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Species-group organization of the Pan-American *Dissomphalus* (Hymenoptera, Bethylidae)

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Abstract: *Dissomphalus* is a cosmopolitan genus with 424 described species. Here, all 287 Pan-American species of *Dissomphalus* are analyzed in order to be allocated to species groups under an alpha taxonomic approach. Thirty-four species groups composed of species with known males were initially considered. The following six species-groups are newly proposed: *chiapanus*, *confusus*, *cornutus*, *fungosus*, *lamellatus* and *napo*. The following eleven species groups are fused into four: *dissomphaloides* with *amplus*, *altivolans* with *apertus*, *xanthopus* with *microstictus*, *kansanus* with *secretus*, *basidentatus* and *stellatus* with *vallensis*, and *strabus* with *tuberculatus*. Forty-seven *incertae sedis* species are grouped and 29 are newly grouped. A total of 35 species groups are now recognized and all of the 11 species known exclusively by females remain unallocated to groups. A pictorial key to the species groups is first proposed.

Keywords: Alpha taxonomy - Chrysidoidea - Nearctic - Neotropical - Pristocerinae - synopsis.

INTRODUCTION

Dissomphalus Ashmead (Fig. 1) is hitherto the largest genus of Bethylidae with 442 valid species worldwide (Azevedo *et al.,* 2018b; Colombo *et al.,* 2018), of which 287 occur in the New Word. Nine species are recorded from the Nearctic region, and five of them are restricted to this regions, three range to Central America, and only *D. krombeini* Azevedo reaches South America (Azevedo, 2003). All the others 278 are distributed throughout the Neotropical region.

Evans (1955 [1954]) was the first to organize *Dissomphalus* into species groups, when he proposed the *xanthopus* and *apertus* species groups for the eight North American species valid at that time. Soon after, Evans (1962) added the *kansanus* species group and included species from Mexico and the Caribbean islands. However, some species were left unallocated.

Alencar & Azevedo (2006, 2008), Azevedo (1999a, 2000, 2001, 2003), Colombo & Azevedo (2016) and Redighieri & Azevedo (2006) organized the Neotropical *Dissomphalus* in 32 groups. During these years, hundreds of new species were described, many of them in studies focused on a particular geographical area, such as Azevedo (1999b), Brito & Azevedo (2017), Colombo & Azevedo (2016), Colombo *et al.* (2018) and Redighieri & Azevedo (2004, 2006). However, many species published in these studies were not allocated in any species group.

Today there are four main problems with the alpha taxonomy of Pan-American *Dissomphalus* related to the species-group organization. First, the organization by Evans was focused mostly on Nearctic species at a time when the genus had few valid species, and Azevedo and collaborators were focused mostly on Neotropical species. Both systems were not fully congruent. Second, there are about 50 species not allocated in any species group. Third, there are several fragmented keys for species group or at the species level covering restricted geographical areas. Thus, identifying any species of Pan-American *Dissomphalus* is a tough task because no key encompassing all species groups or species is available. Fourth, Evans's and Azevedo's group organizations were based on characters of the second metasomal tergal process, a structure of male metasoma, and on male genitalia, but mostly on the former. Thus, species known exclusively by females were never arranged in groups.

Given this scenario, the objective of this contribution is to solve the three first problems aforementioned by proposing a single species-group organization embracing all Pan-American species of *Dissomphalus* known from males.

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Fig. 1. Habitus of *Dissomphalus*. (A) Species group *bicavatus*. (B) Species group *conicus*. Scale bars 2 mm.

MATERIALS AND METHODS

This contribution is fully based on the original descriptions, further information and redescriptions of all species recorded from the Pan-Americas, their type series and any other voucher found in Alencar & Azevedo (2006, 2008), Ashmead (1893, 1894), Azevedo (1999a, b, c, 2000, 2001, 2003), Azevedo *et al.* (2016, 2018a, b), Brito & Azevedo (2017), Bruch (1916), Colombo & Azevedo (2016) Colombo *et al.* (2018), Evans (1955 [1954], 1962, 1963, 1964, 1966, 1969, 1978, 1979), Kieffer (1904, 1906 [1905], 1908, 1910a, b, 1911, 1914a, b), Ogloblin (1930), Redighieri & Azevedo (2004, 2006), Snelling (1996), Vargas & Terayama (2002), Wasmann (1899), Westwood (1839).

The dichotomous keys were drawn up by juxtaposition to identify the species-group, according to their most important characters. Most of the couplets are new, but those of species-groups with median tergal processes are mostly based on Azevedo (1999a). The main characters of each couplet are illustrated. The hand drawings are digitally prepared and represent fictitious specimens. Most of these illustrations are related to tergal processes on the second metasomal segment, which can have a wide range of structures.

I adopted a convention of three different structures in the line drawings. Depressions are a lowering of the surface with a smooth edge, drawn with dashed lines in all illustrations, for instance figure A at couplet 5 in the key. On the other hand, pits are holes on the surface with a sharp edge, clearly outlined, they are drawn with regular lines, for instance figure B at couplet 5 in the key. If the pit is very wide, I used the term concavity, for instance figure A at couplet 34 in the key.

The habitus of Figure 1 was photographed with a Leica Z16 APO stereomicroscope coupled to a Leica DFC 2 video camera with Leica Application Suite V3.6.0 by Leica Microsystems (Switzerland). The image stacks were combined with Helicon Focus (HeliconSoft) and posteriorly edited with Gimp 2.10 software.

The tubercles of the tergal processes are nodular protuberances on the surface of metasomal segment II. They have three orientations. When the tubercles are directed anterad, they are drawn turned forward, for instance figure A in couplet 21 in the key. When the tubercles are directed mesad, they are drawn toward median plane of the metasoma, for instance figure B at couplet 3 in the key. When the tubercles are directed dorsad, they are drawn directed posterad, otherwise the setae would appear in the illustrations as dots rather than filaments, for instance figure A at couplet 3 in the key.

The scope of this contribution is focused on species-group rank other than species level. Thus, the section with check lists of each species-group is not intended to be a catalog. So, only a list of all valid species is presented, without nomenclatural heading. The terms applied to structures follow Lanes *et al.* (2020).

RESULTS

I recognize 287 species of *Dissomphalus* occurring in the New World, organized in 35 species groups, six of them newly proposed. Eleven species known only from female specimens were not grouped.

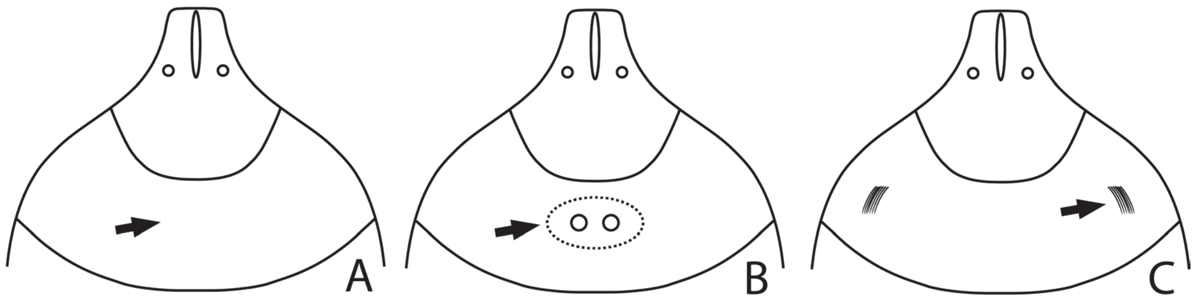
Key to species-groups of Pan-American *Dissomphalus* (♂)

Shortcuts to major groupings

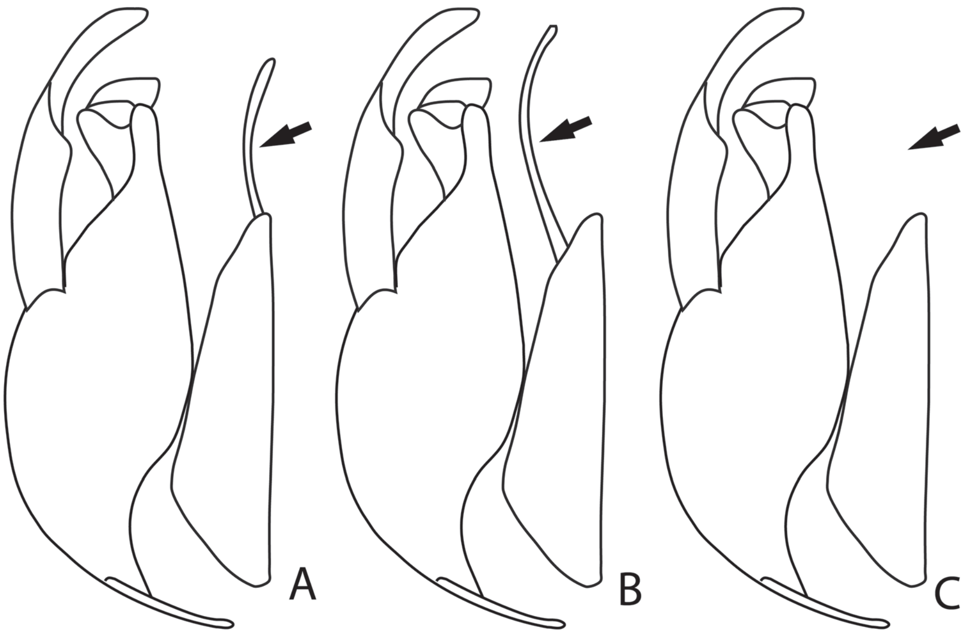
Tergal process absent 2
Tergal process present 5
Median tergal process 6
Lateral tergal process 16
Tergal process without tubercles 19
Tergal process with pair of pits 18
Tergal process with pair of tufts of setae, without any pit 20
Tergal process with pair of tubercles 28

Key to groups

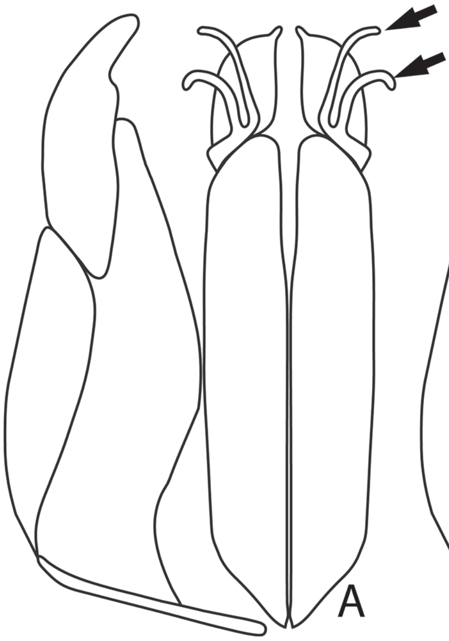
1. Tergal process absent (A) 2
– Tergal process present (B, C) 5



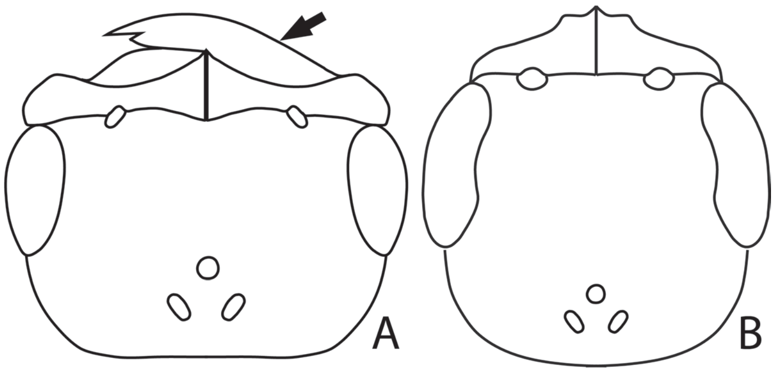
2. Apex of aedeagal ventral ramus with apical (A) or subapical (B) filament .... *microstictus* (E.8)
– Apex of aedeagal ventral ramus without such filament (C) 3



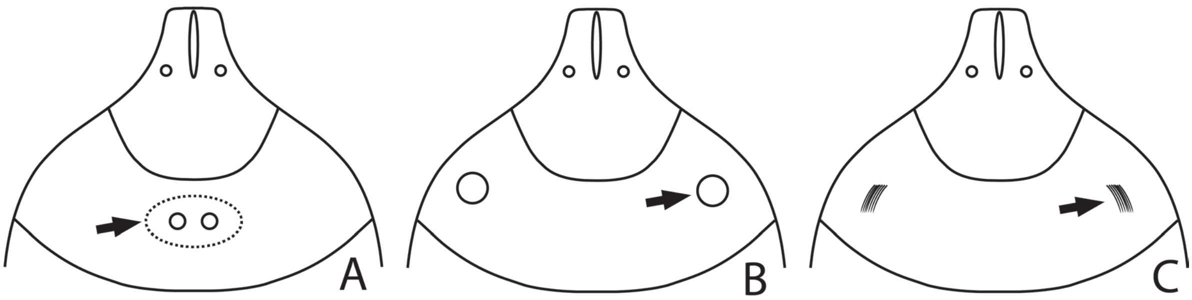
3. Aedeagal dorsal body with two pairs of flagella (A).. *incomptus* (E.6)
– Aedeagal dorsal body without flagella (B)..4



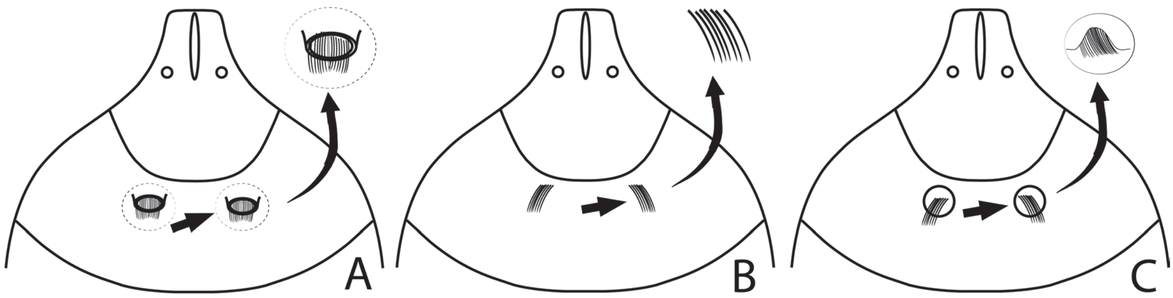
4. Mandibles unusually long, at least ~0.75 × as long as distance between their bases; head unusually wide, head much wider than long (A).. *laticephalus* (E.7)
– Mandibles overlapping just a little bit when closed; head about as wide as long (B).......................... *amplus* (A.1)



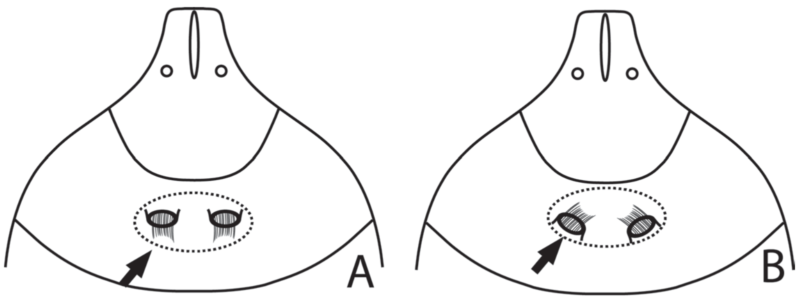
5. Tergal processes close to each other, located at middle of median third of tergal width (A)...................................6
– Tergal processes far from each other, located at lateral third of tergal width, or at most between lateral and median thirds (B, C)..16



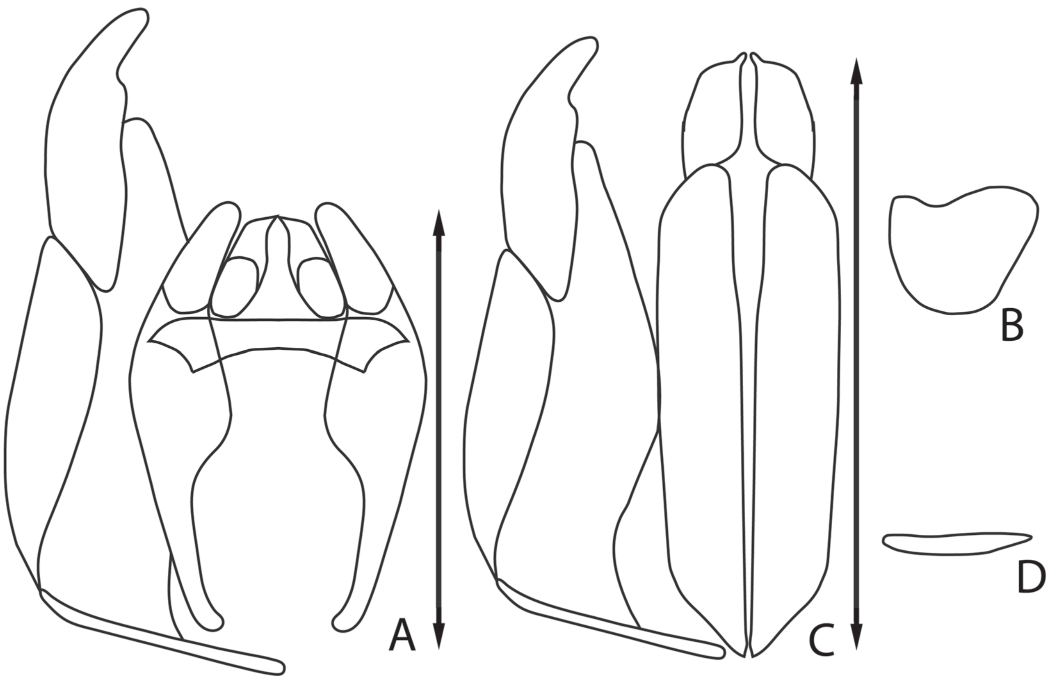
6. Tuft of setae of tergal processes raising from tubercles (A)..7
– Tuft of setae of tergal processes emerging from flat surface (B) or from pits (C), but never from tubercles 10



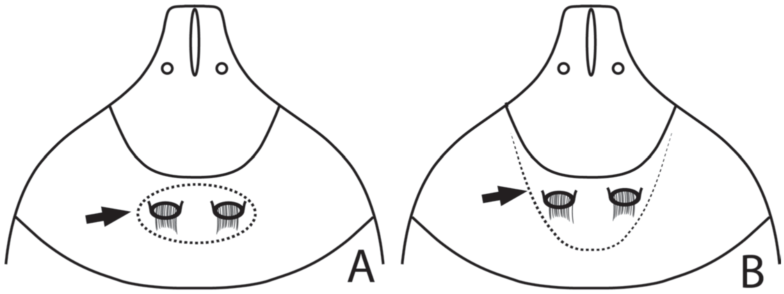
7. Tubercles of tergal processes located at middle of depression, tubercles in vertical position and running parallel (A)..8
– Tubercles of tergal processes located close to distal margin of depression, tubercles at least slightly directed towards each other (B)... *vallensis* (B.11)



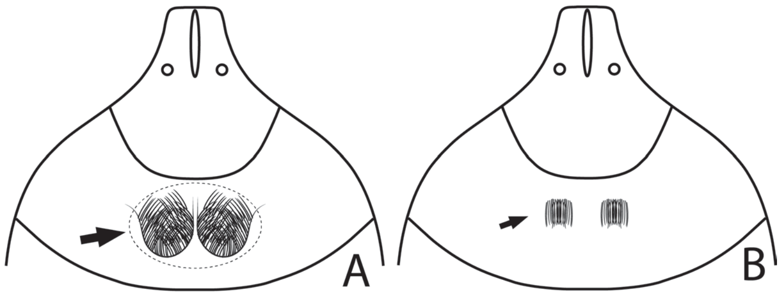
8. Aedeagal dorsal body very short, apex anterior to base of digitus (A); cross-section of aedeagal ventral ramus tubular (B)...*brasiliensis* (B.4)
– Aedeagal dorsal body long, apex posterior to base of digitus (C); cross-section of aedeagal ventral ramus flat (D) 9



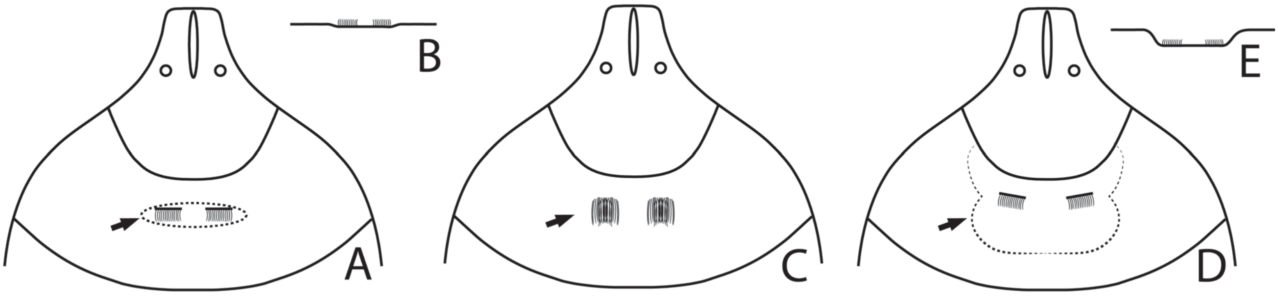
9. Depression of tergal processes elliptical, deep, not embracing posterior margin of metasomal tergite I (A)............ ....*longiclypeus* (B.7)
– Depression of tergal processes half-moon-shaped, shallow, embracing posterior margin of metasomal tergite I (B).. *rasissimus* (B.8)



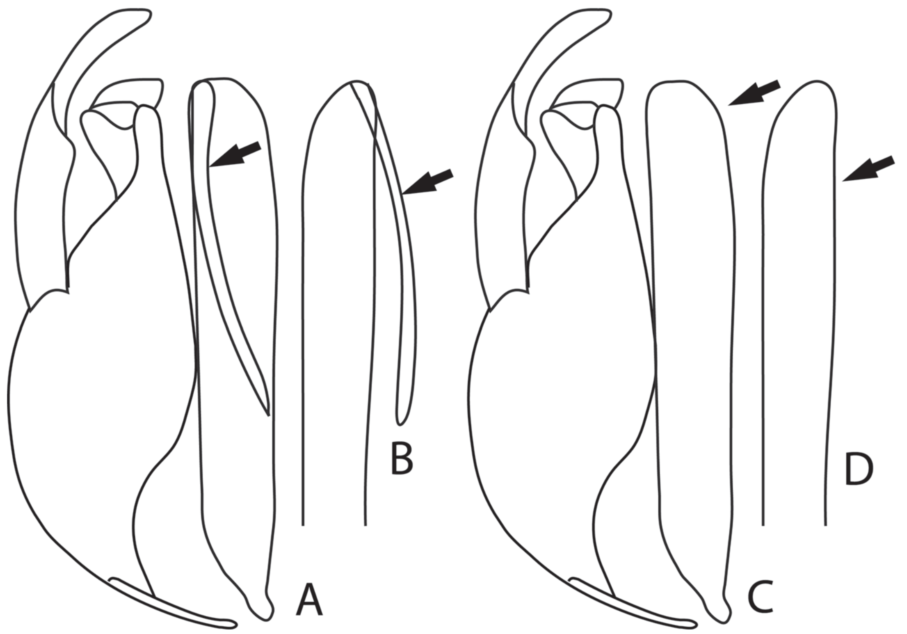
10. Tufts of setae of tergal processes emerging from pair of huge median pits (A)..........................*curvifoveatus* (B.5)
– Tufts of setae of tergal processes emerging directly from surface (B)...11



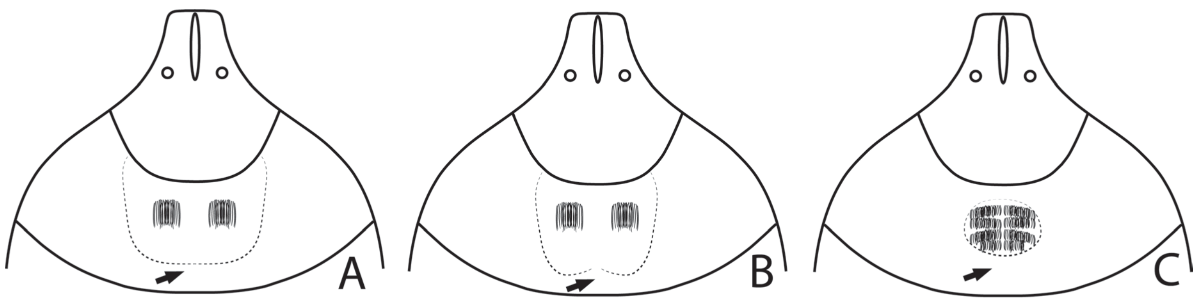
11. Tufts of setae of tergal processes pair linear and transverse (A) in shallow depression (B)............... *bisulcus* (B.3)
– Tufts of setae of tergal processes either non-linear (C), or linear in deep and broad depression (D, E)................12



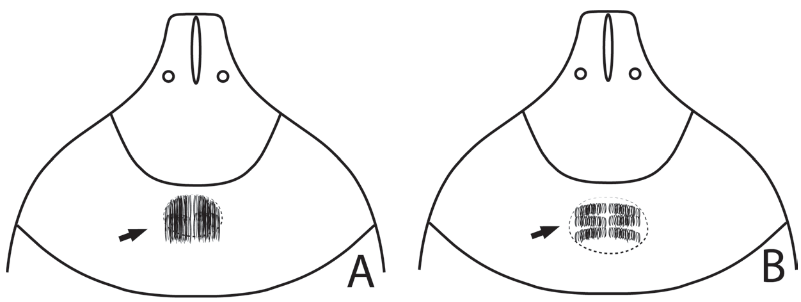
12. Aedeagal ventral ramus with filament strongly angled anterad and ventrad (A, ventral view; B, lateral view)........ .... *bifoveatus* (B.2)
– Aedeagal ventral ramus without such filament (C, ventral view; D, lateral view)..13



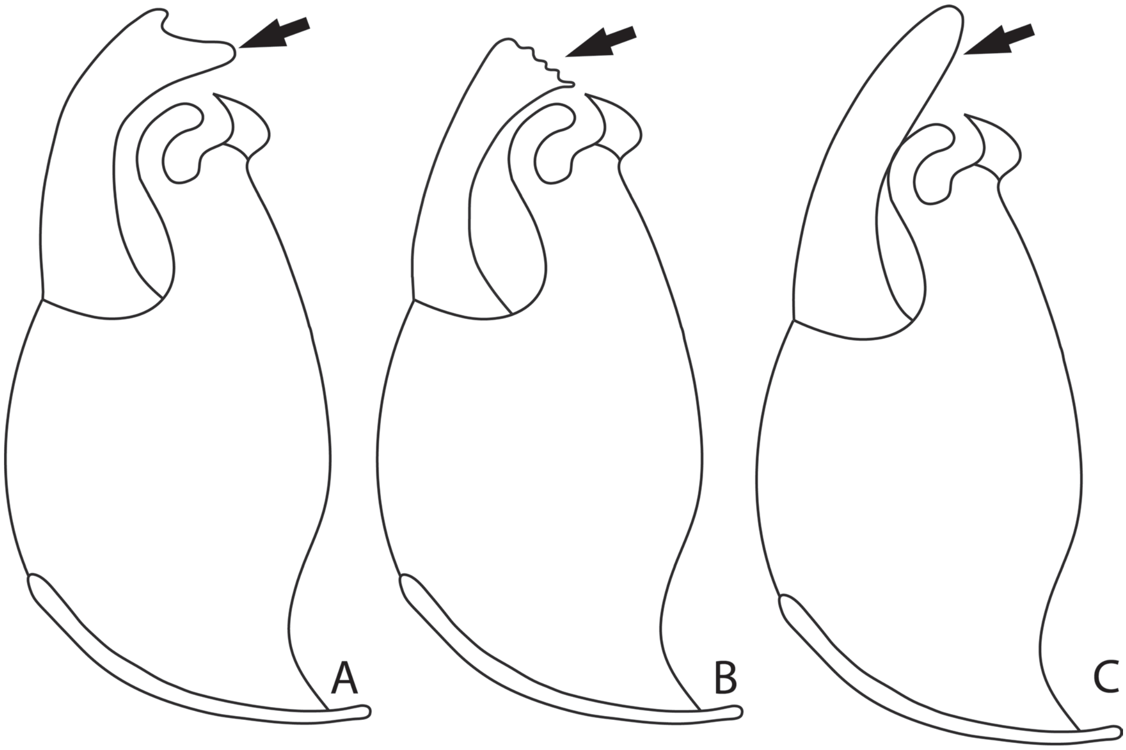
13. Depression of tergal processes half-moon-shaped or nearly so, with posterior margin complete (A) or partially faded (B) .... *linearis* (B.6)
– Depression of tergal processes usually elliptical, subcircular or nearly so (C), but never half-moon-shaped.......14



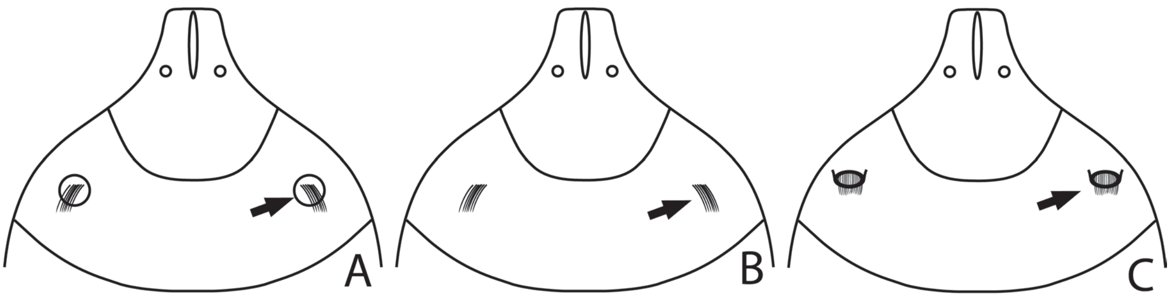
14. Tufts of tergal processes with setae as long as depression (A)... *unitus* (B.10)
– Tufts of tergal processes with setae shorter than depression (B)...15



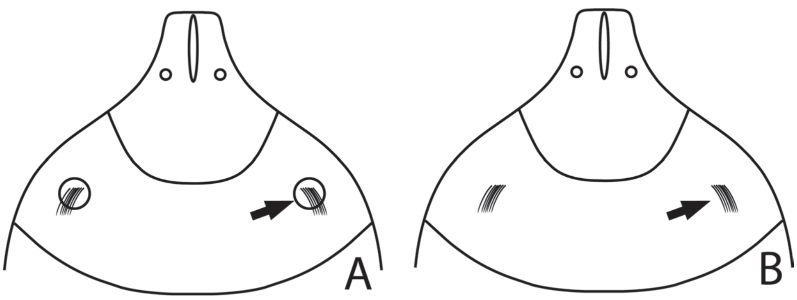
15. Corners of harpe apex angulate, margin between corners truncate, incurved (A) or dentate (B) ..... *ulceratus* (B.9)
– Apex of harpe smoothly tapering and rounded (C) .... *apertus* (B.1)



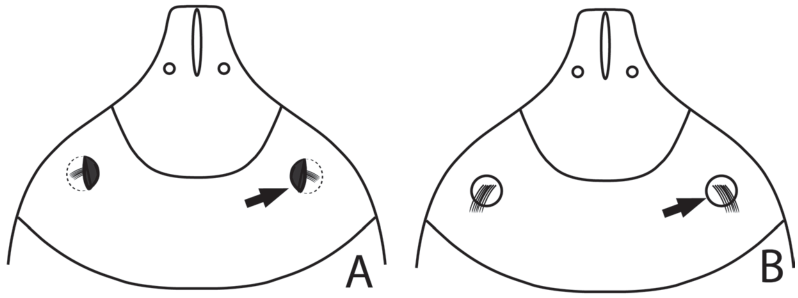
16. Tergal process with tuft of setae placed inside pit (A) or on surface (B), but never with tubercle 17
– Tergal process with tubercle (C)...28



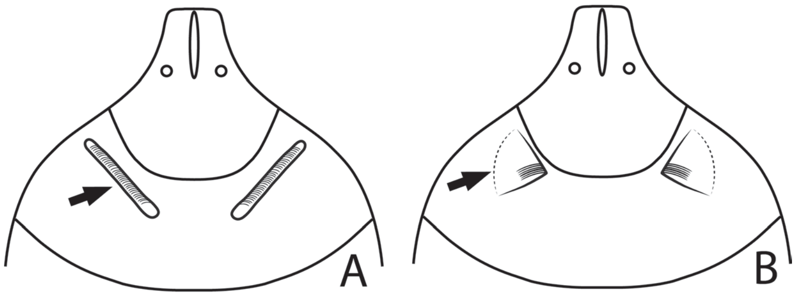
17. Tergal processes with tufts of setae in conspicuous lateral pit (A)..18
– Tergal processes with tufts of setae emerging directly from surface without any pit (B) 20



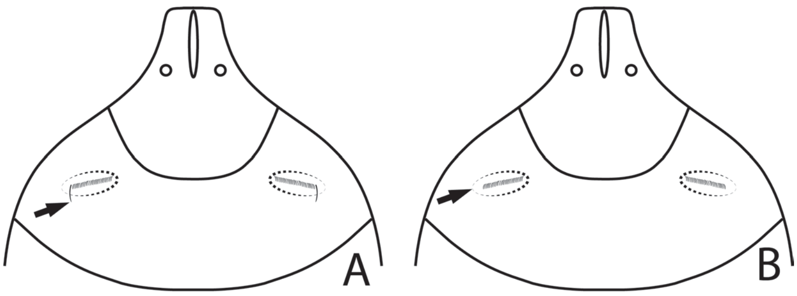
18. Pits of tergal processes subcircular with inner part covered by translucent integument, so that hole is hemispheric (A).. *hemisphaericus* (C.1)
– Pits of tergal processes fully exposed, not partially covered by any expansion (B) 19



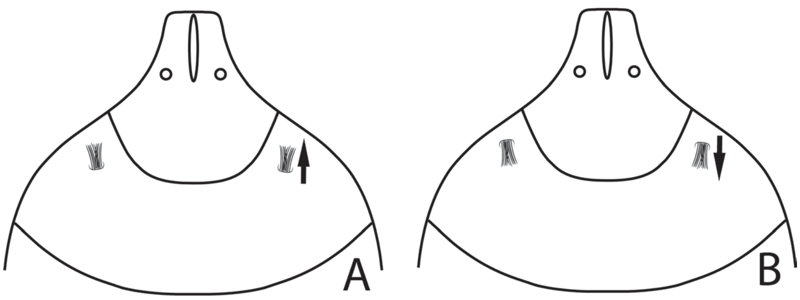
19. Pits of tergal processes elongate, inclined and deeply slit (A) ....*lamellatus* (C.2)
– Pits of tergal processes circular in subtriangular depression (B)... *rettenmeyeri* (C.3)



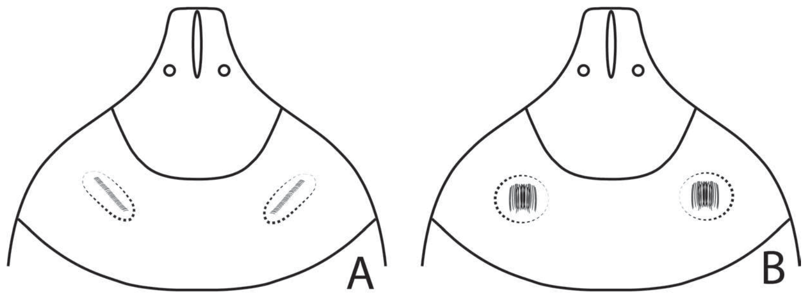
20. Tufts of setae of tergal processes each with one lateral seta distinctly longer than regular ones (A) ..*gilvipes* (D.6)
– Tufts of setae of tergal processes without such distinctly longer seta (B)...21



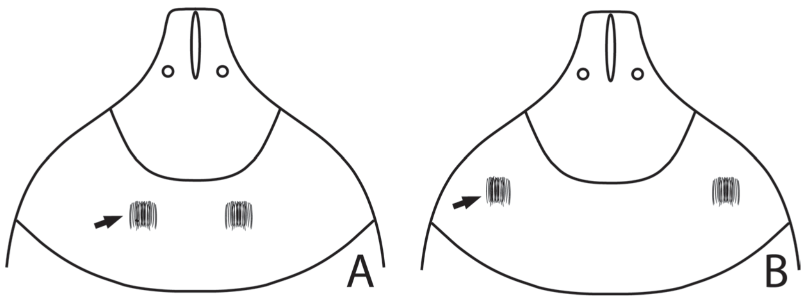
21. Tufts of setae of tergal processes entirely directed anterad (A) .... *amana* (D.1)
– Tufts of setae of tergal processes directed posterad (B) 22



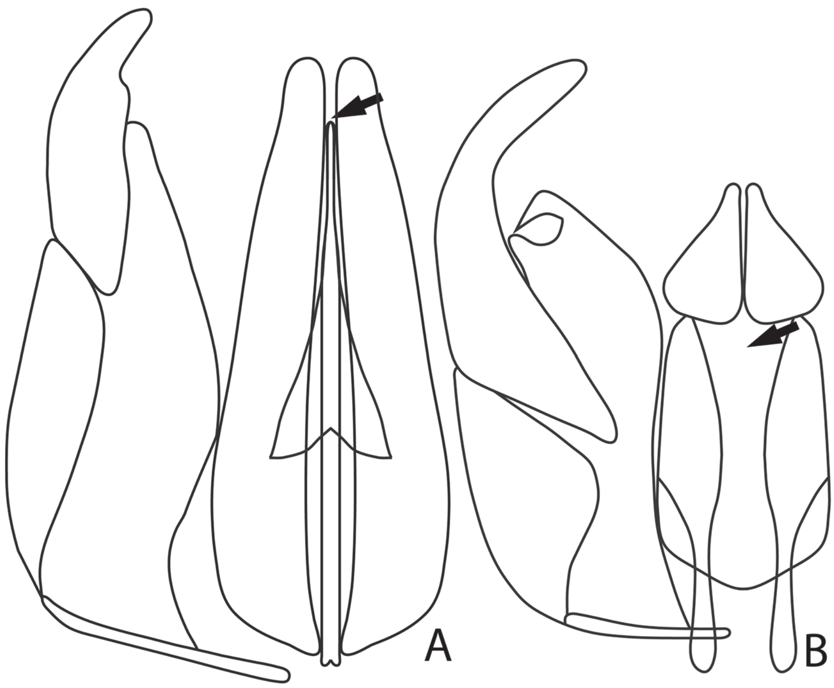
22. Tufts of setae of tergal processes inclined and linear (A).. *rufipalpis* (D.9)
– Tufts of setae of tergal processes usually circular, but never linear (B)..23



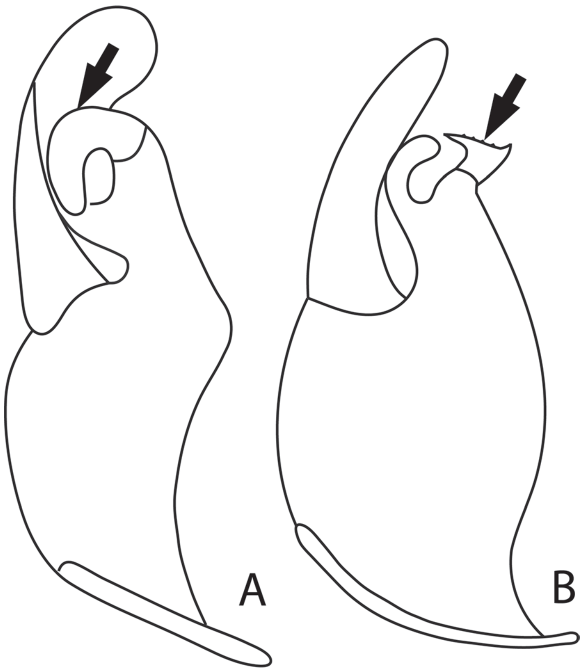
23. Tergal processes located at border between median and lateral thirds of tergal width (A)...................................24
– Tergal processes located on lateral third of tergal width (B)...25



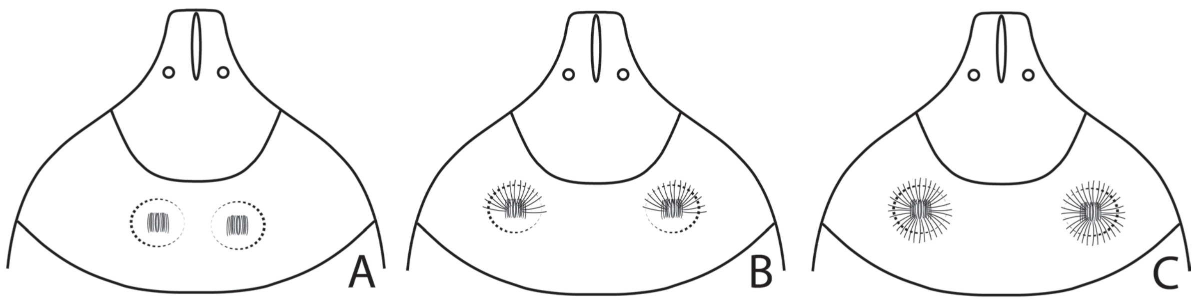
24. Aedeagal dorsal body with elongate median filament; harpe not prominently projected antero-dorsally (A) .... *punctatus* (D.8)
– Aedeagal dorsal body without filament; harpe prominently projected antero-dorsally (B)..............*cornutus* (D.3)



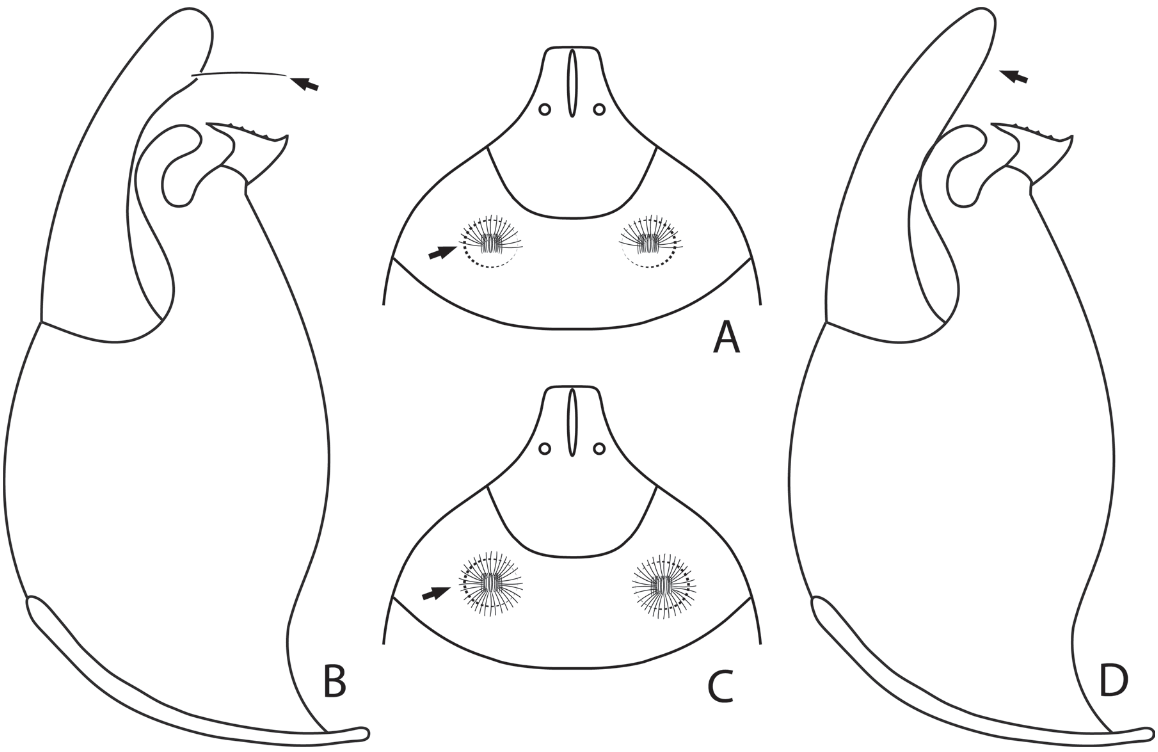
25. Digitus stout, posterior surface including inner corner smooth and without any denticulation (A) .... *napo* (D.7)
– Digitus not stout, posterior surface serrated, inner corner sharpened (B) 26



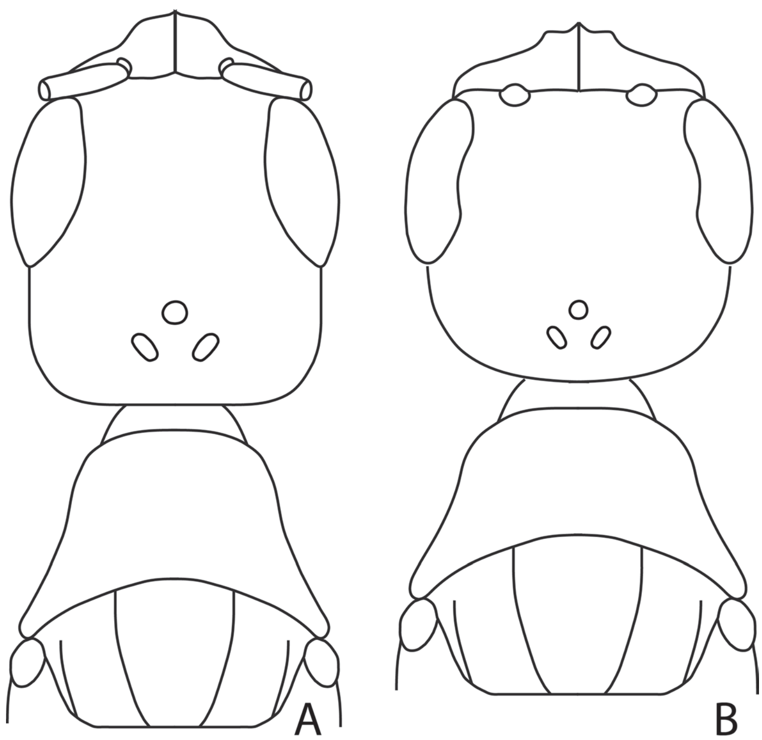
26. Tufts of setae of tergal processes not covered by any set of setae at all (A) .... *confusus* (D.2)
– Tufts of setae of tergal processes at least partially covered by set of longer anterior setae directed posterad (B, C) 27



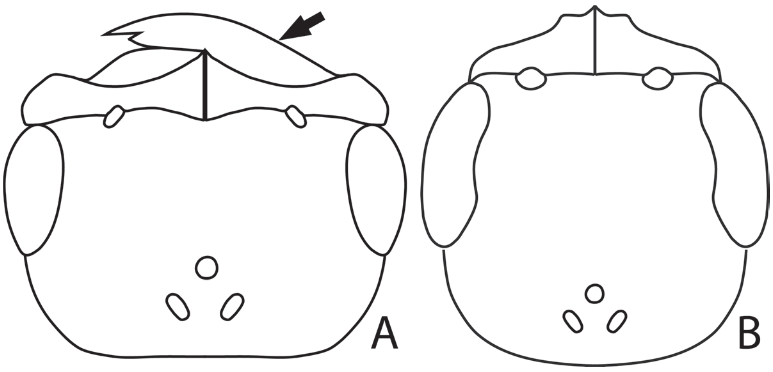
27. Tufts of setae of tergal processes directed posterad, and covered only partially by anterior set of setae, directed posterad (A); inner harpe surface with distinct apical seta (B) .... *coronatus* (D.3)
– Tufts of setae of tergal processes directed mesad, and fully covered by circular set of setae directed mesad (C); inner harpe surface without distinct apical seta (D) .... *fungosus* (D.5)



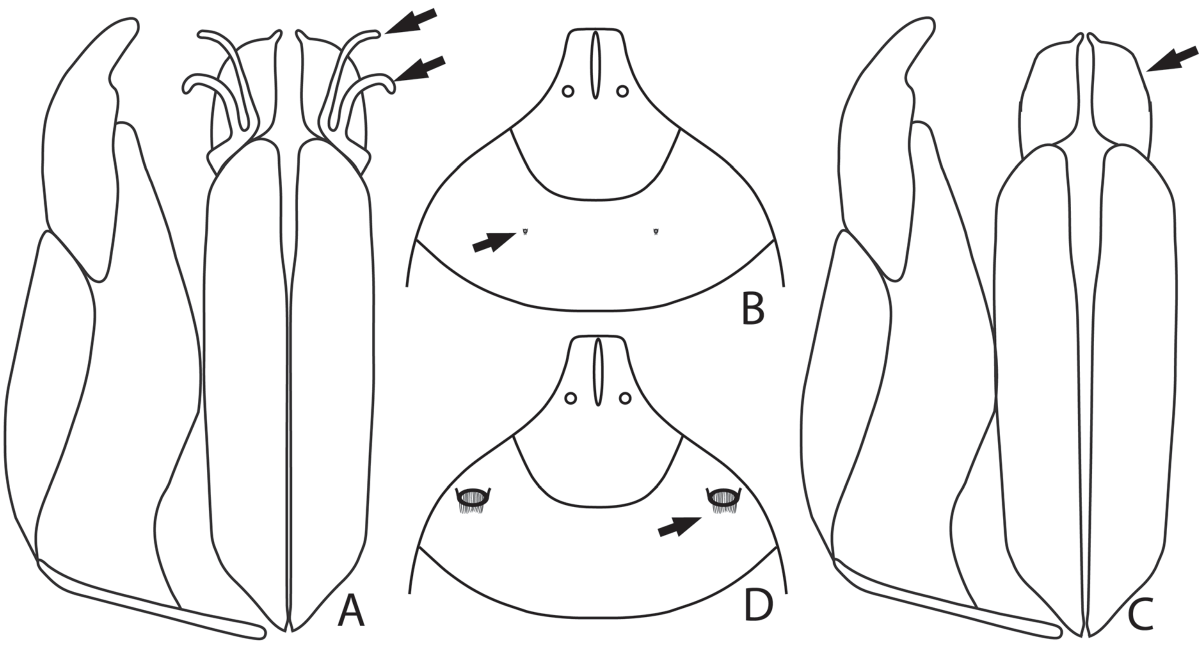
28. Body very elongate; head much longer than wide; dorsal pronotal area nearly as long as mesoscutum, when measured medially (A) .... *dumosus* (E.4)
– Body not so elongate; head most as long as wide; dorsal pronotal area much shorter than mesoscutum, when measured medially (B)..29



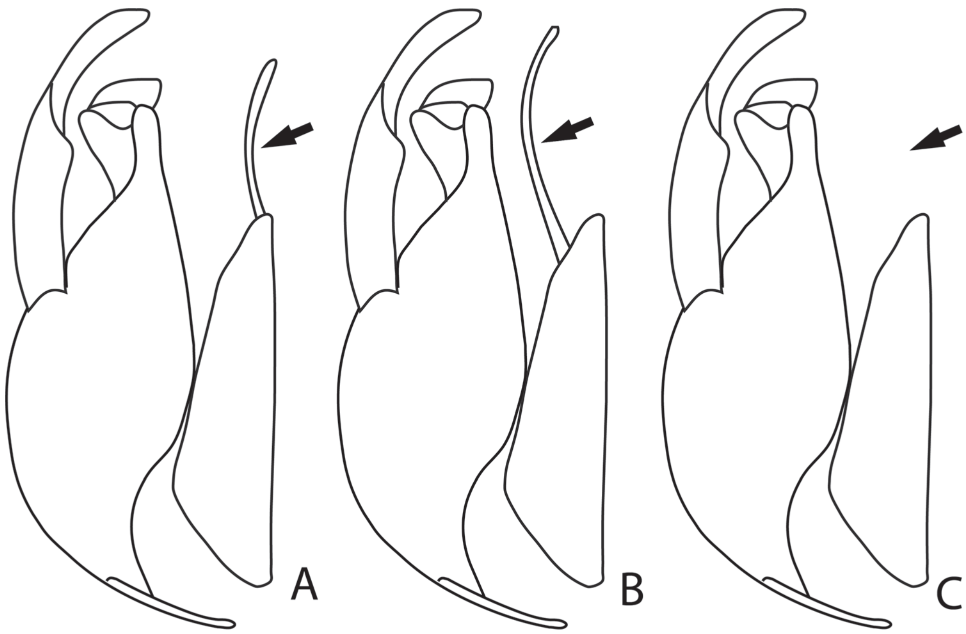
29. Mandibles unusually long, at least ~0.75 × as long as distance between their bases; head much wider than long (A)..*laticephalus* (E.7)
– Mandibles not so long, overlapping each other just little bit when closed; head about as long as wide (B) 30



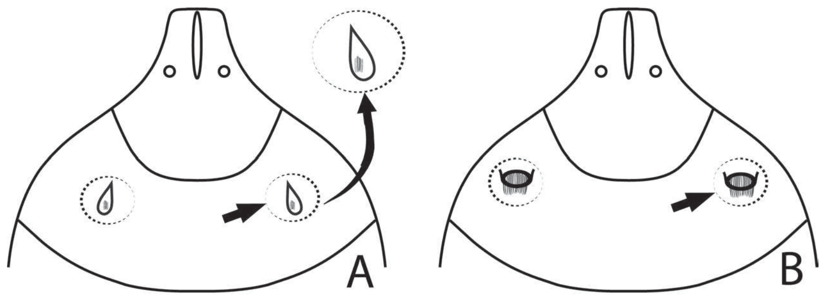
30. Tubercles of tergal processes tiny (A); aedeagal dorsal body with two pairs of flagellae (B) .... *incomptus* (E.6)
– Tubercles of tergal processes small to large (C); aedeagal dorsal body without such flagellae (D) 31



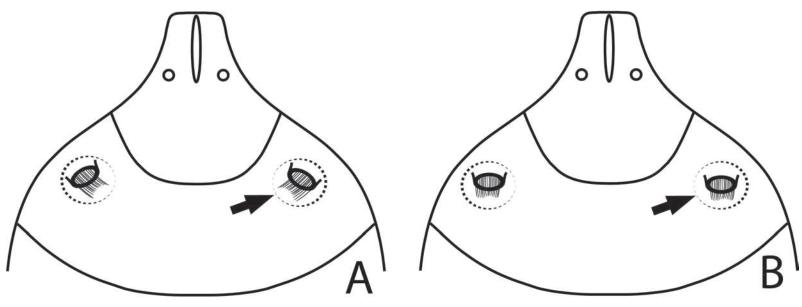
31. Apex of aedeagal ventral ramus with very thin and long filament (A, B).................................... *microstictus* (E.8)
– Apex of aedeagal ventral ramus without such filament (C) 32



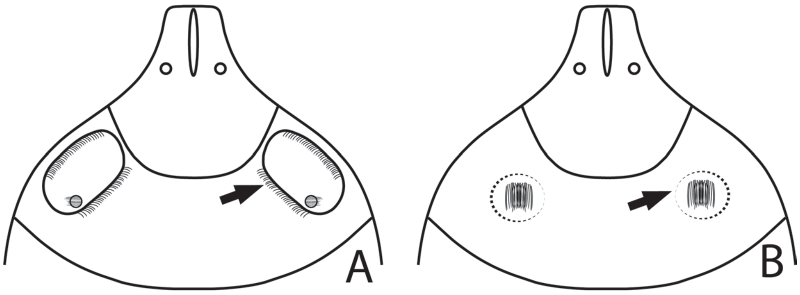
32. Tergal processes with lateral drop-shaped pits, with high rim, sharply pointed anteriorly and rounded posteriorly (A)...*guttus* (E.5)
– Pits of tergal processes never drop-shaped (B)...33



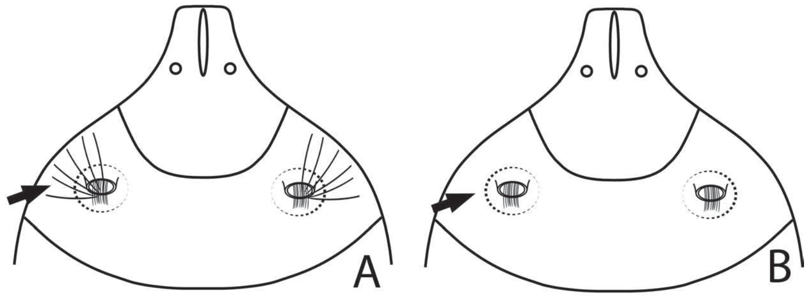
33. Tubercles and tufts of tergal processes at least slightly directed towards each other (A) ....*tuberculatus* (E.11)
– Tubercles of tergal processes not directed towards each other (B) 34



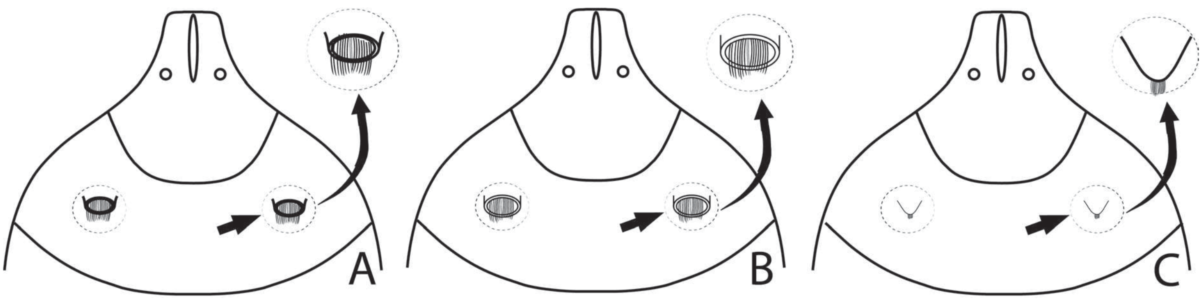
34. Tergal processes very large, occupying more than two thirds of tergal length, and with deep concavity (A) .... *bicavatus* (E.1)
– Tergal processes small or with mid-sized depression, occupying less than half of tergal length, (B) 35



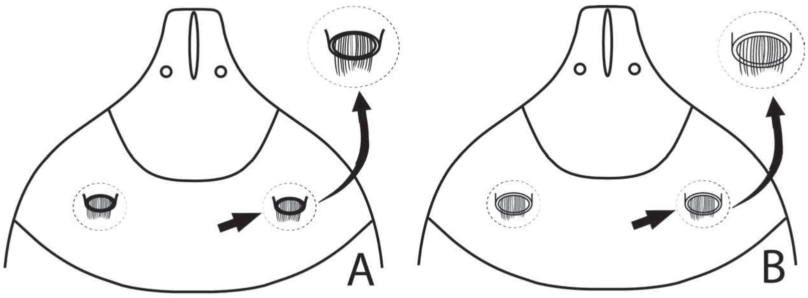
35. Antero-lateral area of depression of tergal process with conspicuous and long set of setae (A) ....*setosus* (E.10)
– Metasomal tergite II without such set of long setae (B)..36



36. Tubercles mostly crater-shaped, tops with pit and tuft of setae (A, B) 37
– Tubercles callus-shaped, progressively narrowing apicad, conical in lateral view, tops without pit, but with tuft of setae (C).. *chiapanus* (E.2)



37. Tubercles navel-shaped, with highly raised and rounded rim, pits usually densely setose, tufts covering pits (A) .. .. *conicus* (E.3)
– Tubercles ring-shaped, with low raised and sharply edged rim, pits usually wide and tufts usually not covering pits (B).. *secretus* (E.9)



The species groups

A. *Species group without tergal process*

A.1. *amplus* species-group

This group is the result of the fusion of *amplus* and *dissomphaloides* species-groups. The *dissomphaloides* species-group was proposed by Evans (1963) to accommodate two species "remarkably *Dissomphalus*-like" (in his words), because the aedeagus is divided in ventral rami and dorsal body. However, he allocated these species in *Apenesia* Westwood because of the absence of a tergal process. Alencar *et al.* (2018) transferred this group to *Dissomphalus* based on molecular and morphological phylogenetic analyses.

This group joins all species without tergal processes on the metasomal tergite II, whose genitalia do not have any filament on the aedeagal ventral ramus as in the *microstictus* species-group, and no apical flagellae on the aedeagal dorsal body as in *incomptus* species-group.

Check list, 17 species:
amplus Redighieri & Azevedo, 2006
asfartus Brito & Azevedo, 2017
azagus Brito & Azevedo, 2017
boitata Colombo & Azevedo, 2018
boto Colombo & Azevedo, 2018
caribbeanus (Evans, 1969) from *incertae sedis*
clovisi Colombo & Azevedo, 2016
denticulatus (Evans, 1963) from *dissomphaloides* species group
dissomphaloides (Evans, 1963) from *dissomphaloides* species group
insulanus (Evans, 1969) from *dissomphaloides* species group
iozus Brito & Azevedo, 2017
kuara Colombo & Azevedo, 2016
lilloanus (Evans, 1969) from *dissomphaloides* species group
miriamae Colombo & Azevedo, 2016
pyata Colombo & Azevedo, 2016
pygmaeus (Evans, 1969) from *dissomphaloides* species group
simulatus (Evans, 1969) from *dissomphaloides* species group

B. *Species groups with median tergal process*

B.1. *apertus* species group

The tergal processes of this group consist of tufts of short setae, not longer than the tuft diameter. Some species like *D. megomphalus* Evans and *D. deformis* Evans have the largest tufts of the genus. The depression is always single and median, but the range of variation is wide, it can be deep or shallow, large or small. The harpe of the male genitalia is evenly outcurved, without any denticulation.

Except for *D. parvus*, the male genitalia of this group have the aedeagal ventral rami wide and short, much shorter than the aedeagal dorsal body. The inner lobe of the dorsal body is semicircular and has a protuberance directed ventrad, with both inner surface and ventral margin wholly setose.

The new composition of this group is mostly the result of the fusion of the *apertus* and *altivolans* groups.

Check list, 11 species:
albipes (Kieffer, 1904) from *incertae sedis*
altivolans Evans, 1955 [1954] from *altivolans* species-group
apertus Kieffer, 1914
deformis Evans, 1969 from *altivolans* species-group
evansi Azevedo, 1999
isteus Brito & Azevedo, 2017 from *altivolans* species-group
lanceolatus Azevedo, 1999 from *altivolans* species-group
megomphalus Evans, 1969 from *altivolans* species-group
parvus Azevedo, 1999
subdeformis Azevedo, 1999 from *altivolans* species-group
subpilosus Azevedo, 1999

B.2. *bifoveatus* species-group

This group is defined on characters of the male genitalia. The aedeagal ventral rami have on the apex an elongated filament, which is strongly angled anterad and ventrad. This feature is unique in the genus. The tergal processes of this group are located in a single depression, which can be very shallow or slightly deep, and occupies the median third of the tergal width or a little more. Inside the depression there is a pair of tufts of setae.

Check list, six species:
angulatus Azevedo, 1999
asitius Brito & Azevedo, 2017
bifoveatus Kieffer, 1906 [1905]
ibocius Brito & Azevedo, 2017
microculus Azevedo, 1999
tisinus Brito & Azevedo, 2017

B.3. *bisulcus* species-group

The tergal processes of this group consist of median linear and transverse tufts of setae. These tufts are placed close to each other, almost touching, and located inside a single depression, which occupies the median third of the tergal width, or slightly more. This depression is so shallow that it is difficult to distinguish from the tergal surface.

Check list, two species:
bisulcus Ashmead, 1894
horizontalis Azevedo, 1999

B.4. *brasiliensis* species-group

This group is defined on characters of the male genitalia. That is because the aedeagus has two features which are very unusual and unique in *Dissomphalus*. The aedeagal ventral rami are tubular, with a circular cross-section or nearly so, and the aedeagal dorsal body is noticeably short, with its apex anterior to the base of the digitus (Redighieri & Azevedo, 2006). The clypeus is broadly projected forward, so that the median lobe is not as clearly defined as in the *gilvipes* species-group, for example.
The tergal processes of this group are placed in shallow median depressions. Each depression has a small, tufted navel-shaped tubercle. The species of this group have a small body, with a delicate metasoma, which usually collapses when the specimen is dry pinned. In this case, the depressions seem to be fused into a single one.

Check list, two species:
brasiliensis Kieffer, 1910
tubulatus Redighieri & Azevedo, 2006

B.5. *curvifoveatus* species-group

The tergal processes of this group consist of very large median pits, strongly arched inward medially, totally covered by a lot of long setae directed mesad and posterad. These pits are located in a single median depression, which occupies the median third of the tergal width. This depression is deep, wide and somewhat triangular (Azevedo, 1999).

Check list, one species:
curvifoveatus Azevedo, 1999

B.6. *linearis* species-group

The tergal processes of this group are placed in a single depression. This depression is large and embraces broadly the posterior margin of metasomal tergite I, so that it has a half-moon shape in dorsal view (Azevedo, 1999), like in the *rasissimus* species-group. However here the depression is somewhat deep and occupies slightly more than the median third of the tergal width. Another important difference is that *linearis* does not have tubercles, whereas in *rasissimus* the tubercles are present, although not clearly defined. In one species the posterior margin is missing, so that it seems an open depression. Nevertheless, this aspect should not be interpreted as a double depression.

Check list, three species:
completus Azevedo, 1999
incompletus Azevedo, 1999
linearis Azevedo, 1999

B.7. *longiclypeus* species-group

The tergal processes of this group consist of navel-shaped tubercles, located in a single transversally elliptical depression, which occupies the median third of the tergal width. The tubercles are located medially, far from the edge, so that they do not modify the margin of the depression.

Check list, five species:
gigantus Azevedo, 1999
longiclypeus Azevedo, 1999
multicoriaceus Azevedo, 1999
scamatus Azevedo, 1999
serratus Azevedo, 1999

B.8. *rasissimus* species-group

The tergal processes of this group are placed in a single depression. This depression is large and embraces broadly the posterior margin of metasomal tergite I, so that it has a half-moon shape in dorsal view (Azevedo, 1999), like in the *linearis* species-group. However here the depression is very shallow to such an extent that is hardly observable and occupies almost the two median thirds of the tergal width. Besides, the male genitalia have the harpes deeply divided medially, forming two distinct lobes.

Check list, two species:
bilobatus Azevedo, 1999
rasissimus Azevedo, 1999

B.9. *ulceratus* species-group

The tergal processes of this group are placed in a single depression. This depression occupies the median third of the tergal width or even more. It is elliptical, biconcave or subcircular, and can be shallow, but occasionally conspicuous (Azevedo 1999). The depression has a pair of tufts with short setae, not longer than their diameter. The tufts display a wide range of variation, they can be circular, elliptical, small or large.
The harpes of the male genitalia have a peculiar shape, their apices have corners that are produced and angulate, the apical margin is truncate or dentate, and the base is wide. Analyzing the harpes is the easiest way to recognize the group.

Check list, six species:
concavatus Azevedo, 1999
congo Colombo & Azevedo, 2016
dentiformis Azevedo, 1999
rectilineus Azevedo, 1999
terbius Brito & Azevedo, 2017
ulceratus Evans, 1969

B.10. unitus species-*group*

The tergal processes of this group are located in a single depression. This depression occupies the median third of the tergal width. It is elliptical or subcircular, only slightly deep, and almost totally covered by a pair of joined tufts of long setae directed posterad (Azevedo, 1999), longer than the diameter of each tuft. The *apertus* species-groups have a similar pattern, but here the depression is smaller, and the setae of tufts are much longer.

Check list, two species:
delgatus Azevedo, 1999
unitus Azevedo, 1999

B.11. *vallensis* species-group

The tergal processes of this group consist of median tubercles, located in a single elliptical or subcircular depression, which occupies the median third of the tergal width. The tubercles are located laterally close to the margin, so that they are slightly or strongly directed mesad. Because of that, the depression seems to be biconcave in dorsal view. The tubercles are not exactly navel-shaped because their base is conical and only the apex is somewhat evenly wide, then it should be more appropriate to treat them as subnavel-shaped.
The clypeus has one or three median teeth. The male genitalia are complex, the aedeagal dorsal lobe is richly ornamented, and the base of several species is also ornamented with filaments or dentition.
The new composition of this group is the result of the fusion of the *vallensis*, *stellatus* and *basidentatus* groups.

Check list, 20 species:
basidentatus Azevedo, 1999 from *basidentatus* species-group
bicarinatus Azevedo, 1999 from *stellatus* species-group
bifurcatus Azevedo, 1999
bisserratus Azevedo, 1999
cerutus Azevedo, 1999 from *basidentatus* species-group
digitatus Azevedo, 1999
dilatatus Azevedo, 1999
extrarramis Azevedo, 1999
largidentatus Azevedo, 1999 from *stellatus* species-group
planus Azevedo, 1999
polidentatus Azevedo, 1999
rosangelae Colombo & Azevedo, 2016
rotundus Azevedo, 1999 from *basidentatus* species-group
scavatus Azevedo, 1999 from *stellatus* species-group
stellatus Azevedo, 1999 from *stellatus* species-group
strictus Azevedo, 1999
torem Colombo & Azevedo, 2018
tortuosus Azevedo, 1999 from *stellatus* species-group
triangularis Azevedo, 1999
vallensis Evans, 1979

C. *Groups with lateral pitted process*

C.1. *hemisphaericus* species-group

The tergal processes of this group consist of lateral pitted modifications with a tuft of setae, but never have any tubercle. The pits of this group are large and elliptical because their inner part is covered by a translucent sclerite, so that the hole is hemispheric, which makes the group easily recognized (Azevedo, 2003).

Check list, six species:
ferocus Azevedo, 2003
fredi Colombo & Azevedo, 2016
gordus Azevedo, 2003
hemisphaericus Azevedo, 2003
undatus Azevedo, 2003
vampirus Azevedo, 2003

C.2. *lamellatus* species-group, new

The tergal processes of this group consist of lateral pitted modifications with a tuft of setae, but never has any tubercle. The main character of this group is that the pit is very deep, elongated, and with an inclined slit. This slit is unique in *Dissomphalus*.

Check list, three species:
collaris Evans, 1962 from *incertae sedis*
lamellatus Redighieri & Azevedo, 2006 from *incertae sedis*
ubracus Brito & Azevedo, 2017 from *incertae sedis*

C.3. *rettenmeyeri s*pecies-group, new

The tergal processes of this group consist of lateral pitted modifications with a tuft of setae, but never has any tubercle. The pits of this group are somewhat circular or nearly so, their opening is subvertical. The pits are located in an opened subtriangular depression, with the vertex located medially and the outer margin outcurved and opened. The combination of characteristics is unique in the genus.

Check list, one species:
rettenmeyeri Evans, 1964 from *incertae sedis*

D. *Species-groups with lateral tufted process*

D.1. *amana* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle and pits. The main character of this group is that the setae of tufts are directed anterad, which is unique in the genus. The tufts are located inside a depression (Colombo & Azevedo, 2016).

Check list, two species:
amana Colombo & Azevedo, 2016
potyra Colombo & Azevedo, 2016

D.2. *confusus* species-group, new

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts are composed by short setae. This character seems to be not strong enough, so that it should be a waste basket of those groups with lateral tufted processes. However, it is useful for alpha taxonomic purposes.
Some species, such as *Dissomphalus clypeatus* Evans, were described as having a tiny pit, but Azevedo (2003) examined its holotype and was not able to see any pit. Such tiny pits can cause a misinterpretation of key couplet 19. However, to follow the first entrance the pits have to be conspicuous. *Dissomphalus taiabocu* Colombo & Azevedo seems to have this issue.

Check list, four species:
abarus Brito & Azevedo, 2017 from *incertae sedis*
clypeatus Evans, 1955 [1954] from *incertae sedis*
confusus Ashmead, 1894 from *incertae sedis*
taiabocu Colombo & Azevedo, 2016 from *incertae sedis*

D.3. *cornutus* species-group, new

The tergal processes of this group consist of tufted modifications, without any tubercle or pit. The tufts are located between the median and lateral thirds of the tergal width. Because of that, key couplet 5 can cause misinterpretations, but considering that the tergal processes are not located within the median third of the tergal width, this group is regarded as having lateral processes. The surface of metasomal tergite II is flat, without any depression. The tufts have few and long setae compared with the average found in the genus. In the male genitalia, the harpe is strongly projected antero-dorsally.

Check list, three species:
cornutus Evans, 1964 from *incertae sedis*
fimbriatus Redighieri & Azevedo, 2006 from *incertae sedis*
scopatus Redighieri & Azevedo, 2004 from *incertae sedis*

D.4. *coronatus* species-group

The tergal processes are characterized by having a pair of tufts with setae directed posterad, without any tubercle pit. Each tuft is located inside a conspicuous depression. This depression has also setae directed posterad circulating its anterior board, so that it partially covers the tufts. Another important character is the presence of a distinct seta on the inner surface of the harpe in the male genitalia. This group is similar to the *fungosus* species-group (see it for details).
Alencar & Azevedo (2006) defined this group based on the presence of a crown-like structure on the aedeagal dorsal body. However, such structure is present in most of the species of *Dissomphalus*, it is placed on the base of the aedeagal dorsal body, which supports the apical lobe. Thus, it does not work for diagnosing any group.

Check list, 14 species:
aculeatus Alencar & Azevedo, 2006
afestus Brito & Azevedo, 2017
auritus Alencar & Azevedo, 2006
coronatus Alencar & Azevedo, 2006
culteratus Alencar & Azevedo, 2006
declinatus Alencar & Azevedo, 2006
decussatus Alencar & Azevedo, 2006
flexuosus Alencar & Azevedo, 2006
hirtus Alencar & Azevedo, 2006
galeatus Alencar & Azevedo, 2006
pronus Alencar & Azevedo, 2006
ramosus Alencar & Azevedo, 2006
sinatus Alencar & Azevedo, 2006
uber Alencar & Azevedo, 2006

D.5. *fungosus* species-group, new

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. They are characterized by having a tuft of setae converging mesad. Each tuft is located inside a conspicuous depression, which has setae circulating its board. This group is similar to the *coronatus* species-group (Alencar & Azevedo 2006), because both groups have the setae circulating the board of the depression. However, in the former the setae circulate all of the board, whereas in the latter they circulate only the anterior half of the board. Another difference in the tergal processes is related to the orientation of the setae. Both sets of setae of the tufts and the depression are mesad in the former, whereas they are directed posterad in the latter.
In the genitalia, the inner harpe surface of the *coronatus* species-group has a distinct seta directed mesad or nearly so. This seta is absent in the *fungosus* species-group.

Check list, one species:
fungosus Evans, 1979 from *incertae sedis*

D.6. *gilvipes* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts of the tergal processes can be somewhat circular or even a little elongated, but almost always have the most lateral seta distinctly longer than others, which is the most important diagnostic character of this group. In addition, the clypeus is broadly projected forward, so that the median lobe is not clearly defined (Azevedo, 2003).

Check list, six species:
alticlypeatus Azevedo, 2003
arbeius Brito & Azevedo, 2017
bicerutus Azevedo, 2003
gilvipes Evans, 1979
irupe Colombo & Azevedo, 2018
krombeini Azevedo, 1999

D.7. *napo s*pecies-group, new

The tergal processes of this group consist of a lateral tufted modifications, without any tubercle or pit. The male genitalia have the digitus stout, large, with the posterior surface without denticulation and the inner corner on the posterior margin without any protuberance, so that the posterior surface is wholly and evenly convex. The digitus also has the distal tip narrowly rounded, but not sharp. All these characteristics in the digitus are unique among the American species. Its single species was placed at the *punctatus* species-group, because of the similarity of the tergal processes. However, the tergal processes in the *napo* species-group are much more lateral than in the *punctatus* species-group.

Check list, one species:
napo Evans, 1979 from *punctatus* species-group

D.8. *punctatus* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts are located between the median and lateral thirds of the tergal width. Because of that, key couplet 5 can cause misinterpretations, but considering that the tergal processes are not located within the median third of the tergal width, this group is regarded as having lateral processes. These characteristics are the same as in the *cornutus* species-group. However, in the former group the tergal processes are located inside a circular depression, with densely setose margins which are not angulate, and setae directed posterad. In addition, the male genitalia have an elongate median filament in the aedeagal dorsal body (Azevedo, 2003).

Check list, six species:
acutipupu Colombo & Azevedo, 2018
bahiensis Redighieri & Azevedo, 2006
cuca Colombo & Azevedo, 2018
jurupari Colombo & Azevedo, 2018
punctatus (Kieffer, 1910)
tupinikim Colombo & Azevedo, 2016

D.9. *rufipalpis* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts are located inside an elliptical and inclined depression, and consequently the tufts follow the depression's shape, so that the tufts are clearly linear and oblique. That is the most important diagnostic character of this group (Azevedo, 2003).

Check list, five species:
ellipticus Evans, 1969
guarani Colombo & Azevedo, 2016
inclinatus Redighieri & Azevedo, 2006
infissus Evans, 1969
rufipalpis Kieffer, 1910

E. *Species-groups with lateral tubercled processes*

E.1. *bicavatus* species-group

The tergal processes of this group consist of antero-lateral depressions, which are exceptionally large, usually more than 0.5 × the median length of metasomal tergite II, and usually deep, with the cross-section somewhat subcircular. Each depression has a tufted navel-shaped tubercle located at the medial surface, the inner and outer margins have rows of short setae directed posterad. Such depressions are unique in the genus (Azevedo, 2001).
I have seen many undescribed species with depressions similar to those found in the *bicavatus* species group, but smaller, which can cause confusion.

Check list, 35 species:
abruptus Azevedo, 2001
alticarinatus Azevedo, 2001
archeatus Azevedo, 2001
bicavatus Evans, 1979
basivolsellus Azevedo, 2001
bivolsellus Azevedo, 2001
curvilongus Azevedo, 2001
elongatus Azevedo, 2001
falcatus Evans, 1962
falciformis Azevedo, 2001
flagellatus Azevedo, 2001
geniculatus Azevedo, 2001
gladius Azevedo, 2001
intradentatus Azevedo, 2001
largimanus Azevedo, 2001
latus Azevedo, 2001
lobisserratus Azevedo, 2001
longimerus Azevedo, 2001
longipilosus Azevedo, 2001
mantoides Azevedo, 2001
megadentatus Azevedo, 2001
microdentatus Azevedo, 2001
octavus Azevedo, 2001
pedipalpoides Azevedo, 2001
piscicercus Azevedo, 2001
rectangularis Azevedo, 2001
retorcerens Azevedo, 2001
sinuatus Azevedo, 2001
spiculus Azevedo, 2001

strepsus Azevedo, 2001
subtriangularis Azevedo, 2001
tetracerutus Azevedo, 2001
tetralobatus Azevedo, 2001
trogon Azevedo, 2001
tropoides Azevedo, 2001

E.2. *chiapanus* species-group, new

The tergal processes of this group consist of lateral tufted callus-shaped tubercles. This kind of tubercles are usually smaller than navel-shaped tubercles, progressively narrowing apicad, so that they have pyramidal features. On the top of each tubercle, a tuft of setae is raising.

Sometimes, it is difficult to distinguish ring- and callus-shaped tubercles because of their small size, as in *D. borus* Brito & Azevedo. In *D. arteobius* Brito & Azevedo, the depressions have setae lateral to them, which can cause confusion with the *setosus* species-group.

Check list, seven species:
arteobius Brito & Azevedo, 2017 from *incertae sedis*
borus Brito & Azevedo, 2017 from *incertae sedis*
caparao Colombo & Azevedo, 2016 from *incertae sedis*
chiapanus Evans, 1962 from *kansanus* species-group
trilobatus Redighieri & Azevedo, 2006 from *incertae sedis*
trisus Brito & Azevedo, 2017 from *incertae sedis*
ilarius Brito & Azevedo, 2017 from *incertae sedis*

E.3. *conicus* species-group

The tergal processes of this group consist of lateral tufted navel-shaped tubercles. The tubercles are located in an inconspicuous depression. This kind of tubercles are evenly wide along their height, with rounded rim, tuft of setae on the top (Azevedo, 2003).

The available information on *D. clausus* Kieffer, *D. flavipes* Kieffer and *D. ocellatus* Kieffer is very poor, but Kieffer (1914b) mentioned the presence of a tergal process that I interpreted as navel-shaped tubercles. I have never examined *D. clausus* and *D. flavipes* Kieffer. Besides, *D. ocellatus* deposited in the Natural History Museum (London, UK) has its metasoma missing. Thus, the placement of these three species at the *conicus* species-group is weakly supported and needs future studies to better understand them.

Three species, *D. archboldi* Evans, *D. nanellus* Evans and *D. isortus* Brito & Azevedo, have their tubercles exceedingly small, and because of that they remind of a ring-shaped style. That can cause confusion. The tubercles of *D. geortus* Brito & Azevedo, *D. mendicus* Evans and *D. peculiaris* Redighieri & Azevedo are even smaller.

Three species, *D. amplexus* Redighieri & Azevedo, *D. caipora* Colombo & Azevedo and *D. differens* Redighieri & Azevedo, have some setae on the antero-lateral surface of metasomal tergite II, which can be interpreted as a character of the *setosus* species-group style. However, in these three species the setae are not thick, as in the *setosus* species-group. Thus, the difference between the *conicus* and the *setosus* species-group is sometimes confusing.

Check list, 38 species:
amplexus Redighieri & Azevedo, 2006 from *incertae sedis*
amplifoveatus Redighieri & Azevedo, 2006 from *incertae sedis*
archboldi Evans, 1969 from *incertae sedis*
ardonius Brito & Azevedo, 2017
arteus Brito & Azevedo, 2017
botocudus Colombo & Azevedo, 2016
caipora Colombo & Azevedo, 2018 from *incertae sedis*
capixaba Colombo & Azevedo, 2016 from *incertae sedis*
cervoides Azevedo, 2003
clausus Kieffer, 1908 from *incertae sedis*
conicus Azevedo, 2003
connubialis Evans, 1966 from *incertae sedis*
curupira Colombo & Azevedo, 2018
curviventris Azevedo, 2003
differens Redighieri & Azevedo, 2006 from *incertae sedis*
elegans Redighieri & Azevedo, 2006 from *incertae sedis*
ettus Brito & Azevedo, 2017
filus Azevedo, 2003
flavipes Kieffer, 1910 from *incertae sedis*
geortus Brito & Azevedo, 2017 from *incertae sedis*
h-ramus Redighieri & Azevedo, 2004
iara Colombo & Azevedo, 2018
ibirapitanga Colombo & Azevedo, 2016 from *incertae sedis*
ibrastus Brito & Azevedo, 2017
isortus Brito & Azevedo, 2017 from *incertae sedis*
laminaris Redighieri & Azevedo, 2004
manus Azevedo, 2003
nanellus Evans, 1969 from *incertae sedis*
ocellatus Kieffer, 1911 from *incertae sedis*
personatus Redighieri & Azevedo, 2006 from *incertae sedis*
racarus Brito & Azevedo, 2017
saci Colombo & Azevedo, 2018
spinosus Azevedo, 2003
teraus Brito & Azevedo, 2017
truncatus Azevedo, 2003
umbilicus Azevedo, 2003
urazius Brito & Azevedo, 2017
verrucosus Redighieri & Azevedo, 2004

E.4. *dumosus* species-group

This group has two main characters. First, the body is elongated, especially the head, with the area posterior to the supra-ocular line very developed. Also, the median clypeal lobe, the dorsal pronotal area and the metapectal-propodeal disc are elongated. That is unusual because *Dissomphalus* has the body robust (short and wide) in most of its species. This makes the group easily recognizable. Second, the male genitalia have the aedeagal ventral rami very long and the ventral side of the gonostipe much more developed than the dorsal side (Azevedo, 2000). That is unique among species of the genus.

There are two kinds of very distinct tergal processes. One consists of lateral tufted navel-shaped tubercles, both located in a conspicuous depression. Another consists of elliptical lateral depressions with the surface apparently areolate.

Check list, three species:
dumosus Evans, 1966
longicephalus Azevedo, 2003
mirabilis Evans, 1966 from *incertae sedis*

E.5. *guttus* species-group

The tergal processes of this group consist of tufted ring-shaped tubercles. The tubercles are drop-shaped, because they are sharpened anteriorly and rounded posteriorly, so that they resemble a drop. That shape is unique in the genus. Each tubercle has a large pit partially covered by a tuft of setae (Azevedo, 2003).

Check list, two species:
guttus Azevedo, 2003
latimerus Azevedo, 2003

E.6. *incomptus* species-group

The main diagnostic character of this group is in the male genitalia, which have two pairs of flagellae on the aedeagal dorsal body of aedeagus. No other Pan-American species of *Dissomphalus* has such flagellae. The tergal processes of this group are much reduced or even absent (Azevedo, 2003).

Check list, two species:
incomptus Evans, 1964
microtuberculatus Azevedo, 1999

E.7. *laticephalus* species-group

The main diagnostic character of this group is in the head. First, the mandibles are unusually long, at least about 0.75 × as long as the distance between their bases. Second, the vertex of the head is strongly angled or unusually wide. Besides, the head is very wide in comparison with the majority of species in the genus, with its width about 1.2 × its length. The tergal processes of this group are absent or not very conspicuous in size (Azevedo, 2003).

Check list, five species:
contractus Azevedo, 2003
cristatus Redighieri & Azevedo, 2004
laticephalus Azevedo, 2003
lobicephalus Azevedo, 2000
mandibulatus Azevedo, 2003

E.8. *microstictus* species-group

The main diagnostic character of this group is in the male genitalia, which have the apex of the aedeagal ventral ramus with an elongated filament inserted subapically (Alencar & Azevedo, 2008) in the majority of species, and apically only in *D. xanthopus* Ashmead. Thus, the inclusion of this species here broadens the concept of this group. The tergal processes do not only vary among the species, but also intraspecifically. *Dissomphalus microstictus* Evans can have ring- or callus-shaped tubercles, or the tubercles can be even absent (Alencar & Azevedo, 2008). That makes the tergal processes not useful for diagnosing the group.

Check list, 17 species:
balteus Alencar & Azevedo, 2008
divaricatus Alencar & Azevedo, 2008
flaviscapus (Evans, 1969) from *incertae sedis*
forceps Alencar & Azevedo, 2008
incurvatus Alencar & Azevedo, 2008
microstictus Evans, 1969
osseus Alencar & Azevedo, 2008
paululus Alencar & Azevedo, 2008
perparvus Alencar & Azevedo, 2008
perturbatus Alencar & Azevedo, 2008
perventriosus Alencar & Azevedo, 2008
pilus Alencar & Azevedo, 2008
raziogus Brito & Azevedo, 2017
refertus Alencar & Azevedo, 2008
signatus Alencar & Azevedo, 2008
uncus Alencar & Azevedo, 2008
xanthopus Ashmead, 1893 from *xanthopus* species-group

E.9. *secretus* species-group

The tergal processes of this group consist of lateral tufted ring-shaped tubercles. The tubercles are located in an inconspicuous or a conspicuous depression. This kind of tubercles are short, evenly wide along their height, with a sharp rim, each with a tuft of setae on the top. The pits are usually wide, and the tufts do not cover the whole pit, so that the pits are easily observable.

Check list, four species:
cacirus Colombo & Azevedo, 2016
excellens Redighieri & Azevedo, 2006 from *incertae sedis*
secretus Colombo & Azevedo, 2016
puteolus Evans, 1969 from *incertae sedis*

E.10. *setosus* species-group

The tergal processes of this group consist of lateral tufted navel-shaped tubercles. Each tubercle is located in a depression varying from inconspicuous to conspicuous. The lateral surface of metasomal tergite II has thick setae close to the depressions, which represent the main character of this group.

Many species of this group have a small body with inconspicuous tergal processes which have reduced tubercles, as in the Nearctic species *D. arizonicus* Evans, *D. barberi* Evans, *D. californicus* Ashmead, and *D. kansanus* Evans. However, some species with small bodies can have large tubercles, as the Neotropical *D. boiuna*.

Check list, 30 species:
areius Brito & Azevedo, 2017
aretisus Brito & Azevedo, 2017
arizonicus Evans, 1962 from *kansanus* species-group
barberi Evans, 1955 [1954] from *xanthopus* species-group
boibumba Colombo & Azevedo, 2018
boiuna Colombo & Azevedo, 2018 from *incertae sedis*
californicus Ashmead, 1893 *xanthopus* species-group
capelobo Colombo & Azevedo, 2018
caviclypeus Evans, 1969 from *incertae sedis*
citus Brito & Azevedo, 2017
crassus Redighieri & Azevedo, 2006
distans Redighieri & Azevedo, 2006
divisus Redighieri & Azevedo, 2006
filiformis Redighieri & Azevedo, 2006
firmus Redighieri & Azevedo, 2006
inflexus Redighieri & Azevedo, 2006
iracema Colombo & Azevedo, 2018
joaquinae Colombo & Azevedo, 2018
kansanus Evans, 1955 [1954] from *kansanus* species-group
magnus Redighieri & Azevedo, 2006 from *incertae sedis*
mapinguara Colombo & Azevedo, 2018 from *incertae sedis*
matintaperera Colombo & Azevedo, 2018 from *incertae sedis*
mirim Colombo & Azevedo, 2016 from *secretus* species-group
politus Ashmead, 1894 from *incertae sedis*
purius Colombo & Azevedo, 2016 from *incertae sedis*
sartus Brito & Azevedo, 2017
setosus Redighieri & Azevedo, 2006
spissus Redighieri & Azevedo, 2006
teobus Brito & Azevedo, 2017
w-aedeagus Colombo & Azevedo, 2016

E.11. *tuberculatus* species-group

The tergal processes of this group consist of sublateral or lateral tufted ring- or navel-shaped tubercles. Each tubercle is located in a depression, which can be inconspicuous or not. The tubercles and their tufts are slightly directed mesad (Azevedo, 2003). This kind of orientation is also present in some groups with median processes like *stellatus*, *basidentatus* and *vallensis*, but is unique among the *Dissomphalus* with lateral tergal processes.

The *strabus* species-group is here fused with the *tuberculatus* species-group. In the former group the tergal processes are slightly more sublateral, and this subtle variation does not justify a separate group as proposed by Azevedo (2003).

Check list, four species:
plaumanni Evans, 1964
strabus Azevedo, 2003 from *strabus* species-group
thysanus Azevedo, 2003 from *strabus* species-group
tuberculatus Ashmead, 1894

F. *Species known only from females*

The taxonomic position of the species known only from females remain unsolved. That is because the dimorphism is expressed in small blind apterous females and large macropterous males (Azevedo, 2003). Thus, only couples taken in phoretic copulation are able to be solved the problem of conspecific association (Azevedo *et al.,* 2016), or molecular tools.

Check list, 11 species:
attaphilus (Bruch, 1916)
azarai (Ogloblin, 1930)
catalinae Vargas & Terayama, 2002
claviger Evans, 1955 [1954]
crassicornis (Wasmann, 1899)
luscus Evans, 1964
mexicanus (Westwood, 1839)
platensis (Bruch, 1916)
scrupeus Evans, 1964
singularis Evans, 1962
yu Snelling, 1996

DISCUSSION

When I started working on *Dissomphalus* in the late 1990s, the genus had 52 Neotropical species and eight Nearctic species, five of them ranging also through Central America, as listed by Gordh & Móczár (1990). These numbers are nothing compared to the almost 300 valid New World species and the hundreds of undescribed ones I have seen throughout this time. Because of this hyper diversity, organizing *Dissomphalus* in species groups in order to facilitate its alpha taxonomy is crucial, and it has been a big challenge over the last 50 years.

The genitalia of *Dissomphalus* offer very useful characters to separate species because they vary immensely among species with clear morphological gaps, but with few intraspecific variations. On the other hand, at the species-group level, these gaps are sometimes not clear. Thus, in many cases, doubts can come up while utilizing the keys or even when studying the groups.

Except for the *napo* group, the new groups proposed here are partially (*chiapanus*) or fully (*lamellatus*, *rettenmeyeri*, *confusus*, *cornutus*, and *fungosus*) composed by species never allocated in any group before. These constitute the majority of the *incertae sedis* species in the genus in the Neotropical region, all of them having lateral processes. I established categories according to the shape of the processes in pitted, tufted and tubercled processes in order to accommodate the *incertae sedis* species in the groups. The latter was also subdivided according to the possession of navel-, ring- or callus-shaped tubercles. Thus, these groups differ from each another in details of the tergal process morphology, and because of that sometimes distinguishing groups is a hard task.

One example that illustrates this difficulty in group delimitation are the *conicus* and *setosus* species-groups, two large groups in numbers of species. They have the classical lateral navel-shaped tubercles in depressions, which vary from inconspicuous to conspicuous, or they can even be absent. Anyway, the surface lateral to the depressions or the corresponding area when without the depressions, have conspicuous and somewhat thick setae in *setosus* (Redighieri & Azevedo, 2006). These setae are few and delicate in *conicus* (Azevedo, 2003). Nonetheless, there are some species in the *conicus* group, whose setae are not so delicate, or in some species of the *setosus* group not so thick. This problem has already been raised by Colombo & Azevedo (2018), when indicating *D. matintaperera*, *D. mapinguari* and *D. caipora* as species which link both groups. Thus, in cases of doubt in couplet 35 of the keys, I recommend following both ways.

Problems of ambiguity can even occur between clusters of groups. In some instances, affirming that the tergal processes are median or lateral is hard. By definition, the tergal processes are considered median when located inside the median third of the tergal width, but sometimes the process can expand further than this limit. The tergal processes are considered lateral when located on the lateral thirds of the tergal width, but sometimes the processes are located exactly on the limit of the median and lateral tergal width. So, the position of the tergal processes when lateral can be more mesad or more laterad, but always not connected by a single median depression. The *cornutus* and *punctatus* species-groups are two examples in which the lateral tergal processes are located at the limit of the median and lateral tergal width (Azevedo 2003), and consequently are a matter of precaution at couplet 5 in the key. On the other hand, *brasiliensis* is an example of a species-group with median tergal processes (Redighieri & Azevedo, 2006), which needs precaution in the same couplet because it does have a single depression medially. Thus, the important tip to help understanding if the processes are median or lateral is to check if the species have single or double depressions.

Several new groups were created here to accommodate the huge diversity held in this genus. Nevertheless, I also fused several groups in order to avoid concept overlapping among them. That is the case in the *basidentatus*, *vallensis* and *stellatus* species-groups (Azevedo, 1999a). These groups were defined in a combination of characters that are always partially present in at least two of these three groups. Another case are the *strabus* and *tuberculatus* species-groups, defined by having tubercles slightly directed to each other (Azevedo, 2003). The only significant difference is the depth of the depression, which seems to me very little to justify splitting this group.

I also took this opportunity to improve or set up the definition of some groups. For instance, the original definition of the *secretus* species-group is inconsistent. It is based on four characters, such as metasomal tergum II with lateral depressions or not, 2) well-defined side pits, circular-shaped, higher edges, 3) tubercle below the surface of the tergite, many setae at the apex, and 4) bristles on the edge of the depressions or not (Colombo & Azevedo, 2018). The characters 1 and 4 are useless, because both conditions of presence and absence are possible, so that they do not help to understand the identity of the group. Anyway, when the depression has bristles, then the species belongs to the *setosus* species group, like for instance *D. mirim*. Character 2: 'well defined pit', refers to a wide pit located at the top of the tubercle. Thus, characters 2 and 3 have to be combined as: 'tubercle with pit at the top, from where a tuft of setae is raised'. This structure is quite common in the genus. And, because of that, it would run to the *conicus* species-group, except by the fact that in this latter group the tubercle is navel-shaped, whereas in the *secretus* group it is ring-shaped. However, it is not easy to distinguish navel and ring-shaped tubercles, because of their tiny size and range of variation. Therefore, we need precaution at couplet 37 in the key. As a result, the definition of this group was fully redesigned.

The species-group organization that I propose here is the first attempt to encompass all species, and I am sure that much is still necessary to improve the system and make the key more accurate. I am also conscious that there still are many undescribed species which can provoke instability in this group organization, because of two reasons. First, new species can be in the limit of two groups, and second, new groups can arise.

It is necessary to emphasize that the species-groups were conceived under an alpha taxonomic approach unlinked from a phylogenetic perspective. That is the justification of why I have utilized the word organization in the title instead of classification. I adopted this approach because of some reasons. First, a species-group is an informal rank and not subject to nomenclatural rules (ICZN, 1999). Second, the establishment of species-groups is supposed to be useful only to help people to identify species in this huge genus. Third, morphological and molecular phylogenetic analyses of a genus with more than 400 species is time consuming, and the key for the species-group is urgent, otherwise species identification is a big hurdle.

Finally, I have seen more than 20 thousand unidentified specimens of Pan-American *Dissomphalus*, likely representing hundreds of new species. Certainly, there will be species that cannot be allocated to any species-group proposed here. Thus, I foresee the need for proposing in the future additional new species-groups in this speciose genus of flat wasps.

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REFERENCES

Alencar I.D.C.C., Azevedo C.O. 2006. Definition of Neotropical *coronatus* species-group (Hymenoptera: Bethylidae, *Dissomphalus*) with description of thirteen new species. *Zootaxa* 1330: 1-26. DOI: 10.11646/zootaxa.1330.1.1

Alencar I.D.C.C., Azevedo C.O. 2008. A new species-group of *Dissomphalus* (Hymenoptera: Bethylidae), with description of thirteen new species. *Zootaxa* 1851: 1-28. DOI: 10.11646/zootaxa.1851.1.1

Alencar I.D.C.C., Waichert C. & Azevedo C.O. 2018. Opening Pandora's box of Pristocerinae: molecular and morphological phylogenies of *Apenesia* (Hymenoptera, Bethylidae) reveal several hidden genera. *Systematic Entomology* 43: 481-509. DOI: 10.1111/syen.12295

Ashmead W.H. 1893. A monograph of the North American Proctotrypidae. *Bulletin of the United States National Museum* 45: 1-472. DOI: 10.5479/si.03629236.45.1

Ashmead W.H. 1894. Report on the parasitic Cynipidae, part of the Braconidae, the Ichneumonidae, the Proctotrypidae, and part of the Chalcididae. Part III. *Journal of Linnean Society of London, Zoology* 25: 188-254.

Azevedo C.O. 1999a. Revision of the Neotropical *Dissomphalus* Ashmead, 1893 (Hymenoptera, Bethylidae) with median tergal process. *Arquivos de Zoologia* 35: 301-394. DOI: 10.11606/issn.2176-7793.v35i4p301-394

Azevedo C.O. 1999b. On Nearctic *Dissomphalus* (Hymenoptera, Bethylidae), with the description of two new species from Florida. *Iheringia, Série Zoológica* 87: 49-56.

Azevedo C.O. 1999c. Additional notes on Systematic of Neotropical *Dissomphalus* Ashmead (Hymenoptera, Bethylidae). *Revista Brasileira de Zoologia* 16: 921-949.

Azevedo C.O. 2000. The *dumosus* group of *Dissomphalus* (Hymenoptera, Bethylidae): definition and description of a new Amazonian species. *Boletim do Museu Paraense Emílio Goeldi* 16: 91-97.

Azevedo C.O. 2001. Systematics of the Neotropical *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) of the *bicavatus* group. *Revista Brasileira de Entomologia* 45: 173-205.

Azevedo C.O. 2003. Synopsis of the Neotropical *Dissomphalus* (Hymenoptera, Bethylidae). *Zootaxa* 338: 1-74. DOI: 10.11646/zootaxa.338.1.1

Azevedo C.O., Colombo W.D., Alencar I.D.C.C., Brito C.D. de, Waichert C. 2016. Couples in phoretic copulation, a tool for male-female association in highly dimorphic insects of the wasp genus *Dissomphalus* Ashmead (Hymenoptera: Bethylidae). *Zoologia* 33(6): e20160076. 7p. DOI: 10.1590/S1984-4689zool-20160076

Azevedo C.O., Alencar I.D.C.C., Colombo W.D. 2018a. Pairs in copulation of the highly dimorphic genus *Pristocera* Klug (Hymenoptera, Bethylidae) from Madagascar solve taxonomic problems of male-female associations. *Zootaxa* 4433: 1-49. DOI: 10.11646/zootaxa.4433.1.1

Azevedo C.O., Alencar I.D.C.C., Ramos M.S., Barbosa D.N., Colombo W.D., Vargas R. J.M., Lim J. 2018b. Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4489: 1-294. DOI: 10.11646/zootaxa.4489.1.1

Brito C.D., Azevedo C.O. 2017. Review of *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) from Panama, with key to the Central American species. *Zootaxa* 4335: 1-72. DOI: 10.11646/zootaxa.4335.1.1

Bruch C. 1916. Descripción de dos himenópteros mirmecófilos pertenecientes á los Bethylidae. *Physis* 2: 19-23.

Colombo W.D., Azevedo C.O. 2016. Review of *Dissomphalus* Ashmead, 1893 (Hymenoptera, Bethylidae) from Espírito Santo, Brazil, with description of twenty-one new species. *Zootaxa* 4143: 1-84. DOI: 10.11646/zootaxa.4143.1.1

Colombo W.D., Alencar I.D.C.C., Limeira-de-Oliveira F. & Azevedo C.O. 2018. New species and records of *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) from Cerrado, Caatinga and relicts of the Atlantic Forest from northeastern Brazil. *Zootaxa* 4462: 1-40. DOI: 10.11646/zootaxa.4462.1.1

Evans H.E. 1955 [1954]. The North American species of *Dissomphalus* (Hymenoptera, Bethylidae). *Proceedings of the Entomological Society of Washington* 56: 288-309.

Evans H.E. 1962. Further studies on the genus *Dissomphalus* in the United States, Mexico, and Greater Antilles (Hymenoptera, Bethylidae). *Proceedings of the Entomological Society of Washington* 64: 65-78.

Evans H.E. 1963. A revision of the *Apenesia* in the Americas (Hymenoptera, Bethylidae). *Bulletin of the Museum of Comparative Zoology* 130: 249-359.

Evans H.E. 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology* 132: 1-222.

Evans H.E. 1966. Further studies on Neotropical Pristocerinae (Hymenoptera, Bethylidae). *Acta Hymenopterologica* 2: 99-117.

Evans H.E. 1969. The genera *Apenesia* and *Dissomphalus* in Argentina and Chile (Hymenoptera, Bethylidae). *Breviora* 311: 1-23.

Evans H.E. 1978. The Bethylidae of America North of Mexico. *Memoirs of the American Entomological Institute* 27: 1-332.

Evans H.E. 1979. The genus *Dissomphalus* in Northwestern South America (Hymenoptera: Bethylidae). *Proceedings of the Entomological Society of Washington* 81: 276-284.

Gordh G., Móczár L. 1990. A catalog of the world Bethylidae

(Hymenoptera: Aculeata). *Memoirs of the American Entomological Institute* 46: 1-364.

ICZN International Commission on Zoological Nomenclature. 1999. International Code on Zoological Nomenclature. Published by International Trust for Zoological Nomenclature c/o The Natural History Museum, London, UK. Available online at http://iczn.org/iczn/index.jsp.

Kieffer J.J. 1904. Description de nouveaux Dryininae et Bethylinae du Musée Civique de Gênes. *Annali del Museo Civico di Storia Naturale di Genova* 41: 351-412.

Kieffer J.J. 1906 [1905]. Beschreibung neuer Proctotrypiden aus Nord- und Zentralamerika. *Berliner Entomologische Zeitschrift* 50: 237-290.

Kieffer J.J. 1908. Nouveaux proctotrypides et cynipides d'Amérique recueillis par M. Baker. *Annales de la Société Scientifique de Bruxelles* 32: 7-64.

Kieffer J.J. 1910a. Description de nouveaux microhyménoptères du Brésil. *Annales de la Société Entomologique de France* 78: 287-348.

Kieffer J.J. 1910b. Description de nouveaux Béthylides (Hymen). *Annales de la Société Entomologique de France* 79: 31-56.

Kieffer J.J. 1911. Nouveaux Béthylides et Dryinides exotiques du British Museum de Londres. *Annales de la Société Scientifique de Bruxelles* 35: 200-233.

Kieffer J.J. 1914a. Trois nouveaux Béthylides. *Bulletin de la Société Entomologique de France*, 1: 60-61.

Kieffer J.J. 1914b. Bethylidae. *Das Tierreich* 41: 228-595.

Lanes G.O., Kawada R., Azevedo C.O., Brothers D. 2020. Revisited morphology applied for Systematic of flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4752: 1-127. DOI: 10.11646/zootaxa.4752.1.1

Ogloblin A.A. 1930. Notes on Bethylidae with the description of two new species from Misiones. *Revista de la Sociedad Entomologica Argentina* 3: 15-27.

Redighieri E.S., Azevedo C.O. 2004. New species and notes on *Dissomphalus* (Hymenoptera, Bethylidae) from Estação Biológica de Santa Lúcia, Santa Teresa, ES, Brazil. *Iheringia, Série Zoológica* 94: 329-333. DOI: 10.1590/S0073-47212004000300018

Redighieri E.S., Azevedo C.O. 2006. Fauna de *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) da Mata Atlântica Brasileira, com descrição de 23 espécies novas. *Revista Brasileira de Entomologia* 50: 297-334. DOI: 10.1590/S0085-56262006000300001

Snelling R.R. 1996. Systematic notes on some Bethylidae from the Virgin Islands and Puerto Rico (Hymenoptera: Chrysidoidea). *Memoirs of the Entomological Society of Washington* 17: 194-208.

Vargas R. J.M., Terayama M. 2002. Five new species of the subfamily Pristocerinae (Insecta, Hymenoptera, Bethylidae) from Colombia. *Biogeography* 4: 25-31.

Wasmann E. 1899. Die Psychischen Fähigkeiten der Ameisen. *Zoologica*,11: 1-133.

Westwood J.O. 1839. Monograph upon the hymenopterous genus *Scleroderma*. *Transactions of the Royal Entomological Society of London* 2: 164-172.