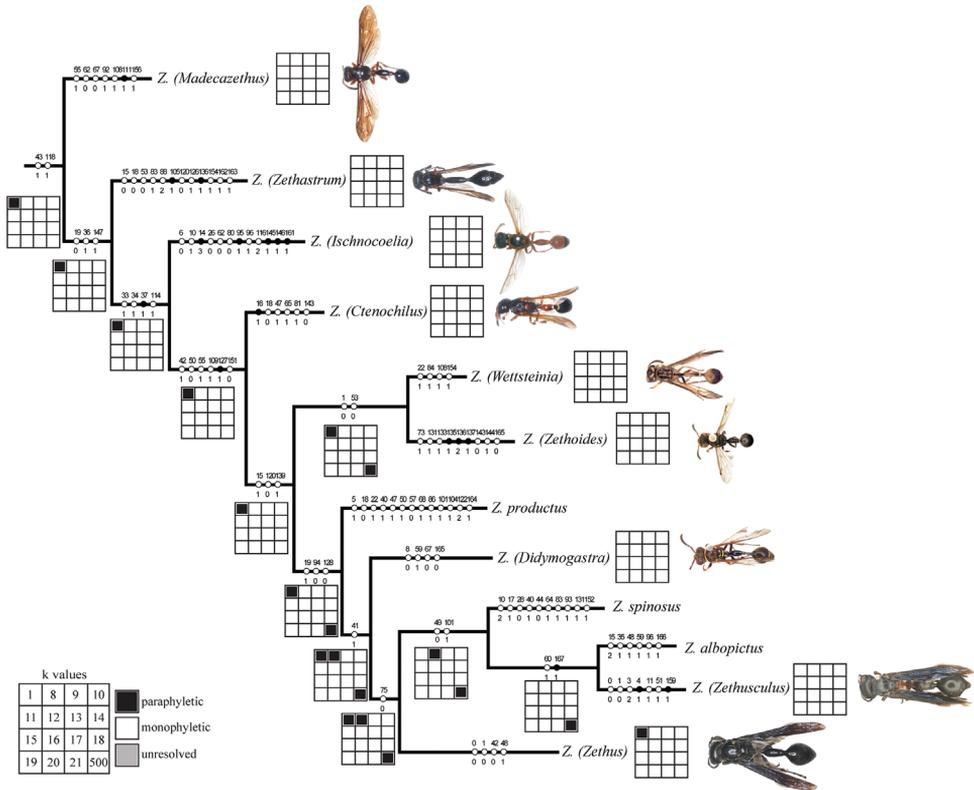


Figure 3. Simplified phylogeny of *Zethus*. Square plots indicate distinct recovery status of clades under different k values.

Description. Frons projected over antennal socket. Gena angled. Occipital carina ventrally complete, with small branch or completely absent. Pronotal carina short or lamellar. *Proepisternum* with posterior margin lamellar (Fig. 2A), rarely blunt. Metanotum bent, rarely flat. Mid tibia with one or two spurs. Propodeum without apical rim. Propodeum with or without apical lamella, orifice slit like. Valvula projected, with superior margin free, infero-posterior angle straight. T1 variable. T2 with evident stem (Fig. 2C), occasionally absent.

Observations. The large diversity included in *Zethus* reflects diagnostic features, of which few encompass the entirety of the genus, only the projected frons, angled gena, absence of the apical rim in the propodeum, orifice slit like and traits of the valvula being constant within the group. Also, the absence of the apical rim in propodeum is constant throughout the entire genus while it is present in most of the other Zethini. The subgenera are more defined in more detail.

Distribution. Cosmopolitan (specified under each subgenus)

Included species. 298 (listed under each subgenus in Suppl. material 3)

Identification key to subgenera of *Zethus* Fabricius

- 1 Pronotal carina short, not lamellar, and at most slightly sinuous laterally (Fig. 2C, D).....**2**
- Pronotal carina usually lamellar and strongly sinuous laterally (Fig. 2E); if short or regular, then vertex is raised after ocelli or lamella of T3 laterally tapered and secondary lamella present**3**
- 2 T1 with lateral margins touching ventrally (Fig. 7B). Apical lamella of T3 without any indents.....**Z. (*Madecazethus*)**
- T1 with lateral margins clearly separated from each other. Apical lamella of T3 with a confluent lateral indent (Fig. 9D)**Z. (*Zethastrum*)**
- 3 Labial palpi 3-segmented (Figs 4B, 6B).....**4**
- Labial palpi usually 4-segmented, if 3-segmented, stem of T2 elongated.....**5**
- 4 Labial palpi psamophore with numerous long and thick setae (Fig. 4B); maxillary palpi 6-segmented; apical propodeal lamella triangular and isolated; posterior face of metanotum flat (Fig. 4C); dorsal aperture of propodeum present.....**Z. (*Ctenochilus*)**
- Labial palpi regular, with no outstanding setae; maxillary palpi 3-segmented (Fig. 6B); apical propodeal lamella rounded and contiguous (Fig. 6C); metanotum flat or more evenly convex; dorsal aperture of propodeum absent.....**Z. (*Ischnocoelia*)**
- 5 Male antennae rolled (Fig. 12D); females with clypeus microstriate (Fig. 12B); tegula with outer margin raised and only medially interrupted (Fig. 12C)
.....**Z. (*Zethusculus*)**
- Male antennae hook-like; female clypeus without microstriae; outer margin of tegula either completely raised or limited to posterior half.....**6**
- 6 T3 posterior margin projected, with apical lamella tapered laterally with indented secondary lamella present (Fig. 10B, C); S3 with apical lamella reduced and a medial lamellar lobe projecting subapically from sclerite (Fig. 10C)**Z. (*Zethoides*)**
- T3 not projected, with apical lamella of regular length throughout and no secondary lamella; S3 without medial lamellar lobe and apical lamella regular.....**7**
- 7 Propodeum with apical lamella developed.....**Z. (*Wettsteinia*)**
- Propodeum without apical lamella, if developed, then vertex is raised after ocelli.....**8**
- 8 Notauli absent; vertex of head flat; pre-tegular carina present.....
.....**Z. (*Didymogastra*)**
- Notauli present; vertex usually raised after ocelli; pre-tegular carina absent ...
.....**Z. (*Zethus*)**

A synopsis of each taxon in the key will follow, in alphabetical order, with a taxonomic catalog, description, observations, distribution and included species number. A

list of species in each subgenus is provided in Suppl. material 3 (available in OSF, under <https://doi.org/10.17605/OSF.IO/FJV32>). The description will consist of a core description, where general characters are cited and the synapomorphies, which will be in **bold**. Unique synapomorphies will be in ***bold italic***.

***Zethus* (*Ctenochilus*) de Saussure, 1856, stat. nov.**

Fig. 4

Ctenochilus de Saussure, 1856: 323 (name for division III of *Pterocheilus* in de Saussure 1852); 1875: 372 (genus). Bequaert and Ruiz 1942: 220. Giordani Soika 1962 (treatment of three species).

Type species: *Epipona pilipalpa* Spinola, 1851.

Description. Male antennae hooked. Interantennal carinas present. Clypeus of female short or long, with or without apical teeth, always without microstriae. Male mandible 4-toothed. Galea reaching fore coxae. **Labial palpi with *psamophore* aspect, 3-segmented** (Fig. 4B) **and palpomere I straight**. Only small branch of occipital carina ventrally. Vertex flat. Gena evenly convex. Pronotal carina lamellar with lateral portion strongly sinuous. Pre-regular carina present, incomplete. **Welts present** (Fig. 4C) or absent. Notaulices present, complete or incomplete. Tegula evenly convex with outer margin raised only on posterior half. Epicnemial carina usually complete. Posterior carina of mesepimeron absent. Two midtibial spurs. **Metanotum anteriorly margined, with lateral carina restricted to anterior half and posterior face flat** (Fig. 4D). Posterior tibia of females with spines in one line. Marginal cell with obtuse apex. Propodeum with dorsal aperture, lateral carina on dorsal half and sublateral carina present. **Dorsal margin of dorsal aperture present**. Apical lamella of propodeum present. T2 with short stem. T3 lamella simple, no indents. S3 lamella reduced, no medial lobe. S5 and 6 of males without carinas.

Observations. Due to the lowered status of *Ctenochilus* to subgenus, the species belonging to this group require new combinations. These are given in Suppl. material 3.

Distribution. Neotropical (Argentina and Chile).

Included species. 5



Figure 4. Synapomorphic characters of *Zethus* (*Ctenochilus*) indicated in *Z. pilipalpa* **A** habitus **B** labial palpi **C** mesoscutum, dorsal view; arrow indicates welt **D** metanotum, oblique view; arrow indicates flat surface. Scale bars: 1.0 mm.

***Zethus (Didymogastra)* Perty, 1833 stat. rev.**

Fig. 5

Didymogastra Perty, 1833: 144 (genus). Bohart and Stange 1965: 25 (jr. syn. of *Zethus*).Type species: *Didymogastra fusca* Perty, 1833.*Zethus (Didymogastra)* Dalla Torre, 1892: 9 (subgenus of *Zethus*).

Description. Interantennal carinas present. Clypeus of female short, without microstriae. **Clypeal teeth absent** or present. Male mandible 4-toothed. Galea length variable. Labial palpi segmentation variable. Occipital carina ventrally complete, occasionally incomplete. Vertex flat. Genal margin evenly convex. Pronotal carina lamellar with lateral portion strongly sinuous. Pre-tergular carina present, incomplete. Welts present or absent. Notaulices absent. Tegula evenly convex with outer margin raised only on posterior half. Epicnemial carina variable. **Posterior carina of mesepimeron present** (Fig. 5B). Two midtibial spurs. Metanotum anteriorly margined. **Lateral carina of metanotum absent**. Posterior tibiae of females with one row of spines. Marginal cell apically obtuse. Dorsal aperture of propodeum present, varying from slit, to wide orifice, to two orifices. Propodeum presenting only lateral carina, restricted to dorsal half, and without apical lamella. Propodeal orifice with rounded dorsal margin. T1 with long stem and medium expansion. Anterior margin of S1 elliptical or quadrate. **Stem of T2 elongated** (Fig. 5C). Lamella of T2 well developed, sometimes reflexed. Lamellas of T3 and S3 developed and simple, without indents. S5 and 6 of males without carinas.

Observations. Although here the very long stem of T2 is marked as a synapomorphy, it is not constant throughout the entire subgenus. Some representatives from the *hilarianus* group have a medium-sized stem. Part of the *hilarianus* group (former *Z. smithii* group) has been revised and phylogenetically analysed by Lopes et al. (2015).

Distribution. Nearctic and Neotropical.

Included species-groups: *fuscus* and *hilarianus*.

Included species. 25.



Figure 5. Synapomorphic characters of *Zethus (Didymogastra)* indicated in *Z. fusca* **A** habitus **B** mesepimeron, posterior view; arrow indicates posterior carina **C** second metasomal tergum; arrow indicates stem. Scale bars: 1.0 mm.

***Zethus (Ischnocoelia)* Perkins, 1908 stat. nov.**

Fig. 6

Ischnocoelia Perkins, 1908: 28, 32 (genus). Perkins 1912: 118 (distinct from *Elimus*).

Meade-Waldo 1913: 44; 1914: 459 (note on synonymy). Bohart and Stange 1965: 11. Giordani Soika 1969: 66 (key to species). Cardale 1985: 177–179 (cat.).

Type species: *Ischnocoelia xanthochroma* Perkins, 1908.*Stenolabus* von Schulthess, 1910: 189 (genus). Meade-Waldo 1914: 459 (jr. syn. of *Ischnocoelia*).Type species: *Stenolabus fulvus* von Schulthess, 1910.

Description. Male antennae as a hook. Interantennal carinas variable. **Clypeus of female long, considerably passing acetabulum with convex apical margin**, without microstriae nor apical teeth. **Maxillary and labial palpi 3-segmented** (Fig. 6B). Galea reaching first pair of coxae. Male mandible 4-toothed. **Small ventral branch of occipital carina ventrally.** Vertex flat. Genal margin evenly convex. Pronotal carina lamellar, strongly sinuous laterally. Pretegular carina absent. Welts variable. Notaulices present, incomplete. Tegula evenly convex, with outer margin raised only on posterior half. Epicnemial carina variable. Mesepimeron without carina. Mid tibia with two spurs. **Metanotum not anteriorly margined** with lateral carina reaching posterior half of sclerite. Posterior tibiae of females with one row of spines. Apical angle of marginal cell variable. **Dorsal aperture of propodeum absent.** Propodeum only with lateral carina. Dorsal margin of propodeal orifice rounded. **Apical lamella of propodeum rounded and contiguous** (Fig. 6C). T1 with short or long stem and medium expansion. **Anterior margin of S1 quadrate.** Apical lamellae of T2 and T3 and S3 developed and simple, without lateral indents. **S5 and S6 in males with transverse carina. Volselar crest axe-like.**

Observations. The ICZN establishes that a species' epithet should agree with the gender of the genus. Since *Ischnocoelia* is female and *Zethus*, male, there is a mandatory spelling change (Art. 34.2, ICNZ) for names that are female. While most of the specific epithets could simply be converted into masculine form due to the new com-



Figure 6. Synapomorphic characters of *Zethus (Ischnocoelia)* **A** habitus of *Z. xanthochromus* **B** labial palpus of *Z. elongatus* **C** propodeum of *Z. integrus*, oblique view; arrow indicates continuity between both apical lamellae. Scale bars: 1.0 mm.

bination under *Zethus* and kept similar to the current valid one, a new name had to be given to *Ischnocoelia ferruginea* due to homonymy. The new combinations of other species are given in the Suppl. material 3.

Distribution. Australian.

Included species. 14.

***Zethus (Ischnocoelia) rutilus* Lopes, nom. nov.**

Elimus ferrugineus Meade-Waldo, 1910: 38 (male, “S. Australia” – London, no. 18.129). 1913: 45 (not *Elimus*, assigned to *Ischnocoelia*).

Ischnocoelia ferruginea Bequaert, 1928: 151 (cat.). Bohart and Stange 1965, 40: 11 (note). Giordani Soika 1969: 71 (key), 76 (fig, Victoria: Melbourne, Broad Meadows). Cardale 1985: 178 (cat.). Borsato 2003: 511 (female); 517 (figs, syn. sr. of *D. ecclesiasticus* Rayment, Western Australia: Fremantle, New South Wales: Sydney, Victoria: 3 localities, Australian Capital Territory: Canberra). Carpenter and Brown 2021: 12 (cat.).

Discoelius ecclesiasticus Rayment, 1954 (female, male, nest). Borsato 2003: 511, 517 (syn. jr. of *I. ferruginea* (Meade-Waldo)).

Ischnocoelia ecclesiastica; van der Vecht, 1981: 443, 456 (not *Discoelius*, assigned to *Ischnocoelia*, probable syn. of other species). Cardale 1985: 177 (cat.).

Observations. The new combination for *I. ferruginea* would be *Zethus ferrugineus*, which is a secondary junior homonym of *Zethus ferrugineus* de Saussure, 1852, which is a junior synonym of *Zethus biglumis* Spinola, 1841. Therefore, a new name has to be proposed.

Etymology. The new name follows the intention of the name it is replacing, an epithet referring to color, which translates to a yellowish red.

***Zethus (Madecazethus)* Giordani Soika, 1979**

Fig. 7

Zethus (Madecazethus) Giordani Soika, 1979: 20 (key to subgenus), 53 (subgenus, key to species).

Type species: *Labus madecassus* Schulthess, 1907

Description. Male antennae as a hook. Interantennal carinas present. Clypeus of female short without microstriae, apical teeth present or absent. Male mandible 4-toothed. Labium with short to medium galea, palpi 4-segmented with first segment curved. Occipital carina ventrally complete. Vertex flat. Genal margin evenly convex. Pronotal carina short, straight laterally. Pre-regular carina, when present, incomplete. Welts and notaulices absent. Tegula evenly convex or posteriorly angled, with outer margin raised completely or restricted to posterior half. **Dorsal portion of epicnemial**



Figure 7. Synapomorphic characters of *Zethus* (*Madecazethus*) **A** habitus of *Z. madecassus* **B** petiole of *Z. rhodesianus*; arrow indicates point where the two sides of the first tergum meet. Scale bars: 1.0 mm.

carina present, sometimes absent. Mesepimeron without carina. Two midtibial spurs. **Metanotum usually not anteriorly margined. Lateral carina of metanotum usually absent.** Posterior tibiae of females with spines restricted to basal portion or as a row along entire tibia. Apical angle of marginal cell obtuse. Dorsal propodeal aperture present. Propodeum with lateral carina always present, submedian rarely and sublateral variable, but incomplete when present. **Dorsal margin of propodeal orifice acute**, rarely rounded. Apical propodeal lamella triangular. T1 with short stem, **lateral margins of sclerite touching ventrally** (Fig. 7B) and narrow expansion. Anterior margin of S1 variable in shape. Stem of T2 developed. Apical lamella of T2 present, reduced in Malagasy species. Lamellae of T3 and S3 developed and simple, without lateral indent. S5 and 6 of male without carinas. **Aedeagus with apically flattened apodemes.**

Observations. Although *Z. madecassus* and *Z. seyrigi* were the only representatives of *Z. (Madecazethus)* they are not sister groups and thus, should not be placed in a species group of their own. A wider analysis of the African *Zethus* is needed to verify the validity of the already proposed *pubescens* group (represented by *Z. empeyi*, *Z. rhodani* and *Z. rotschildianus*), since it may also be paraphyletic.

Distribution. Palearctic and Afrotropical

Included species-groups. *delagoensis*, *favillaceus*, *pubescens*.

Included species. 17

Zethus (*Wettsteinia*) Dalla Torre, 1904 stat. nov.

Fig. 8

Wettsteinia Dalla Torre, 1904: 10 (genus). Bohart and Stange 1965: 25 (jr. syn. of *Zethus*).

Type species: *Labus sichelianus* de Saussure, 1875 (= *Zethus sichelianus* (de Saussure, 1875)).

Laboides Zavattari, 1912: 65 (division of *Zethus*). Bohart and Stange 1965: 25 (jr. syn. of *Wettsteinia*).

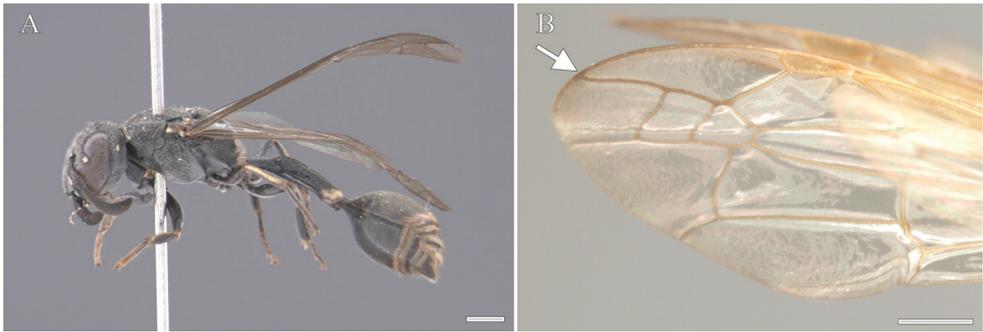


Figure 8. Synapomorphic characters of *Zethus* (*Wettsteinia*) **A** habitus of *Z. sichelianus* **B** forewing of *Z. adonis*; arrow indicates acute apex of marginal cell. Scale bars: 1.0 mm.

Type species: *Labus sichelianus* de Saussure, 1875 (= *Zethus sichelianus* (de Saussure 1875)).

Description. Male antennae hook-like. Interantennal carinas present or absent. Clypeus of female short, without microstriae, with or without apical teeth. Number of teeth in male mandible variable. Galea length at most short. Labial palpi 4-segmented. Occipital carina ventrally complete. Vertex flat. **Genal margin sinuous.** Pronotal carina lamellar, strongly sinuous laterally. Pre-tegular carina present, incomplete. Welts and notaulices variable. Tegula evenly convex with outer margin usually raised along entire margin, occasionally restricted to posterior half. Epicnemial carina dorsally complete or incomplete. Mesepimeron without carina. Mid tibia with one or two apical spurs. Metanotum anteriorly margined. Lateral carina of metanotum reaching at most half of sclerite. Spines of posterior tibiae of females, when present, scattered or distributed in a row. Apex of marginal cell usually acute. Dorsal propodeal aperture present. **Propodeal submedian carina complete**, when present. Propodeal lateral carina limited to dorsal half and sublateral carina absent. Dorsal margin of propodeal orifice rounded. Apical lamella of propodeum present. **Apex of marginal cell acute** (Fig. 8B). T1 with long or short stem and **narrow expansion**. Anterior margin of S1 elliptical or quadrate. Lamellae of T2 and 3 and S3 well developed and simple, without indents. S5 and 6 of male without carinas. **Basal plate of aedeagus short.**

Observations. Bohart and Stange (1965) already suspected a close relationship between the species-groups in this subgenus but left it as part of *Z.* (*Zethus*). A curious trait of females of many species here present is the three-spotted clypeus (on apical spot and a pair of lateral spots). Although it is not constant along the entire group, it is a pattern rarely seen outside this clade.

Distribution. Nearctic and Neotropical.

Included species-groups. *cubensis*, *heydeni*, *montezuma*, *sichelianus*, *sulcatus* and *strigosus*.

Included species. 58

Zethus (Zethastrum) Lopes, subg. nov.

<http://zoobank.org/07FE7FD8-2DDE-4603-8622-F32BEBD8DF5C>

Fig. 9

Type species. *Zethus ceylonicus* de Saussure, 1867.

Description. Male antennae hook-like. Interantennal carinas present or absent. Clypeus of female without microstriae, short, usually with apical teeth. Male mandible with three or four teeth. **Galea stub-like.** Labial palpi 4-segmented with **palpomere I straight** (Fig. 9B). Occipital carina ventrally complete. Vertex flat. Genal margin evenly convex. Pronotal carina short, slightly sinuous laterally. Pre-regular carina absent. Welts absent. **Notaulices complete.** Tegula evenly convex with **outer margin completely raised.** Epicnemial carina variable. Mesepimeron without carina. Mid tibia with two spurs. Metanotum usually anteriorly margined, with lateral carina of variable length. Spines in posterior tibiae of females, when present, restricted to basal portion. Apical angle of marginal cell obtuse. Dorsal aperture of propodeum present. **Submedian carina present** (Fig. 9C), but variable in the group; lateral carina present, with variable length; **sublateral carina complete.** Dorsal margin of propodeal orifice rounded or acute. Apical propodeal lamella triangular. T1 with short stem and long expansion with semi-parallel sides, **with basal dorsal carina** (Fig. 9C). S1 with elliptical anterior margin. **Lamella of T2 well developed. T3 with depression and lamella with confluent indent** (Fig. 9D). Lamella of T3 and S3 simple. S5 and 6 of males without carinas. **Aedeagus with short basal plate. Digitus with basal projection and basal tuft.**

Observations. Only three of four species-groups from the Oriental region were sampled: *Z. quadridentatus* group (represented by *Z. varipunctatus*); *Z. luzonensis* group (represented by *Z. fulgens*); and *Z. dolosus* group (all the other Oriental *Zethus*). Although the present analysis shows the basal longitudinal carina and weak apical constriction of T1 as



Figure 9. Synapomorphic characters of *Zethus (Zethastrum)* indicated in *Z. ceylonicus* **A** habitus **B** labial palpus **C** propodeum and basal portion of petiole, posterior view; arrowhead indicates submedian carina; arrow indicates basal longitudinal carina in first tergum **D** third metasomal tergum, lateral view; arrow indicates confluent indent. Scale bars: 1.0 mm.

synapomorphies for the subgenus and constant throught the clade, the sampling may not be as optimal as presumed, leaving out species with different traits than what was portrayed.

Wang et al. (2019) recently published three new species and a key to the Oriental species. The constriction of T1 is occasionally used in their key, highlighting the existence of specimens with a stronger constriction. However, this is not illustrated, making it impossible to determine to what degree the sclerite narrows. Still, clearly strong constrictions are illustrated for the newly described species *Z. asperipunctatus* Wang and Li and *Z. nullimarginatus* Wang and Li. The basal longitudinal carine of T1 was not used in the key, but in the two aforementioned species, the structure was not observed.

The *Z. dolosus* species group appears to be paraphyletic in relation to the *Z. quadridentatus* group. A thorough analysis is needed of *Z. (Zethastrum)* including representatives from the *trimaculatus* species group to verify the validity of the assemblages.

Although Gusenleitner (2007) described *Z. fulgens* comparing it to *Z. nigerrimus*, a species in the *trimaculatus* group, the type was examined, and it fits more properly the *Z. luzonensis* group. Selis (2017) recently revised this group, but left *Z. fulgens* out, just as Wang et al. (2019) did not key it in couplets along with the group. However, in its description (Gusenleitner, 2007), more emphasis is given to punctuation and color and little attention is given to the pilosity, an outstanding and diagnostic trait of the group and so, it is no surprise Selis did not consider examining this species.

Distribution. Palearctic and Oriental.

Included species-groups. *dolosus*, *luzonensis*, *quadridentatus*, *trimaculatus*.

Etymology. The subgeneric name comes from the radical *Zethus* accompanied by the suffix *-astrum* which stands for incomplete resemblance.

Included species. 29.

***Zethus (Zethoides)* Fox, 1899**

Fig. 10

Zethoides Fox, 1899: 436 (genus). Brèthes 1903: 249 (questions as distinct genus); Zavattari 1912: 6 (key), 76 (questions distinct genus).

Type species: *Zethoides smithii* Fox, 1899 (= *Zethus (Zethoides) chapadensis* Bohart and Stange 1965).

Baeoprymna Cameron, 1912: 224 (genus). Bohart and Stange 1965: 150 (jr. syn. of *Zethus (Zethoides)*)

Type species: *Baeoprymna rufoornata* Cameron, 1912 (= *Zethus miniatus* de Saussure, 1858).

Protozethus Bertoni, 1925: 75 (genus). Bohart and Stange 1965: 150 (jr. syn. of *Zethus (Zethoides)*).

Type species: *Zethus olmecus* de Saussure, 1875 by monotypy.

Zethus (Zethoides) Bohart & Stange, 1965: 20 (dendrogram), 25 (key to subgenera), 150 (subgenus of *Zethus*, sr. syn. of *Baeoprymna* and *Protozethus*), 203, 204 (figs). Lopes and Noll 2018 (phylogenetic analysis).

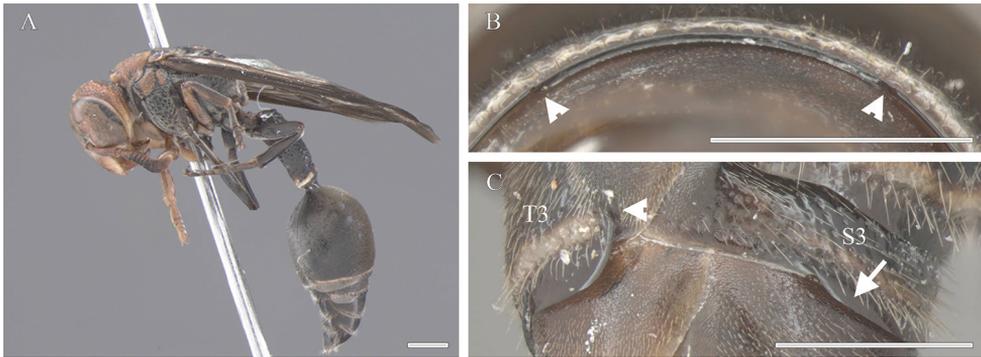


Figure 10. Synapomorphic characters of *Zethus* (*Zethoides*) **A** habitus of *Z. miniatus* **B** end-on view of primary (lower) and secondary (upper) lamellae of the third tergum; arrowheads delimit extent of primary lamella **C** third metasomal tergum and sternum, lateral view; arrowhead indicates perpendicular indent; arrow indicates medial lamellar lobe. Scale bars: 1.0 mm.

Description. Male antennae hook-like. Longitudinal interantennal carin present, transversal may be absent. Female clypeus short, not microstriae, usually with apical teeth. Male mandible with three to four teeth. Galea length variable. Labial palpi 4-segmented, with palpomere one curved or straight. Occipital carina ventrally complete. Vertex flat. Genal margin rarely evenly convex, sinuous in more derived groups. Pronotal carina lamellar with lateral portion strongly sinuous, rarely straight (in *olmecus* group). Pre-tregular carina usually incomplete, sometimes absent. Welts absent. Notaulices rarely present. Tegula angled or evenly convex, with outer margin usually completely raised. Epicnemial carina complete. Posterior carina of mesepimeron usually absent, present only in *Z. binodis* group. Two or one midtibial spur. Metanotum anteriorly margin. Lateral carina of metanotum variable, from very short to extending as a transverse carina. **Coxa usually with reflexed socket margin.** Spines in posterior tibiae of females in one row, when present. Apical angle of marginal cell variable. Dorsal aperture of propodeum present. Propodeum with submedian carina usually present (absent only in *aztecus* and *minimus* groups); lateral carina present of variable length; sublateral usually absent. Apical propodeal lamella present or absent. T1 variable. Margin of S1 variable. Stem of T2 variable (especially elongated in *binodis* group). Lamella of T2 well developed. **T3 tuberculate and apical margin posteriorly projected. Apical lamella of T3 tapered laterally** (Fig. 10B). **Secondary lamella present on T3** (Fig. 10B) **with perpendicular lateral indent** (Fig. 10C). **Lamella of S3 reduced. Medial lamellar lobe on S3 present** (Fig. 10C). S5 and 6 of males without carinas. **Basoventral projection of cuspis absent.**

Observations. *Zethus* (*Zethoides*) stands out among all the other subgenera of *Zethus*. While its synapomorphies are concentrated in the third metasomal segment, its representatives do not share a similar body plan and show the greatest morphological variation within one subgenus. The species-groups here present may show similarity to other lineages (or subgenera) of *Zethus* and may mislead one into supposing a closer

relationship to others than *Z. (Zethoides)* (e.g.: *Z. aztecus* to some *Z. (Zethusculus)*; *Z. binodis* group to *Z. (Didymogastra)*; *Z. biglumis* group to the *Z. pallidus* group). This may suggest a faster diversification in the lineages of *Z. (Zethoides)* when compared to other subgenera.

Distribution. Nearctic and Neotropical.

Included species-groups. *aztecus*, *biglumis*, *binodis*, *carinatus*, *olmecus*, *parvulus*.

Included species. 43

Zethus (Zethus) Fabricius, 1804

Fig. 11

Zethus Fabricius, 1804: 282 (genus). Giordani Soika 1958: 75 (revision of Oriental species). Bohart and Stange 1965 (revision new world species). Giordani Soika 1979: 20 (revision African species). Carpenter, 1986

Type species: *Zethus coeruleopennis* (Fabricius, 1798) (= *Vespa coeruleopennis* Fabricius, 1798).

Lethus Say, 1837: 387 (misspelling).

Heros de Saussure, 1856: 115 (division of *Zethus*).

Euzethus Dalla Torre, 1904: 14 (name for division I of *Zethus* in de Saussure 1852).

Type species: *Vespa coeruleopennis* (Fabricius, 1798)

Zethus (Zethus) Bohart & Stange, 1965: 20 (dendrogram), 25 (key to subgenera, subgenus of *Zethus*), 197–201 (figs). Lopes and Noll 2018 (paraphyletic).

Description. Male antennae hook-like. **Interantennal longitudinal and transversal carinas absent.** Clypeus of females short, without microstriae and with or without apical teeth. Male mandible with two to four teeth. Galea short. Labial palpi usually 4-segmented with first palpomere curved. Occipital carina ventrally present or absent (Fig. 11B). Vertex generally raised behind ocelli. Genal margin evenly convex. Pronotal carina lamellar or short with lateral portion straight or sinuous. **Pre-tegular carina absent.** Welts absent. **Notaulices present, incomplete** (Fig. 11C) or complete in more derived groups. Tegula evenly convex or posteriorly angled, with outer margin beveled or raised on posterior half. Dorsal carina usually complete, sometimes dorsally incomplete. Mesepimeron without carina. Usually two tibial spurs, rarely one. Metanotum anteriorly margined, usually without lateral carina. Spines of hind tibia scattered. Marginal cell apically obtuse. Dorsal aperture of propodeum mostly present. Propodeum with submedian carina absent (present only in *Z. wileyi*), lateral and sublateral carinas present. Apical lamella of propodeum absent (present only in *Z. prominens*). T1 variable. S1 with anterior margin elliptical or quadrate. Lamellae of T3 and S3 usually developed. S5 and 6 of males without carinas.

Observations. The inclusion of *Z. wileyi* in this clade was unexpected. As observed by Lopes et al. (2017), this taxon ran in Bohart and Stange's (1965) key as closely related to the species-groups within *Z. (Didymogastra)*, but in the present analysis it is



Figure 11. Synapomorphic characters of *Zethus* (*Zethus*) **A** habitus of *Z. coeruleopennis* **B** head of *Z. infundibuliformis*, oblique posterior view. 42. Mesoscutum of *Z. discoelioides*, dorsal view; arrowhead indicates incomplete notaulus. Scale bars: 1.0 mm.

recovered in *Z.* (*Zethus*). The former relationship may have been an artifact due to poor sampling of representatives in the nominotypical subgenus.

Distribution. Nearctic and Neotropical.

Included species-groups. *chalybeus*, *coeruleopennis*, *discoelioides*, *infundibuliformis*, *magretti*, *prominens*, *spinipes*, *stangei*, *wileyi*.

Included species. 52

Zethus (*Zethusculus*) de Saussure, 1855

Fig. 12

Zethusculus de Saussure, 1855: 118 (division of genus *Zethus*); 1875: 18 (division of *Zethus*).

Type species: *Zethus jurinei* de Saussure.

Zethusculus Howes, 1917: 407 (misspelling).

Zethus (*Zethusculus*) Bohart & Stange, 1965: 20 (dendrogram), 25 (key to subgenera), 125 (subgenus of *Zethus*, key to species), 202 (figs). Lopes and Noll 2018 (paraphyletic).

Description. **Interantennal longitudinal and transversal carinas absent.** **Male flagellum rolled** (Fig. 12D). **Female clypeus microstriate** (Fig. 12B), short and without apical teeth. **Male mandible 3-toothed.** Galea short. Labial palpi 4-segmented with first palpomere curved. Occipital carina ventrally complete or as small branch. Vertex usually raised (flat only in the *imperfectus* group). Genal margin mostly evenly convex (sinuous in the *imperfectus* group). Pronotal carina lamellar with lateral portion strongly sinuous. Pre-tegular carina incomplete. Welts and notaulices absent. **Tegula with outer margin usually angled, raised except for medial interruption** (Fig. 12C). Epicnemial carina complete. Mesepimeron without carina. Mid tibia with one apical spur. Metanotum anteriorly margined with lateral carina extending at most to anterior half of the sclerite. Spines in posterior tibia scattered. Apical angle of marginal cell variable. Dorsal aperture of propodeum only present in *imperfectus* group. Propodeum



Figure 12. Synapomorphic characters of *Zethus* (*Zethusculus*) **A** habitus of *Z. jurinei* **B** close-up of female clypeus of *Z. mexicanus* **C** tegula of *Z. mexicanus*; arrowheads indicate length of interruption on raised margin **D** male flagellum of *Z. mexicanus*. Scale bars: 1.0 mm.

with lateral carinas and without submedian and sublateral carinas. Apical lamella of propodeum only present in *imperfectus* group. T1 with short stem and medium expansion. S1 with elliptical anterior margin. S2 with apical lamellae. T3 with apical lamella only in *imperfectus* group. S3 without lamellae only in *mexicanus* group. S5 and 6 without carinas. **Anterior margin of ventral lobe of aedeagus reflexed outward.** Cuspis with apical tuft.

Observations. While Lopes and Noll (2018) recovered this subgenus as paraphyletic, the results here present support the wider analysis of the group (Golfetti et al. 2020) where it is recovered as monophyletic.

Distribution. Nearctic and Neotropical.

Included species-groups. *arietis*, *imperfectus*, *mexicanus*.

Included species. 27.

Nomen dubium

These taxa of doubtful application lack evidence that allows a proper affiliation to species-groups or subgenera, thus considering them *incertae sedis* as well. Three of the taxa are already cited in Bohart and Stange (1965): *Z. assimilis* (Brèthes), *Z. holmbergii* Brèthes and *Z. medius* Brèthes. Three species are added to this list: *Z. didymogastra* Spinola, *Z. rufipes* Fox and *Z. scandens* Zavattari.

Zethus didymogastra Spinola, 1841 – After its description, de Saussure (1852) synonymized it under *Z. binodis* Fabricius, only to go back and validate *Z. didymogastra* again after two decades (de Saussure, 1875). The last mention of this species was by Cameron (1912) when he synonymized it once again also under *Z. binodis*. Nevertheless, the taxonomic catalog of *Z. binodis* in Bohart and Stange (1965) does not bring the synonym nor is the species brought up anywhere else in their study.

Zethus rufipes Fox, 1899 – This taxon makes a rather curious case, where Bohart and Stange (1962) designated a lectotype, but never mentioned it in their great revision of 1965. The fact that this species was omitted in Bohart and Stange (1965) was noted by Carpenter and Vecht (1991).

Zethus scandens Zavattari, 1913 – This species was described by Zavattari and only again cited by Rasmussen and Asenjo's (2009) catalog for Peruvian fauna. No remarks or lists were made by any other authors, not even Bohart and Stange (1965).

Concluding remarks

This is the first broad phylogenetic analysis of *Zethus* and corroborates an already predicted paraphyly of the genus in relation to *Ischnocoelia* and *Ctenochilus*. Still, the study suggests an expansion regarding the subgeneric classification, as nine robust lineages were recovered and labeled as subgenera. Despite the fact that the clades comprising each subgenus are at least moderately supported, their relationships are not, and there are also three species-groups (*albopictus*, *pallidus* and *spinus*) that require deeper investigation in order to assign them to a subgenus or create one of their own. Thus, this study reveals an incongruence with traditional classification, proposes a new one and forms a base for more specific approaches on the genus.

Acknowledgements

We thank all who supported the completion of this study, especially all collections and curators who provided loans that allowed wide sampling. We also thank Dr. Cintia Lopes, Dr. Dalton Amorim, Dr. Marcel Hermes and Dr. Yuri Grandinete for insights on early versions of the manuscript. We also thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing scholarships for RBL's doctorate in the Universidade de São Paulo and research internship at the American Museum of Natural History.

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Supplementary material 1

List of characters and states used in the study

Authors: Rogério Botion Lopes, James M. Carpenter, Fernando Barabosa Noll

Data type: morphological characters

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Supplementary material 2

Topologies recovered from using distinct k values for implied weighting in parsimony searches

Authors: Rogério Botion Lopes, James M. Carpenter, Fernando Barabosa Noll

Data type: phylogenetic analysis

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Link: <https://doi.org/10.3897/jhr.82.65760.suppl2>

Supplementary material 3

List of all *Zethus* species according to the new proposed subgeneric division

Authors: Rogério Botion Lopes, James M. Carpenter, Fernando Barabosa Noll

Data type: species data

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Supplementary material 4

Matrix used in the searches included in this studie's phylogenetic analysis

Authors: Rogério Botion Lopes, James M. Carpenter, Fernando Barabosa Noll

Data type: morphological matrix

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