Zootaxa 2862: 1–38 (2011)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Phylogenetic review of dobsonflies of the subfamily Corydalinae and the genus *Corydalus* Latreille (Megaloptera: Corydalidae)

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Abstract

Phylogenetic relationships of the World genera of dobsonflies, subfamily Corydalinae, are reappraised, as well as those of species of the New World genus *Corydalus*, both on the basis of morphological characters. Previous phylogenetic hypotheses of dobsonfly genera by Glorioso, Penny, and Contreras-Ramos, respectively, are re-evaluated, and a fourth revised phylogeny is presented. Ninety-five characters of 10 taxa, one outgroup and nine ingroup taxa, were used in the updated analysis of Corydalinae. It recognizes four lineages, with *Chloroniella* as sister to the other three, of which the *Nevromus* lineage (*Acanthacorydalis* + *Nevromus* + *Neoneuromus*) is sister to the *Corydalus* lineage (*Chloronia* + *Platyneuromus* + *Corydalus*), and both as a group are sister to the *Protohermes* lineage (*Protohermes* + *Neurhermes*). The main changes in the updated Corydalinae phylogeny are the placement of *Chloroniella* as sister to all other dobsonfly genera, and the placement of *Acanthacorydalis* as a member of the *Nevromus* lineage. Previously, Penny had proposed *Chloroniella* as sister to all dobsonfly genera except the *Protohermes* lineage, and both Glorioso and Penny, respectively, placed *Acanthacorydalis* as sister to the *Corydalus* lineage. About *Corydalus*, its species phylogeny is herein updated, as four species from Venezuela were added to the genus after its taxonomic revision. For the new phylogeny, 120 characters of 35 taxa, two outgroup and 33 ingroup taxa, were used. It produced a strict consensus of two trees, better resolved than the previous one. The *C. arpi* species group is moved to sister of all other species except the *C. cephalotes* species pair, while the *C. batesii* species group is conserved, being the only unresolved group within the phylogeny. Two of the species added, *C. hayashii* and *C. mayri*, belong to the well defined *C. arpi* species group, of Guayana Shield affinity, whereas *C. crossi* is sister to a large and widespread group beginning with the *C. nubilus* species group, and *C. clavijoi* is sister to *C. tesselatus* within the latter group.

Key words: Phylogeny, dobsonfly, Corydalinae, *Corydalus*, classification

Accepted by E. DeWalt: 28 Jan. 2011; published: 2 May 2011

Introduction

The Megaloptera is a small holometabolous taxon with an estimated World fauna of 348 extant species (modified from Cover & Resh 2008). It generally receives ordinal status and has been clearly placed within the Neuropterida (Kristensen 1981, 1991; Whiting *et al.* 1997; Aspöck *et al.* 2001). As recognized by most authors, the order contains two families, Corydalidae and Sialidae (alderflies), the former with two subfamilies, Corydalinae (dobsonflies) and Chauliodinae (fishflies), although family status has been proposed for each of the three main lineages (Theischinger 1983). Additionally, the monophyly of Corydalidae has been challenged (Contreras-Ramos 2004a). The alpha taxonomy of the order is in fairly good shape, particularly after recent taxonomic efforts led by Liu on the Asian fauna (e.g., Liu & Yang 2004, Liu *et al.* 2009, Yang & Liu 2010). A general account of biological knowledge of the order has been elaborated by New & Theischinger (1993), however phylogenetic knowledge is still incomplete. Although there is a genus-level hypothesis for the Chauliodinae (Liu & Yang 2006), there is none yet for the Sialidae. Several group level phylogenies have been proposed (e.g., Liu *et al.* 2005). Nine dobsonfly genera are currently recognized (Table 1), of which *Chloronia*, *Corydalus*, and *Platyneuromus* are present in the New World. Although all three have been revised, no formal phylogenies have been proposed for *Chloronia* or *Platyneuromus*. *Corydalus* is the most species-rich genus of New World dobsonflies, currently including 34 described species.

TABLE 1. Taxonomic status of dobsonfly (Corydalinae) genera of the World.

Taxon	Distribution	Status	Selected references
Acanthacorydalis Weele	Oriental Region, northeastern India to Vietnam and China	Ca. 8 species; no general systematic revision, phylogeny for Chinese species	Glorioso 1981; New & Theischinger 1993; Liu *et al.* 2005
Chloronia Banks	Neotropical Region, Brazil through Mexico, Lesser Antilles	17 species described; revised, no formal phylogeny	Penny & Flint 1982; Contreras-Ramos 2000, 2002, 2004c; Azevêdo 2003
Chloroniella Esben-Petersen	South Africa	1 species, redescribed	Penny 1993
Corydalus Latreille	North, Central, and South America	34 species described; revised, phylogeny proposed	Contreras-Ramos 1998, 2002; Azevêdo & Hamada 2006, 2007
Neoneuromus Weele	Oriental Region, northeastern India to Malay Peninsula and China	8 species described; revised for China, no general phylogeny	Liu & Yang 2004
Neurhermes Navás	Oriental Region, northwest India to Indonesia and China	8 species described; no systematic revision, no phylogeny	Glorioso 1981; New & Theischinger 1993
Nevromus Rambur	Oriental Region, northwest India to Indonesia and China	4 species described; no systematic revision, no phylogeny	Glorioso 1981; New & Theischinger 1993
Platyneuromus Weele	Central America to northeastern Mexico	3 species described; revised, no phylogeny	Glorioso & Flint 1984; Contreras-Ramos 1999a; Contreras-Ramos & Harris 1998
Protohermes Weele	Oriental Region, northwest India to Indonesia, China, and Japan	60 species described; 10 species groups revised, phylogenies for species groups proposed	Glorioso 1981; New & Theischinger 1993; Liu & Yang 2009

This contribution attempts to summarize current knowledge on the phylogeny of the subfamily Corydalinae and of the genus *Corydalus*. It is not a formal attempt to review the genus level systematics of the subfamily, a goal that was successfully accomplished by Glorioso (1981). Following Glorioso, it is assumed that dobsonfly genera are monophyletic, as is the major taxon Corydalinae (but see *Conclusions* ahead). The revised Corydalinae analysis involved removal of several *Corydalus* species that were included previously in order to test the monophyly of *Corydalus* (Phylogenetic Analysis Phase I in Contreras-Ramos 1998). The main challenge here was to assign representative character states to *Corydalus*, as a supraspecific taxon, for which character states present in species held by basal nodes (i.e., states hypothesized as ancestral) were selected. As a complementary task, the phylogenies proposed by Glorioso (1981) and Penny (1993) were reanalyzed from compiled data matrices. This implied not only extraction of characters from their presented cladograms, where characters were mapped, but scoring of actual character states in the outgroup. The results obtained were very close but not identical to the original analyses, which means that outgroup characters were sometimes assigned a plesiomorphic state, 0, without checking the true state present in the specimens. It is intended that these analyses further stimulate research using morphological and molecular characters to challenge or support current hypotheses.

Phylogeny of Corydalinae. An excellent genus-level revision of this subfamily was performed by Glorioso (1981). He studied specimens from various representative species of each genus and so was able to define or redefine all dobsonfly genera. His cladistic analysis was performed manually as that was still a pre-computer period for phylogenetic analyses. He used 70, mostly binary morphological characters which were polarized *a priori* through outgroup comparison. No data matrix was included. His resulting phylogeny (Fig. 1A) lacked only *Chloroniella*, because specimens of this South African genus were unavailable to him. Glorioso's study is still essential for anyone wishing to do taxonomic research on dobsonfly genera. Later on, Penny (1993) obtained specimens of *Chloroniella peringueyi* Esben-Petersen, the only species in the genus, and incorporated this taxon into Glorioso's data set with a few modifications. Glorioso's characters 1, 2, 3, and 18, were deleted, and characters 47, 50, 57, 58, and 60 were new in Penny's analysis, leaving a total of 71 characters. The program PAUP was utilized to develop a phylogeny, yet no data matrix was made available in the paper. One tree was obtained (Fig. 1B) identical to that of Glorioso, except for the inclusion of *Chloroniella* as sister to the *Nevromus* + *Corydalus* assemblages. The present study rebuilds a character matrix from character states mapped on Glorioso's and Penny's cladograms. Unfortunately, character states were not mapped for the outgroups, requiring study of actual specimens. Table 1 lists the World Corydalinae genera with comments on their taxonomic status.

As part of a systematic revision of *Corydalus* (Contreras-Ramos 1998), several atypical species from South America (*C. affinis* Burmeister, *C. arpi* Navás, *C. colombianus* Contreras-Ramos, *C. ecuadorianus* Banks, *C. flinti* Contreras-Ramos, *C. hecate* MacLachlan, *C. ignotus* Contreras-Ramos, *C. imperiosus* Contreras-Ramos, *C. nubilus* Erichson, and *C. tesselatus* Stitz) were studied for their effects on the monophyly of *Corydalus*. First, some of the species were incorporated into Glorioso's data set, following his character polarization criteria (Contreras-Ramos 1993). Then, a thoroughly revised analysis was performed studying specimens from all dobsonfly genera and from the outgroup, Chauliodinae (Fig. 2). Surprisingly, these results differed from those of Glorioso and Penny, but because they were a test of monophyly for *Corydalus*, they have passed unnoticed as an independent generic phylogeny of Corydalinae. In order to highlight its novel nature, the data matrix is reanalyzed here excluding the atypical *Corydalus* and leaving a single *Corydalus* taxon.

Phylogeny of *Corydalus*. There is one previous phylogenetic analysis of *Corydalus*, which is part of the systematic revision of the genus (Contreras-Ramos 1998). In that analysis, 30 species (Table 2, Fig. 3) and two outgroups were codified for 120 morphological characters (*C. amazonas* Contreras-Ramos was removed because males were unknown, so many data are missing) and three most parsimonious trees were obtained (Fig. 4). After the revision, four species, all from Venezuela, were added to the genus (Contreras-Ramos 2002): *C. clavijoi* Contreras-Ramos, *C. crossi* Contreras-Ramos, *C. hayashii* Contreras-Ramos, and *C. mayri* Contreras-Ramos. These four species are incorporated here into a revised phylogenetic analysis of the genus. Characters were re-evaluated, in part because a well preserved second male of *C. ecuadorianus* Banks became available (Contreras-Ramos 2004b), so a few changes were made to the data matrix, which are mentioned in the character list (Appendix 7) on the corresponding character entry.

Material and methods

Terminology and taxa studied. Morphological terms used in the analyses, including wing venation and genitalia, follow Glorioso (1981), as modified by Contreras-Ramos (1998). In particular, the use of Glorioso's tenth gonostyli, referring to a pair of digitiform or papilliform processes of the tenth sternum, is avoided, as there is wide support for insect abdominal segment 10 to lack appendages before the origin of extant hexapods (*cf*. Contreras-Ramos 1998, Tables 1–2). However, the original terminology used by Glorioso (1981) and Penny (1993) in their analyses, respectively, was maintained in their character lists (Appendix 1, 3). Common structures used in descriptions and as characters for the analyses are in Contreras-Ramos (1998, figs. 1, 12, 13). Illustrations of most of the characters used in the phylogenies are available in Glorioso (1981), Penny (1993), and Contreras-Ramos (1998, 2002). Specimens of each of the nine dobsonfly genera were studied for the Corydalinae analysis (Table 1). A detailed list of species, specimens, and collections is in Appendix 2 of Contreras-Ramos (1998). Similarly, a complete list of specimens studied for the *Corydalus* phylogeny may be found in the material examined sections in Contreras-Ramos (1998, 2002, 2004b). In the case of *C. amazonas*, it was excluded from the analysis because only females are known. The lack of male characters might increase the number of equally parsimonious trees. Only the adults of both sexes were studied. All specimens were curated and dissected as explained in Contreras-Ramos (1998).

TABLE 2. Known species of the dobsonfly genus *Corydalus*. Detailed species distributions are in Contreras-Ramos (1998, 1999b, 2002, 2004b) and Azevêdo (2003).

Species	Distribution
C. affinis Burmeister, 1839	Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Venezuela
C. amazonas Contreras-Ramos, 1998	Brazil
C. armatus Hagen, 1861	Argentina, Bolivia, Colombia, Ecuador, Peru, Venezuela
C. arpi Navás, 1936	Brazil, Venezuela
C. australis Contreras-Ramos, 1998	Argentina, Brazil, Uruguay
C. batesii MacLachlan, 1868	Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Suriname, Peru, Venezuela
C. bidenticulatus Contreras-Ramos, 1998	Mexico, United States
C. cephalotes Rambur, 1842	Brazil
C. clauseni Contreras-Ramos, 1998	Colombia, Costa Rica, Ecuador
C. clavijoi Contreras-Ramos, 2002	Venezuela
C. colombianus Contreras-Ramos, 1998	Colombia
C. cornutus (L.), 1758	Canada, United States
C. crossi Contreras-Ramos, 2002	Venezuela
C. diasi Navás, 1915	Argentina, Brazil, Paraguay
C. ecuadorianus Banks, 1948	Ecuador
C. flavicornis Stitz, 1914	Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Panama, Peru, Venezuela
C. flinti Contreras-Ramos, 1998	Venezuela
C. hayashii Contreras-Ramos, 2002	Venezuela
C. hecate MacLachlan, 1866	Brazil, Peru, Venezuela[1]
C. holzenthali Contreras-Ramos, 1998	Bolivia, Peru
C. ignotus Contreras-Ramos, 1998	Brazil, French Guiana
C. imperiosus Contreras-Ramos, 1998	Argentina
C. longicornis Contreras-Ramos, 1998	Argentina, Bolivia, Ecuador
C. luteus Hagen, 1861	Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, United States
C. magnus Contreras-Ramos, 1998	Costa Rica, El Salvador, Guatemala, Mexico
C. mayri Contreras-Ramos, 2002	Venezuela
C. neblinensis Contreras-Ramos, 1998	Venezuela
C. nubilus Erichson, 1848	Brazil, French Guiana, Guyana, Venezuela
C. parvus Stitz, 1914	Ecuador, Peru
C. peruvianus Davis, 1903	Argentina, Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Peru, Venezuela
C. primitivus Weele, 1909	Argentina, Bolivia
C. tesselatus Stitz, 1914	Colombia[1], Venezuela
C. texanus Banks, 1903	Guatemala, Mexico, United States
C. tridentatus Stitz, 1914	Brazil

[1] Doubtful record

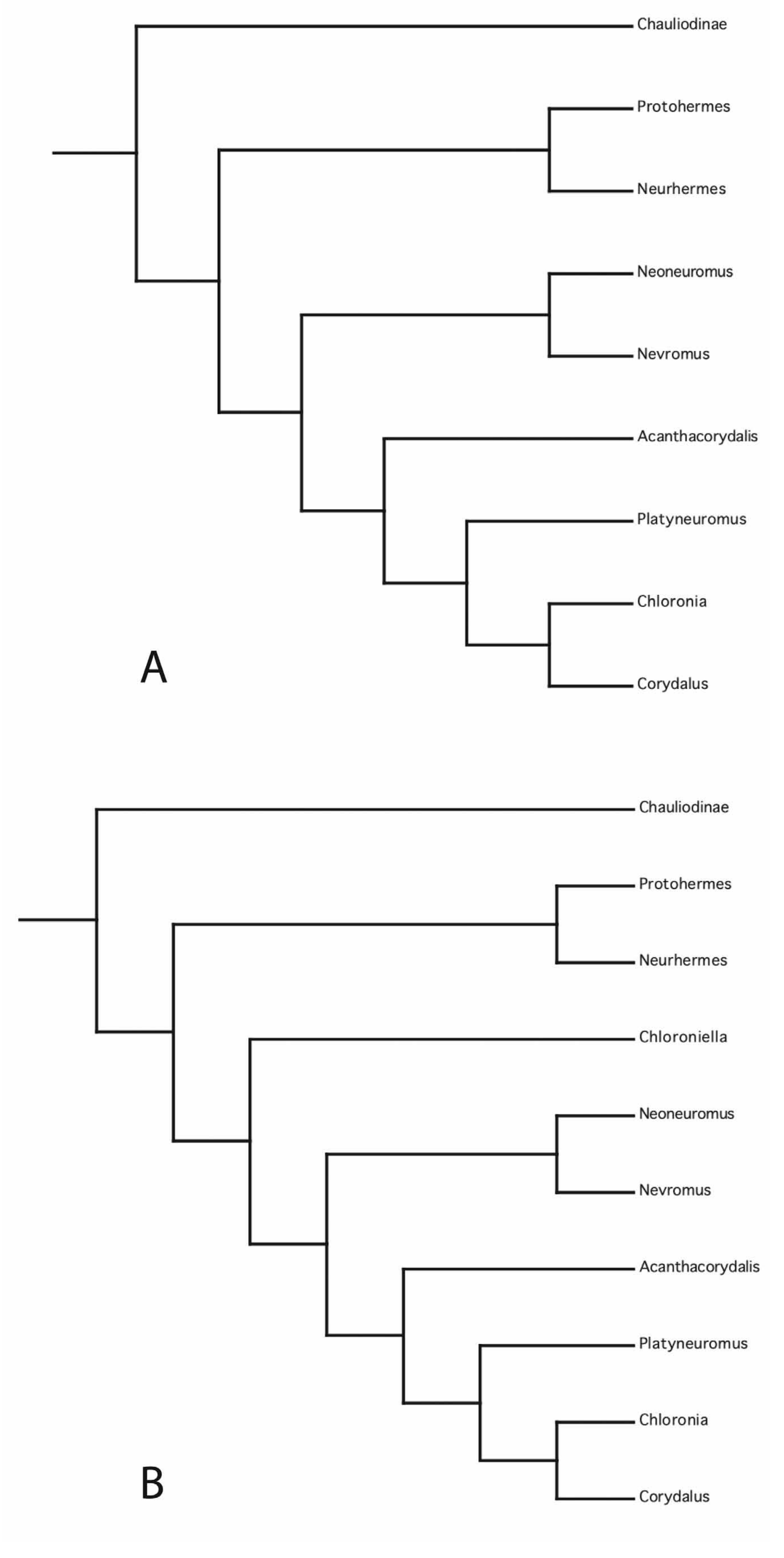

FIGURE 1. Previous phylogenies of Corydalinae genera. A, Glorioso's (1981) original cladogram; B, Penny's (1993) original cladogram.

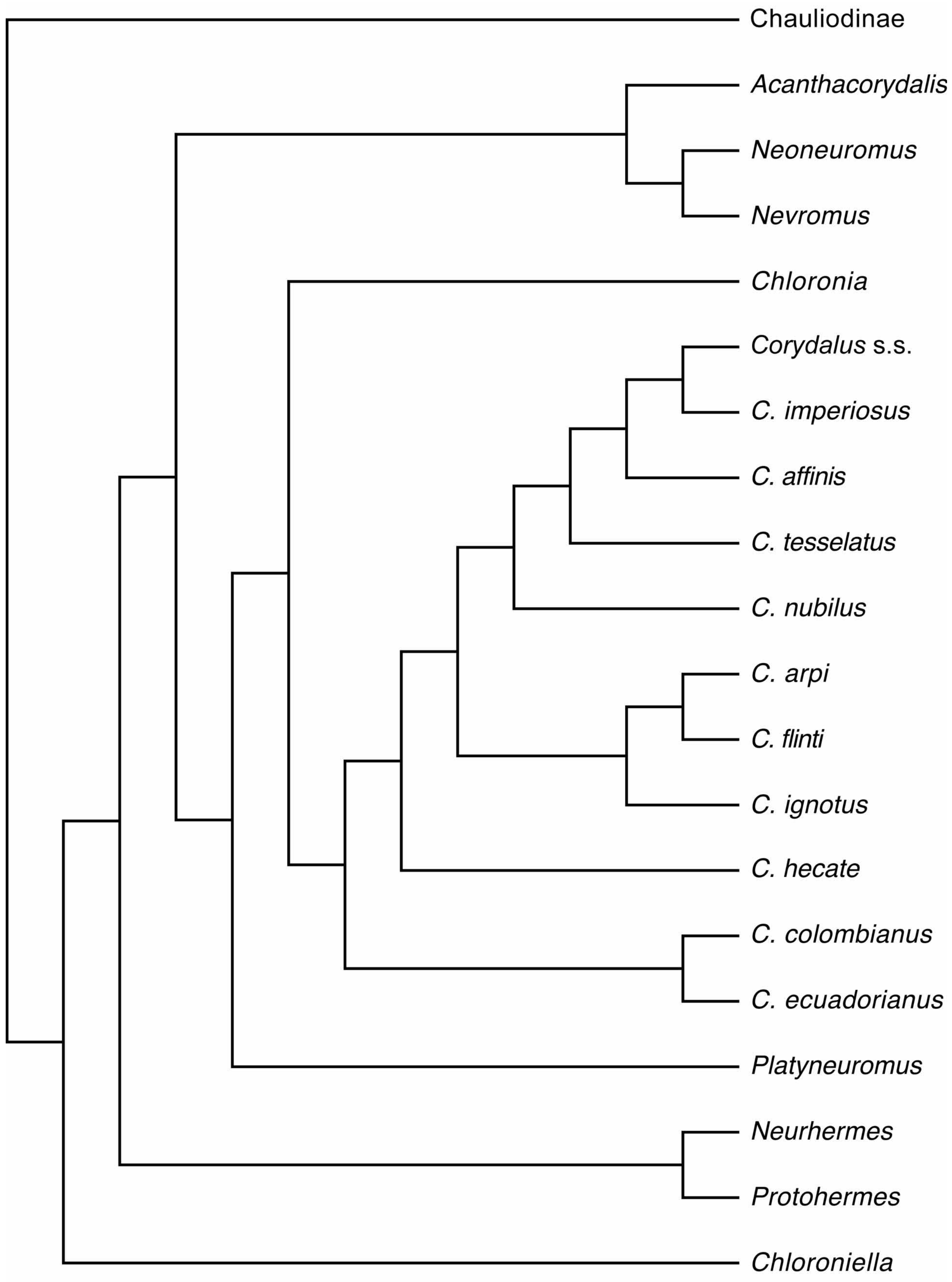

FIGURE 2. Dobsonfly phylogeny presented as a test of monophyly for *Corydalus* (Contreras-Ramos 1998).

Characters. All characters were considered unordered and of equal weight. For Glorioso's and Penny's analyses, characters were extracted as they were originally mapped on their respective cladograms and incorporated into a data editor window of MacClade (Maddison & Maddison 2003). When multistate, a third character state was added as a 2. For instance, in Glorioso's character 13, states plesiomorphic and apomorphic, and 13', apomorphic, were coded as character 13 with states 0, 1, and 2, respectively.

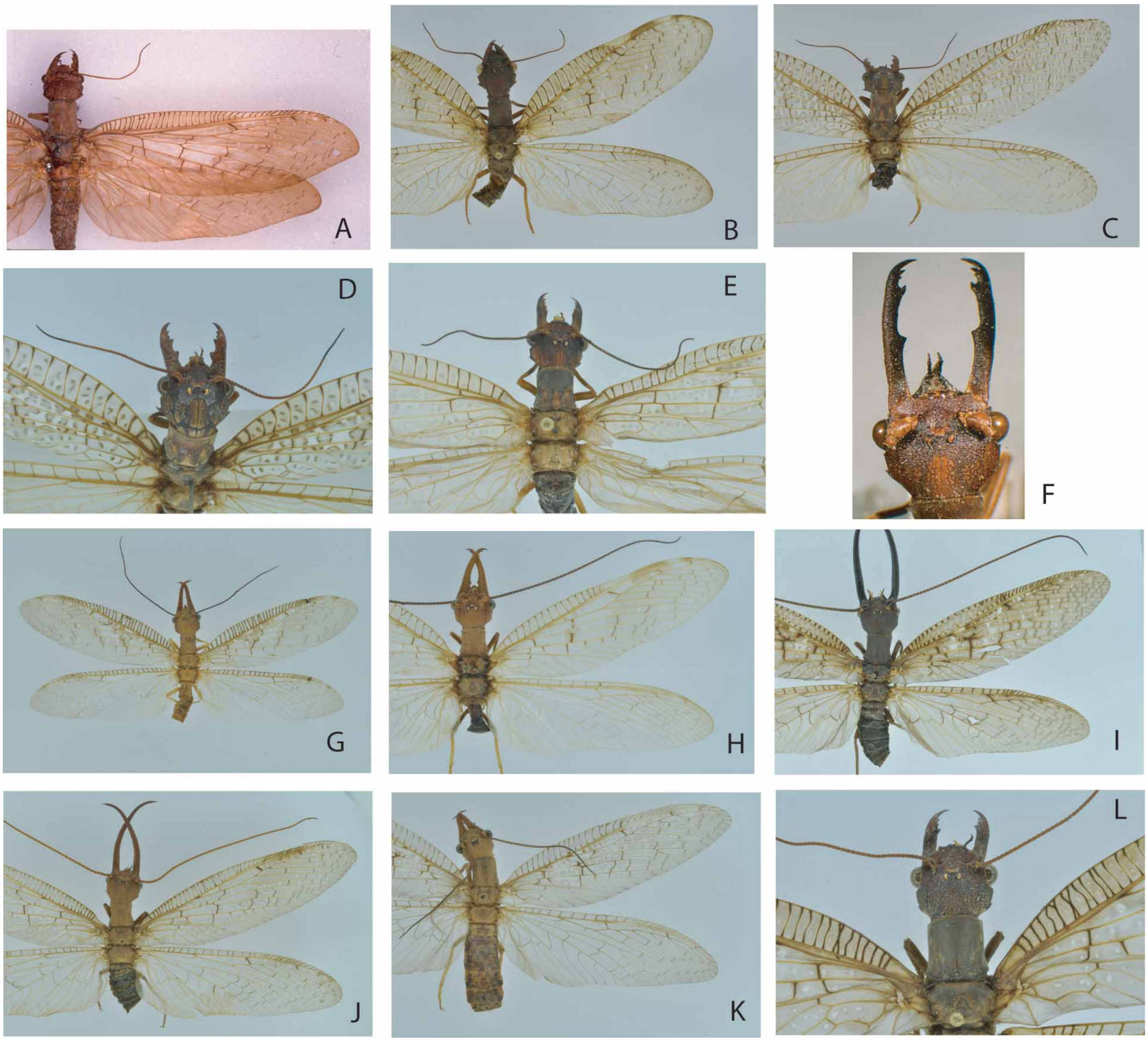

FIGURE 3. Habitus of *Corydalus* species. A, *Corydalus hecate*, male; B, *C. arpi*, male; C, *C. flinti*, male; D, *C. flinti*, male head; E, *C. ecuadorianus*, male; F, *C. colombianus*, male head; G, *C. affinis*, male; H, *C. tesselatus*, male; I, *C. imperiosus*, male; J, *C. australis*, male; K, *C. primitivus*, male; L, *C. holzenthali*, female head.

In Glorioso's cladogram, character 30 was assigned to *Protohermes* and *Neurhermes*, as well as character 41 to *Acanthacorydalis*, as both characters were not mapped. A few characters had coding problems, notably characters 37 and 38 (both a single character with several character states), similarly 54 and 55, and 68 through 70 (overlapping, difficult to apply to all taxa). Nonetheless, his coding was respected, but attempts were made to overcome these problems in the updated analysis. An *a priori* polarization worked out well, with some minor exceptions. For instance, character 46, lack of dorsolateral incisions on the male ninth tergum, was interpreted by Glorioso as apomorphic supporting several taxa, but it turns out that the presence of incisions in *Neoneuromus* is autapomorphic. Similarly, in character 60, the absence of an 11th tergum in several taxa was considered apomorphic, but actually the presence of such a plate is again an autapomorphy for *Neoneuromus*. Some of Glorioso's coding perhaps was limited by the availability of specimens. For instance, character 52, anterolateral corner of 10th gonocoxites with acute projection, was assigned as absent (plesiomorphic) to *Platyneuromus*, but it is actually a synapomorphy for the American genera (i.e., *Chloronia*, *Corydalus*, and *Platyneuromus*). However, the main problem with characters was how they were assigned in the outgroups (Chauliodinae and *Sialis*, of which I focused on the former). In a couple of characters, such as 53 and 54, character states are difficult to assign to the outgroup. Finally, when characters are evaluated for the outgroup, several of them, specifically 21, 25, 27, 29, 46, 50, 56, 60, 66, and 68, cannot be assigned as plesiomorphies (Appendix 2), and so most likely, the reinterpreted data matrix was responsible for slightly different results compared to what Glorioso presented.

Similarly, in Penny's cladogram (his cladogram 1), characters 29' and 37 were assigned to *Acanthacorydalis*, but they were not mapped. Also, characters 55 and 67, grouping *Neoneuromus* through *Corydalus*, should be 55r and 67r, respectively; character 30 for the American lineage of dobsonflies should also be 30r. Finally, character 37, an autapomorphy for *Chloronia*, should actually be 37'. Penny excluded Glorioso's characters 1, 2, 3, and 18, and added the new characters 47, 50, 57, 58, and 60, the first two and the fourth of which are autapomorphies for *Chloroniella*. As with Glorioso's analysis, when character states for Chauliodinae are actually scored one by one, it turns out that for characters 12, 17, 21, 23, 25, 42, 46, 54, 55, 61, 67, and 69 (Appendix 4), it is not assigned a plesiomorphic character state. Again, this might have accounted for the slightly different results obtained when Penny's analysis was re-executed. The problem with *a priori* polarization in Glorioso's analysis was avoided in Penny's because the latter used PAUP. For instance, in character 42, *Neoneuromus* has a reversal to state 0, while all other taxa have state 1.

In the updated Corydalinae analysis, several characters were recoded. For instance, Penny's character 1 (updated analysis character 4) was assigned a state 0 for *Chloroniella*, the same with Penny's character 4 (updated analysis character 8). In Penny's character 15, *Chloroniella* was assigned a 0, while in the corresponding character 17 of the new analysis it received a 1. In Penny's character 46, both *Acanthacorydalis* and *Nevromus* received a 0 (trait present), while in the corresponding character 53 of the new analysis the same taxa received a 0 (trait absent). In Penny's character 51, *Chloroniella* received a state 1, while in the corresponding character 59 of the new analysis, it received a state 3. Other characters in Penny's study that were interpreted differently are 54 (character 55 new analysis), 67 (67 of the new analysis). Finally, all autapomorphies were removed from the data matrix, as well as several characters that turned out invariable as several ingroup taxa were removed from the original analysis: characters 45, 62, 63, 73, 85, 86, 87 in Contreras-Ramos (1998, Phylogenetic Analysis Phase I). When the several *Corydalus* species were removed from the original data matrix (i.e., *C. affinis*, *C. arpi*, *C. colombianus*, *C. ecuadorianus*, *C. flinti*, *C. hecate*, *C. ignotus*, *C. imperiosus*, *C. nubilus*, and *C. tesselatus*; Table 33 in Contreras-Ramos 1998), a new, single, *Corydalus* taxon had to be conformed, for which several variable characters between species were uniformed through a general criterion of assigning the state present in species held by basal nodes (e.g., characters 57, 58, 71, 74, 75, 95), that is, a state thought to be ancestral.

With respect to the *Corydalus* analysis, there were no major changes in the data matrix (Contreras-Ramos 1998, Phylogenetic Analysis Phase II), except for the four Venezuelan species that were incorporated. However, a few characters were re-scored for a couple of species (characters 76, 86, 91, 92, 97, 99, and 101). Changes effected are mentioned in the respective character entry in Appendix 7. Files of data matrices used for all analyses are available from the author upon request.

Cladistic techniques. Selected pinned specimens of each terminal taxon were placed within entomological drawers arranged one species next to the other. The specimens were placed in an *a priori* phylogenetic sequence (e.g., according to a previously published work). Characters were then searched by body region, in an anterior-posterior and dorsal-ventral sequence, comparing one by one across taxa, and then moving to the next character. In a large tabulation sheet, a draft list of characters was written as provisionally defined, considering taxa in the columns and characters in rows (so new sheets may be added as needed). Selected characters were then codified in a second tabulation sheet, this time having taxa in rows and characters in columns, with a revised brief description for each character state. Subsequently, a data matrix was built using MacClade (Maddison & Maddison 2003) and searches for the shortest tree were run using PAUP (Swofford 1998). All characters were treated as unordered and of equal weight. Branch-and-bound searches were performed for all analyses, except for *Corydalus*, for which heuristic searches through a stepwise addition algorithm were applied (replicates $n = 30$). Bootstrap (50% majority rule consensus tree, replicates $n = 1000$) and Bremer support values were also calculated. Seventy-one characters, one outgroup (Chauliodinae), and nine ingroup taxa, were included in the Corydalinae analysis; whereas 120 characters, two outgroups (*Chloronia*, *Platyneuromus*), and 33 ingroup taxa, were incorporated into the *Corydalus* analysis (Appendices 5–8). Revised analyses by Glorioso (1981) and Penny (1993) contained 70 and 71 characters, and nine and 10 taxa, respectively. MacClade's tree window and its trace character function were utilized to determine character evolution, in addition to lists of character changes and apomorphies from PAUP. A Macintosh Power PC G4 computer with 768 MB of SDRAM and operating system 10.1.5 was utilized to run the applications.

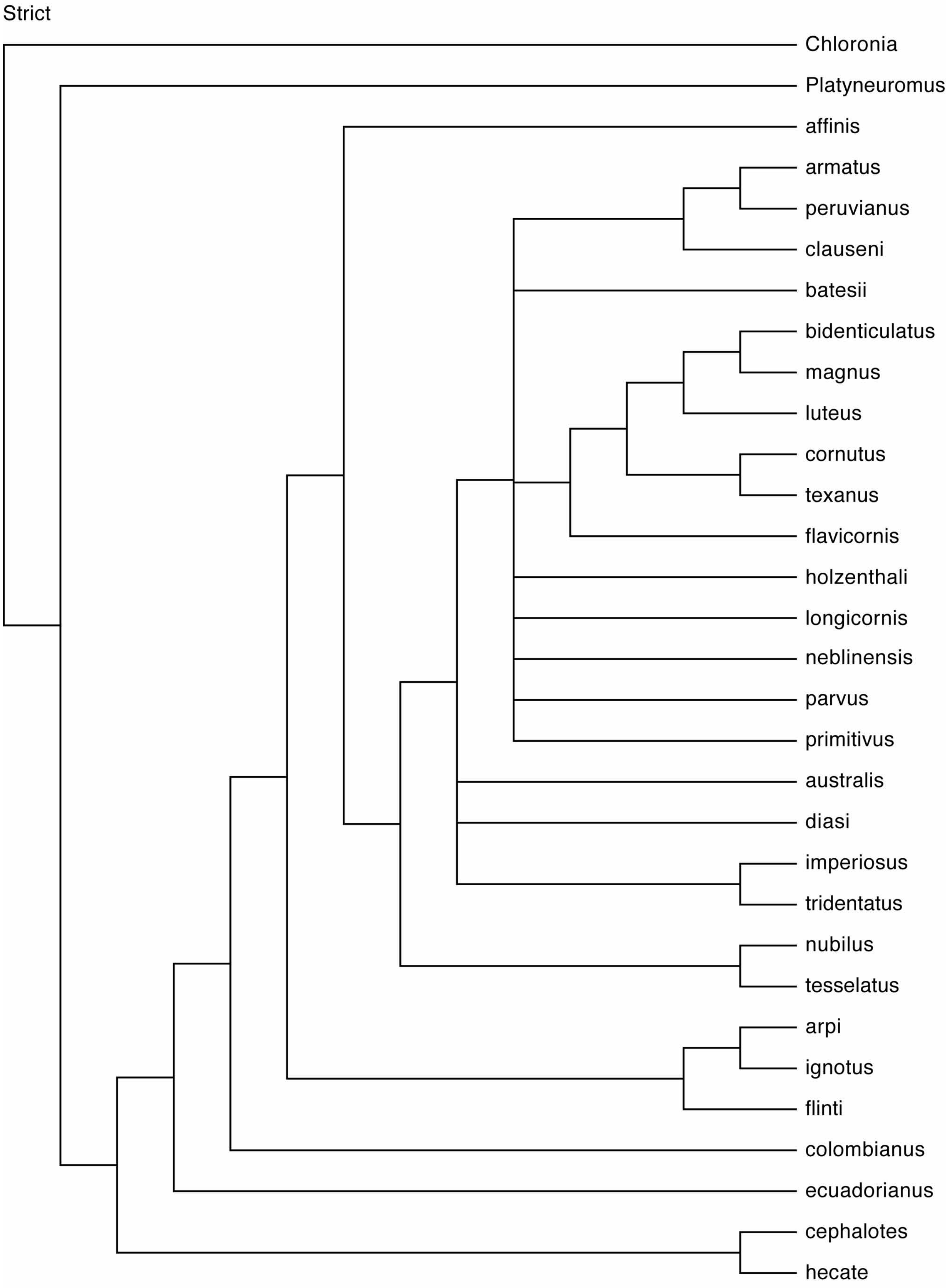

FIGURE 4. Strict consensus of three most parsimonious trees from the analysis of *Corydalus* species by Contreras-Ramos (1998).

Results and discussion

Corydalinae: Glorioso's analysis. Glorioso's study has been a solid starting point for our understanding of genus level relationships within the Corydalinae (Fig. 1A, Appendix 1). However, when character states assigned to the outgroup were revised (Appendix 2), two equally most parsimonious cladograms were obtained (length = 99 steps, consistency index = 0.768, retention index = 0.723, rescaled consistency index = 0.555). One is identical to the one he presented, but in the second one *Acanthacorydalis* is sister to *Nevromus* + *Neoneuromus*. Essentially, Glorioso's data give a partially determined position of *Acanthacorydalis* (Fig. 5). Applying a bootstrap analysis, the weakest node is the one supporting *Acanthacorydalis* (Fig. 6). In fact, redoing a bootstrap some times yields a consensus tree with *Acanthacorydalis* as sister to *Nevromus* + *Neoneuromus*, or forming a polytomy with *Nevromus* + *Neoneuromus* and *Platyneuromus* + *Chloronia* + *Corydalus*. When considering Bremer support values (Fig. 5), the less supported nodes are those of *Chloronia* + *Corydalus* and *Platyneuromus* + *Chloronia* + *Corydalus*, with 2 and 3 Bremer support values respectively; then the *Protohermes* + *Neurhermes* and *Nevromus* + *Neoneuromus* nodes follow in strength, with 4 and 5 as Bremer support values, respectively. Finally, the major group from *Neoneuromus* through *Corydalus*, with a value of 8, is the strongest portion of the phylogeny. In summary, Glorioso's *Protohermes* and *Nevromus* assemblages, as well as the American assemblage (*Platyneuromus* + *Chloronia* + *Corydalus*), are the most solid clades, with *Acanthacorydalis* in an uncertain position.

From Glorioso's original analysis, his characters 46, 48, 54, 56, 60, 65, and 67, are supporting *Acanthacorydalis* position as sister to the American clade. Of these, characters 46 and 60 are dismissed, as they do not provide any support (i.e., they are autapomorphies for *Neoneuromus*). His character 54, shape of ninth gonostylus, is oversimplified (cf., character 54 in Appendix 5); whereas character 56, densely setose ninth gonostylus, is a generalized condition absent only in *Protohermes* and *Nevromus* + *Neoneuromus*, which in addition has been interpreted differently for the updated phylogeny (cf., character 55, Appendix 5). Characters 65 and 67, bursa copulatrix and spermathecal duct, respectively, appear to have been misinterpreted (cf., characters 66 and 68, Appendix 5; and Contreras-Ramos 1998, p. 202). In conclusion, Glorioso's placement of *Acanthacorydalis* as part of the *Corydalus* assemblage seems unwarranted.

Corydalinae: Penny's analysis. Penny's study used a computer application to perform a parsimony analysis and added five new characters (Appendix 3). The addition of *Chloroniella* to the analysis, the only omitted genus from Glorioso's study, also was an improvement. Penny reported one most parsimonious cladogram (Fig. 1B; length = 109 steps, consistency index = 0.688). He also reported a second cladogram (his cladogram 2; length = 113 steps, consistency index = 0.664), which will not be discussed here. His most parsimonious cladogram is essentially equal to Glorioso's, except for *Chloroniella* present as sister to the major group conformed by the *Nevromus* + *Corydalus* assemblages. When Penny's data matrix reassigned a few apomorphic character states in the outgroup (Appendix 4), the analysis yielded two equally most parsimonious trees (length = 111, consistency index = 0.694, retention index = 0.663, rescaled consistency index = 0.460). Again, the position of *Acanthacorydalis* shifts between sister to *Nevromus* + *Neoneuromus* to sister to *Platyneuromus* + *Chloronia* + *Corydalus*, while *Chloroniella* remains stable (Fig. 7). When a bootstrap resampling is applied to the data, a result similar to that of Glorioso is obtained, with the *Acanthacorydalis* node being weakest (Fig. 8). *Chloroniella*'s node is rather strong with a bootstrap value of 86. Bremer support values present a somewhat different pattern (Fig. 7). *Chloronia* + *Corydalus* are a weak group, however the node supporting the *Nevromus* lineage + *American* lineage + *Acanthacorydalis* is also weak, both with Bremer values of 2. The rest of the nodes are fairly strong, with values ranging from 4 (*Chloroniella*'s node), to 5 (American lineage and *Nevromus* lineage nodes), and 6 (*Protohermes* lineage node).

Support in Penny's original analysis for *Acanthacorydalis* as sister to the American lineage is given by characters 52, 54, 66, and 68. Character 52, clavate ninth gonostylus is, as in Glorioso's analysis, a simplification for the taxa involved (*cf*., character 54 in Appendix 5), and so its support for such a clade is questionable. Character 54, densely setose ninth gonostylus, is also present in *Neurhermes* and the outgroup, so its support is partial, however this character has been reinterpreted for *Acanthacorydalis* (*cf*., character 55 in Appendix 6). Characters 66 and 68 have been discussed above for Glorioso's corresponding characters 65 and 67 (*cf*., Contreras-Ramos 1998, p. 202). In conclusion, available evidence, including Penny's results with a revised data matrix (i.e., with outgroup characters rescored), renders the position of *Acanthacorydalis* uncertain.

Regarding *Chloroniella*, Penny's original analysis places *Chloroniella* as sister to the *Nevromus* + *Corydalus* lineages (Fig. 1B) and is supported by his characters 1, 3, 4, 6, 13, 29, 44, and 64. Character 1, a flattened head shape, has been reinterpreted as robust for *Chloroniella* (*cf*., character 4 in Appendix 6). Character 3, moderately to well developed postocular spine, is not a particularly strong character, which might be interpreted differently (*cf*., character 7 in Appendix 6). Character 4, arcuate posterior tentorial pits, has been reinterpreted as linear for *Chloroniella* (*cf*., character 8 in Appendix 6). Character 6, filiform antennae, has been questioned as too general to be assigned to all taxa involved (Contreras-Ramos 1998, p. 203). Characters 13, relatively elongate maxilla; 29, four M-Cu crossveins (*cf*., character 32 in Appendix 6); 44, an inverted V-shaped ninth tergal internal inflection (*cf*., character 43 in Appendix 6); and 63, female gonostylus fused with gonocoxite (*cf*., character 60 in Appendix 6), do support Penny's placement of *Chloroniella*.

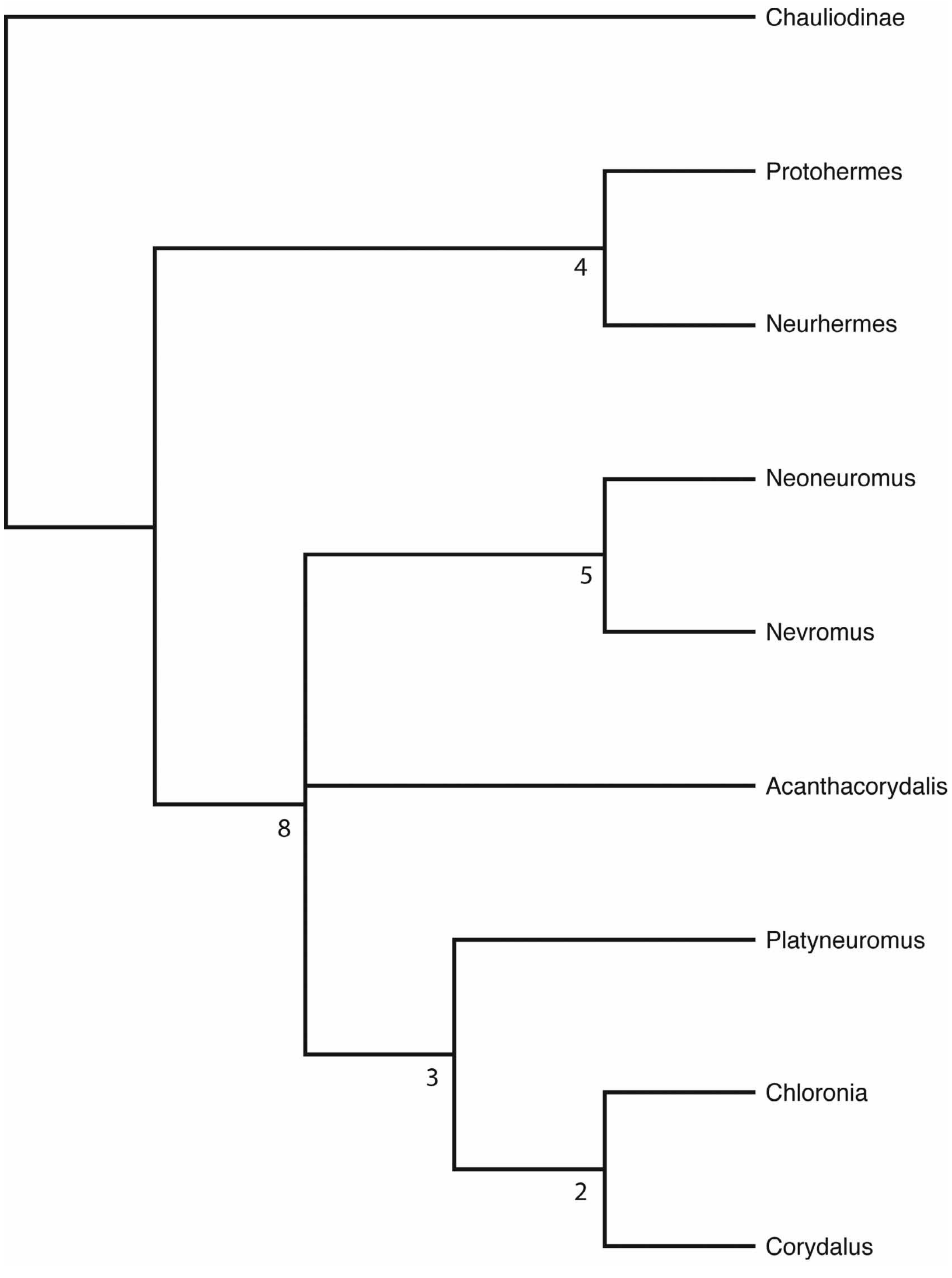

FIGURE 5. Strict consensus of two most parsimonious trees from the revised data matrix extracted from Glorioso (1981). Numbers indicate Bremer support values.

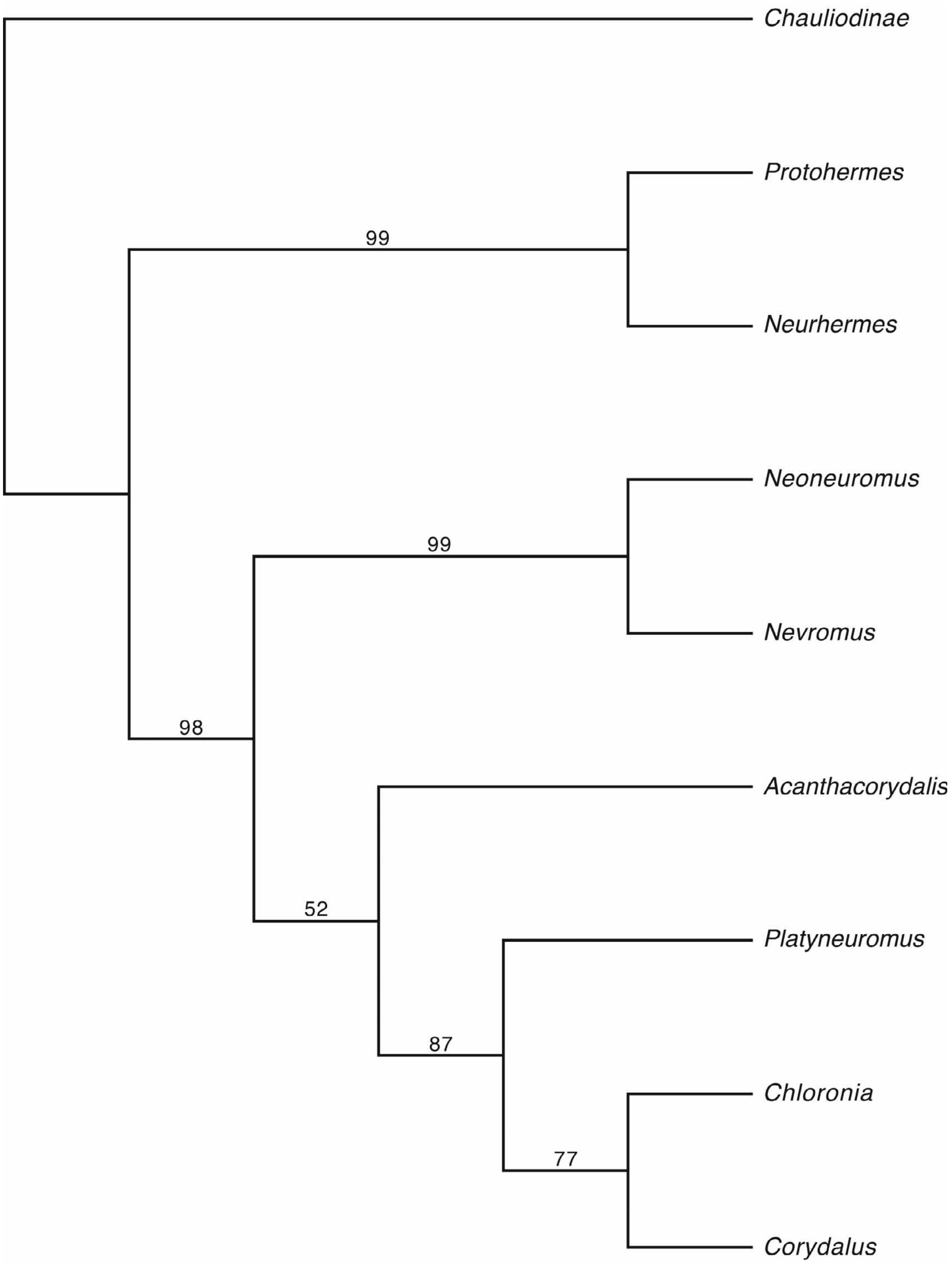

FIGURE 6. Bootstrap 50% majority rule consensus tree ($n = 1000$ replicates) from the revised data matrix extracted from Glorioso (1981).

Corydalinae: phylogenetic update. A test of monophyly for *Corydalus* (Contreras-Ramos 1998) became an independent evaluation of Glorioso's and Penny's phylogenies (Fig. 2). That study, and its updated version presented herein, question former hypotheses with respect to the phylogenetic position of *Acanthacorydalis* and *Chloroniella*. In the present version, utilizing 71 morphological characters, a single most parsimonious tree was obtained (Fig. 9; length = 137 steps, consistency index = 0.686, retention index = 0.642, rescaled consistency index = 0.440). In this tree, *Acanthacorydalis* is part of the *Nevromus* lineage, as sister to *Nevromus* + *Neoneuromus*, while *Chloroniella* is sister to all other ingroup taxa. Also, within the American lineage, *Platyneuromus* emerged as sister to *Corydalus*, instead of *Chloronia*, as had occurred in all former hypotheses. Bootstrap resampling produced a tree (Fig. 10) in which *Platyneuromus* + *Corydalus* was not conserved, and the weakest clade was the *Corydalus* lineage with a value of 67. Overall, most groups have fairly high bootstrap values, especially *Neurhermes* + *Protohermes* and *Nevromus* + *Neoneuromus*, with 100 and 99, respectively, as well as the major clade formed by the *Nevromus* + *Corydalus* lineages, with a value of 93. Weaker values are those of the *Nevromus* lineage and of the major clade *Protohermes* + *Nevromus* + *Corydalus* lineages, with 76 and 69, respectively. Bremer support values are not as encouraging (Fig. 9), particularly because the major group formed by all ingroup taxa except *Chloroniella* collapses with a Bremer value of 1. Also with fairly low values, the *Corydalus* and the *Nevromus* lineages both disappear with a value of 2. All other groups have values of 4 or more.

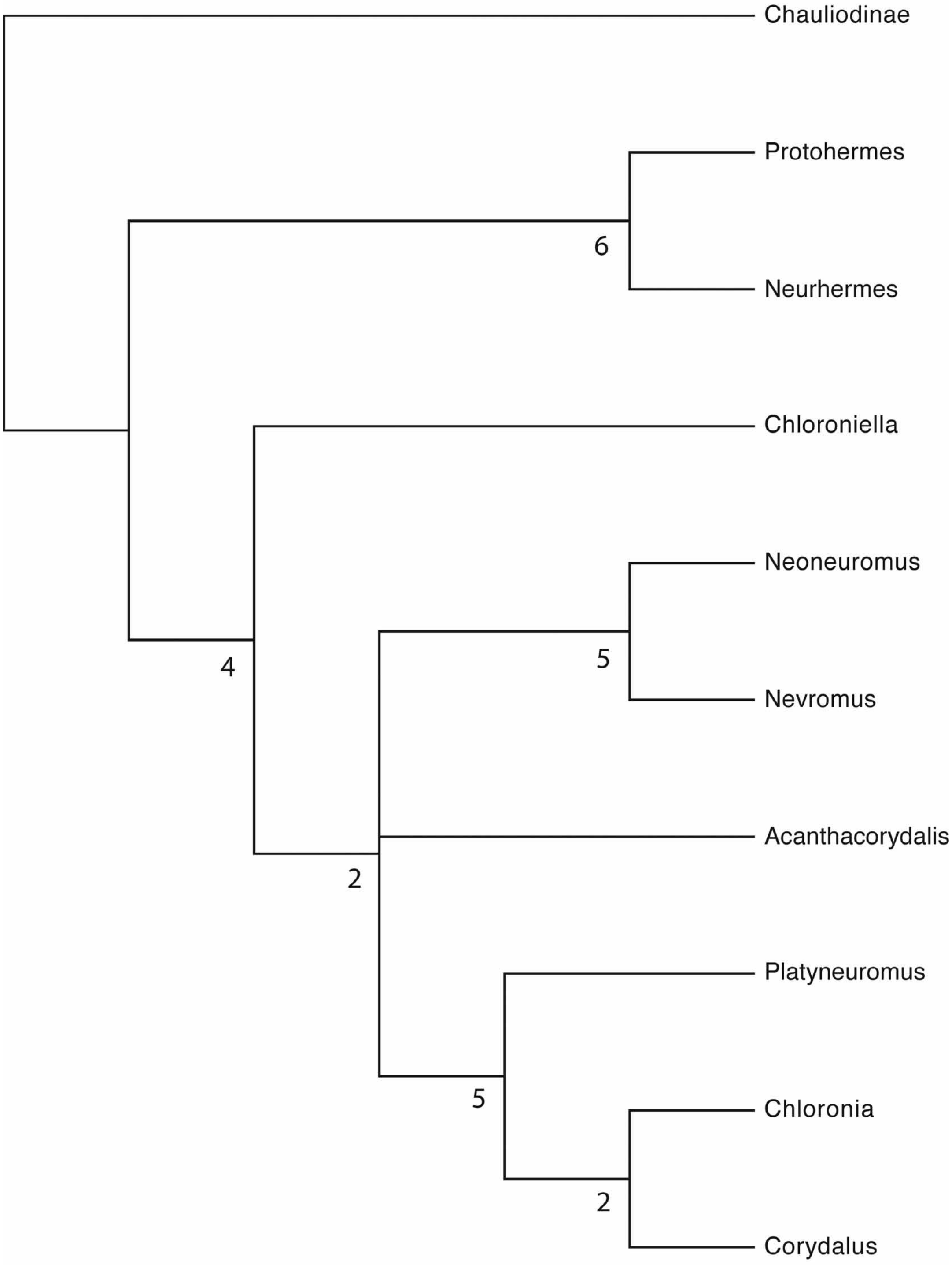

FIGURE 7. Strict consensus of two most parsimonious trees from the revised data matrix extracted from Penny (1993). Numbers indicate Bremer support values.

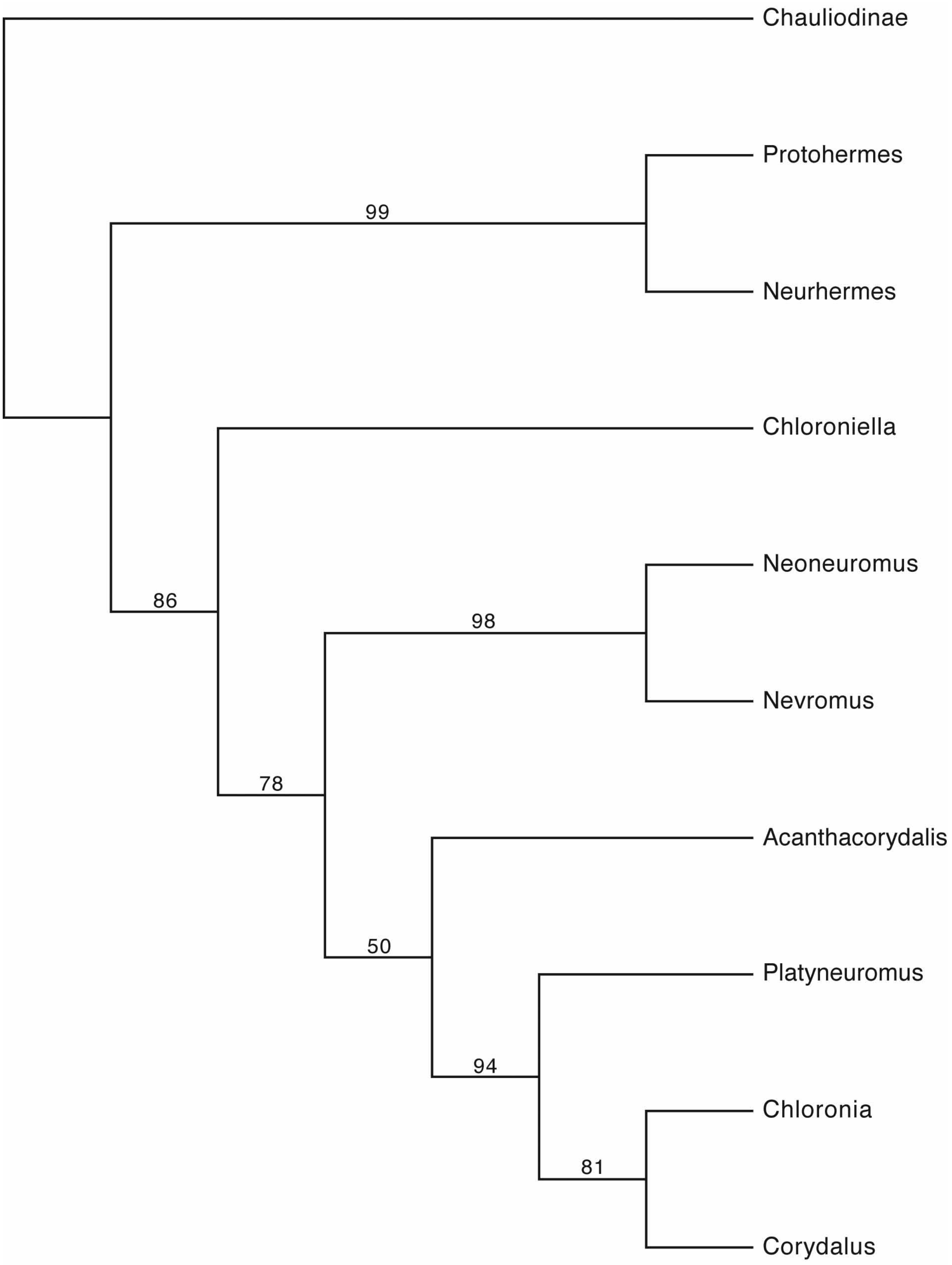

FIGURE 8. Bootstrap 50% majority rule consensus tree (*n* = 1000 replicates) from the revised data matrix extracted from Penny (1993).

Characters that support the monophyly of the *Nevromus* lineage, and thus the membership of *Acanthacorydalis* in such a group, are a reduction of the number of maxillary palp and labial palp sensory areas from two to one (characters 21 and 24, respectively; Appendix 5). Although the consistency index of these characters is 0.5, because state 0 is also present in Chauliodinae, these reductions should be considered apomorphic, as the co-occurrence in the outgroup is an unrelated event. Another synapomorphy (ci = 1.0) is the presence of cubital accessory crossveins (character 33, Appendix 5). A fourth synapomorphy (ci = 1.0) is the migration of the ninth gonostyli posteriorly in relation to the base of the tenth tergites (character 40, Appendix 5). Several *Corydalus* species also have this condition, but it was considered secondarily derived, and not representative of the ancestral condition for the genus. Characters 20, a broadly rounded apex of maxillary palp, and 46, tenth tergites distant from anal tubercle, relegate *Acanthacorydalis* (and all Old World taxa) as nonmembers of the *Corydalus* lineage.

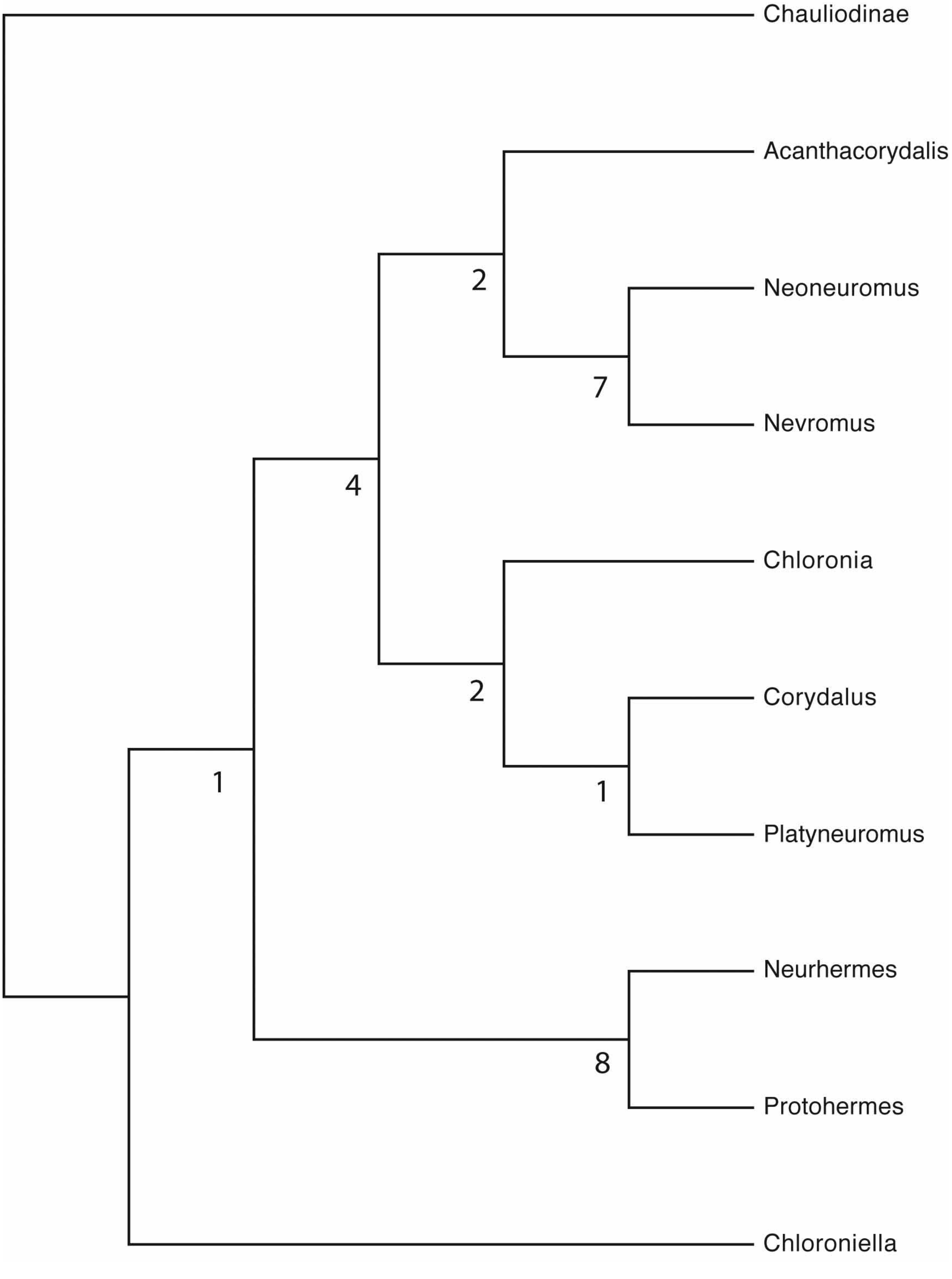

FIGURE 9. Single most parsimonious tree from the updated phylogenetic analysis of Corydalinae genera (length = 137 steps, consistency index = 0.686, retention index = 0.642). Numbers indicate Bremer support values.

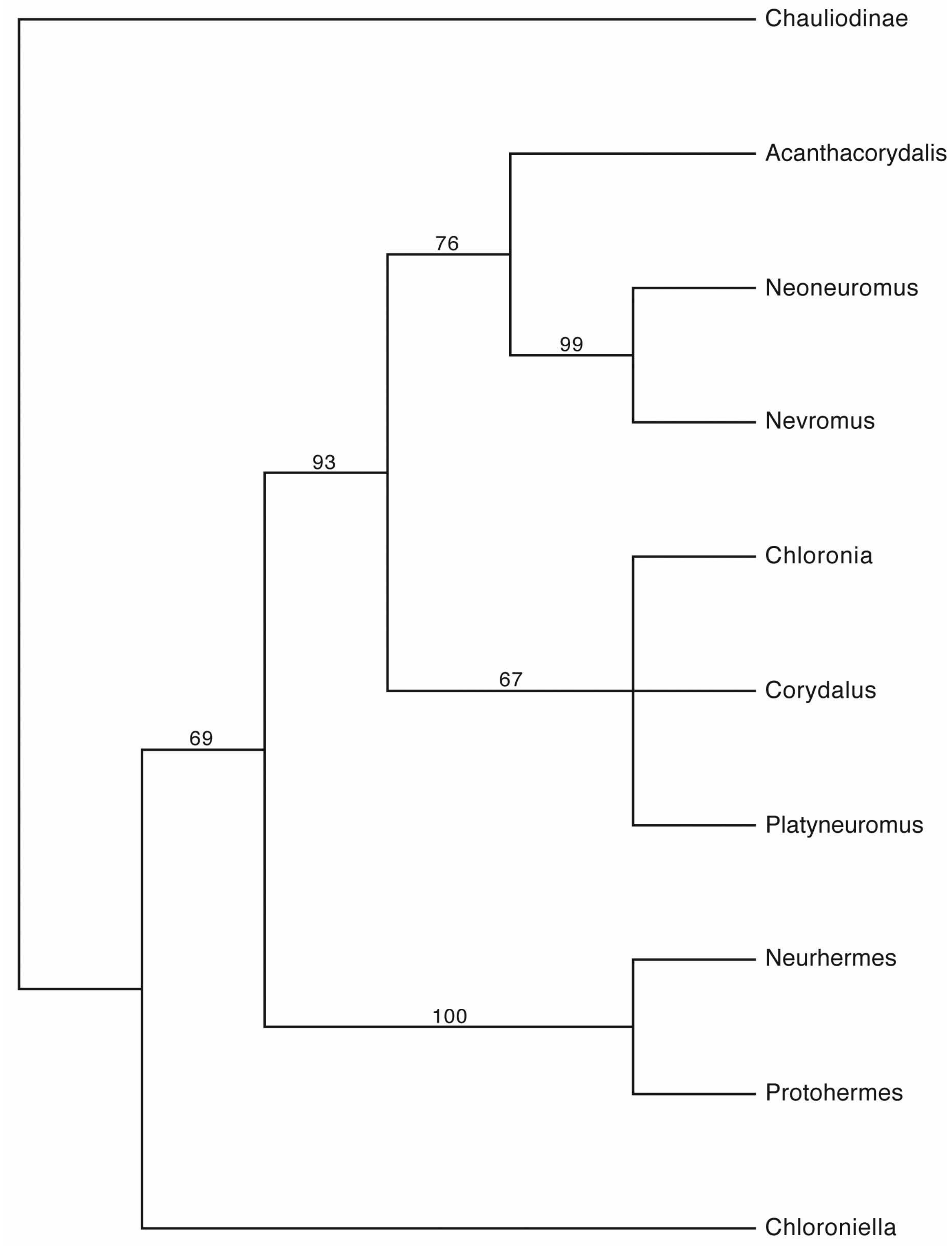

FIGURE 10. Bootstrap 50% majority rule consensus tree (n = 1000 replicates) from the updated phylogenetic analysis of Corydalinae genera.

The lack of the following characters (Appendix 5) in *Chloroniella* contradicts its sister relationship to the major clade *Nevromus* lineage + *Corydalus* lineage (as in Penny's hypothesis; Figs. 1B, 7): flattened head (character 4), complete mandible dentition (character 5), anteclypeus articulated to postclypeus (character 6), arcuate posterior tentorial pits (character 8), inconspicuous stipital setae (character 16), elongate tubular tenth tergites (character 44), apodemes of ninth gonostyli parallel to ninth tergum (character 56), and a posterior internal ingrowth of ovipositor (character 70). Two characters absent in *Chloroniella* exclude it from the group formed by the *Protohermes* + *Nevromus* + *Corydalus* lineages: eight or more Rs branches (character 34), and distinct, articulate ninth gonostyli (character 37). A third character, partly excluding *Chloroniella* from the rest of ingroup taxa is its lack of two M_{3+4} branches (character 28, ci = 0.333). Finally, it is also excluded by the presence of hairlike or spinelike setae on the inner basal side of tenth tergites (character 45, ci = 0.5), which in *Chloroniella*, as in Chauliodinae and a few *Corydalus* species, are conical.

***Corydalus*: phylogenetic update.** Four species from Venezuela, *Corydalus clavijoi*, *C. crossi*, *C. hayashii*, and *C. mayri* (Contreras-Ramos 2002) were studied for characters and incorporated into a pre-existing data matrix (Contreras-Ramos 1998), which consisted of 120 morphological characters. In both analyses, *C. amazonas* was removed, as it is known only from females and missing data increases the number of optimal trees to four (Fig. 11). The original phylogeny consisted of three equally most parsimonious trees (Fig. 4). The updated analysis produced two equally most parsimonious trees (length = 477 steps, consistency index = 0.373, retention index = 0.662, rescaled consistency index = 0.247), with one minor difference between them. In tree 1, *C. holzenthali* is sister to *C. batesii*, whereas in tree 2 *C. holzenthali* is sister to *C. neblinensis* (strict consensus in Fig. 12). Comparing the old and new phylogenies some differences are evident: the *C. arpi* species group was excluded as sister of all species except *C. cephalotes* + *C. hecate*; two major groups, the one including *C. armatus* through *C. primitivus* + *C. australis* + *C. diasi* + *C. tridentatus* species pair (node 54), and the one including *C. armatus* through *C. primitivus* (node 50), both are resolved; and the *C. batesii* species group is conserved, although it contains a polytomy (node 40). The newly incorporated species emerged as follows: *C. hayashii* as sister to *C. arpi* + *C. flinti* and *C. mayri* as sister to *C. ignotus*, both within the *C. arpi* species group (node 65); *C. crossi* as sister to the major group *C. armatus* through *C. nubilus* (node 57); and *C. clavijoi* as sister to *C. tesselatus*.

A bootstrap analysis produced a tree with several polytomies (Fig. 13). Groups with strongest bootstrap values are the *C. cephalotes* species pair (96), the *C. arpi* species group (99), the *C. tesselatus* species pair (87), the *C. tridentatus* species pair (74), the *C. armatus* through *C. tridentatus* species group (79; node 54 in Fig. 12), the *C. armatus* through *C. primitivus* species group (80; node 50 in Fig. 12), and within the latter the *C. luteus* species group (90; node 42 in Fig. 12), *C. bidenticulatus* + *C. magnus* (81), and the *C. armatus* species group (73; node 38 in Fig. 12). The ingroup as a whole had a bootstrap value of 100 (node 68 in Fig. 12). Bremer support (Fig. 12) demonstrated the strongest nodes to be the *C. luteus* species group (3, node 42), the *C. tesselatus* species pair (4), the *C. armatus* through *C. primitivus* species group (4, node 50), the *C. cephalotes* species pair (≥ 5), the *C. arpi* species group (≥ 5, node 65), and the ingroup itself (≥ 5, node 68). Nonetheless, most of the structure of the tree collapses at two extra steps.

Corydalus hayashii is weakly placed as sister to *C. arpi* + *C. flinti* because of several homoplasious character changes (nodes 65 to 63), of which character 87 (ci = 0.375), tenth sternite as a very narrow plate, and character 106 (ci = 0.333), bare to microsetose tenth sternite lobes, offer some support. Similarly, *C. mayri* is sister to *C. ignotus* by several homoplasious character changes (nodes 65 to 64), of which character 26 (ci = 0.400), a triangular labrum, and character 41 (ci = 0.250), seven to eight Rs branches, offer stronger support. About the *C. arpi* group, its position as sister to all *Corydalus* species, except the *C. cephalotes* species pair (node 66), is supported by several character changes (nodes 68 to 66), for instance character 40 (ci = 1.000), last branch of Rs a single vein, and character 98 (ci = 0.5), absence of a sclerotized plate posterior to the tenth sternite. *C. crossi* occupies the sister position to a major clade resting on node 57, supported by several homoplasious character changes (nodes 59 to 58) such as character 4 (ci = 0.250), a concave basal side of the first preapical tooth; character 56 (ci = 0.333), laterally flattened tenth tergites; character 68 (ci = 0.250), anal tubercle with lateral sclerites; character 77 (ci = 0.250), ninth gonostyli and tenth tergites differing in length; and character 78 (ci = 0.333), ninth gonostyli and tenth tergites differing in shape. Finally, *C. clavijoi* is solidly sister to *C. tesselatus*, a relationship supported by several character changes such as character 71 (ci = 0.500), presence of ninth sternum internal ridges; character 72 (ci = 0.667), V-shaped ninth sternum internal ridges; character 111 (ci = 0.500), female eighth sternum well sclerotized; and character 115 (ci = 0.500), female ninth and tenth abdominal segments received by expanded eighth sternum.

Other differences with the previous study are the permanence in the new phylogeny of nodes 52, 51, 49, 48, 47, and 46. Also, the *C. batesii* species group (node 40), is sustained by several homoplasious changes worth mentioning: character 60 (ci = 0.750), a dorsoventrally enlarged apex of tenth tergites, and character 92 (ci = 0.500), a partly subdivided tenth sternite. Node 50 (*C. armatus* through *C. primitivus*; Contreras-Ramos, 1998, fig. 176, node 16) is quite solid in both phylogenies.

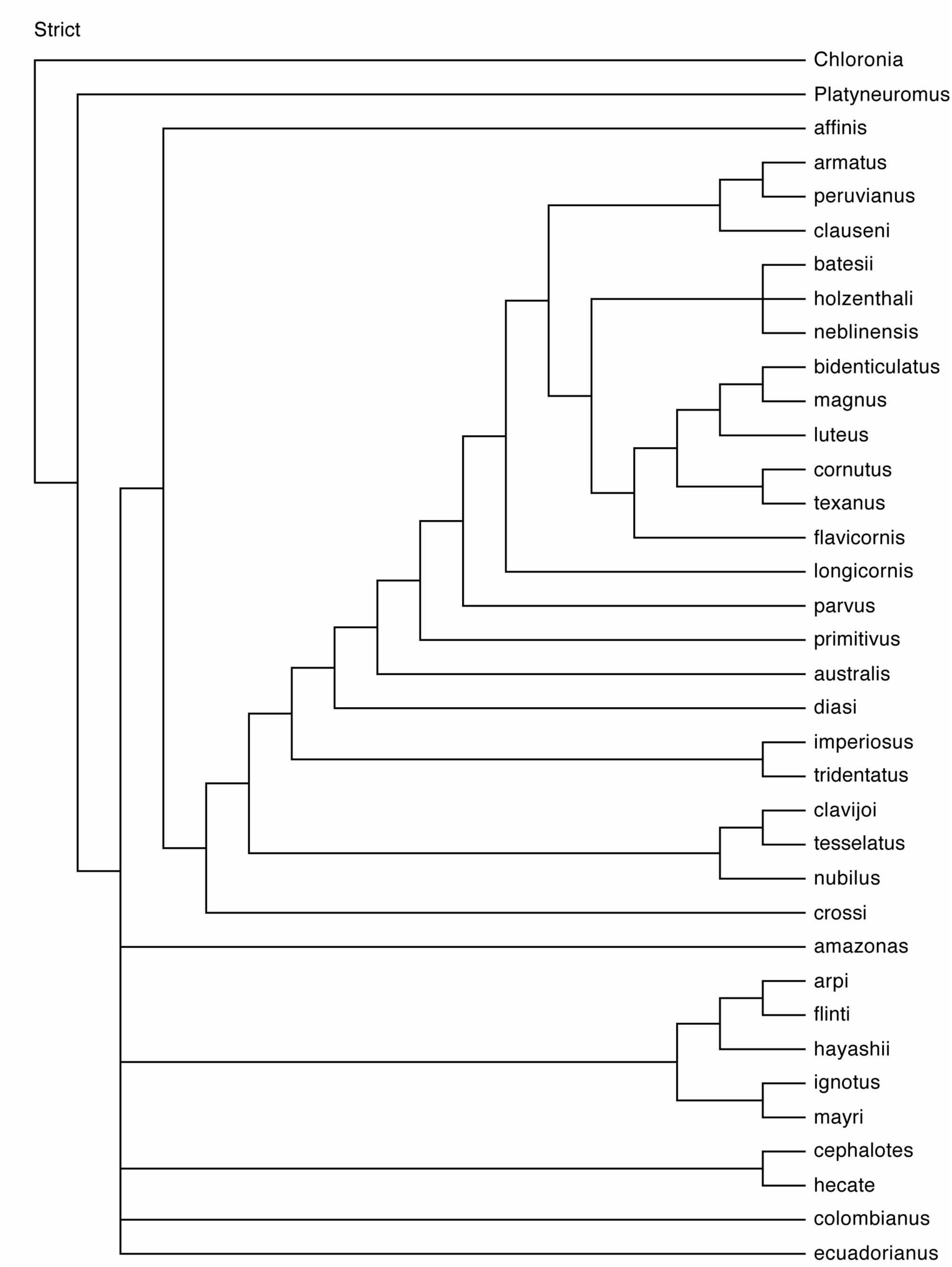

FIGURE 11. Strict consensus of four most parsimonious trees from the updated phylogenetic analysis of *Corydalus* including *C. amazonas*.

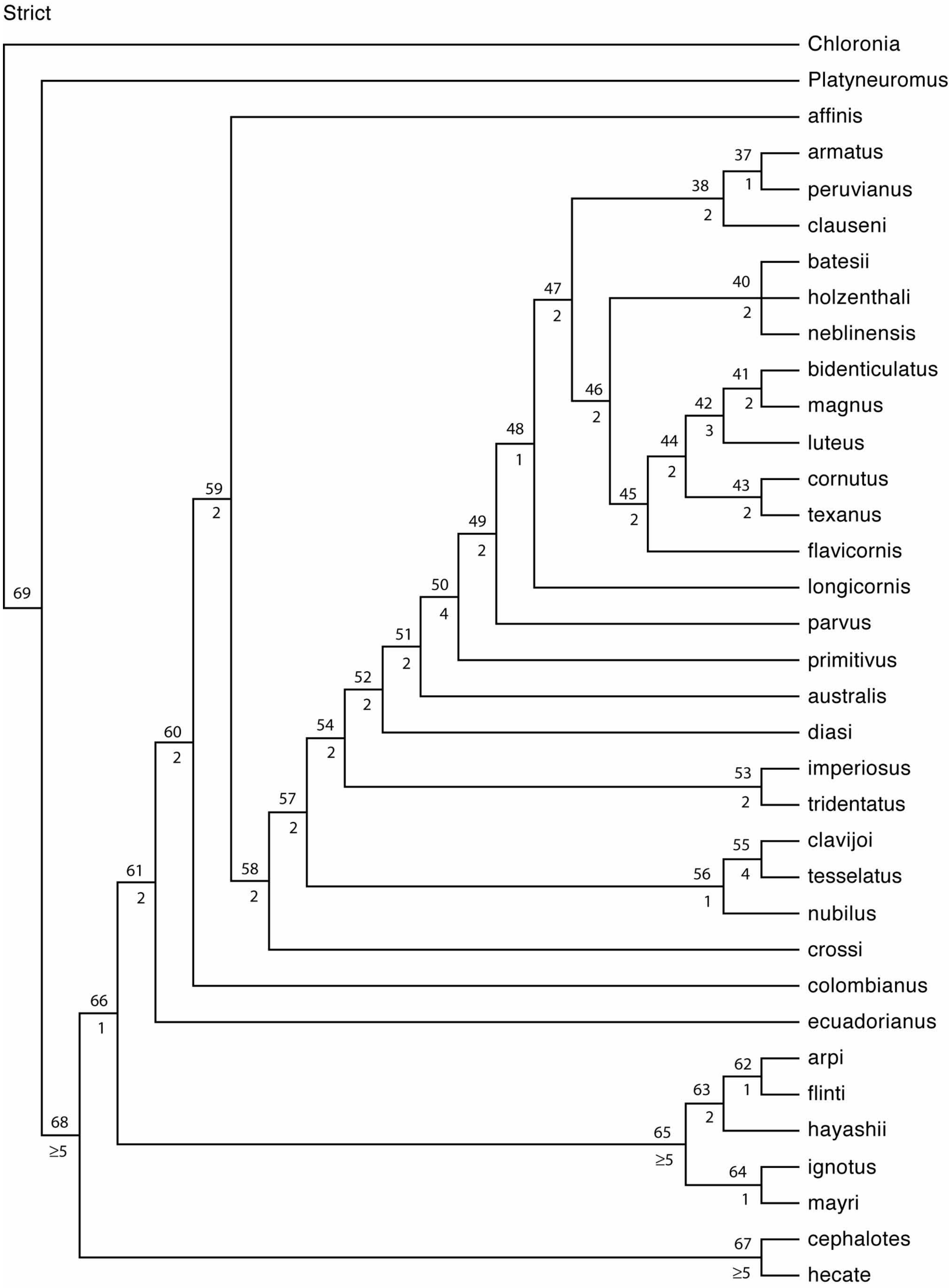

FIGURE 12. Strict consensus of two most parsimonious trees from the updated phylogenetic analysis of *Corydalus*. Numbers at nodes correspond to node numbers, above, and Bremer support values, below.

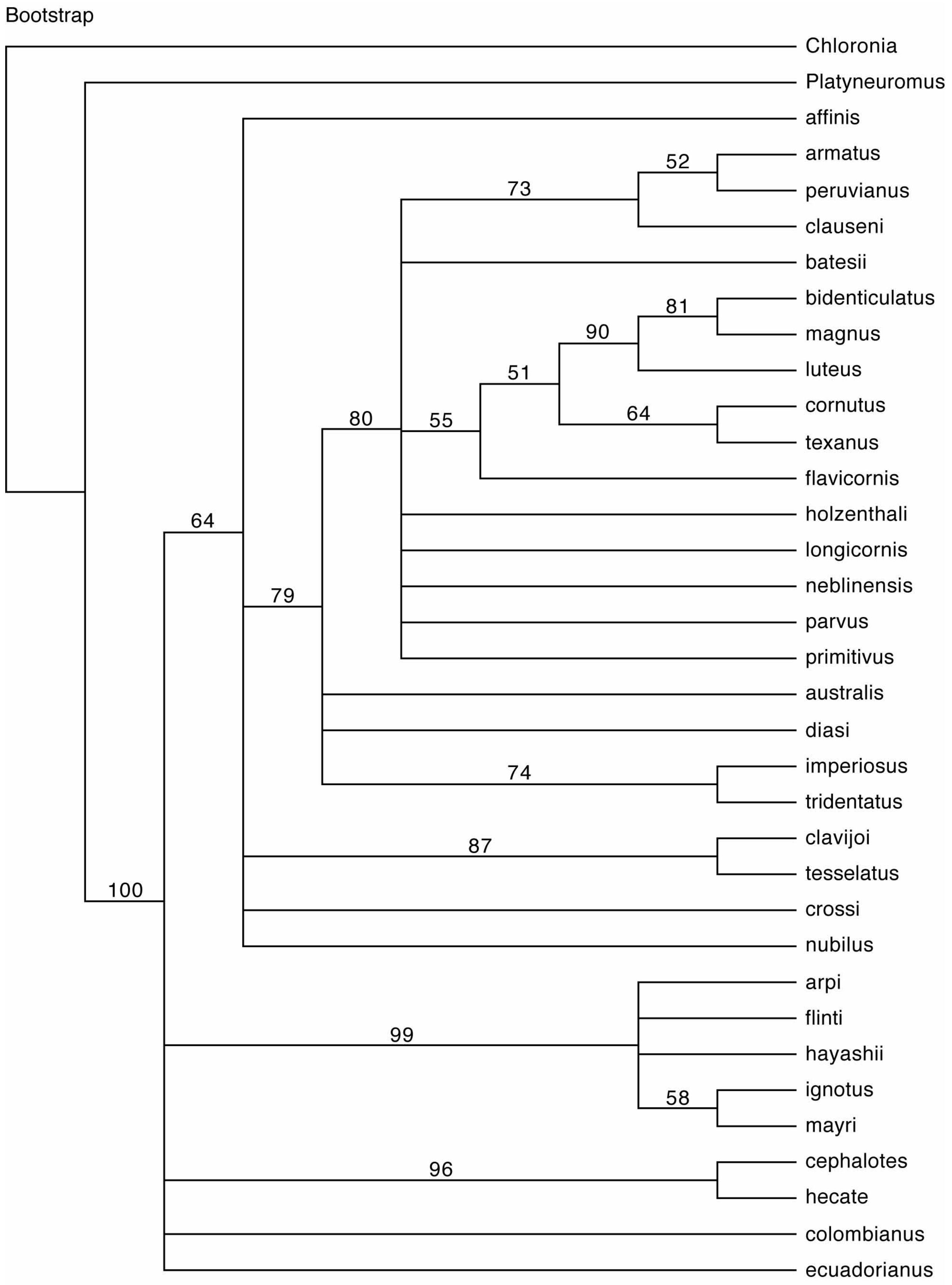

FIGURE 13. Bootstrap 50% majority rule consensus tree (*n* = 1000 replicates) from the updated phylogenetic analysis of *Corydalus*.

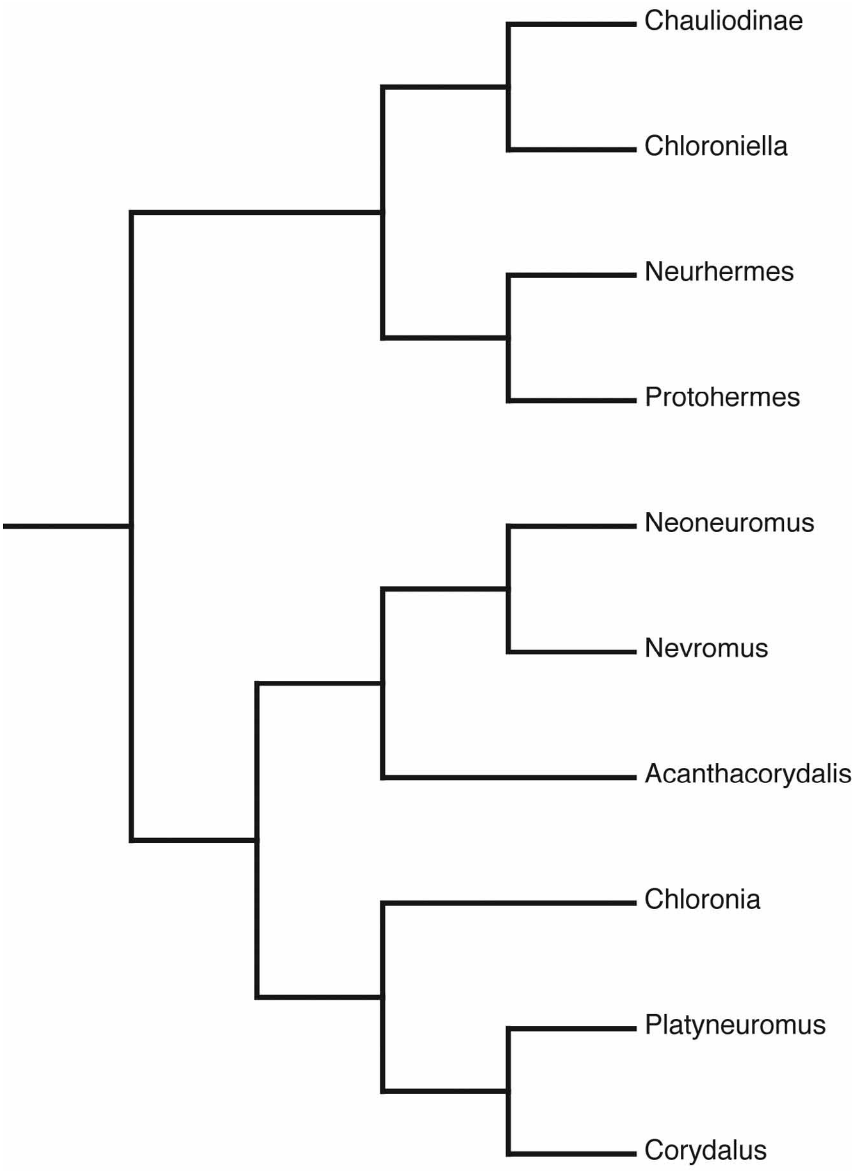

FIGURE 14. Thought-provoking phylogeny of dobsonfly genera and Chauliodinae assuming two main subgroups and *Chloroniella* as sister to fishflies.

Conclusions

Corydalinae. A revised phylogenetic analysis of the World genera of dobsonflies (Fig. 9) questions former hypotheses of the relationships within the group (Figs. 1, 5, 7). In particular, *Acanthacorydalis* is proposed to be a member of the *Nevromus* lineage, sister to *Nevromus* + *Neoneuromus*, and not sister to the *Corydalus* lineage. The analysis also shows that the South African *Chloroniella* is sister to all other dobsonfly genera, and not sister to the *Nevromus* + *Corydalus* lineages. The relationship of the members of the American lineage remains weakly resolved. A classification portraying the aforementioned proposal is presented in Table 3.

Corydalus. Four species from Venezuela have been added to the preexisting data matrix of the genus (Fig. 12). Both, *C. hayashii* and *C. mayri* clearly belong in the monophyletic *C. arpi* species group, although their internal placement in the group is weakly supported; *C. crossi* emerged as sister to the major group sustained in node 57, and *C. clavijoi* came out with certainty as the sister species of *C. tesselatus*. Differences with the former analysis (Fig. 4) are the transfer of the *C. arpi* species group to sister of all *Corydalus* species except the *C. cephalotes* pair, the permanence of the *C. batesii* species group, as well as of nodes 52, 51, 49, 48, 47, and 46, rendering the new phylogeny almost fully resolved. An updated classification of the genus is presented in Table 4.

TABLE 3. Phyletic sequence classification for Corydalinae based on its updated phylogeny (Fig. 9).

- *Chloroniella* Esben-Petersen
- *Protohermes* lineage
  - *Protohermes* Weele
  - *Neurhermes* Navás
- *Nevromus* lineage
  - *Acanthacorydalis* Weele
  - *Nevromus* Rambur
  - *Neoneuromus* Weele
- *Corydalus* lineage
  - *Chloronia* Banks
  - *Platyneuromus* Weele
  - *Corydalus* Latreille

TABLE 4. Phyletic sequence classification for *Corydalus* based on its updated phylogeny (Fig. 14).

- *Corydalus cephalotes* species pair (*C. cephalotes* Rambur + *C. hecate* MacLachlan)
- *Corydalus arpi* species group
  - *Corydalus ignotus* species pair (*C. ignotus* Contreras-R. + *C. mayri* Contreras-R.)
  - Unnamed group 1
    - *Corydalus hayashii* Contreras-R
    - *Corydalus flinti* Contreras-R.
    - *Corydalus arpi* Navás
- *Corydalus ecuadorianus* Banks
- *Corydalus colombianus* Contreras-R.
- *Corydalus affinis* Burmeister
- *Corydalus crossi* Contreras-R.
- *Corydalus nubilus* species group
  - *Corydalus nubilus* Erichson
  - *Corydalus clavijoi* Contreras-R.
  - *Corydalus tesselatus* Stitz
- *Corydalus tridentatus* species pair (*C. imperiosus* Contreras-R. + *C. tridentatus* Stitz)
- *Corydalus diasi* Navás
- *Corydalus australis* Contreras-R.
- *Corydalus primitivus* Weele
- *Corydalus parvus* Stitz
- *Corydalus longicornis* Contreras-R.
- *Corydalus armatus* species group
  - *Corydalus clauseni* Contreras-R.
  - *Corydalus peruvianus* Davis
  - *Corydalus armatus* Hagen
- *Corydalus cornutus* species group
  - *Corydalus flavicornis* Stitz
  - *Corydalus cornutus* species pair (*C. texanus* Banks + *C. cornutus* (L.))
  - *Corydalus luteus* species group
    - *Corydalus luteus* Hagen
    - *Corydalus bidenticulatus* Contreras-R.
    - *Corydalus magnus* Contreras-R.
- *Corydalus batesii* species group
  - *Corydalus holzenthali* Contreras-R., *sedis mutabilis*
  - *Corydalus neblinensis* Contreras-R., *sedis mutabilis*
  - *Corydalus batesii* MacLachlan, *sedis mutabilis*

Final thoughts. I look forward to tests of the hypotheses presented here, especially through molecular characters. A recent morphological study has challenged the monophyly of Corydalidae (Contreras-Ramos 2004a), proposing that Chauliodinae might be closer to Sialidae than to Corydalinae. The main argument is that several fusions and reductions, both in the body and genitalia, if interpreted as apomorphies, would support fishflies and alderflies as sister taxa. Here, admittedly on speculative grounds, if a similar argument is applied to Corydalinae, the possibility exists for a portion of the subfamily to be closer to fishflies (Fig. 14), as two subgroups conform, one with a condition closer to the one assumed as derived for Chauliodinae (*Protohermes* lineage and *Chloroniella*). The distribution of several characters, such as 4, 5, 6, 8, 16, 35, 56, and 70, would not contradict this possibility (Appendix 6, Fig. 9). Moreover, characters 26, 28, 30, 31, 34, 37, and 45, may be interpreted as derived, supporting a sister relationship between *Chloroniella* and fishflies. In other words, if the assumption of a monophyletic Corydalinae is put to rest for a moment, *Chloroniella* might best be classified as a fishfly rather than a dobsonfly. A molecular analysis could help address these questions.

Acknowledgments

I would like to thank the curators that supported the previous *Corydalus* revision, from which this paper is derived. Thanks also to José Clavijo and Marco Gaiani (Universidad Central de Venezuela, Maracay), as well as G. Onore (Pontificia Universidad Católica del Ecuador), for loans which contained several interesting specimens. Financial support from the Mini-PEET Program (2003) of the Society of Systematic Biologists, as well as general support from my home institution (Tila-María Pérez, Fernando Cervantes, Patricia Escalante, Noemí Chávez, and Georgina Ortega) are gratefully acknowledged. Special thanks to Ollie Flint (National Museum of Natural History) for his hospitality during a visit to the NMNH in 2009. Shaun Winterton (California Department of Food & Agriculture), David Bowles (Missouri State University), and Norm Penny (California Academy of Sciences), critically revised an earlier draft of this paper, but the final version is my responsibility. Finally, I express my gratitude to Phil Clausen (University of Minnesota), the late Earle Cross, Ollie Flint, Steve Harris (Clarion University), the late Marek Kalicewski, Rick Mayden (St. Louis University), Norm Penny, Milton Ward (University of Alabama), and especially to my former Ph.D. advisor, Ralph Holzenthal (University of Minnesota), for all their teaching and encouragement.

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APPENDIX 1. Characters used for the phylogenetic analysis of Corydalinae by Glorioso (1981). Characters are from Glorioso's table 1 and were recoded as 0 for the plesiomorphic state and 1 or 2 for the apomorphic ones. Character number and character states correspond with those in Appendix 2.

Characters of the head

1. Gular setation: (0) conspicuously setose; (1) microsetose.
2. Postocular ridge: (0) absent; (1) present.
3. Postocular plane: (0) absent; (1) present.
4. Head shape: (0) robust; (1) flattened.
5. Postocular flange: (0) absent; (1) present.
6. Postocular spine: (0) feebly developed; (1) moderately to well developed.
7. Posterior tentorial pits: (0) linear; (1) arcuate.
8. Cranial disk: (0) without spines; (1) with spines.
9. Antennae: (0) feebly subserrate; (1) filiform.
10. Clypeal margin: (0) entire; (1) incised medially.
11. Male mandibles: (0) not enlarged; (1) enlarged.
12. Female mandibles: (0) Three-fourths head length or shorter; (1) length of head.

13. Labrum shape: (0) triangular; (1) ovoid; (2) broadly truncate.
14. Labral position: (0) over mandibles; (1) between mandibles.
15. Labral anterior margin: (0) sparsely setose; (1) fimbriate.
16. Maxilla shape: (0) short and broad; (1) relatively elongate.
17. Lacinia apex: (0) with three elongate setae; (1) without elongate setae.
18. Stipital setae: (0) conspicuous; (1) inconspicuous.
19. Galeal setae: (0) flattened, lanceolate; (1) bristlelike.
20. Galeal sensory peg: (0) well developed; (1) poorly developed; (2) absent.
21. Maxillary palp: (0) five-segmented; (1) four-segmented.
22. Maxillary palp apex: (0) conical; (1) broadly rounded.
23. Maxillary palp setae: (0) long; (1) short.
24. Maxillary palp sensory areas: (0) one at apex; (1) two at apex.
25. Labial palp: (0) four-segmented; (1) three segmented.
26. Labial palp sensory areas: (0) one at apex; (1) two at apex.

Characters of the thorax

27. Last branch of radial sector: (0) bifurcate; (1) not bifurcate.
28. M_{1+2} branches: (0) two; (1) four or more.
29. M_{3+4} branches: (0) two; (1) one.
30. 1A branches: (0) two; (1) three.
31. R_1-Rs crossveins: (0) three; (1) four or more.
32. Medial crossveins: (0) two; (1) three or more.
33. M-Cu crossveins: (0) three; (1) four; (2) six or more.
34. Cubital accessory crossveins: (0) absent; (1) present.
35. Costal crossveins: (0) vertical or oblique; (1) reticulate.

Male terminalia characters

36. Ninth sternum: (0) hind margin entire or projecting; (1) hind margin widely and deeply cleft.
37. Ninth sternum: (0) more or less quadrate; (1) attenuate.
38. Ninth sternum: (0) without median projection; (1) with median projection.
39. Ninth sternum: (0) without postero-lateral lobes; (1) with postero-lateral lobes.
40. Ninth sternum: (0) without setiferous lateral protuberances; (1) with setiferous lateral protuberances.
41. Ninth sternum: (0) with normal setae; (1) with short, stout setae; (2) with fine setae.
42. Ninth sternum: (0) not sclerotized dorsally; (1) sclerotized dorsally.
43. Ninth sternum: (0) without internal ridges; (1) with internal ridges.
44. Ninth sternum: (0) Not locking with tenth sternite; (1) locking with tenth sternite.
45. Ninth tergum: (0) more or less quadrate; (1) short, with broad median incision.
46. Ninth tergum: (0) with dorso-lateral incisions; without dorso-lateral incisions.
47. Ninth tergal internal inflection: (0) without median fossa; (1) with median fossa.
48. Ninth tergal internal inflection: (0) arched; (1) inverted V-shaped.
49. Membrane between ninth and tenth sternites: (0) thin; (1) thickened, bilobate; (2) thickened, regularly convoluted.
50. Genital papillae: (0) present; (1) absent.
51. Tenth gonocoxites: (0) without median projection; (1) with median projection.
52. Tenth gonocoxites: (0) antero-lateral corner without acute projection; (1) anterolateral corner with acute projection.
53. Tenth gonostylus: (0) digitiform; (1) short, broad; (2) papilliform.
54. Ninth gonostylus: (0) unguiform; (1) clavate.
55. Ninth gonostylus: (0) relatively short; (1) long, bent.
56. Ninth gonostylus: (0) sparsely setose; (1) densely setose.
57. Ninth gonostylus apodeme: (0) parallels ninth tergum; (1) directed medially.
58. Tenth tergites: (0) short; (1) long, thin.
59. Tenth tergites: (0) not biramous; (1) biramous.
60. Eleventh tergum: (0) present; (1) absent.

Female terminalia characters

61. Lateral sclerite of ovipositor: (0) well sclerotized; (1) weakly sclerotized.
62. Gonostylus: (0) articulated with gonocoxite; (1) fused with gonocoxite.
63. Sternal pouch: (0) absent; (1) present.
64. Sclerites between eighth sternum and gonopore: (0) absent; (1) present.

65. Bursa copulatrix: (0) not saclike; (1) saclike.
66. Number of spermathecae: (0) two; (1) one.
67. Spermathecal duct: (0) continuous with bursa; (1) separate from bursa, T-shaped.
68. AccesoryAccessory glands: (0) present; (1) absent.
69. AccesoryAccessory glands: (0) short; (1) long.
70. Accessory glands: (0) sigmoid; (1) linear.

APPENDIX 2. Input data matrix for Glorioso's (1981) phylogenetic analysis of Corydalinae. The matrix was extracted from the cladogram (Glorioso's Figure 53) according to its mapped characters and character states. Character states in the outgroup were not specified and so were filled by inference from specimens or from additional sources (e.g., Contreras-Ramos 1998) when necessary.

	Character						
	1	2	3	4	5	6	7
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Chauliodinae	0000000000	0000000000	1000101010	0000000000	0000010001	0000010001	0000010100
Acanthacorydalis	1111011111	1101011110	0000000000	1121100011	1000010100	0001010001	0100101000
Chloronia	1111011011	0020010110	0101010010	0010000001	2000010111	0121010101	1110101100
Corydalus	1111011011	0001011110	1101111010	0110000000	0000010121	0121010001	0110101100
Neoneuromus	1111011011	0010010111	0000000100	1111001000	0010001001	1000000000	0100000001
Neurhermes	1110000000	0000000002	0001010101	1000000100	0100110000	0000111011	0001111010
Nevromus	1111011011	0010111111	0000000100	1111000000	0011011000	0010000001	0100010001
Platyneuromus	1111111011	0020010110	0101010000	0010000000	0000010110	0001010001	0110101100
Protohermes	1110000000	0000000000	0011010101	1000010000	0000010000	0000001001	0000111010

APPENDIX 3. Characters used for the phylogenetic analysis of Corydalinae by Penny (1993). Characters are from Penny's table 1 and were recoded as 0 for the plesiomorphic state and 1 or 2 for the apomorphic ones. Character number and character states correspond with those in Appendix 4.

Characters of the head

1. Head shape: (0) robust; (1) flattened.
2. Postocular flange: (0) absent; (1) present.
3. Postocular spine: (0) feebly developed; (1) moderately to well developed.
4. Posterior tentorial pits: (0) linear; (1) arcuate.
5. Cranial disk: (0) without spines; (1) with spines.
6. Antennae: (0) feebly subserrate; (1) filiform.
7. Clypeal margin: (0) entire; (1) incised medially.
8. Male mandibles: (0) not enlarged; (1) enlarged.
9. Female mandibles: (0) Three-fourths head length or shorter; (1) length of head.
10. Labrum shape: (0) triangular; (1) ovoid; (2) broadly truncate.
11. Labral position: (0) over mandibles; (1) between mandibles.
12. Labral anterior margin: (0) sparsely setose; (1) fimbriate.
13. Maxilla shape: (0) short and broad; (1) relatively elongate.
14. Lacinia apex: (0) with three elongate setae; (1) without elongate setae.
15. Galeal setae: (0) flattened, lanceolate; (1) bristlelike.
16. Galeal sensory peg: (0) well developed; (1) poorly developed; (2) absent.
17. Maxillary palp: (0) five-segmented; (1) four-segmented.
18. Maxillary palp apex: (0) conical; (1) broadly rounded.
19. Maxillary palp setae: (0) long; (1) short.
20. Maxillary palp sensory areas: (0) one at apex; (1) two at apex.
21. Labial palp: (0) four-segmented; (1) three segmented.
22. Labial palp sensory areas: (0) one at apex; (1) two at apex.

Characters of the thorax

23. Last branch of radial sector: (0) bifurcate; (1) not bifurcate.
24. M_{1+2} branches: (0) two; (1) four or more.
25. M_{3+4} branches: (0) two; (1) one.
26. 1A branches: (0) two; (1) three.
27. R_1-Rs crossveins: (0) three; (1) four or more.
28. Medial crossveins: (0) two; (1) three or more.
29. M-Cu crossveins: (0) three; (1) four; (2) six or more.
30. Cubital accesoryAccessory crossveins: (0) absent; (1) present.
31. Costal crossveins: (0) vertical or oblique; (1) reticulate.

Male terminalia characters

32. Ninth sternum: (0) hind margin not notched; (1) hind margin notched.
33. Ninth sternum: (0) more or less quadrate; (1) attenuate.
34. Ninth sternum: (0) without median projection; (1) with median projection.
35. Ninth sternum: (0) without posterolateral lobes; (1) with posterolateral lobes.
36. Ninth sternum: (0) without setiferous lateral protuberances; (1) with setiferous lateral protuberances.
37. Ninth sternum: (0) with normal setae; (1) with short, stout setae; (2) with fine setae.
38. Ninth sternum: (0) not sclerotized dorsally; (1) sclerotized dorsally.
39. Ninth sternum: (0) without internal ridges; (1) with internal ridges.
40. Ninth sternum: (0) Not locking with tenth sternite; (1) locking with tenth sternite.
41. Ninth tergum: (0) more or less quadrate; (1) short, with broad median incision.
42. Ninth tergum: (0) with dorso-lateral incisions; without dorso-lateral incisions.
43. Ninth tergal internal inflection: (0) without median fossa; (1) with median fossa.
44. Ninth tergal internal inflection: (0) arched; (1) inverted V-shaped.
45. Membrane between ninth and tenth sternites: (0) thin; (1) thickened, bilobate; (2) thickened, regularly convoluted.
46. Genital papillae: (0) present; (1) absent.
47. Genital papillae medially: (0) separated; (1) fused.
48. Tenth gonocoxites: (0) without median projection; (1) with median projection.
49. Tenth gonocoxites: (0) antero-lateral corner without acute projection; (1) anterolateral corner with acute projection.
50. Tenth gonocoxites: (0) medially joined; (1) medially separated.
51. Tenth gonostylus: (0) digitiform; (1) short, broad; (2) papilliform.
52. Ninth gonostylus: (0) unguiform; (1) clavate.
53. Ninth gonostylus: (0) relatively short; (1) long, bent.
54. Ninth gonostylus: (0) sparsely setose; (1) densely setose.
55. Ninth gonostylus apodeme: (0) parallels ninth tergum; (1) directed medially.
56. Tenth tergites: (0) short; (1) long, thin.
57. Tenth tergites: (0) without sensory field on apical surface; (1) with sensory field on apical surface.
58. Tenth tergites: (0) rounded; (1) laterally compressed.
59. Tenth tergites: (0) uniramous; (1) biramous.
60. Tenth tergites: (0) not bearing basal tuft of hairs; (1) bearing basal tuft of hairs.
61. Eleventh tergum: (0) present; (1) absent.

Female terminalia characters

62. Lateral sclerite of ovipositor: (0) well sclerotized; (1) weakly sclerotized.
63. Gonostylus: (0) articulated with gonocoxite; (1) fused with gonocoxite.
64. Sternal pouch: (0) absent; (1) present.
65. SleritesSclerites between eighth sternum and gonopore: (0) absent; (1) present.
66. Bursa copulatrix: (0) not saclike; (1) saclike.
67. Number of spermathecae: (0) two; (1) one.
68. Spermathecal duct: (0) continuous with bursa; (1) separate from bursa, T-shaped.
69. AccesoryAccessory glands: (0) present; (1) absent.
70. AccesoryAccessory glands: (0) short; (1) long.
71. AccesoryAccessory glands: (0) sigmoid; (1) linear.

APPENDIX 4. Input data matrix for Penny's (1993) phylogenetic analysis of Corydalinae. The matrix was extracted from the cladogram (Penny's cladogram 1) according to its mapped characters and character states. Character states in the outgroup were not specified and so were filled by inference from specimens or from additional sources (e.g., Contreras-Ramos 1998) when necessary.

	characters							
	1	2	3	4	5	6	7	
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Chauliodinae	0000000000	0100000000	1010100000	0000000000	0100010000	0001100000	1000001010	0
Acanthacorydalis	1011111110	0011100000	0000001121	1000111000	0101000000	0101000000	1010010100	0
Chloronia	1011011002	0010100101	0100100010	0000012000	0101110010	2101010000	1111010110	0
Chloroniella	1011010000	0010000000	0010100010	0100100000	0101001001	1000101001	1010001000	0
Corydalus	1011011000	1011101101	1110100110	0000000000	010 1210010	2101000000	1011010110	0
Neoneuromus	1011011001	0010110000	0001001111	0010000010	0010010100	0000000000	0010000000	1
Neurhermes	0000000000	0000020001	0101011000	0001000100	1100000000	0011100010	1000111101	0
Nevromus	1011011001	1111110000	0001001111	0000000011	0110000000	1000000100	1010001000	1
Platyneuromus	1111011002	0010100101	0100000010	0000000000	0101100000	0101000000	1011010110	0
Protohermes	0000000000	0000000011	0101011000	0100000000	0100000000	0000101001	1000011101	0

APPENDIX 5. Characters used for the updated phylogenetic analysis of Corydalinae (modified from Contreras-Ramos 1998). Characters are coded as 0 for the plesiomorphic state and 1, 2, or 3 for the apomorphic ones. Character number and character states correspond with those in Appendix 6. Explanation of characters below may be complemented with Contreras-Ramos (1998, Phylogenetic Anaylyisis Phase I: Test of Monophyly, p. 187).

Characters of the head

1. Gular setation: (0) conspicuously setose; (1) microsetose. This character, along with characters 2, 3, 22, 36, 64, 66, and 67, are invariable within ingroup taxa, supporting the monophyly of Corydalinae (but see "phylogeny of the Corydalinae" above).
2. Postocular ridge: (0) absent; (1) present.
3. Postocular plane: (0) absent; (1) present.
4. Head shape: (0) robust; (1) flattened. Besides *Protohermes* and *Neurhermes*, the plesiomorphic state was assigned to *Chloroniella* (Penny's analysis assigned the apomorphic condition to the latter).
5. Mandible dentition: (0) reduced with apical tooth oblique; (1) complete with apical tooth slightly bent.
6. Anteclypeus: (0) fused to postclypeus; (1) articulated to postclypeus.
7. Postocular spine: (0) absent; (1) feebly to moderately developed; (2) well developed.
8. Posterior tentorial pits: (0) linear; (1) arcuate. The posterior tentorial pits in *Chloroniella* were considered linear (state 0), differing from Penny's analysis in which they were assigned the apomorphic state.
9. Sexual dimorphism: (0) absent; (1) present. Sexual dimorphism might be interpreted as a derived condition present in *Acanthacorydalis*, *Platyneuromus*, and *Corydalus*. In *Platyneuromus*, postocular flanges of males show allometric variation as a function of individual size and tend to be wider than in females. Although both, *C. cephalotes* + *C. hecate*, sister to all other ingroup species lack sexual dimorphism, intermittently other species sister to large species groups (e.g., *C. colombianus*), and a member of a group mostly lacking dimporphism (i.e., *C. flinti*), have males with elongate mandibles.
10. Setose area on venter of mandibles: (0) slightly to well developed; (1) apparently absent. This is a rather homplasious character with its apomorphic state appearing independently derived on three occasions (*Acanthacorydalis*, *Chloroniella*, *Corydalus*).
11. Labrum shape: (0) ovoid; (1) triangular; (2) broadly truncate. In Corydalinae, the primitive condition appears to be a triangular labrum (state 1), but considerable homoplasy in this character indicates an independent origin for an ovoid labrum (Chauliodinae, *Neoneuromus*, *Nevromus*; state 0), as well as for a broadly truncate labrum (*Chloronia*, *Platyneuromus*; state 2) and a regression to a triangular labrum in *Corydalus*.
12. Labral position: (0) over mandibles; (1) between mandibles. A homoplasious character with the apomorphic condition in *Acanthacorydalis* and *Corydalus*.
13. Setation of labral anterior margin: (0) fimbriate; (1) sparsely setose. The labrum is sparsely setose in all dobsonflies, with the exception of *Nevromus* (not *Neoneuromus*, by mistake in Contreras-Ramos 1998), which has the condition present in the outgroup.

14. Maxillae shape: (0) short and broad; (1) relatively elongate. The derived state is present in all dobsonflies except *Neurhermes* and *Protohermes*.
15. Lacinia apex: (0) with one to three distinct setae; (1) without elongate setae. This is a homoplasious character, its apomorphic condition occurring in *Acanthacorydalis*, *Neoneuromus*, and *Platyneuromus*.
16. Stipital setae: (0) conspicuous; (1) inconspicuous. Reduced stipital setae (state 1) occur in the *Nevromus* and *Corydalus* lineages.
17. Shape of galeal setae: (0) flattened, lanceolate; (1) bristlelike. The apomorphic condition is present in the *Nevromus* and *Corydalus* lineages, as well as in *Chloroniella*.
18. Galeal sensory peg: (0) well developed; (1) poorly developed; (2) apparently absent.
19. Maxillary palp: (0) 5-segmented; (1) 4-segmented. This is a defining apomorphy for *Corydalus*, independently derived from the condition in Chauliodinae.
20. Maxillary palp apex: (0) conical; (1) broadly rounded. This is a defining synapomorphy for the American dobsonflies.
21. Sensory areas at apex of maxillary palp: (0) one; (1) two. Within all dobsonflies, the *Nevromus* lineage shows a regression to one sensory area (state 0).
22. Relative length of palpifer: (0) long; (1) short. The apomorphic state is present in all dobsonflies.
23. Labial palp: (0) 4-segmented; (1) 3-segmented. As character 19, labial palp segmentation undergoes an independent reduction in *Corydalus* and the outgroup.
24. Sensory areas at apex of labial palp: (0) one; (1) two. As character 21, within all dobsonflies the *Nevromus* lineage is supported by a regression to one sensory area (state 0).
25. Apical sensory area of labial palp: (0) unmodified, circular; (1) elongate, deforming palp segment. The most apical sensory area of the labial palps has become elongate in *Platyneuromus* and most *Corydalus* species. Although in a few *Corydalus* species (e.g., *C. arpi*, *C. ignotus*) the area retainsed the primitive condition, in *C. cephalotes* + *C. hecate* the area is narrowly elongate without deforming the palpal segment, yet being modified.

Characters of the Wings

26. Last branch of Rs: (0) bifurcate; (1) single vein. The apomorphic condition is present in an independent fashion in *Corydalus*, *Chloroniella*, and fishflies. A bifurcate last branch of Rs is the generalized condition, as it is present in most ingroup taxa and even in a farther outgroup, alderflies.
27. M_{1+2} branches: (0) one; (1) two to three; (2) four or more. There appears to be a trend in dobsonflies for a reduction in M_{1+2} branches (state 1), however this is not without some homoplasy, in particular as the out group has a strong reduction to only one branch (state 0).
28. M_{3+4} branches: (0) one; (1) two. This is a rather homoplasious character. An evolutionary scenario is for state 1 to be the generalized condition with an independent reduction of M_{3+4} branches in *Chloronia*, *Corydalus*, *Chloroniella*, and the outgroup.
29. 1A branches: (0) two; (1) three. This character supports the sister group relationship between *Neurhermes* and *Protohermes*.
30. R_1-Rs crossveins: (0) two to three; (1) four or more. Although homoplasious, this character appears to depict a general trend for reduction in the number of R_1-Rs crossveins, as it occurs in the American genera, but with an independent reduction in *Chloroniella* and the outgroup.
31. Medial crossveins: (0) two; (1) three or more. This is a homoplasious character which offers partial support for grouping the Old World taxa, except *Chloroniella*.
32. M-Cu crossveins: (0) three; (1) typically four; (2) five or more.
33. Cubital accessory crossveins: (0) absent; (1) present. Crossveins uniting the branches of Cu_1 is a synapomorphy for *Neoneuromus*, *Nevromus*, and *Acanthacorydalis*. The latter was codified as 0 by mistake in Contreras-Ramos (1998).
34. Rs branches: (0) five to seven; (1) eight or more. This character supports the grouping of all dobsonfly genera except *Chloroniella*, so it contributes to relegate this genus as sister to all other ingroup taxa.
35. Cu_1 branches: (0) two to three; (1) four or more.

Male Terminalia Characters

36. Cerci: (0) fused to base of tenth tergites; (1) discretely separated from tenth tergites.
37. Ninth gonostyli: (0) reduced to distinct but not articulate; (1) distinct, articulate. In fishflies the ninth gonostyli are reduced, for instance appearing as setose lobes attached to the tenth sternite. In *Chloroniella* the ninth gonostyli are fused to the ninth tergum, and so although distinct, this condition is coded within state 0 under the premise that the gonostyli show a degree of reduction. This character also relegates *Chloroniella* as the most basal ingroup taxon.
38. Ninth tergum shape: (0) more or less subquadrate; (1) short and broad; (2) subquadrate elongate; (3) subtriangular.
39. Wide bands of microsetae on ninth tergum: (0) absent; (1) present. Wide longitudinal bands of microsetae are present in nearly all *Corydalus* species. They support a sister group relationship between *Corydalus* and *Platyneuromus*.
40. Ninth gonostyli position: (0) below base of tenth tergites; (1) posterior to base of tenth tergites. In the *Nevromus* lineage ninth gonostyli have migrated posteriorly by a posterolateral enlargement of the ninth tergum.

41. Posterior margin of ninth tergum: (0) nearly straight to moderately concave; (1) deeply and broadly concave. A conspicuously concave ninth tergum supports a sister group relationship between *Neurhermes* and *Protohermes*.
42. External pregenital sacs: (0) absent; (1) present.
43. Ninth tergal internal inflection: (0) merged with ninth tergum or slightly distinct, typically arched; (1) distinct, arched, with median fossa; (2) distinct, inverted v-shaped, without median fossa. This character is somewhat homoplasious. State 0 is present in the outgroup and the basal *Protohermes* lineage. State 1 supports a sister group relationship between *Neoneuromus* and *Nevromus*.
44. Tenth tergites shape: (0) broad and short; (1) short, developed dorsally and ventrally; (2) elongate tubular. Short and broad tenth tergites (state 0) are present in the outgroup and the basal *Chloroniella* and *Protohermes*. A modification of a short tergite (state 1) is autapomorphic for *Neurhermes*. Tubular, variously modified tenth tergites (state 2), are generalized within the *Nevromus* and *Corydalus* lineages.
45. Setation on inner basal side of tenth tergites: (0) hairlike or spinelike; (1) short conical.
46. Distance of tenth tergites to anal tubercle: (0) close; (1) distant. Typical tenth tergites close or adjacent to the anal tubercle are present in several *Corydalus* species. However, in most American dobsonflies the tergites have separated from the anal tubercle, with the intervening space often sclerotized, and this represents a synapomorphy for the *Corydalus* lineage.
47. Genital cavity: (0) concealed (covered) to slightly exposed; (1) broadly exposed caudally. A dorsoventrally wide genital cavity, broadly exposed caudally, is a synapomorphy for the *Protohermes* lineage.
48. Ninth sternum shape: (0) flaplike, reduced; (1) subquadrate; (2) broadly convex, sclerotized; (3) attenuate. The generalized condition appears to be a subquadrate ninth sternum (state 1), somewhat reduced in the outgroup (state 0), modified into a convex and sclerotized cover in the *Protohermes* lineage (state 2), and with an autapomorphous attenuate shape in *Neoneuromus* (state 3).
49. Ninth sternum setation: (0) moderately thick tapering setae (normal); (1) short, stout setae; (2) fine, hairlike setae.
50. Ninth sternum internal ridges: (0) absent; (1) present. Sclerotized internal ridges on the ninth sternum support a sister group relationship between *Neoneuromus* and *Nevromus*. These lines may represent ancestral lines of fusion in the formation of the ninth sternum, perhaps related to an appendicular origin as a paired structure. A few *Corydalus* species display a convergent presence of similar structures.
51. Membrane between ninth and tenth sternites: (0) smooth to wrinkled; (1) bilobate; (2) convoluted.
52. Sclerotization of membrane between ninth and tenth sternites: (0) unsclerotized; (1) lightly to well sclerotized. The apomorphic condition is present in *Acanthacorydalis*, as well as in part supporting a sister group relationship between *Corydalus* and *Platyneuromus*.
53. Genital papillae: (0) absent; (1) present. These eversible sacs (lobes) adjacent anteriorly to the tenth sternite have a somewhat homoplasious distribution. They are conspicuous and somewhat thickened in *Protohermes* and *Neurhermes*, and less developed and semimembranous in *Chloroniella* and *Platyneuromus*. Unlike Glorioso (1981), I could not observe these papillae in *Acanthacorydalis* (but material was scarce), nor in *Nevromus*.
54. Ninth gonostyli shape: (0) reduced; (1) narrowly elongate unguiform; (2) subclavate unguiform; (3) elongate tubular to subclavate.
55. Setation of ninth gonostyli: (0) sparsely setose; (1) densely setose. The apomorphic condition offers partial support for the monophyly of the *Corydalus* lineage.
56. Apodemes of ninth gonostyli: (0) directed medially; (1) parallel to ninth tergum. The apomorphic condition is a synapomorphy for the major group formed by the *Nevromus* and *Corydalus* lineages.
57. Tenth sternite shape: (0) fused plate (thick bar) strongly produced caudally; (1) narrow band, nearly flat to slightly convex; (2) moderately convex band, strongly produced caudally. A state for a moderately to strongly convex band, more or less developed caudally as a plate was eliminated, as this state occurs in higher *Corydalus* and state 1 was assigned instead, as the latter occurs in several basal species of that genus. The generalized condition in the ingroup is state 1, whereas state 2 supports a sister group relationship between *Nevromus* and *Neoneuromus*.
58. Tenth sternite posterolateral corners: (0) widely open; (1) with shallow concavity. A state for moderate to deep conical concavities was eliminated from the test of monophyly data set, as it was not considered representative for *Corydalus*.
59. Tenth sternite lobe shape: (0) reduced to absent; (1) digitiform; (2) fused to tenth sternite; (3) papilliform.

Female Terminalia Characters

60. Gonostylus: (0) indistinct; (1) distinct, semiarticulate (sclerotized); (2) distinct, fused to gonocoxite (unsclerotized). Semiarticulate, sclerotized gonostyli (state 1) support the monophyly of the *Protohermes* lineage.
61. Sternal pouch: (0) absent; (1) well developed; (2) slightly developed or reduced. A sternal pouch between segments six and seven is well developed (thickened, it cannot be unfolded by distending intersegmental juncture) in *Chloronia*, *Platyneuromus* and several basal *Corydalus* (state 1). It is only slightly developed in *Acanthacorydalis* and has undergone reduction (i.e., it is small and can be unfolded by distension) in several *Corydalus*.
62. Membrane between eighth sternum and gonopore (laterally): (0) bare; (1) with spinous setae with sclerotized base. This specialized setation appears independently in *Chloroniella* and *Neurhermes*. It corresponds to Glorioso's (1981) character 64 and Penny's (1993) character 65, which was coded as absent (bare) for *Chloroniella*.
63. Eighth sternum sclerotization: (0) light to moderate; (1) strong.

64. Cerci: (0) fused to base of tenth tergites; (1) not fused to base of tenth tergites.
65. Membrane between eighth sternum and gonopore (ventrally): (0) bare to sparsely setose; (1) with conspicuous spinous setae. Such conspicuous setation (state 1) supports the monophyly of the *Protohermes* lineage.
66. Bursa copulatrix: (0) reduced; (1) saclike.
67. Number of spermathecae: (0) one; (1) two. Two spermathecae (state 1) are present in all observed ingroup taxa, whereas fishflies have single spermathecae (state 0). Glorioso (1981) recorded one spermathecae for *Protohermes*, *Neurhermes*, and *Nevromus*, as well as Penny (1993), who also did it for *Chloroniella*. However, my observations do not correspond with their findings.
68. Spermathecal duct: (0) thin, saclike; (1) short to moderately long, tubular; (2) very long, tubular.
69. Accessory glands: (0) absent; (1) long irregular; (2) short; (3) reduced.
70. Posterior internal ingrowth of ovipositor: (0) absent; (1) present. The presence of this structure supports the monophyly of the major clade formed by the *Nevromus* and *Corydalus* lineages.
71. Thickened membranous receptacle of bursa: (0) absent to slightly developed; (1) moderately to well developed.

Autapomorphies

The following characters are autapomorphies for some of the genera and were not included in the data matrix. They are listed below as they might help diagnose the different taxa, as well as provide potential evidence for groups in the event of new taxa being discovered.

1. Postocular flange. This is an autapomorphic condition for *Platyneuromus*.
2. Spines on cranial disk. A pair of short, conical protrusions (“spines”) on the cranial disk is an autapomorphy for *Acanthacorydalis*. There is a pair of analogous round convexities in *Corydalus flinti*, but not as developed.
3. Male antennae with papilliform setae. In males of most *Corydalus*, setation has been modified from hairlike setae into thick and short papilliform setae. However, a few *Corydalus* species maintain the primitive condition.
4. Male antennae long. In most taxa, the primitive condition is for antennae to be similarly short in both male and female. Males of *Acanthacorydalis* and those of typical *Corydalus* (Contreras-Ramos 1998, p. 187) have noticeably longer antennae than do females. However, as this derived condition does not appear to be the ancestral condition in *Corydalus*, this trait is considered an autapomorphy for *Acanthacorydalis*.
5. Male mandibles elongate. Male mandibles are, in the generalized condition, unmodified, similar to those in females. Elongate mandibles have evolved independently in *Acanthacorydalis* and several *Corydalus* species. However, because the ancestral condition of Corydalus species is unmodified mandibles, it is considered that this condition is an autapomorphy for *Acanthacorydalis* (as did Glorioso 1981).
6. Female mandibles long with reduced dentition. This is an autapomorphy of *Acanthacorydalis*. In one *Corydalus* species, *Corydalus amazonas*, mandibles show a similar, but less accentuated condition, which evolved independently.
7. Labral dorsal surface with two pairs of distinct setae. This apomorphic condition was observed only in *Chloroniella*. Galeal setae crowned with very long setae. This is an autapomorphy for *Nevromus*.
8. Costal crossveins reticulate. Simple vertical or oblique costal crossveins is the generalized condition for most taxa. Reticulate (irregularly branching) crossveins are an autapomorphy for *Acanthacorydalis*.
9. Male ninth abdominal segment retractile into eighth segment. This modification is unique to *Neoneuromus*.
10. Internal pregenital sacs on the eighth abdominal segment of males. Probable scent glands, occupying a large portion of the eighth segment, are considered autapomorphic in *Acanthacorydalis*. Less developed pregenital sacs, yet visible, are also present in several *Corydalus*.
11. Male ninth tergum dorsolateral incisions. This is an autapomorphic condition for *Neoneuromus*. Contrastingly, the absence of incisions was considered apomorphic by Glorioso (1981; his character 46).
12. Male anal tubercle covered with eleventh tergum. The generalized condition is an unmodified, semimembranous, tubular structure. In *Neoneuromus*, an autapomorphic condition conforms the anal tubercle under a sclerotized plate possibly representing an eleventh tergum. Convergently, in a few *Corydalus* species a similar anal tubercle condition appears, but only covering its base (*C. clavijoi*, *C. flinti*, *C. ignotus*) or fully developed in one (*C. tesselatus*), although in most it consists only of a pair of lateral sclerites.
13. Anterolateral apodemes of the male tenth sternite moderately to well developed. These ingrowths of the tenth sternite, probably serving as apodemes, are present in most *Corydalus* species, which constitutes an autapomorphic condition.
14. Setation of the male tenth sternite lobes inconspicuous to microsetose. This condition is considered autapomorphic for *Corydalus*, as it is present in most species of this genus.
15. Lateral sclerite of female ovipositor lightly sclerotized. This condition is autapomorphic for *Chloronia*.
16. Eighth sternum of female abdomen as a movable plate. This modification is an autapomorphy for *Neurhermes*.

APPENDIX 6. Data matrix for the updated phylogenetic analysis of Corydalinae.

				characters				
	1	2	3	4	5	6	7	
Taxon	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Chauliodinae	0000000000	0000000010	0010010000	0000000000	0000100000	0000100000	0010000000	0
Acanthacorydalis	1111112111	1111111000	0100001101	1201111001	0122000110	1102011112	2001011101	0
Chloronia	1111111100	2011011001	1101001000	0101011300	0122010120	1002111032	1001011101	0
Chloroniella	1110001001	1011001000	1101011000	0100010000	0020100100	0011001132	0101011130	0
Corydalus	1111111111	1111011011	1111111000	1201111310	0022110100	2103111032	1001011101	1
Neoneuromus	1111111100	0011111100	0100002101	1111111201	0012000301	0001012012	0001011221	1
Neurhermes	1110001000	1010000200	1101002111	1001011100	1001001200	0011001011	0111111110	0
Nevromus	1111111100	0001011100	0100002101	1111111001	0012000101	0001112022	0001011221	0
Platyneuromus	1111111110	2011111001	1101101100	0101111010	0022010100	1111111112	1001011101	0
Protohermes	1110001000	1010000000	1101002111	1101011100	1000001200	0011001011	0001111110	0

APPENDIX 7. Characters used for the updated phylogenetic analysis of *Corydalus* (modified from Contreras-Ramos 1998). Characters are coded as 0 for the plesiomorphic state and 1, 2, or 3 for the apomorphic ones. Character number and character states correspond with those in Appendix 8. Explanation of characters below may be complemented with Contreras-Ramos (1998, Phylogenetic Anaylisis Phase II: Species Relationships, p. 205).

Characters of the Head

1. Width (thickness) of mandible dentition (in females if males have elongate mandibles): (0) flattened, plate like; (1) thickened. Most ingroup taxa, including the *C. arpi* species group, show somewhat thickened teeth.
2. Distance between preapical teeth (in females if species has males with elongate mandibles): (0) approximately equidistant; (1) basal tooth moderately separated; (2) basal tooth strongly separated. There is a clear trend in mandibles, with slight homoplasy, for the basal tooth to separate from the pair of preapical teeth.
3. Orientation of basal preapical tooth (in females if species has males with elongate mandibles): (0) oblique; (1) abruptly angled. There is a trend for the basal tooth to become orientated in at an abrupt angle in several species (beginning with *C. parvus*; Fig. 14, node 49), with the *C. batesii* species group and the *C. cornutus* species pair, retaining the plesiomorphic condition.
4. Shape of posterior (basal) side of first (most proximal) preapical tooth (in females if species has males with elongate mandibles): (0) more or less straight; (1) concave.
5. Thickness of posterior (basal) side of first (most proximal) preapical tooth (in females if species has males with elongate mandibles): (0) thin; (1) moderately widened, round; (2) widened, forming perpendicularly flat surface. With slight homoplasy, there is a trend for this transformation series to change from state 0 in the outgroup, to state 1 in several species (e.g., from the *C. arpi* species group to the *C. nubilus* species group), and then to state 2 in a large group (e.g., from *C. diasi* to *C. magnus*).
6. Preapical teeth relative size (in females if species has males with elongate mandibles): (0) approximately subequal; (1) first and second teeth smaller; (2) middle tooth smaller. This character resembles in distribution, but with some degree of difference, that of character 5.
7. Preapical teeth shape (in females if species has males with elongate mandibles): (0) broadly triangular; (1) canine like. This character lacks homoplasy. State 1 helps define a large group, from *C. ecuadorianus* to *C. magnus* (Fig. 14, node 61).
8. Mandible longitudinal line of fusion (in females if species has males with elongate mandibles): (0) more or less evident; (1) apparently absent. In mandibles of a few species, such line (state 0) might indicate the ancestral fusion of lacinia with stipes of the first pair of maxillae. In most species such a line is indistinguishable (state 1).
9. Setose area on venter of mandibles (in females if species has males with elongate mandibles): (0) slightly to well developed; (1) apparently absent. There seems to be a phylogenetic trend, with little homoplasy, for this setose area to disappear (e.g., from *C. primitivus* to *C. magnus*).
10. Male mandible length: (0) short, female-like; (1) slightly to strongly elongate. The apomorphic condition includes several degrees of modification. In *C. cephalotes* and *C. flinti* mandibles are only slightly elongate. In *C. nubilus* mandibles vary with individual body size, so small males might be confused with females at first sight. In most species, particularly those considered typical, males have clearly elongate mandibles.
11. Male mandible dentition: (0) discrete; (1) moderately reduced; (2) highly reduced. This transformation series shows a similar phylogenetic gradient to character 10.
12. Male mandible basal protrusion: (0) absent; (1) present. This is a rather homplasious character. The basal protrusion

appears to correspond with the original mandible base, as if the mandibles have been pulled. It might represent a transitional stage towards fully modified mandibles, in which the protrusion is absent.

13. Male mandible papilliform cuticular outgrowths: (0) absent; (1) present. These cuticular papillae are of unknown function, although it was speculated in the genus revision that they may have a sensory function (chemoreception). Their presence helps define a clade from *C. colombianus* to *C. magnus* (Fig. 14, node 60).
14. Sexual dimorphism: (0) absent; (1) present. Although with some homoplasy (its presence in *C. cephalotes*, *C. flinti*, and one outgroup), this character provides support for the same clade as character 13.
15. Anteclypeus: (0) normal, a conspicuous plate; (1) reduced, a narrow plate. A reduced anteclypeus, typically hidden underneath the clypeal margin was found in *C. amazonas*, *C. cephalotes*, and *C. hecate*. Having removed the former from the analysis, this character acts as a synapomorphy for the latter two species.
16. Postclypeus: (0) slightly distinguishable from frons; (1) clearly fused to frons. The apomorphic condition supports the monophyly of the ingroup taxa.
17. Lateral corners of frons: (0) moderately convex; (1) strongly convex, directed anteriorly. The apomorphic condition supports the monophyly of the *C. arpi* species group.
18. Clypeal margin shape: (0) nearly flat (straight) to having slightly developed projections; (1) having moderately to well developed projections. With slight homoplasy, the apomorphic condition supports a large clade beginning with the *C. arpi* species group through *C. magnus* (Fig. 14, node 66).
19. Middle of clypeal margin: (0) incised; (1) not incised. State 1 of this character partly supports the clade from *C. parvus* through *C. magnus* (Fig. 14, node 49), with a reversal to the plesiomorphic condition in *C. batesii* and *C. holzenthali*.
20. Postocular spine: (0) feebly to moderately developed; (1) well developed. The apomorphic state offers partial support for the *C. arpi* species group, as one species of the group lacks the condition.
21. Length of male antennae: (0) short; (1) moderately long; (2) very long. There are two main conditions, state 0 and state 1. Nearly all species with elongate male mandibles show state 1. However, on three occasions a second apomorphic state for very long antennae has arisen, on the *C. tridentatus* species pair, *C. longicornis*, and *C. magnus*, respectively.
22. Thickness of male antennae: (0) slender; (1) moderately thick; (2) conspicuously thick.
23. Setation of male antennae: (0) finely setose, hairlike to fine spinelike; (1) papilliform setae. There is a clear trend for species with elongate-mandible males to present the apomorphic condition, beginning from *C. colombianus* (Fig. 14, node 60) with the exception of *C. nubilus* and *C. crossi*. The function of the papillae is unknown, but it may be chemoreceptive as has been speculated for similar structures of the male mandibles.
24. Shape of male antennae: (0) filiform to slightly subserrate; (1) subserrate; (2) denticulate. The generalized condition is state 0. The apomorphic conditions are rather homoplasious, subserate antennae appearing independently in *C. parvus*, *C. clauseni*, *C. flavicornis*, and *C. magnus*, while unique denticulate antennae are present in *C. luteus* and *C. bidenticulatus*.
25. Antennae color: (0) approximately uniform or only apically infuscate; (1) basal, middle, and apical thirds discretely colored. A specialized condition of tricolored antennae (basal, middle, and apical thirds discretely colored) supports the monophyly of the *C. arpi* species group.
26. Labrum shape: (0) broadly truncate; (1) ovoid; (2) triangular. This is a somewhat homoplasious character. The majority of species, beginning from *C. affinis* (Fig. 14, node 59) with the exception of *C. tesselatus* (with state 0), posses a triangular labrum. However, *C. arpi*, *C. ignotus*, and *C. mayri*, also have state 2. Only one species, *C. hecate*, bears state 1.
27. Labral position: (0) over mandibles; (1) between mandibles. The apomorphic condition is present throughout the ingroup, with the exception of *C. arpi*, *C. flinti*, and *C. ecuadorianus*.
28. Anterior margin of submentum: (0) flat; (1) dorsoventrally developed, with lateral sclerites. State 1 supports the monophyly of the ingroup.
29. Submental projections: (0) short, blunt; (1) moderately to well developed, sharply pointed; (2) moderately developed, broadly blunt; (3) moderately developed, slightly pointed. Two main apomorphic states are present in the ingroup, state 1 from *C. cephalotes* through *C. clavijoi* (Fig. 14, nodes 68 through 55) while state 3 is present in nearly all species from *C. nubilus* through *C. magnus* (node 57). Exceptions are *C. affinis*, with autapomorphic state 2, and *C. clavijoi* with state 1.
30. Maxillary palp: (0) 5-segmented; (1) 4-segmented. This is a defining synapomorphy for *Corydalus*, although a convergent reduction in segmentation occurred in fishflies and alderflies.
31. Stipes: (0) relatively short to moderately long; (1) relatively long. Originating twice, the apomorphic condition supports a sister group relationship between *C. cephalotes* and *C. hecate*, as well as between *C. imperiosus* and *C. tridentatus*.
32. Stipital setae: (0) apparently absent, inconspicuous; (1) present, microsetose. The apomorphic condition supports the monophyly of the *C. arpi* species group.
33. Lacinia apex: (0) with 2-3 elongate setae; (1) without elongate setae. The apomorphic condition is present in the majority of the ingroup, beginning from *C. colombianus* (Fig. 14, node 60) but excluding *C. affinis*.
34. Shape of lacinia apex: (0) moderately round; (1) subacute. The apomorphic state is present throughout the ingroup.
35. Labial palp: (0) 4-segmented; (1) 3-segmented. This is a synapomorphy for *Corydalus*, which appears to be correlated with character 30. This reduction also occurred in fishflies and alderflies.
36. Shape of apical segment of labial palp: (0) unmodified; (1) moderately elongate; (2) strongly elongate. There is a somewhat homoplasious trend for the apical segment to become elongate.
37. Apical sensory area of labial palp: (0) circular; (1) elongate, narrow; (2) moderately elongate, wide; (3) strongly elongate, wide. There is similarly a somewhat homoplasious but stepwise increase in elongation and width of the sensory area of the labial palp.

Characters of the Thorax

38. Costal area of forewing: (0) with indistinct single stigma; (1) with distinct double stigma. The specialized condition appears independently in three members of the *C. arpi* species group and in *C. tesselatus*.
39. Costal crossveins: (0) vertical or oblique; (1) sinuate. According to the current phylogenetic hypothesis, sinuate veins have evolved in parallel in *C. ecuadorianus* and *C. colombianus*.
40. Last branch of Rs: (0) bifurcate; (1) single vein. The apomorphic condition groups all *Corydalus* species, except the sister *C. cephalotes* and *C. hecate*.
41. Rs branches: (0) nine or more; (1) seven to eight. The derived state is present in three members of the *C. arpi* species group, *C. ignotus*, *C. mayri*, and C. *flinti*, as well as in *C. crossi* and *C. texanus*.
42. M_{1+2} branches: (0) two; (1) three or variably two to three; (2) four or variably three to four.
43. Medial crossveins: (0) two or typically two; (1) three or more. There is an apparent trend for the apomorphic condition to prevail in several species species, beginning from *C. ecuadorianus* (Fig. 14, node 61) although state 1 is also present in *C. cephalotes* and *C. hecate*, and state 0 is present in *C. nubilus*.
44. Cu_1 branches: (0) three; (1) four or more. State 1 is present throughout the ingroup, as well as in one outgroup, *Platyneuromus*.
45. Pronotum: (0) with four spots; (1) with broad vittae; (2) slightly to moderately patterned.

Male Terminalia Characters

46. Eighth sternum setation: (0) densely setose, with long hairlike setae; (1) moderately setose, short to moderately long setae. State 1 is distributed throughout the ingroup.
47. External pregenital sacs: (0) present; (1) apparently absent. Most *Corydalus* species and one outgroup present the apomorphic state.
48. Internal pregenital sacs: (0) apparently absent; (1) slightly developed; (2) moderately to well developed. This is a rather homplasious character, although it shows a trend for state 2 to prevail above, and includesing, the *C. armatus* species group.
49. Ninth tergum shape: (0) subtriangular; (1) subquadrate. There is a trend for a subqudrate ninth tergum to predominate within *Corydalus*, as only *C. hecate*, *C. ecuadorianus*, *C. colombianus*, and *C. crossi* retain the plesiomorphic condition, which is present in *Chloronia* as well.
50. Wide bands of microsetae on ninth tergum: (0) absent to barely noticeable; (1) present, distinct. Nearly all *Corydalus* species display state 1, as does *Platyneuromus*, while *Chloronia*, *C. cephalotes*, and *C. colombianus*, retain the primitive condition.
51. Anterodorsal apodeme of ninth tergum: (0) long, platelike, pointed; (1) short, blunt. Although this character might be a potential synapomorphy for *Platyneuromus* and *Corydalus*, an outgroup for such an hypothesis is required in order to determine the direction of change.
52. Ninth tergal internal inflection: (0) reaching about midlength of tergum; (1) deep, nearly touching posterior tergal edge. State 1 is widespread, while the *C. arpi* species group, *C. affinis*, and the *C. nubilus* species group, display the plesiomorphic condition, present in *Chloronia* as well.
53. Posterior margin of ninth tergum: (0) nearly straight to slightly concave; (1) moderately to conspicuously concave. State 1 appears more or less intermittently throughout the ingroup.
54. Cerci: (0) flattened; (1) more or less bulging. Only *C. arpi* and *C. hayashii* show flattened cerci (state 0), which might be interpreted as a reversal to a state in *Chloronia*.
55. Tenth tergite shape: (0) elongate, tubular; (1) short, blunt. Truly short and blunt tenth tergites support a sister group relationship between *C. arpi* and *C. flinti*.
56. Tenth tergite shape: (0) subcylindrical; (1) dorsoventrally flattened; (2) laterally flattened. This is a homoploasious character. State 1 offers partial support for the *C. cephalotes* species pair and the *C. arpi* species group, respectively. State 2 predominates on species held by node 58 (Fig. 14).
57. Tenth tergite shape (width): (0) approximately uniform or gradually narrowing; (1) distal half noticeably narrower; (2) mid portion slightly narrower. Assignment of states was reinterpreted, with *C. arpi*, *C. flinti*, and *C. ignotus* having received state 1 instead of the original state 0.
58. Tenth tergite shape (direction): (0) more or less straight; (1) bending in at about 90° angle; (2) abruptly changing direction. State 0 is the generalized condition. State 1 is present only in *C. ignotus*, *C. mayri*, and *C. hayashii*, of the *C. arpi* species group, while state 2 occurs in a parallel series of species from *C. australis* through *C. longicornis*.
59. Inner side of tenth tergite base: (0) more or less straight; (1) broadly round; (2) protruding, elbowed. Although fairly characteristic traits, the states of this character have a homoplasious distribution. State 1 is present in *C. ignotus*, *C. hayashii*, and *C. nubilus*, while state 2 occurs in *C. imperiosus* and *C. australis*.
60. Apex of tenth tergites: (0) more or less digitiform; (1) truncate, biramous; (2) dorsoventrally enlarged; (3) with incurvation. The generalized condition is for a digitiform apex, which occupies the basal half of the phylogeny except for *C. arpi* which has autapomorphic state 1. State 2 is rather homoplasious, being present in the *C. tridentatus* species pair, *C. diasi*, and the *C. batesii* species group, while state 3 displays a trend for a portion of the tree resting on node 51 (Fig. 14).
61. Relative size of tenth tergite apex: (0) somewhat narrowing or not noticeably enlarged; (1) enlarged, capitate. The specialized condition originates several times in a parallel fashion on *C. australis*, *C. primitivus*, *C. parvus*, and *C. longicornis*.
62. Setation on inner basal side of tenth tergites: (0) fine to moderately thick, hairlike; (1) thick tapering to conical setae; (2)

fine to moderately thick spinelike setae. Hairlike setae conform to the generalized condition. A specialized type of setae, state 1, is present in *C. arpi*, *C. flinti*, and *C. hayashii*, a monophyletic subgroup of the *C. arpi* species group, as well as in *C. ecuadorianus*, *C. colombianus*, *C. tesselatus*, and *C. tridentatus*.

63. Tenth tergites sclerotization: (0) lightly sclerotized, semimembranous; (1) moderately to well sclerotized. State 1 is widespread, whereas state 0 occurs only on in *C. affinis* and the outgroup *Chloronia*.
64. Tenth tergites ventral line of sclerotization: (0) inconspicuous; (1) moderately to clearly evident. The specialized condition is present in a homoplasious fashion on in *C. ignotus*, *C. nubilus*, the *C. tridentatus* species pair, *C. holzenthali*, and *C. neblinensis*, although it partiallly provides support for the sister group relationship of *C. imperiosus* and *C. tridentatus*.
65. Tenth tergites setation: (0) fine, clear; (1) moderately thick, tapering, dark. Modified setae are present dorsally on the tenth tergites in a homoplasious fashion on *C. ecuadorianus*, *C. primitivus*, and the *C. armatus* species pair, offering partial support for the monophyly of the latter.
66. Distance of tenth tergites to anal tubercle: (0) widely separated; (1) moderately separated; (2) very close, adjacent.
67. Tenth tergites relative size: (0) subequal to about 1.5 times length of ninth tergum; (1) between 1.5 times to about twice as long as ninth tergum; (2) slightly more than twice as long as ninth tergum; (3) about half length of ninth tergum.
68. Anal tubercle: (0) semimembranous to lightly sclerotized; (1) with eleventh tergum; (2) with lateral sclerites. State 0 suffers a regression on the *C. cornutus* species group, while state 1 is restricted to *C. ignotus* and *C. flinti*, yet supports the sister group relationship of *C. tesselatus* and *C. clavijoi*.
69. Venter of anal tubercle: (0) bare to very slightly setose; (1) moderately setose. A setose venter of the anal tubercle occurs twice, once on *C. affinis*, and a second time providing support for *C. bidenticulatus* and *C. magnus* as sister species.
70. Ninth sternum shape: (0) subquadrate; (1) with posterior margin convex; (2) moderately to strongly subattenuate. State 0 is generalized throughout the phylogeny. State 1 occurs in parallel on the *C. tridentatus* species pair, as well as on *C. diasi* and *C. australis*, while state 2 supports, respectively, the monophyly of the *C. arpi* and the *C. nubilus* species groups.
71. Ninth sternum internal ridges: (0) absent; (1) present. The presence of these structures supports, respectively, the monophyly of the *C. arpi* species group and the sister group relationship between *C. clavijoi* and *C. tesselatus*.
72. Ninth sternum internal ridges: (0) absent; (1) longitudinal, linear; (2) v-shaped. Among species with internal ridges, linear ones predominate within the *C. arpi* species group, while v-shaped ridges support a sister relationship between *C. clavijoi* and *C. tesselatus*, although the latter type is also present in *C. flinti* of the former group.
73. Ninth sternum posterolateral lobes: (0) apparently absent; (1) slightly developed; (2) moderately developed; (3) well developed.
74. Ninth sternum setation: (0) long, fine, hairlike; (1) short to moderately long, fine, tapering; (2) moderately long, thick, tapering. State 0 is autapomorphic for *Chloronia*, state 1 is the widespread condition, and state 2 supports a sister relationship between *C. cephalotes* and *C. hecate*, although it is also present in *C. ecuadorianus* and *C. colombianus*.
75. Membrane between ninth and tenth sternites: (0) bilobate; (1) smooth to wrinkled; (2) convoluted. This is a somewhat homoplasious character, particularly on states 0 and 1, whereas state 2 does contribute to the monophyly of a large species group that begins with *C. primitivus* (Fig. 14, node 50).
76. Sclerotization of membrane between ninth and tenth sternites: (0) non- sclerotized; (1) slightly sclerotized; (2) well sclerotized, thickened. State 0 is present in the outgroup *Chloronia*, as well as in *C. cephalotes*. State 1 occurs in several species, including all members of the *C. arpi* species group. State 2 is present in the outgroup *Platyneuromus*, as well as in *C. colombianus* and *C. affinis*, and offers partial support for *C. tesselatus* and *C. clavijoi* as sister, as well as to the monophyly of the group held by node 54 (Fig. 14). Score of this character was changed to 1 for *C. ecuadorianus*.
77. Ninth gonostyli versus tenth tergites: (0) differing in length; (1) about the same length.
78. Ninth gonostyli versus tenth tergites: (0) differing in shape; (1) similar in shape. Only a few species have a similar shape of ninth gonostyli and tenth tergites, specifically *C. ecuadorianus*, *C. colombianus*, *C. affinis*, and *C. clavijoi*, so this character has evolved in a parallel fashion.
79. Ninth gonostyli position: (0) below tenth tergite base; (1) slightly posterior to tenth tergite base; (2) conspicuously posterior to tenth tergite base. This is a fairly homoplasious character, although there is a clear trend for state 0 to be the ancestral condition (e.g., occurs in both outgroups), whereas state 1 is present in several species (*C. cephalotes*, *C. hecate*, most of the *C. arpi* species group, *C. affinis*, *C. crossi*, and *C. imperiosus*), and state 2 predominates on the group held by node 52.
80. Ninth gonostyli shape: (0) subclavate; (1) unguiform; (2) elongate, subcylindrical. State 0, although present in the outgroup *Chloronia*, may not be the plesiomorphic condition. Similarly, state 1 is present only in the outgroup *Platyneuromus* and in *C. tesselatus*. It appears that elongate, subcylindrical ninth gonostyli, present from *C. cephalotes* through *C. crossi* (Fig. 14, nodes 68 through 58) may represent the ancestral condition for *Corydalus*. Subclavate gonostyli might be a derived condition, as they prevail in most species, from *C. imperiosus* through *C. magnus* (Fig. 14, node 54).
81. Ninth gonostylus apodeme: (0) thickened; (1) flattened, platelike. A thickened apodeme (deepened below the cuticle) of the ninth gonostylus is plesiomorphic, although it intermixes to some degree into species such as the *C. nubilus* and *C. tridentatus* species groups. Apomorphic apodemes are flattened, superficial, and are present in species such as *C. ignotus*, *C. flinti*, *C. ecuadorianus*, *C. colombianus*, as well as in most members of the group held by node 50 (Fig. 14).
82. Dorsal end of ninth gonostylus apodeme: (0) normal, not projecting; (1) projecting out from base of gonostyli, or with scar of projection. The specialized condition is unique, however it emerged within a homoplasious pattern in *C. ignotus*, *C. arpi*, *C. crossi*, and *C. nubilus*.
83. Base of ninth gonostylus apodeme: (0) more or less exposed; (1) deep into body wall. State 0 is the generalized condition. In the *C. cephalotes* species pair, *C. hayashii*, *C. flinti*, and the *C. nubilus* and *C. tridentatus* species groups, the basal end

of the apodemes are immersed into the membranous body wall.

84. Ninth gonostyli apical claw: (0) present; (1) absent. An apical claw is present only in the two outgroups, as well as in *C. colombianus*, *C. clavijoi*, and *C. tesselatus*, the latter two being sister species.
85. Setae on apex of ninth gonostyli: (0) unmodified, as in rest of gonostyli; (1) distinct from rest; thick, tapering. The apomorphic condition supports a sister group relationship between *C. cephalotes* and *C. hecate*.
86. Tenth sternite shape: (0) nearly flat to slightly convex; (1) moderately convex; (2) strongly convex. On a transverse plane, from one anterolateral projection to the other, a nearly flat to slightly convex tenth sternite (state 0) constitutes a generalized condition, present in both outgroups and many ingroup taxa. A moderately convex tenth sternite (state 1) is present in several species, from *C. primitivus* through *C. peruvianus* as well as in *C. holzenthali*, while a strongly convex sternite (state 2) is present in *C. hayashii*, *C. crossi*, *C. clavijoi*, the *C. tridentatus* species pair, *C. diasi*, and *C. australis*. The condition in *C. arpi* was corrected from state 1 to state 0.
87. Tenth sternite width: (0) narrow to moderately narrow plate; (1) very narrow plate; (2) slightly widened plate; (3) conspicuously widened plate. These character states are observed when considering the tenth sternite on a longitudinal plane, from anterior to posterior margin.
88. Anterolateral projections of tenth sternite: (0) nearly undeveloped to slightly developed; (1) moderately developed; (2) well developed.
89. Shape of anterolateral projections of tenth sternite: (0) sharp, ridge like; (1) round, broad; (2) narrow, elongate. Undeveloped, ridge like projections (state 0) are representative of the outgroups and the *C. arpi* species group.
90. Posterolateral corner of tenth sternite: (0) shallow, broad concavity; (1) shallow, conical concavity; (2) moderately deep, conical concavity; (3) conspicuously deep, rather wide, conical concavity.
91. Anteromedian projection of tenth sternite: (0) absent to very slightly developed; (1) moderately developed; (2) well developed. A state 0 was reassigned to *C. ecuadorianus*, formerly with state 1.
92. Structure of tenth sternite: (0) single plate; (1) partly subdivided; (2) subdivided in two movable halves. The generalized condition is for a tenth sternite structured as a single plate (state 0). However, a tenth sternite partly subdivided in two halves, condition that could be indicated simply as a cleft on the anterior margin (state 1), is present in *C. nubilus*, as well as in the monophyletic *C. batesii* species group. Moreover, in *C. affinis*, and the sister species *C. clavijoi* and *C. tesselatus*, the middle of the sternite is so narrow that each sternite side consists of an independently movable half (state 2). A character state 0 was reassigned to *C. ecuadorianus*, formerly with state 1.
93. Middle region of tenth sternite: (0) more or less uniformly thin; (1) with conspicuous internal thickening. An internal thickening of the tenth sternite is present only in the *C. cephalotes* species pair, as well as in *C. crossi* and *C. nubilus*.
94. Sclerotized band posterior to tenth sternite: (0) absent; (1) present. A slightly to moderately sclerotized transverse band posteriorly adjacent to the tenth sternite is a synapomorphy for *C. cornutus* and *C. texanus*.
95. Tenth sternite median protrusions: (0) absent; (1) present. Sclerotized median protrusions, posteriorly fused to the tenth sternite are a synapomorphy for *C. luteus*, *C. bidenticulatus*, and *C. magnus*.
96. Small mesal membranous sacs anterior to tenth sternite: (0) absent; (1) present. These, possibly reduced genital papillae, close to each other anteromedially on the tenth sternite, are present only in *C. affinis* and *C. tesselatus*.
97. Distance of tenth sternite to anal tubercle: (0) well separated; (1) moderately separated; (2) very close, adjacent. This is a somewhat homoplasious character. State 0 occurs only in both outgroups, as well as in the sister *C. clavijoi* and *C. tesselatus*. State 1 is widespread on the phylogeny, whereas state 2 intermittently occurs in *C. hayashii*, *C. flinti*, *C. ecuadorianus*, *C. affinis*, as well as in the *C. tridentatus* species pair. State 2 was reassigned to *C. ecuadorianus*, formerly with state 0.
98. Sclerotized plate posterior to tenth sternite: (0) present; (1) absent. A sclerotized plate next to the posterior margin the tenth sternite is plesiomorphic. It is present in both outgroups, as well as in the *C. cephalotes* species pair and *C. colombianus*.
99. Membranous fold posterior to tenth sternite: (0) absent; (1) present. A fold of the semimembranous area posterior to the tenth sternite is present in most ingroup species, with the exception of *C. hecate*, *C. hayashii*, *C. arpi*, *C. flinti*, *C. crossi*, *C. tesselatus*, and *C. tridentatus*. State 0 was reassigned to *C. arpi*, formerly with state 1.
100. Setation of area posterior to tenth sternite: (0) mostly bare to slightly setose; (1) spinous setae present; (2) moderately to strongly setose; (3) only sides moderately setose.
101. Tenth sternite lobes shape: (0) papilliform, wide; (1) digitiform; (2) papilliform, slightly elongate; (3) papilliform, long; (4) papilliform, very long; (5) reduced. This is a rather complex character with several states, however it does show a pattern of distribution. Papilliform wide and digitiform lobes (states 0 and 1) are plesiomorphic, present in the outgroups and a few species. Nonetheless, the *C. arpi* species group has a synapomorphous reduced type of lobes (state 5). Three categories of elongate papilliform lobes (states 2, 3, and 4) are distributed throughout the tree, but state 2 clearly supporting the *C. cornutus* species group. In *C. ecuadorianus*, state 0 was reassigned (formerly it had state 2).
102. Tenth sternite lobes orientation (“x-y plane”): (0) slightly to moderately divergent; (1) caudally to slightly directed mesally; (2) moderately directed mesally; (3) strongly directed mesally; (4) directed anteriorly. These states represent the orientation of tenth sternite lobes on a “flat” plane continuous to the tenth sternite, or an “x-y plane”. State 4 was assigned to species with reduced lobes. In *C. arpi* and C. mayri, a pair of small anterior outgrowths might correspond to the tenth sternite lobes, probably an advanced degree of reduction of the adnate condition in *C. ignotus*. States 0 and 1 appear intermittently, whereas state 2 is present on *C. cornutus*, *C. luteus*, and *C. bidenticulatus*. State 3, a well defined condition, emerged as a parallelism.

103. Tenth sternite lobes orientation ("z plane"): (0) well separated, directed posteroventrally; (1) very close to moderately separated to on tenth sternite. These states represent the orientation of tenth sternite lobes on a plane perpendicular to the tenth sternite, a "z plane". The *C. arpi* species group was assigned state 0, assuming the lobes have completed a "rotation" from posteriorly to anteriorly directed and so being well separated from the sternite. State 1 is present in *Platyneuromus*, and then it predominates through most of the tree beginning on node 61 (Fig. 14). The *C. armatus* species group is partly supported by a regression to state 0.
104. Distance between tenth sternite lobes: (0) well separated; (1) moderately separated; (2) very close. State 0 is present in the outgroups and the *C. cephalotes* species pair, *C. ecuadorianus*, and *C. colombianus*, plus *C. holzenthali* and *C. neblinensis* of the *C. batesii* species group. State 1 predominates on the group held by node 59 (Fig. 14) with its presence also in *C. flinti*, while state 2 partly supports the *C. arpi* species group.
105. Sclerotization of tenth sternite lobes: (0) well sclerotized; (1) lightly to moderately sclerotized.
106. Setation of tenth sternite lobes: (0) long, conspicuous; (1) bare to microsetose. The apomorphic condition is present in the major group held by node 60 (Fig. 14), with the exception of *C. crossi*, as well as in the monophyletic subgroup formed by *C. hayashii*, *C. arpi*, and *C. flinti*, within the *C. arpi* species group.
107. Apical claw on tenth sternite lobes: (0) absent; (1) present. State 1 is a synapomorphy for the *C. cephalotes* species pair.

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108. Sternal pouch: (0) moderately to well developed; (1) reduced, apparently absent to slightly developed. The presence of a sternal pouch, the plesiomorphic condition, predominates on both outgroups and several species. Reduction of the sternal pouch has occurred mostly within the group held by node 54 (Fig. 14), although the character is reversed in the *C. batesii* species group and *C. flavicornis*.
109. Seventh sternum: (0) lightly to moderately sclerotized; (1) well sclerotized. State 1 is present in *C. ignotus* and *C. arpi*, and it might be present in the rest of the *C. arpi* species group, but this is unconfirmed at the moment because females of *C. flinti*, *C. hayashii*, and *C. mayri* are unknown.
110. Eighth tergum: (0) lightly to moderately sclerotized; (1) well sclerotized. The apomorphic condition is present in *C. ignotus*, *C. arpi*, and *C. tesselatus*, and it might be present in the unknown females of *C. flinti*, *C. hayashii*, and *C. mayri*.
111. Eighth sternum: (0) lightly to moderately sclerotized; (1) well sclerotized. The apomorphic condition contributes to a sister relationship of *C. clavijoi* and *C. tesselatus*, and it might support the monophyly of the *C. arpi* species group, although its presence has not been confirmed in females of *C. flinti*, *C. hayashii*, and *C. mayri*.
112. Posterior margin of eighth sternum: (0) flat (straight) to slightly concave; (1) slightly to moderately convex; (2) strongly concave. The generalized condition is state 0, while states 1 and 2 each appears seldom but intermittently in an entirely homoplasious manner.
113. Ventral pouch between eighth and ninth segments: (0) slightly developed; (1) moderately developed; (2) well developed. State 0, the plesiomorphic condition, is present in both outgroups, the *C. cephalotes* species pair, as well as in *C. crossi*, *C. nubilus*, and as a reversal supporting the sister relationship between *C. cornutus* and *C. texanus*. State 1 is widespread throughout much of the tree, while state 2 appears independently in *C. arpi*, *C. parvus*, *C. magnus*, and supporting in part the monophyly of the *C. armatus* species group.
114. Spinous setae ventrally between eighth and ninth segments: (0) conspicuous; (1) absent or few, inconspicuous. The derived condition appears supporting the monphyly of the *C. arpi* and *C. nubilus* species groups, respectively, as well as in *C. ecuadorianus*, *C. colombianus*, and *C. crossi*. Reserve Caution should be taken as the condition is undetermined in females of *C. flinti*, *C. hayashii*, *C. mayri*, and *C. ecuadorianus*.
115. Ninth and tenth segments: (0) normal; (1) received by expanded eighth sternum. This unique condition supports the sister relationship between *C. clavijoi* and *C. tesselatus*, although it is also present in *C. ignotus*.
116. Lateral sclerite of ovipositor: (0) lightly to moderately sclerotized; (1) well sclerotized. *Platyneuromus* and most ingroup species show the apomorphic condition. State 0 is present in *Chloronia*, *C. affinis*, and *C. primitivus*.
117. Fine spinous setae on anterior side of ovipositor: (0) present; (1) absent or only few microsetae present. State 1 is present throughout the ingroup.
118. Setose membranous papillae on venter of ninth segment: (0) present; (1) absent. These papillae, located on the ninth segment just anterior to the ovipositor base, are absent in the ingroup.
119. Bursa copulatrix: (0) semimembranous to lightly sclerotized; (1) moderately sclerotized, thickened. State 1 supports the monophyly of the *C. arpi* species group, although it is unconfirmed in *C. flinti*, *C. hayashii*, and *C. mayri*. It is also present in *C. tesselatus*.
120. Thickened membranous receptacle of bursa: (0) absent to slightly developed; (1) moderately to well developed. The apomorphic condition appears to have originated early in *Corydalus*, as it is present in the *C. cephalotes* and *C. arpi* species groups and reappears intermittently in *C. ecuadorianus*, *C. affinis*, *C. nubilus*, *C. tesselatus*, *C. diasi*, and *C. australis*, while the group held by node 50 (Fig. 14) is supported by a regression to the primitive state.

Autapomorphies

A few autapomorphies are listed in Contreras-Ramos (1998). As they are uninformative regarding group support, autapomorphies are not listed here neither has an extensive search taken place in order to detect them, but many might be found from the species diagnoses.

Appendix 8. Data matrix for the updated phylogenetic analysis of *Corydalus*.

			Characters			
					1	1 1
	1 2	3 4	5 6	7 8	9 0	1 2
Taxon	1234567890 1234567890	1234567890 1234567890	1234567890 1234567890	1234567890 1234567890	1234567890 1234567890	1234567890 1234567890
Chloronia	0000000000 0000000000	0000000000 0000000000	0000000000 0000000000	0000000000 0000000000	0000000000 0000000000	0000000000 0000000000
Platyneuromus	0000000000 0001000000	0000000000 0010012000	0001101111 1101020000	0010000000 0011020001	0000000001 1000000001	1110000000 0000010000
affinis	1000111101 2011010000	1010021121 0001112001	0111210211 1001000000	0000011010 0011021112	1001001223 0200012112	3311010100 0210001101
amazonas	110011101? ????110000	????021111 0011101000	02112????? ??????????	?????????? ??????????	?????????? ??????????	???????000 0111011100
armatus	1110221111 2011010110	1210021131 0011123001	0111211211 1101022003	0210111200 0021220020	1001010222 0000001113	3001110100 0020011100
arpi	1000100100 0000011101	0000120111 0101100101	0101211011 1000111001	0110013002 1101110012	0101001000 0000001100	5402010011 1021011111
australis	1100211101 2011010100	1110021131 0011112001	0111211011 1111022223	1010011201 0031020020	0001023122 0000001110	4311110100 0010011101
batesii	1100221111 2011010100	1110021131 0011123001	0111211211 1111020002	0210011000 0011220020	1001000121 1100001110	3111110000 0010011100
bidenticulatus	1210221111 2011010110	1212021131 0011123001	0011211211 1101022003	0010012010 0011220020	1001000121 2000101112	2211110100 0010011100
cephalotes	0001010001 1001110000	0000001111 1001101000	0111211010 1111011000	0010010000 0012101012	0011100010 0010001011	1100001000 0000011101
clauseni	1110221111 2011010110	1211021131 0011123001	0111211211 1101022003	0210011200 0021220020	1001010222 0000001112	3001110100 0020011100
clavijoi	1001111101 2011010100	1110021111 0011101001	0111211011 1011021000	0010020102 1231021112	0010021213 1200000110	3101010000 1011111100
colombianus	1000111011 0111010100	1110001111 0011100011	0111211000 1101001000	0110000000 0012021102	1000001010 0000001010	0010010000 0011011100
cornutus	1200221111 2011010110	1210021131 0011100001	0011211211 1101022003	0010011000 0011220020	1001000121 1001001113	2211110100 0000011100
crossi	1101111101 2111010100	1000021111 0011112001	1111211201 1101021000	0010011200 0011110012	1101021210 0010001100	4311000100 0001011100
diasi	1101211101 2011010100	1110021131 0011112001	0111211211 1111022002	0010010201 0031020020	1001022121 0000001110	4311110100 0010011101
ecuadorianus	0001011000 0000010100	0000000111 0001100011	0011211201 1111001000	0110100200 0012011102	1001000011 0000002112	0010100000 0???01????
flavicornis	1210221111 2011010110	1211021131 0011123001	0011211211 1101022003	0010011200 0021220020	1001000121 1000001113	2011110000 0010011100
flinti	10001201?1 0101011101	0000100111 0101100001	1001211011 1001111000	0110023102 1221111012	1011001001 0000002100	5401010??? ??????????
hecate	1000110010 0000110000	0000011111 1001101000	0211211001 1111011000	0010010000 0012111012	0011100010 0010001001	1100001000 0000011101
holzenthali	1100221111 2011010100	1110021131 0011112001	0111211011 1111022002	0211010200 0011220020	0001010121 0100001110	0010110000 0010011100
hayashii	1000120110 0000011101	0000101111 0101100101	0001211011 1010011110	0110010002 1101111012	0011021000 0000002100	5402010??? ??????????
ignotus	1000100100 0000011100	0000121111 0101100101	100121??11 1011011110	00110001?2 1131??1022	1101003000 000000????	5402000011 1211111111
imperiosus	1001011101 2011010100	2110021131 1011101001	0211211211 1101001022	0011020201 0031020010	0011023121 0000002113	4311010100 0010011100
longicornis	?????????1 2011010110	2210021131 0011123001	0111211011 1101022203	1210011200 0021220020	1001012122 0000001113	3111110??? ??????????
luteus	1210221111 2011010110	1212021131 0011123001	0011211211 1101022003	0010011000 0011220020	1001000121 2000101110	2211110100 0010011100
magnus	1210221111 2011010110	2211021131 0011123001	0011211011 1101022003	0010012010 0011220020	1001000121 2000101112	2111110100 0120011100
mayri	1000100100 0000011101	0000121111 0101100001	1001211011 1011011100	0010000202 1101111012	0001000000 0000001110	5402000??? ??????????
neblinensis	1100221111 2011010110	1110021131 0011123001	0011211211 1111020002	0011011200 0021220020	1001000121 1100001110	3010110?00 001001????
nubilus	0001111101 1111010000	0000021131 0011112001	0101210211 1001012010	0011020202 0001110000	0111003110 0110001110	3101010000 0101011101
parvus	1110221111 2011010110	1111021131 0011123001	0111211011 1101022203	1210011200 0021220020	1001012122 0000001113	3111110100 0020011100
peruvianus	1210221111 2011010110	1210021131 0011123001	0111211011 1101022003	0010111200 0021220020	1001010222 0000001113	3001110100 0020011100
primitivus	1100211111 2011010100	1110021131 0011112001	0111211011 1101022203	1210111200 0021220010	1001012122 0000001110	3111110100 0010001100
tesselatus	1001111101 1111010100	1110001131 0011112101	0111211011 1011022000	0110020102 1231020021	0010001213 0200010100	3111010001 1211111111
texanus	1200221111 2011010110	1110021131 0011112001	1011211211 1101022003	0010010000 0011220020	1001000121 1001001110	2111110100 0000011100
tridentatus	?0012111?1 2011?10100	2110021131 10111??001	0111211211 1101022002	0111020201 0031020000	0011022112 0000002100	0111110100 0???01????