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Is the family Corydalidae (Neuropterida, Megaloptera) a monophylum?[1]

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Abstract: It is suggested, on the basis of 24 morphological characters, that fishflies (Corydalidae, Chauliodinae) might be more closely related to alderflies (Sialidae) than to dobsonflies (Corydalidae, Corydalinae). This hypothesis would render Corydalidae, as it is generally recognized (Chauliodinae + Corydalinae), a paraphyletic taxon. Gathering of data from other sources, such as molecular characters, is encouraged in order to test the aforementioned phylogenetic hypothesis.

Key words: Megaloptera, Corydalidae, monophyly, phylogeny, classification.

Introduction

It is well known in zoology, and entomology is a prime example, that taxa traditionally recognized in classifications often times are artificial groupings based on primitive similarity. Monophyly is to be assumed as the null hypothesis, but whenever possible, characters should be searched in order to support or challenge the accepted classification. As a general scenario, it appears that when rather subtle characters are underestimated against more evident similarity, there is a potential case of paraphyly. Within Megaloptera, three main lineages have been typified since the establishment of the genera *Corydalus* Latreille (1802), *Chauliodes* Latreille (1802), and *Sialis* Latreille (1802) (New & Theischinger 1993), commonly known as dobsonflies, fishflies, and alderflies, respectively. Such lineages have variously been considered as Sialidinae (alderflies) and Corydalinae (dobsonflies + fishflies) of Sialididae by Davis (1903), as Sialidinae and Corydalinae (Neuromini + Chauliodini) of Sialidae by Weele (1910), or more recently as Sialidae and Corydalidae (Corydalinae + Chauliodinae) of Megaloptera (e.g., Glorioso 1981). Nonetheless, Theischinger (1983) considered each of the three lineages as an independent family (Sialidae + Chauliodidae + Corydalidae).

In summary (Tab. 1), the consensual classification implies that dobsonflies (Corydalinae) are the sister group of fishflies (Chauliodinae), and both in turn are sister to Sialidae (alderflies), a view supported by at least one formal phylogenetic study (Aspöck et al. 2001).

Methods

The idea that fishflies could be phylogenetically closer to alderflies than to dobsonflies came out as part of a test of monophyly of *Corydalus*, which included examples of all genera of Corydalinae and utilized Chauliodinae as an outgroup: „...reductions in head structure, mouthpart segmentation, and male genitalia in Sialidae and Chauliodinae question the accepted view of the monophyly of Corydalidae" (Contreras-Ramos 1998: 204). Inspected characters in that study were taken as a starting point.

Specimens of Sialidae (*Sialis*, *Protosialis* Weele [1909]), Chauliodinae (*Archichauliodes* Weele [1909], *Chauliodes* Latreille [1802], *Dysmicohermes* Munroe [1954], *Neohermes* Banks [1908], *Nigronia* Banks [1908]), and Corydalinae (*Acanthacorydalis* Weele [1907], *Chloronia* Banks [1908], *Chloroniella* Esben-Petersen [1924], *Corydalus*, *Neoneuromus* Weele [1909], *Neurhermes* Navás [1915], *Neuromus* Rambur [1842], *Platyneuromus* Weele [1909], *Protohermes* Weele [1907]) were studied (list of material examined is in Contreras-Ramos 1998). Techniques and terminology were based on Glorioso (1981) as modified by Contreras-Ramos (1998). Further inspection of characters was done from descriptions in the literature. Because the phylogenetic question treated involves three taxa and using an outgroup turned out difficult for a morphological study, an a priori process of character polarization through a hypothetical ancestor was performed (i.e., a vector of zeros was used). The rationale for the polarization was to assign the apomorphic condition to reductions in segmentation of mouth parts and of the genitalia, as well as to fusion of head structures, that is, to character states thought as derived or specialized. Characters were given equal weight, treated as unordered, and analyzed through

[1] This paper is respectfully dedicated to Univ.-Prof. Dr. Horst Aspöck, on the occasion of his 65th birthday and as homage for his extensive contributions to neuropterology.

Davis (1903): Order Neuroptera, Family Sialididae (now Megaloptera)	
Subfamily Sialidinae Adults: Accessory veins of radial sector on the front side of vein R3; ocelli wanting; fourth tarsal segment of tarsi prominently bilobed. Larvae: Anal prolegs wanting; lateral filaments only seven pairs, and distinctly jointed.	Subfamily Corydalinae (including both fishflies and dobsonflies) Adults: Accessory veins of radial sector on the posterior side of vein R2; ocelli three; fourth segment of tarsi obscurely or not at all lobed. Larvae: Anal prolegs one pair, provided with claws; lateral filaments eight pairs, slightly or not at all jointed.
Weele (1910): Megaloptera (including Raphidioptera), Family Sialidae	
Subfamily Sialidinae Ocelli wanting, fourth tarsal joint prominently bilobed. Rather small forms.	Subfamily Corydalinae Three ocelli, fourth tarsal joint simple, not bilobed. Large and mediocre forms. Tribe Neuromini Male with a pair of appendices superiores and inferiores. Antennae moniliform in both sexes, never pectinate. Head quadrangular, with a more or less developed tooth at the sides and dendriform pattern on the occiput. Wings with more than 3 crossveins between the radius and radialsector. Large forms. Tribe Chauliodini Male with only a pair of appendices superiores. Antennae mostly pectinate in the male, moniliform to pectinate in the female. Head triangular, no tooth at the sides. The occiput with linguatiform pattern. Wings always with 3 crossveins between the radius and radialsector. Mediocre to large forms.
Glorioso (1981), New & Theischinger (1993), Evans & Neunzig (1996): Megaloptera	
Family Sialidae Adults: Less than 25 mm in length; ocelli absent; 4th tarsal segment dilated. Larvae: With 7 pairs of 4 to 5-segmented lateral filaments on abdominal segments 1-7 and a single long caudal filament; 25 mm or less when full-grown.	Family Corydalidae Adults: Over 25 mm in length; ocelli present; 4th tarsal segment simple. Larvae: With 8 pairs of 2-segmented lateral filaments on abdominal segments 1-8, and a pair of 1-segmented filaments on abdominal segment 10; apex of abdomen with 2 anal prolegs, each bearing a pair of claws; 30-65 mm when full grown. Subfamily Corydalinae Adults: With head subquadrate with postocular ridge, spine and plane; males with well-developed ninth gonostyli. Larvae: With ventral gill tufts. Subfamily Chauliodinae Adults: With head subtriangular without postocular ridge, spine and plane; males without ninth gonostyli. Larvae: Without ventral gill tufts.
Theischinger (1983): Megaloptera (for Australia)	
Sialidae Ocelli wanting; 4th tarsal segment prominently bilobed; wings without conspicuous pigment spots.	Chauliodidae Three ocelli; 4th tarsal segment simple; conspicuous pigment spots in both wings.
Corydalidae (by inference)	

Table 1: Megaloptera classifications and characters used to support them (unless otherwise stated, characters are from adults).

an exact search with PAUP 4.0b10 (Swofford 1998). Building of the data matrix and tree drawing was done with MacClade 3.08a (Maddison & Maddison 1992). Table 2 presents a list of the characters and character states and Table 3 shows the distribution of the character states among taxa.

Results

As expected, a single tree with no homoplasy was obtained (Fig. 1), showing Chauliodinae (fishflies) and Sialidae (alderflies) as adelphotaxa, with Corydalinae as the basal member of the group. Examples of characters grouping fishflies and alderflies are a reduced mandible dentition (character 4, fig. 4-5), anteclypeus fused to postclypeus (character 5, fig. 2, 3), reduction in segmen-

tation of maxillary and labial palps (characters 8 and 9), male abdomen with cerci fused to base of tenth tergites (character 16, fig. 6, 9, 12) and a reduction of the ninth gonostyli and ninth sternum (characters 17 and 18, fig. 7, 10-15, 17-21), as well as larvae lacking tracheal gills (character 21). The monophyly of Megaloptera is not well supported, but possible synapomorphies for the three taxa are a reduction in the terminal forking of the longitudinal veins (character 11), an inconspicuous pterostigma (character 12), and the aquatic mode of life of the larvae (character 24). Autapomorphies for Sialidae, the most specialized member of the group in this scenario, are absence of ocelli (character 6, cf. fig. 2-3), fourth tarsal segment dilated (character 10), reduced male tenth abdominal tergites (character 19, fig. 20-21), as well as in the larvae a reduction in the number of abdominal lateral filaments (character 22) and substitution of anal prolegs for a single caudal filament (character 23). Few or no defining characters for Corydalinae and Chauliodinae question the monophyly of these taxa as well.

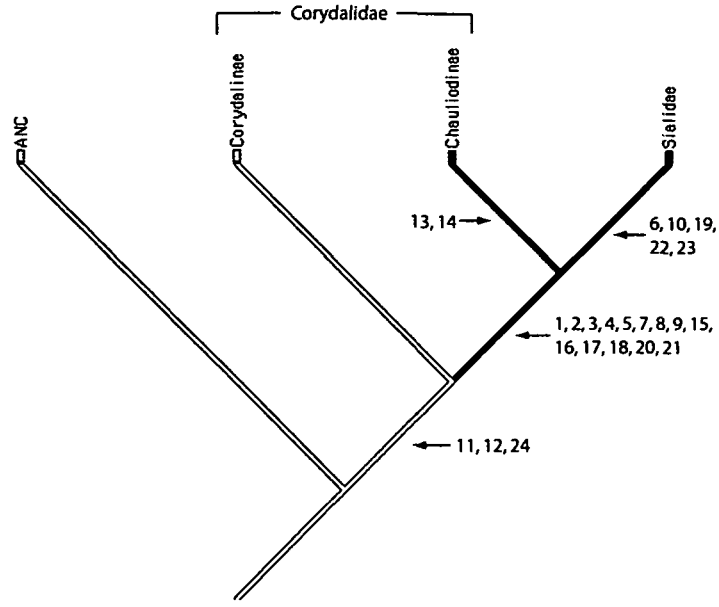

Fig. 1: Hypothetical phylogeny of major taxa of Megaloptera showing fishflies (Corydalidae, Chauliodinae) and alderflies (Sialidae) as adelphotaxa. An a priori polarization of 24 morphological characters, using a hypothetical ancestor, was effected. Each number indicates a corresponding character in its apomorphic state.

Discussion

The main premise of the phylogenetic hypothesis is that reductions and fusions are apomorphic. Examples of reductions involve the postocular plane (character 1),

Table 2. Characters and character states used in the analysis.

Character	Plesiomorphic state (0)	Apomorphic state (1)
Adult head		
1. Postocular plane	Present	Absent
2. Postocular spine	Present	Absent
3. Head shape	Flattened	Robust
4. Mandible dentition	Complete, apical tooth slightly bent	Reduced, apical tooth oblique
5. Anteclypeus	Articulated to postclypeus	Fused to postclypeus
6. Ocelli	Present	Absent
7. Posterior tentorial pits	Arcuate	Linear
8. Maxillary palp	5-segmented	4-segmented
9. Labial palp	4-segmented	3-segmented
Adult thorax		
10. Tarsal segments	Unmodified	4th segment dilated
11. Terminal bifurcations	Present	Reduced of main longitudinal veins
12. Pterostigma	Present, pigmented	Apparently absent, without pigment
13. Last branch of Rs	Bifurcate	Single vein
14. M_{3+4} branches	2 branches	Single vein
15. Rs branches	≥8	4–7
Male abdomen		
16. Cercus	Free, between 9th gonostylus and 10th tergite	Incorporated to base of 10th tergite
17. Ninth gonostylus	Entire	Reduced
18. Ninth sternum	Well developed, plate like	Reduced
19. Tenth tergite	Well developed	Reduced
20. Tenth sternite	Simple, plate like	Modified, produced (fused) plate or reduced
Larva		
21. Tracheal gills	Present	Absent
22. Lateral filaments	8	7
23. Segment 10	Pair of prolegs, each with filament	Prolegs absent, single caudal filament present
24. Habitat	Terrestrial	Aquatic

Table 3: Data matrix showing character state distribution.

Character																								
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corydalinae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Chauliodinae	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	0	1
Sialidae	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1

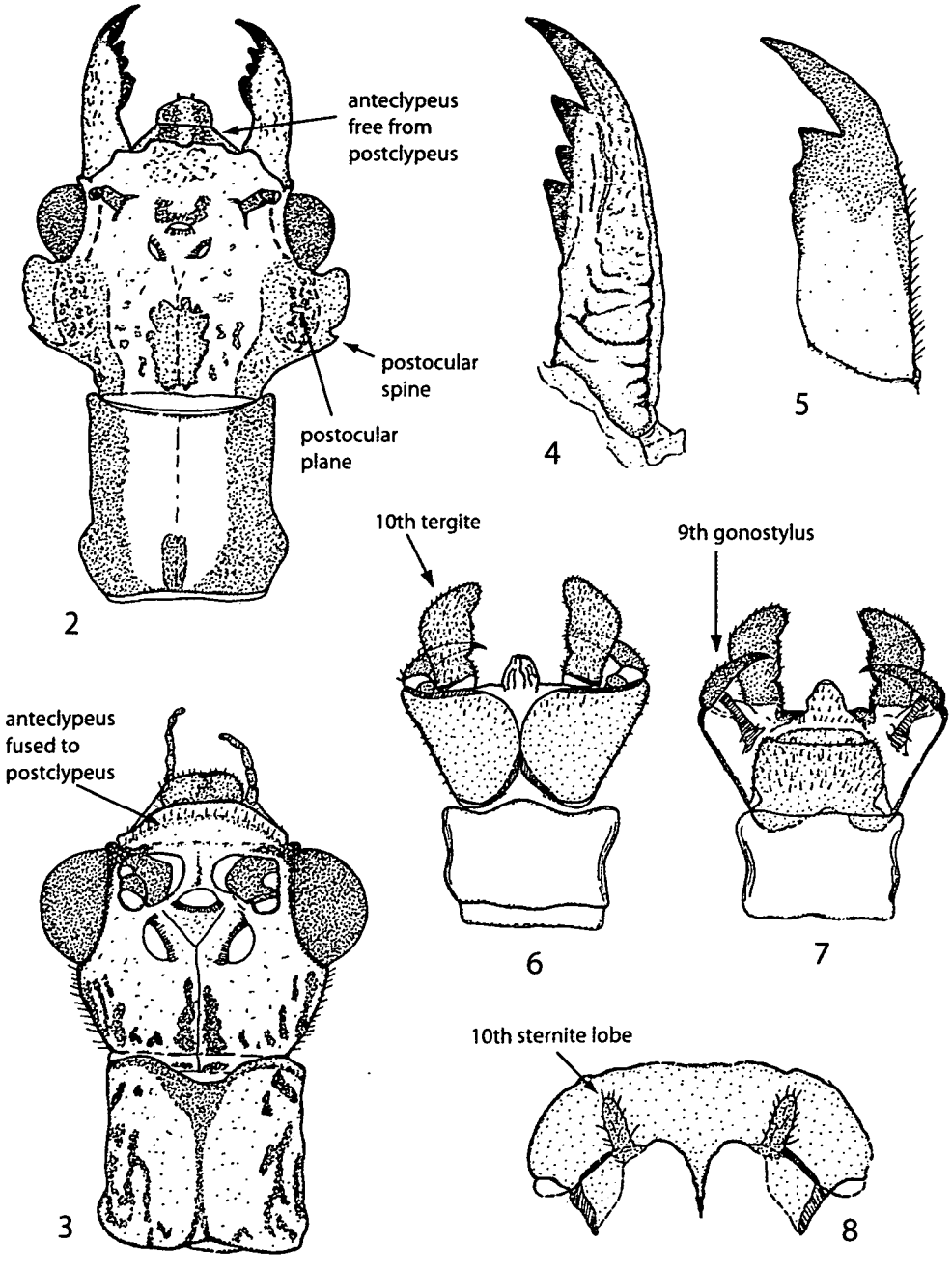

Fig. 2–8: Structures and characters: (2) *Platyneuromus soror* (Hagen 1861), head and pronotum; (3) *Neohermes filicornis* (Banks 1903), head and pronotum; (4) *Corydalus mayri* Contreras-Ramos 2002, right mandible; (5) *Nigronia* sp., right mandible; (6) *Platyneuromus honduranus* Navás 1928, male genitalia, dorsal; (7) Same, ventral; (8) *P. honduranus* (Navás 1928), tenth sternite.

postocular spine (character 2, fig. 2-3), mandible dentition, branches of Rs (character 15), ninth gonostyli, ninth sternum, tenth sternite, and larval tracheal gills, whereas examples of fusions involve head shape (character 3, fig. 2-3), anteclypeus, posterior tentorial pits (character 7), maxillary and labial palps segmentation, and cerci. All these putative apomorphies have the same distribution, being present in Chauliodinae + Sialidae and absent in Corydalinae. Further reductions or modifications present only in one taxon, mainly Sialidae, may be interpreted as autapomorphies, such as the absence of ocelli, a dilated tarsal segment, tenth tergites reduced, larval abdomen with seven lateral filaments, and the replacement of anal prolegs by a caudal filament. From Table 1, most characters used to place Corydalinae and Chauliodinae within Corydalidae might be interpreted as plesiomorphies, such as presence of ocelli (absent in Sialidae), fourth tarsal segment unmodified (bilobed in Sialidae), 8 pairs of lateral filaments on larval abdomen (7 in Sialidae), and a pair of larval anal prolegs (a single filament in Sialidae). At this point, the hypothesis that Sialidae is the sister group of Chauliodinae, needs further testing. I suggest maintaining the current classification unless the above hypothesis is corroborated by other studies (e.g., molecular techniques). It should also be further demonstrated that Corydalinae, Chauliodinae, and Sialidae, are monophyletic entities themselves.

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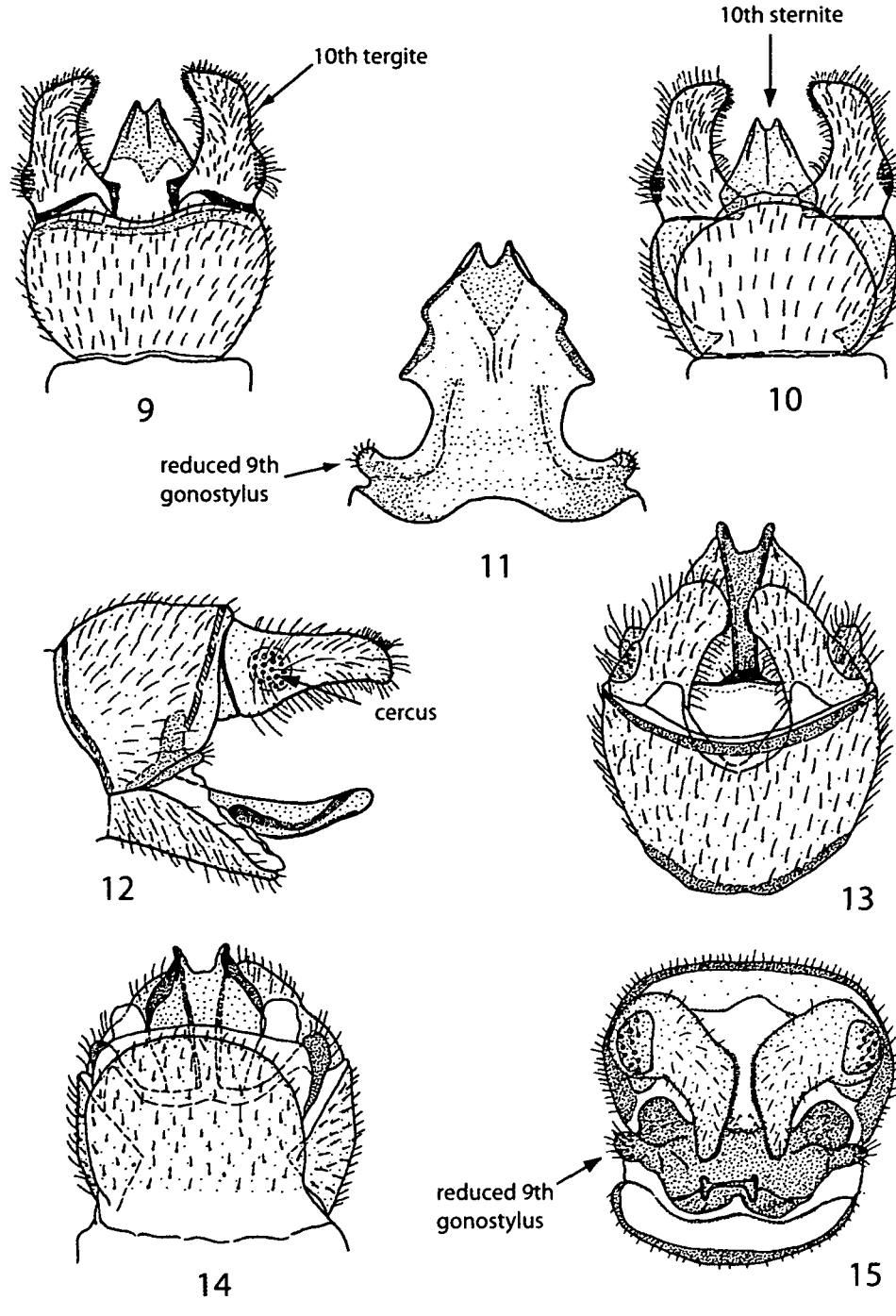

Fig. 9-15: Structures and characters: (9) *Neohermes angusticollis* (HAGEN 1861), male genitalia, dorsal; (10) Same, ventral; (11) *N. angusticollis*, tenth sternite, dorsal; (12) *N. angusticollis* (HAGEN 1861), male genitalia, lateral; (13) *Neohermes filicornis* (BANKS 1903), male genitalia, dorsal (anal tubercle retracted); (14) Same, ventral; (15) Same, caudal.

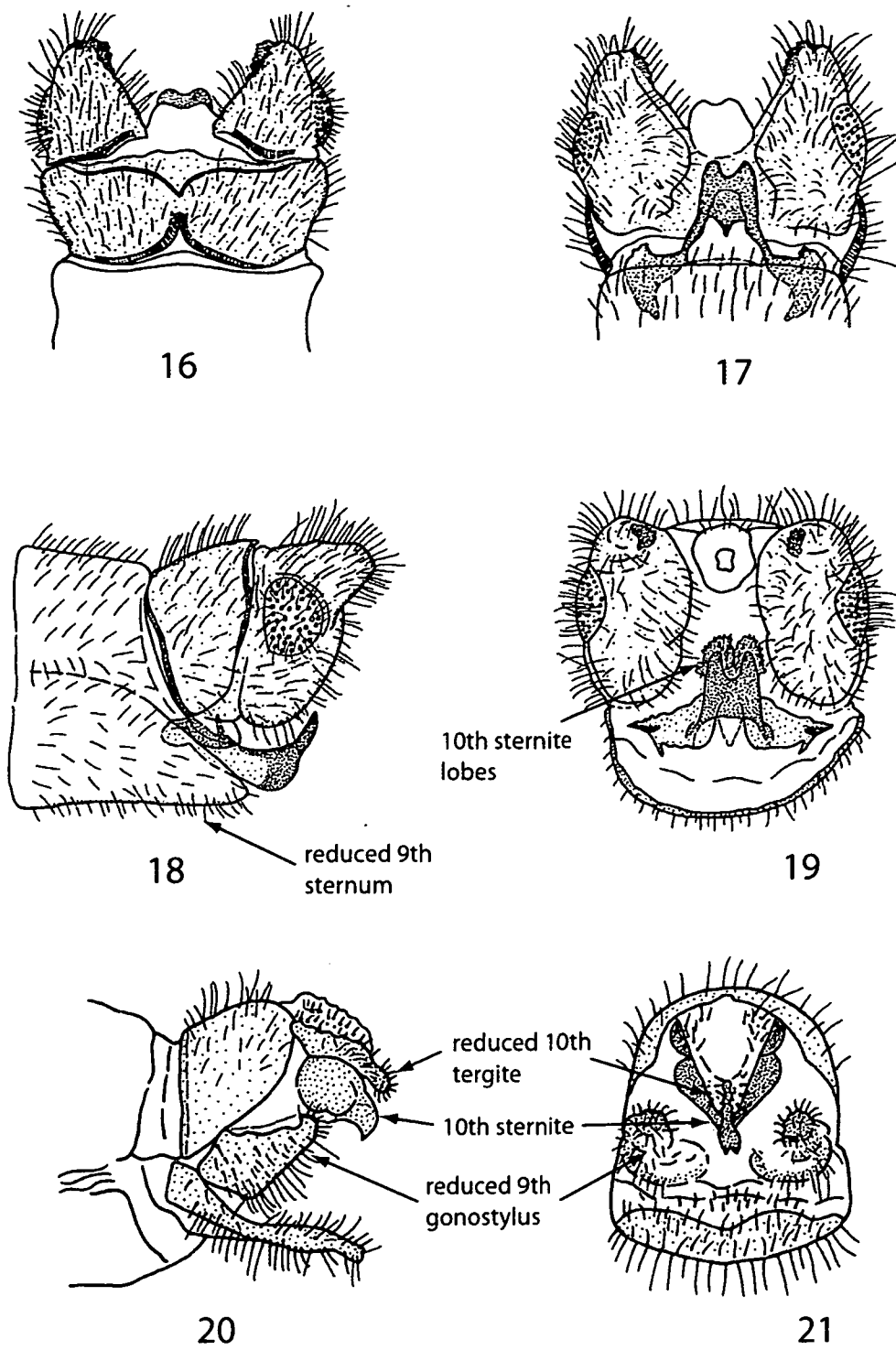

Fig. 16-21: Structures and characters: (16) *Chauliodes rastricornis* RAMBUR 1842, male genitalia, dorsal; (17) Same, ventral; (18) Same, lateral; (19, Same, caudal; (20) Sialis vagans ROSS 193), male genitalia, lateral; (21) Same, caudal.

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