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Phylogeny of the genera of the parasitic wasps subfamily Doryctinae (Hymenoptera: Braconidae) based on morphological evidence

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The evolutionary relationships among most (143 genera) of the currently recognized genera of the braconid wasp subfamily Doryctinae were investigated using maximum parsimony analysis, employing 100 characters from external morphology and four additional, less well-studied character systems (male genitalia, ovipositor structure, venom apparatus and larval cephalic structure). We investigated the 'performance' of characters from external morphology and the other character systems and the effects of abundant missing entries by comparing the data decisiveness, retention and consistency indices of four different character partitions. The results indicate that the performances of the different partitions are not related to the proportions of missing entries, but instead are negatively correlated to their proportion of informative characters, suggesting that the morphological information in this group is subject to high levels of homoplasy. The external morphological partition is significantly incongruent with respect to a data set comprising the other character systems based on the ILD test. Analyses supported neither the monophyly of the large tribes Doryctini and Hecabolini, nor the monophyly of the Spathiini and Heterospilini. Relationships obtained from successive approximation weighting analysis for the complete data differ considerably from the currently accepted tribal and subtribal classifications. The only exceptions were the Ypsistocerini and the Ecphylini, whose recognized members were recovered in single clades. A close relationship between the Binaerini and Holcobraconini, and also *Monarea*, is consistently supported by venom apparatus and ovipositor structure characters but is not indicated by external morphological data. Low bootstrap values obtained for most of the recovered clades in all analyses do not allow us to propose a meaningful reclassification for the group at this time. A complete list of the recognized genera and their synonymies is given.

ADDITIONAL KEYWORDS: classification – consistency index – data decisiveness – insect – retention index – systematics.

INTRODUCTION

The braconid wasp subfamily Doryctinae is a large, heterogeneous group currently known from more than 1000 described species in more than 150 genera (Marsh, 1997, 2002; Belokobylskij, 2001). Doryctine wasps are mostly tropical and subtropical in distribution and are especially diverse in the New World tropics, where two thirds of the world's described genera occur (Shenefelt & Marsh, 1976; Belokobylskij, 1992a; Marsh, 1993, 1997). Most species are idiobiont ectoparasitoids of larvae of xylophagous or bark-boring Coleoptera, although several taxa attack the larvae of Lepidoptera (especially leaf miners) and Symphyta (especially Xiphydriidae), and in unusual cases they are endoparasitoids of adults of Embioptera (*Sericobracon* Shaw) or phytophagous (e.g. *Allorhogas* Gahan, *Psenobolus* Reinhard and possibly *Donquick-*

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eia Marsh) (Shaw & Edgerly, 1985; de Macêdo & Monteiro, 1989; Belokobylskij, 1996; Ramírez & Marsh, 1996; Penteado-Dias, 1999). Furthermore, a few genera have been found living within termite nests (some treated previously as Ypsistocerinae, but see Quicke *et al.*, 1992c), suggesting that they might possibly also present unusual biologies, although these still remain to be discovered (Brues, 1923; Cushman, 1923; Kistner, Jacobson & Elliot, 2000; Belokobylskij, 2002).

The most recent higher-level classifications of the Doryctinae are those of Fischer (1981a) and Belokobylskij (1992a, 1993). Following study of the external morphology of 34 different genera, mainly from the tropics, Fischer (1981a) proposed nine tribes, with the Doryctini further subdivided into seven subtribes (Table 1). More recently, Belokobylskij's study (1992a) reassessed the limits and composition of the Doryctinae and its tribes based on examination of the type specimens of almost all the included genera, as well as a large amount of principally Palaearctic material. This resulted in recognition of several putative generic synonymies, and the creation of three new tribes and 12 new subtribes, giving totals of 13 and 21 tribes and subtribes, respectively (Table 1). Following this, Belokobylskij (1993) assessed the evolutionary relationships among the doryctine tribes based on apparent synapomorphies but without any formal analysis. However, most of these 'synapomorphies' are better regarded simply as trends rather than all-or-nothing characters.

Table 1. Tribal and subtribal classifications of the Doryctinae proposed by Fischer (1981a) and Belokobylskij (1992a). For generic composition of these taxa see Appendix 1

Belokobylskij (1992a)		Fischer (1981a)	
Tribes	Subtribes	Tribes	Subtribes
Binareini	Acanthodoryctina	Doryctini	Binaerina
	Binaerina		Dendrosotina
Doryctini	Caenophanina		Doryctina
	Dendrosotina		Heterospilina
	Doryctina[1]		Neoclinocentrina
	Doryctomorphina[1]		Pedinotina
	Rhaconotina		Stenocorsina
Ecphylini		Ecphylini	
Evaniodini		Evaniodini	
Hecabolini	Hecabolina	Hecabolini	
	Pambolideina	Histeromerini	
	Percnobraconoidina	Odontobraconini	
	Stenocorsina	Rhaconotini	
Heterospilini		Spathiini	
Holcobraconini	Holcobraconina	Stephaniscini	
	Ivondroviina		
	Odontobraconina		
Labaniini			
Leptorhaconotini			
Percnobraconini			
Sericobraconini[2]			
Siragrini[3]			
Spathiini	Psenobolina		
	Ptesimogastrina		
	Sisupalina		
	Spathiina		
	Spathiplitina		
	Spathiostenina		
	Trigonophasmina		
Stephaniscini			
Syngastrini			

[1]Taxa with at least some of their genera currently placed in other subfamilies. [2]Placed as a tribe of the Hecabolini by Belokobylskij (1995a). [3]Proposed by Belokobylskij (1994).

As with the attempts at tribal classification, descriptions of many of the genera of Doryctinae continue to be based largely on the possession of particular character combinations, and this in turn suggests that the external morphology of this group might be quite homoplastic. Although in recent years several internal character systems have been investigated and incorporated in phylogenetic analyses within the Braconidae (e.g. Quicke & van Achterberg, 1990; Whitfield, 1992; Quicke & Belshaw, 1999; Dowton *et al.*, 2002), these have been employed primarily to investigate relationships at the subfamily level because they are still known only for a small proportion of the genera. However, surveys of these alternative character systems within the Doryctinae suggest that they may provide additional valuable phylogenetic information (e.g. Rahman, Fitton & Quicke, 1998a, b; Quicke *et al.*, 1992c).

In the present work, all the available internal and external morphological information for 143 of the 162 currently recognized doryctine genera was used for the first time to investigate their phylogenetic relationships using a comprehensive phylogenetic reconstruction method. We also compared the phylogenetic hypotheses obtained with the most recent tribe level classification for this group and explored the performance of analyses based on different character systems and proportions of missing entries.

MATERIAL AND METHODS

Taxa and characters

In this study, we considered genera as the terminal taxa, extracting information from specimens of one to a few representative species for each genus (see below). Although this approach makes a priori assumptions about the monophyly of the selected supraspecific taxa, an exemplar approach (*sensu* Yeates, 1995; Prendini, 2001) would have been impractical owing to the very small overlap between those species examined for external morphological characters and those examined for other character systems such as venom apparatus and ovipositor microsculpture.

One hundred characters were initially scored for each of the 143 included doryctine genera. A list of the genera recognized by the senior author, together with their synonyms is provided in Appendix 1. Several genera previously proposed by Belokobylskij (1992a) to form part of the Doryctinae were not considered within this group as a consequence of recent molecular and morphological studies, which have confirmed that they actually belong either to the separate, rather more basal cyclostome subfamily Rhyssalinae (namely *Rhyssalus* Haliday, *Oncophanes* Foerster, *Dolopsidea* Hincks, *Thoracoplites* Fischer, *Metaspathius* Brues and *Caenopachyella* Szépligeti), or within an enlarged concept of the Mesostoinae (e.g. *Doryctomorpha* Ashmead) (Belshaw *et al.*, 1998, 2000; Belshaw & Quicke, 2002; Belokobylskij, Iqbal & Austin, 2004; A. Zaldivar-Riverón & D. L. J. Quicke, unpubl. data).

Four characters systems were included: (1) adult external morphology; (2) male genitalia; (3) venom apparatus; and (4) ovipositor structure, including the microsculpture of the egg canal. Additionally, a single character of the cephalic larval structure was also scored. In order to incorporate the observed intra- and interspecific variation within many of the genera, variable characters were coded as polymorphic. The character states coded for each terminal taxon are given in Appendix 2. In most cases, the scoring of external characters was based on examination of the type species as well as additional taxa for each genus (see Appendix 3). No specimens were available for 29 genera, although we could incorporate ten of these by extracting external character information from their original descriptions and other references (see References in character list shown below). The remaining 19 genera could not be included in this study because their types are either lost or unavailable and their descriptions are insufficiently detailed (see genera included in Appendix 1). Data on male genitalia, ovipositor structure, venom apparatus and cephalic larval structure were assembled from direct material examination and/or from several published surveys, most of them made by the present authors (see References in character list below).

The monophyly of the Doryctinae was tested by including in the analyses several cyclostome braconid genera belonging to the Exothecinae (*Colastes* Haliday), Hormiinae (*Hormius* Nees), Rhyssalinae (*Dolopsidea*, *Rhyssalus*, *Metaspathius*), Rhysipolinae (*Rhysipolis* Foerster), Rogadinae (*Aleiodes* Wesmael, *Clinocentrus* Haliday, and *Stiropius* Cameron) and Pambolinae (*Phaenodus* Foerster), as well as the Braconinae (treated as a single terminal taxon in our analyses). Additionally, we included the poorly known genus *Monitoriella* Hedqvist, which was originally placed within the Hormiinae, although, based on its overall resemblance, some authors have argued it could actually belong to the Doryctinae (Wharton, 1993; Whitfield & Wharton, 1997). The mesostoine genus *Doryctomorpha* (see above) was designated as the outgroup because it is the least morphologically aberrant of its subfamily as now constituted (*Mesostoa* van Achterberg, *Praonopterus* Tobias, *Proavga* Belokobylskij, *Aspilodemon* Fischer, *Hydrangeocola* Bréthes). The Mesostoinae, which appear principally to be gall-associated, seems to be a suitable outgroup because in molecular studies it consistently comes out at the base of the cyclostome braconid group (Belshaw & Quicke, 2002; Dowton *et al.*, 2002).

Character sets examined

One particular problem with the character systems others than external morphology is that they have not been explored for all doryctine genera, and hence the available data contain a high proportion of missing entries. We have therefore explored the performance of the adult external morphological characters vs. the alternative character systems by analysing the following four character sets: (1) complete data, all taxa (ALL DATA); (2) only external characters, all taxa (ONLY EXTERNAL; characters 1–63); (3) only taxa with ≥ 70% scored characters (> 70% DATA); and (4) characters other than those from external morphology, including only taxa with ≥ 50% of scored characters (REPRODUCTIVE + LARVAL; characters 64–100). The genera included for the REPRODUCTIVE + LARVAL and the > 70% DATA partitions are indicated in Appendix 1.

Phylogenetic analyses

All analyses were carried out using PAUP* v.4.0b10 (Swofford, 1998). Characters with two or more states were coded as polymorphic (*sensu* Wiens, 1995). Three different performance measures for the various character sets were compared: the consistency (CI; Kluge & Farris, 1969), retention (RI; Farris, 1989) and data decisiveness (DD; Goloboff, 1991) indices. It has been noted that the CI value is influenced strongly by the number of taxa included, decreasing as the number of taxa increase (Kitching *et al.*, 1998). On the other hand, the DD has been argued to be a better indicator of phylogenetic signal because of its independence from the number of characters used (Davis *et al.*, 1998; Kitching *et al.*, 1998). Also, DD apparently reflects the intrinsic attributes of the different character sets (Davis *et al.*, 1998). Because autapomorphic states can lead to overestimation of the CI (Davis *et al.*, 1998; Kitching *et al.*, 1998), all the performance measures were calculated by substituting autapomorphic states with missing entries using MACCLADE v.4.0 (Maddison & Maddison, 2000). An approximation of the mean length of all possible trees, necessary for calculation of DD, was obtained from 100 000 randomly generated trees (using the equiprobable model).

The incongruence between the external and the remaining character systems was assessed comparing the ONLY EXTERNAL against the REPRODUCTIVE + LARVAL data sets using the incongruence length difference (ILD; Farris *et al.*, 1994) test with 500 replicates and 100 random additions. The test was run using only those taxa contained in the REPRODUCTIVE + LARVAL data set.

Preliminary analyses showed the data set to be particularly difficult to analyse in terms of time, so we employed the search strategy of Quicke, Taylor & Purvis (2001) (QHS) for large data sets to try to recover the most parsimonious trees for each of the four character sets examined. The initial search with this strategy with equally weighted, unordered characters was carried out using 10 000 random additions with TBR swapping, holding only one tree from each addition. The subsequent iterative searches used a variety of weighting functions (maximum and minimum values of retention and consistency indices). Owing to the computational constraints imposed by the data sets, maxtrees was set at 30 000 and clade support was evaluated using a nonparametric bootstrap (Hillis & Bull, 1993) with 100 replicates and 100 random additions holding only one tree (which was consequently very conservative). Two successive approximations weighting (SAW) analyses (Farris, 1969; Carpenter, 1994) were performed for the ALL DATA set starting from the most parsimonious trees found by the QHS analyses, using the maximum and minimum retention indices separately as the reweighting function (MaRI and MiRI, respectively). We considered the strict consensus trees derived from the latter two analyses as our best phylogenetic hypotheses. The relationships recovered in the strict consensus of all analyses were compared with the previous tribal and subtribal classification of the Doryctinae made by the senior author (Belokobylskij, 1992a). Within this classification we also considered the tribal and subtribal placements suggested for several genera that were described posteriorly (Belokobylskij, 1992b, 1994, 1995b, 1998a, 2000, 2001, 2002; Belokobylskij & Quicke, 2000).

The Wilcoxon signed-ranks test (Templeton, 1983; Felsenstein, 1985) was used to test significance of differences between a randomly chosen sample of 100 of both the most parsimonious trees found for the four character sets analysed and those found in alternative analyses constraining the two largest tribes, Doryctini and Hecabolini (*sensu* Belokobylskij, 1992a), each to be monophyletic (one-tailed probability is presented). Alternative phylogenetic hypotheses were obtained using the QHS strategy as described above.

Characters

External morphology

Terminology follows that of Sharkey & Wharton (1997) except for wing vein terminology, which follows Tobias (1976) [van Achterberg's (1979) wing venation terminology is included in parentheses]. References for the genera whose specimens were not available for examination of external morphological characters are: Ashmead (1900); Cushman (1923); Beardsley (1961); Fischer (1981b); Marsh (1983); Quicke & van Achterberg (1990); van Achterberg, 1995); Barbalho, Penteado-Dias & Marsh (1999); Barbalho & Penteado-Dias, 2002); Kistner *et al.* (2000).

1. *Scape*: 0 = less than two times longer than maximally wide (e.g. Fig. 1G); 1 = two or more times longer than maximally wide. The character 'scape with or without transformations' was included in a previously study (Belokobylskij, 1993); however, modifications of the scape are complex and therefore here we have subdivided that character into three separate ones.
2. S*cape*: 0 = without apical lobe (e.g. Fig. 1G, L); 1 = with apical lobe (e.g. Fig. 1H, J).
3. *Apical lobe of scape, if present, then*: 0 = simple (e.g. Fig. 1H, J); 1 = compound, with a distinct process margined by strong lateral carinae (e.g. Belokobylskij, 1994: fig. 4). The presence of an apical lobe of scape with a distinct process margined by strong lateral carinae was previously proposed as one of the characters that define the tribe Siragrini (Belokobylskij, 1994).
4. *Dense cluster of setae on apical margin of scape and pedicel*: 0 = absent (e.g. Fig. 1H, J); 1 = present (e.g. Fig. 1I, K).

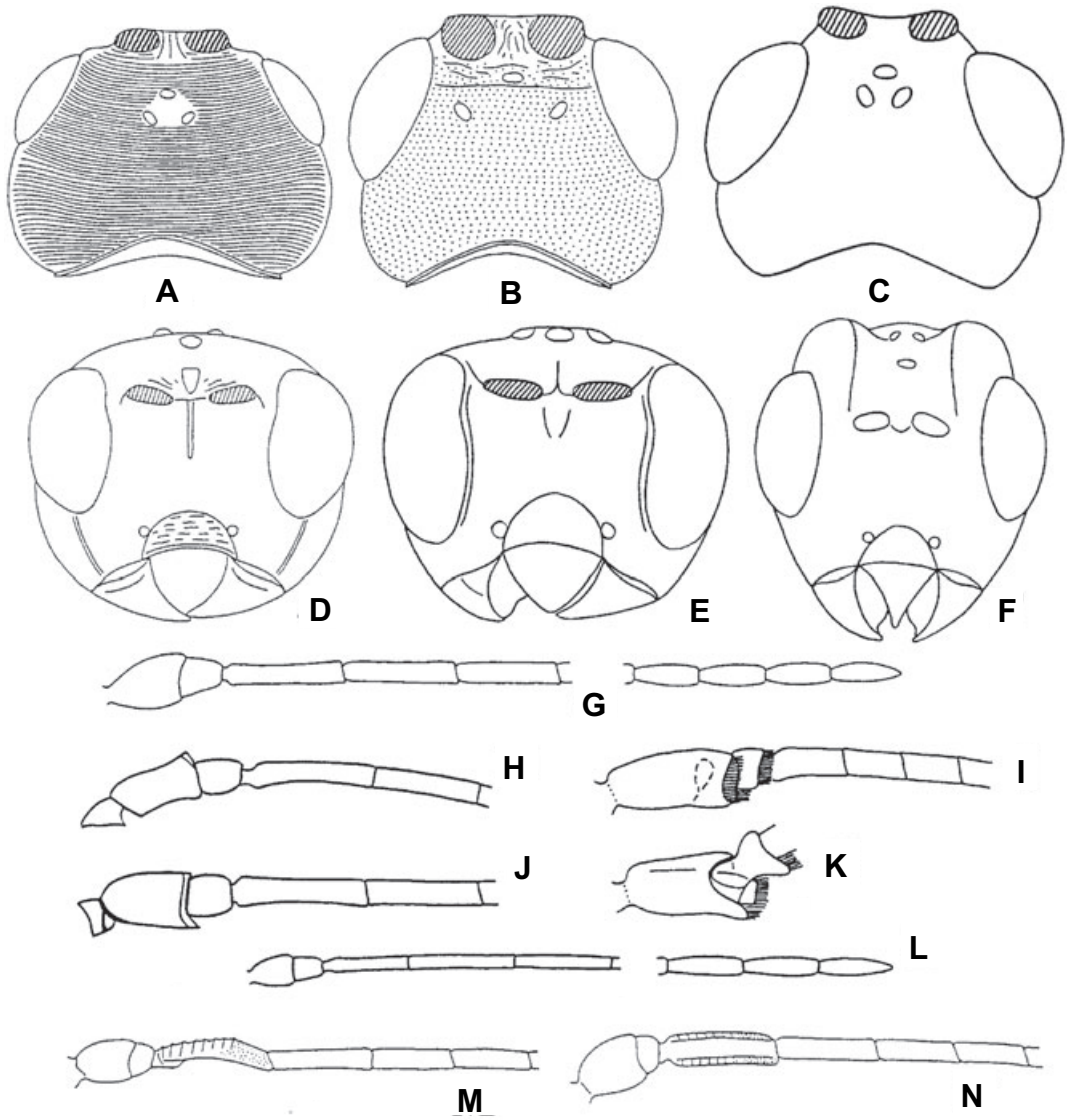

Figure 1. External morphological features in the Doryctinae. A–C, head, dorsal view; D–F, head, frontal view; G–N, basal and apical segments of antenna (dorsal and lateral views). A, *Rhoptrocentrus cleopatrae* Belokobylskij; B, M, N, *Sonanus senzuensis* Belokobylskij & Konishi; C, *Bracodoryctes tergalis* Belokobylskij & Quicke; D, *Doryctes germanicus* Belokobylskij; E, *Stephanospathius ornatipes* (Kieffer); F, *Schlettereriella rufithorax* (Szépligeti); G, *Platyspathius hospitus* Belokobylskij & Ku; H, J, *Synspilus nitidus* Belokobylskij & Quicke; I, K, *Binarea spinicollis* Brullé; L, *Ecphylus brevitergum* Belokobylskij.

5. *First flagellar segment*: 0 = longer than second (e.g. Fig. 1H, I); 1 = equal to or shorter than second (e.g. Fig. 1L). An equal or shorter first flagellar segment, secondary lost of basoventral tubercle on hind coxa, absence of dorsope on the first tergite, and presence of a propodeal bridge were proposed by Belokobylskij (1993) as putative synapomorphies for the Stephaniscini.
6. *First flagellar segment*: 0 = regularly smooth or finely sculptured (e.g. Fig. 1H, K); 1 = smooth dorsally, strongly sculptured ventrally (e.g. Fig. 1M, N).
7. *Maxillary palpi*: 0 = six-segmented; 1 = five-segmented; 2 = four-segmented; 3 = three-segmented (e.g. van Achterberg, 1995: fig. 46); 4 = two-segmented (e.g. van Achterberg, 1995: fig. 56); 5 = one-segmented. Reductions in the number of palpar segments appear to be a widespread trend in ichneumonoids (Tobias, 1967; van Achterberg, 1988). Within the Doryctinae, a maxillary labial palp formula 5 + 3 has been used to define the Ecphylini (Belokobylskij, 1993).
8. *Labial palpi*: 0 = four-segmented; 1 = three-segmented; 2 = two-segmented (e.g. van Achterberg, 1995: fig. 46); 3 = one-segmented; 4 = absent (e.g. van Achterberg, 1995: fig. 56). See character 7.
9. *Third labial palp segment*: 0 = as long as or longer than second; 1 = distinctly shorter than second (e.g. Belokobylskij & Quicke, 2000: fig. 113).
10. *Malar suture*: 0 = absent (e.g. Fig. 1E, F); 1 = present (e.g. 1D). Reference: Belokobylskij (1993).
11. *Frons*: 0 = without lateral protuberances (e.g. Fig. 1D, E); 1 = with lateral protuberances (e.g. 1F).
12. *Occipital carina*: 0 = present (e.g. Fig. 1A, B); 1 = absent (e.g. Fig. 1C). The complete absence of an occipital carina was for a long time considered as a synapomorphy that distinguishes the Braconinae from the Doryctinae (Quicke & van Achterberg, 1990). However, this condition is also present in members of the Opiinae (e.g. *Desmiostoma* Fischer), as well as in a few members of other cyclostome subfamilies, including several Doryctinae.
13. V*ertex*: 0 = not striate (e.g. Fig. 1B, C); 1 = striate (e.g. Fig. 1A).
14. V*ertex, if not striate*: 0 = not granulate or rugulose-granulate (e.g. Fig. 1C); 1 = granulate or rugulose-granulate (e.g. Fig. 1B). Scored as '?' if vertex striate.
15. *Pronotum*: 0 = dorsally without modifications or with convex lobe (e.g. Marsh, 1988: fig. 22); 1 = with pointed spines or tubercles (e.g. Belokobylskij, 1992a: fig. 20; Fig. 2A). Spines or tubercules on the pronotum and the strongly enlarged submedial cell of hind wing were considered by Belokobylskij (1992a, 1993) as synapomorphies that distinguish members of the tribe Binareini.
16. *Pronotum*: 0 = dorsally without modifications or with spines or tubercles; 1 = with convex lobe (e.g. Marsh, 1988: fig. 22) (1).
17. *Notauli*: 0 = complete or at least partly present (e.g. Marsh, 1993: fig. 14; Fig. 2F); 1 = entirely absent (e.g. Belokobylskij & Quicke, 2000: fig. 86).
18. *Prescutellar depression (scutellar sulcus)*: 0 = long and narrow or of medium length; 1 = considerably shortened (e.g. Achterberg, 1995: figs 35, 55).
19. *Prepectal carina*: 0 = present (e.g. Fig. 2D); 1 = absent (e.g. Fig. 2B).
20. *Propodeal bridge between abdominal and coxal foramina*: 0 = absent; 1 = present (e.g. Fig. 2G). The presence of a propodeal bridge between abdominal and coxal foramina was mentioned as a putative synapomorphy for the Percnobraconini, Stephaniscini and Evaniodini (Belokobylskij, 1993). It is also associated with the transformation of abdominal tergite 1 into a petiole and elevation of the metasomal insertion (as in Evaniodini).
21. *Propodeal bridge between abdominal and coxal foramina (if present)*: 0 = narrow (e.g. Fig. 2G); 1 = very wide so metasoma is inserted near the top of propodeum. A wide propodeal bridge between abdominal and coxal foramina was stated by Belokobylskij (1993) as a synapomorphy for the members of the Evaniodini.
22. *Propodeum*: 0 = completely or partly sculptured (e.g. Fig. 2E); 1 = almost entirely smooth.
23. *Propodeal carinated areas*: 0 = present at least basally (e.g. Fig. 2E); 1 = completely absent.
24. *Radial (marginal) cell of fore wing*: 0 = distally closed (e.g. Fig. 3A–E); 1 = open (e.g. Figs 3F, 4A). An open radial cell was proposed as an autapomorphy for the Labaniini (Belokobylskij, 1993). However, this condition is also present in other doryctine genera.
25. *Second radiomedial vein (r-m) of fore wing*: 0 = present (e.g. Fig. 3A–E); 1 = absent (e.g. Figs 3F, 4C, E, G). Absence of the second radiomedial vein together with a short cuspis of the volsella are trends that were employed by Belokobylskij (1993) to define the members of the Hecabolini.
26. *Second radiomedial vein (r-m) of fore wing, when present*: 0 = with wide bulla (e.g. Fig. 3A–E); 1 = largely tubular (e.g. Fig. 4H; Marsh, 1997: figs 16, 18, 30).

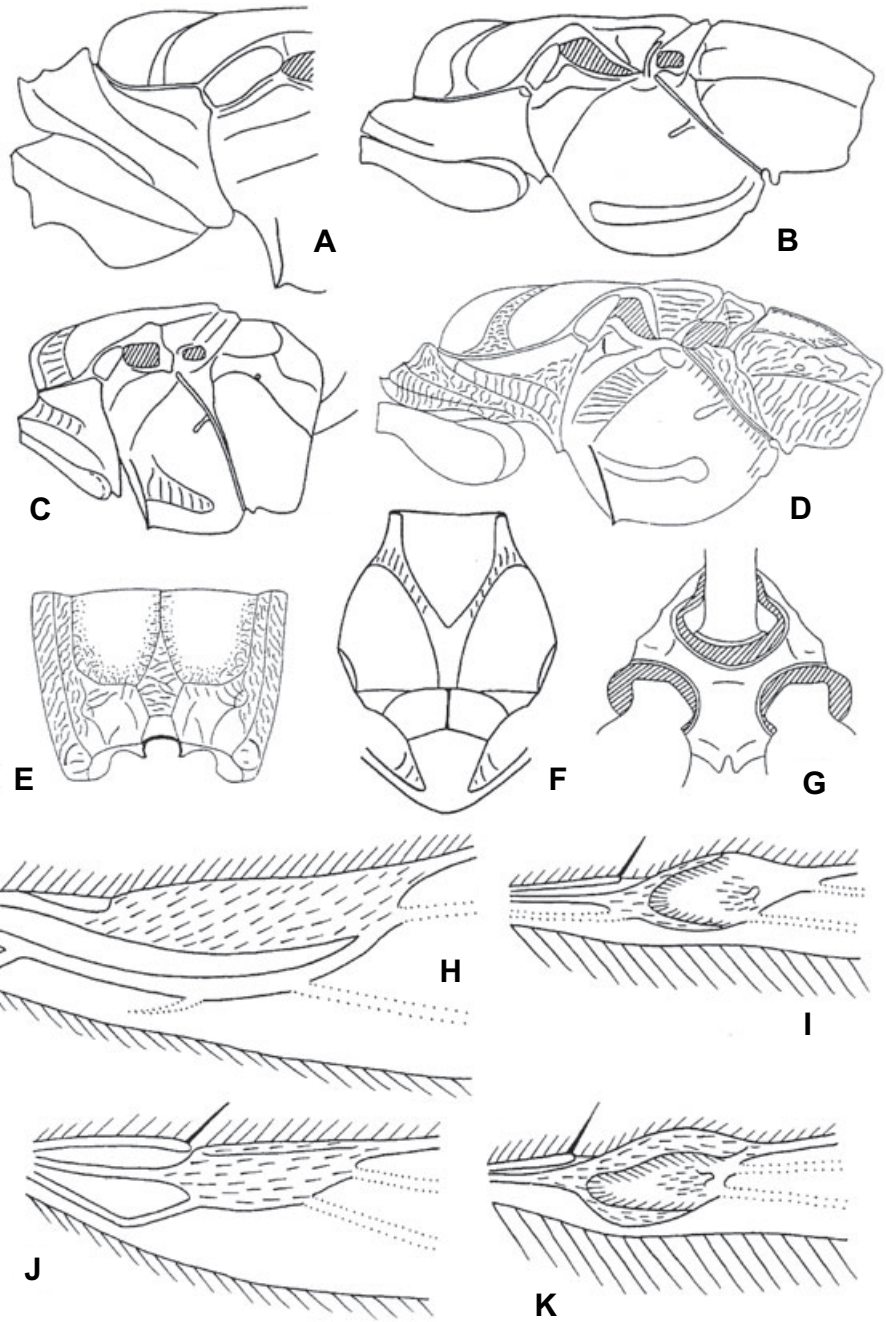

Figure 2. External morphological features in the Doryctinae. A, anterior part of mesosoma, lateral view; B–D, mesosoma, lateral view; E, areas of propodeum; F, mesonotum; G, propodeum, view from behind; H–K, stigma-like enlargement of the hind wing in male. A, *Binarea spinicollis* Brullé; B, *Bracodoryctes tergalis* Belokobylskij & Quicke; C, *Evaniodes areolaris* Szépligeti; D, E, *Doryctes germanicus* Belokobylskij; F, *Fijibracon insularis* Belokobylskij; G, *Stephanospathius ornatipes* (Kieffer); H, *Dendrosoter middendorffi* (Ratzeburg); I, *Heterospilus orientalis* Belokobylskij; *Leluthia asiatica* (Tobias); J, K, *H. separatus* Fischer.

27. *Second radiomedial vein (r-m) of fore wing, if largely tubular*: 0 = with posterior bulla only (e.g. Marsh, 1997: fig. 18); 1 = with two bullae (e.g. Marsh, 1997: fig. 30); 2 = totally sclerotized (e.g. Fig. 4H; Marsh, 1997: fig. 16).

28. *First radiomedial vein (2-SR) of fore wing*: 0 = present (e.g. Fig. 3E, F); 1 = absent or strongly unsclerotized for the most part (e.g. Figs 3B, D, 4A, E, G). An absent or weakly sclerotized first radiomedial vein together with a

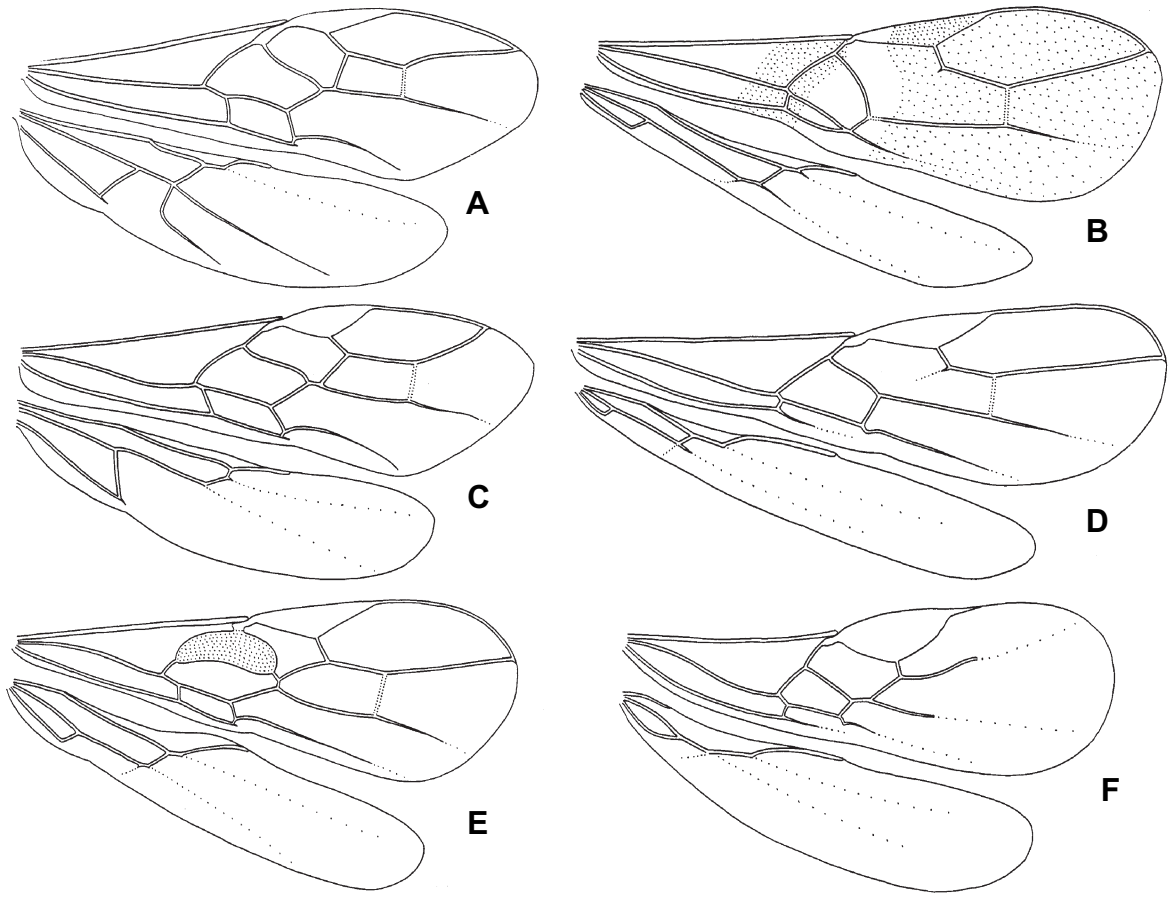

Figure 3. External morphological features in the Doryctinae. Wing venation characters, fore and hind wings. A, *Holcobracon fulvus* Cameron; B, *Caenophanes luculentus* Belokobylskij; C, *Acanthodoryctes morleyi* (Froggatt); D, *Heterospilus tirnax* Papp; E, *Neurocrassus fabimaculatus* Belokobylskij; F, *Pambolidea yuma* Ashmead.

shortened basal ring of male genitalia were features proposed by Belokobylskij (1993) as defining the Heterospilini.

29. *Recurrent vein (m-cu) of fore wing*: 0 = postfurcal (e.g. Figs 3E, 4D, H); 1 = antefurcal or interstitial (e.g. Fig. 3A, C).
30. *Nervellus* (*cu-a) of fore wing*: 0 = postfurcal or interstitial (e.g. Fig. 3A–F); 1 = antefurcal (e.g. Fig. 4E).
31. *Parallel vein (CU1a) relative to cubital vein (2-CU1) of fore wing*: 0 = not interstitial, arising behind middle of distal vein of brachial cell (e.g. Fig. 4D); 1 = interstitial (e.g. Fig. 4F); 2 = not interstitial, arising before or from middle of distal vein of brachial cell (e.g. Fig. 3C, E). Scored as missing data if brachial cell opens distally (see character 32, state 1).
32. *Brachial (1st subdiscal) cell of fore wing*: 0 = distally closed (e.g. Fig. 4B, D, F, H); 1 = open (e.g. Fig. 4A, C). Belokobylskij (1993) proposed that an open brachial cell together with a stigma-like swelling on the hind wing of males, the absence of the volsellar apodema of male genitalia, and the complete or partial transition to unique hosts are useful trends suggesting a close relationship between the Hecabolini and the Heterospilini. Furthermore, the first of these characters, together with hind wing vein R1 being completely or nearly absent, were proposed by Belokobylskij (1993) as trends that group the Labanini + Sericobraconini, although the latter was subsequently synonymized with the Hecabolini (Belokobylskij, 1995a).
33. *Fore wing of male*: 0 = without sclerotized enlargement, including veins 1-m and 1-SR + m (e.g. Fig. 3A–D); 1 = with sclerotized enlargement (e.g. Fig. 3E). Two genera, *Neurocrassus* Snoflak and *Bulvonervus* Shenefelt, have the anterior parts of the first abscissa of medial veins of the fore wing evidently widened and sclerotized.
34. *Number of distal hamuli*: 0 = four to eight;

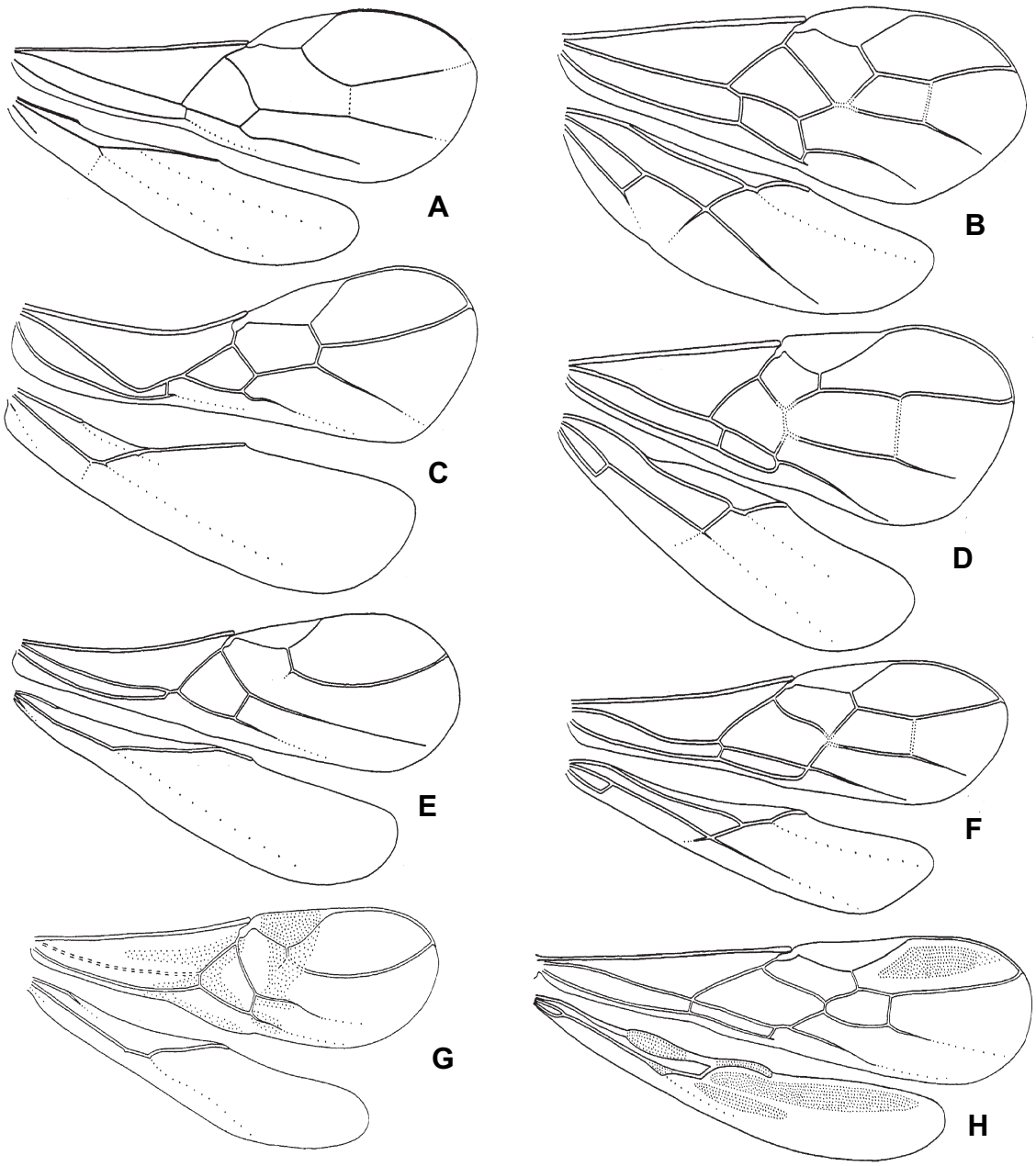

Figure 4. External morphological features in the Doryctinae. Wing venation characters, fore and hind wings. A, *Labania straminea* Hedqvist; B, *Doryctes fulviceps* Reinhard; C, *Percnobracon secundus* Muesebeck; D, *Dendrosoter hartigi* (Ratzeburg); E, *Fijibracon insularis* Belokobylskij; F, *Rhaconotus insularis* Belokobylskij; G, *Nipponecphylus matsumurai* Belokobylskij & Konishi; H, *Doryctophasmus ferrugineiceps* Enderlein.

1 = three. Hamuli are hook-like setae on the anterior margin of the hind wing, which interlock with the recurved posterior edge of the forewing in the Hymenoptera during flight (Basibuyuk & Quicke, 1997). The number of basal hamuli has been shown to be size related in Braconinae (Quicke, 1981) and therefore the number of distal hamuli may also be.

35. *Transverse vein (r) of radial cell of hind wing*: 0 = absent (e.g. Fig. 3B, F); 1 = present (e.g. Marsh, 1997: fig. 12).
36. *Recurrent vein (m-cu) of hind wing*: 0 = present (e.g. Figs 3A, F, 4C); 1 = absent (e.g. Fig. 3C).
37. *Recurrent vein (m-cu) of hind wing (if present)*: 0 = not curved strongly towards apex of wing (e.g. Fig. 4A–D); 1 = strongly curved to apex of wing

(e.g. Fig. 3A). A strong curvature of the recurrent vein towards the apex of the hind wing together with male parameres narrowed along their entire length have previously been suggested a synapomorphies that define the Holcobraconini (= Odontobraconini) (Marsh, 1970; Belokobylskij, 1992a).

38. *Nervellus (cu-a) of hind wing*: 0 = present (e.g. Figs 3E, 4B); 1 = absent (e.g. Fig. 4A, E). Loss of nervellus in the hind wing was suggested by Belokobylskij (1993) as a synapomorphy for the Labaniini, Percnobraconini, Ecphylini and Sericobraconini, although it is also lost in a number of other cyclostome braconids such as *Acrisis*, *Chremylomorpha*, *Cedria*, and *Austrohormius*, as well as in many Aphidiinae.
39. *Stigma-like enlargement in hind wing of male*: 0 = absent (e.g. Fig. 3A, C); 1 = present in distal part of costal (1-SC + R) vein, without incurved marginal parts (e.g. Fig. 2H–K). See character 32.
40. *Stigma-like enlargement in hind wing of male, if present then*: 0 = formed only as widening of the distal part of costal (1-SC + R) vein (e.g. Fig. 2H); 1 = including distal parts of costal (1-SC + R), mediocubital (M + CU, 1-M), and basal (1r-m) veins (e.g. Fig. 2I–K).
41. *Submedial (subbasal) cell of hind wing*: 0 = small or medium sized, first abscissa of M + CU 0.2–1.0 times as long as second abscissa (1-m) (e.g. Fig. 3B, D); 1 = distinctly enlarged, first abscissa of M + CU 1.5–2.0 times as long as second abscissa (e.g. Fig. 3A, C). See character 15.
42. *Medial (basal) cell of hind wing*: 0 = closed (e.g. Fig. 3E); 1 = widely open antero-distally (e.g. Fig. 4G).
43. *Fore tibial spines*: 0 = absent; 1 = present (e.g. Fig. 5G; Marsh, 1997: figs 65–67). The presence

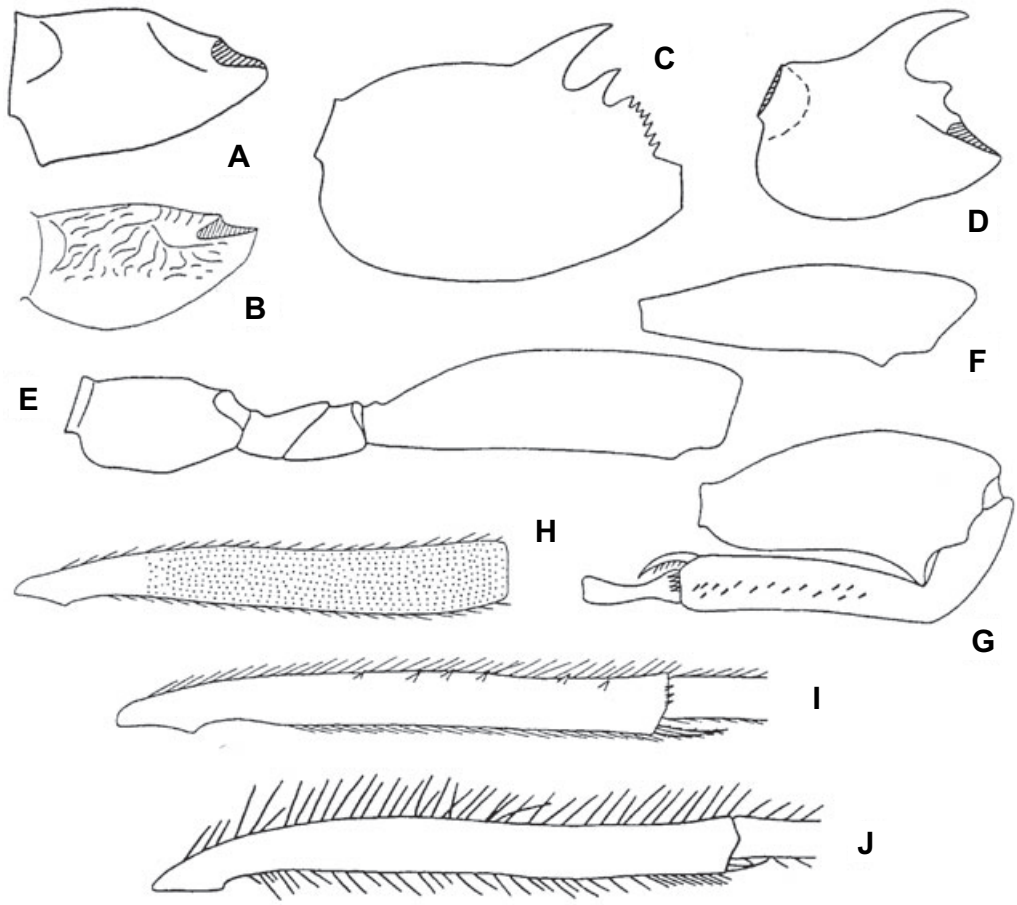

Figure 5. External morphological features in the Doryctinae. A–D, Hind coxa; E, hind coxa, trochanter, trochantellus and femur; F, fore femur; G, fore femur, tibia and basitarsus; H, I, J, hind tibia. A, J, *Bracodoryctes tergalis* Belokobylskij & Quicke; B, I, *Sonanus senzuensis* Belokobylskij & Konishi; C, *Priosphys denticulata* Enderlein; D, *Liodoryctes australiensis* (Szépligeti); E, F, *Termitospathius sumatranus* Belokobylskij; G, *Ceylonspathius nixoni* Belokobylskij; *Rhoptrocentrus cleopatrae* Belokobylskij.

of a row of spines on the outer face of the fore tibia has been considered as an apomorphic, diagnostic condition that distinguishes the subfamily Doryctinae, including also the Ypsistocerini (Marsh, 1965; van Achterberg, 1984). However, several presumably specialized genera lack them (e.g. *Sericobracon* Shaw, *Embobracon* van Achterberg, *Leptorhaconotus* Granger, and some species of *Halycaea* Cameron; van Achterberg, 1995; Quicke, 1996). Additionally, at least weak spines forming a row are present in some braconines, rhyssalines (*Rhyssalus* Haliday) and in the rogadine genus *Yelicones* Cameron (van Achterberg, 1995; Chishti & Quicke, 1995; Quicke & Kruft, 1995; Belokobylskij, 1998b).

44. *Fore tibial spines, if present*: 0 = more or less numerous and dispersed (e.g. Fig. 5G); 1 = usually few and forming a single row (e.g. Marsh, 1997: figs 65–67). See character 43.
45. *Subapical teeth on fore and middle femora*: ventrally 0 = absent; 1 = present (e.g. Fig. 5F, G).
46. *Dorsal spines of hind tibia*: 0 = absent (e.g. Fig. 5H, J); 1 = present (e.g. Fig. 5I).
47. *Basoventral tooth of hind coxa*: 0 = absent (e.g. Fig. 5B–D; Marsh, 1997: fig. 64); 1 = present (e.g. Fig. 5A; Marsh, 1997: fig. 63)(1). The presence of a basoventral tooth on the hind coxa was an important feature employed by Marsh (1997, 2002) in his identification keys for the New World and Costa Rican doryctine genera. However, in Belokobylskij's (1992a) classification this character is variable within most of his proposed tribes.
48. *Hind coxa*: 0 = dorsally without teeth (e.g. Fig. 5A, B, E); 1 = with one to several teeth (e.g. Fig. 5C, D).
49. *Dorsope of first metasomal tergite*: 0 = present and more or less distinct; 1 = very small or indistinct. A distinctive dorsope was mentioned by Barbalho *et al.* (1999) as one of the features that distinguish the Heterospilini from the Spathiini.
50. *Acrosternite of first metasomal tergite*: 0 = short, nearly 0.2–0.25 as long as tergite, not fused with ventral margins of tergite, petiole absent (e.g. Fig. 6F); 1 = long, 0.3–0.5 as long as tergite and fused with its ventral margin anteriorly, petiole present, but incomplete (e.g. Fig. 6D, E); 2 = very long, 0.6–0.85 as long as tergite and entirely fused with it ventral margin, petiole present and long (Fig. 6A, B). An elongated acrosternite is the typical condition found in the Spathiini, Stephaniscini, Evaniodini, Leptorhaconotini and Percnobraconini (Belokobylskij, 1993).
51. *First and second tergites*: 0 = not fused (e.g. Fig. 5G–J); 1 = fused (e.g. Belokobylskij, 2000: figs 10, 11, 23, 24; Barbalho & Penteado-Dias, 2002: fig. 4).
52. *Laterotergites*: 0 = not separated from each other; 1 = separated from each other for at least second and third tergites.
53. *Laterotergites, if separated*: 0 = separated only at second and third tergites; 1 = separated at all tergites.
54. *Second metasomal tergite:* 0 = without apical lenticulate area (e.g. Fig. 6B, E); 1 = with apical lenticulate area (e.g. Fig. 6F, I).
55. *Second metasomal tergite*: 0 = without basal area (e.g. Fig. 6B, F); 1 = with basal area (e.g. Fig. 6G–J). An oval raised area on the second metasomal tergite is a variable character but it is shared by most of the members of the Holcobraconini (= Odontobraconini) (Marsh, 1970).
56. *Basal area of second tergite (if present)*: 0 = connected with second suture (e.g. Fig. 6G, H); 1 = separate from second suture (e.g. Fig. 6I).
57. *Basal area of second tergite (if present and joined with second suture)*: 0 = posteriorly wide, width of its apical part subequal to or slightly less than basal width (e.g. Fig. 6G, J); 1 = narrow, width of its apical part significantly less than basal width (e.g. Fig. 7A, B). An oval raised area on the second metasomal tergite is present in most of the members of the Holcobraconini (= Odontobraconini; Marsh, 1970).
58. *Third metasoma tergite*: 0 = without any transverse narrow depression (e.g. Fig. 6B, F, G); 1 = with a distinct transverse narrow depression (furrow) usually between its anterior third and the middle (e.g. Fig. 6H).
59. *Second metasomal suture*: 0 = present (e.g. Fig. 7C, D, F); 1 = largely or entirely absent (e.g. Figs 6B, E, 7E).
60. *Second metasomal suture*: 0 = straight or evenly curved (e.g. Fig. 7F); 1 = with more or less distinct lateral angulations (e.g. Fig. 6H, J); 2 = with distinct median bend (e.g. Marsh, 1997: fig. 72).
61. *Fifth or sixth metasomal tergites*: 0 = not enlarged, not covering succeeding tergites and entirely smooth (e.g. Fig. 7A, B); 1 = more or less distinctly enlarged, covering succeeding tergites and sculptured at least basally (e.g. Fig. 7C, D, F).
62. *Fourth-sixth metasomal tergites of males*: 0 = simple; 1 = with crenulate basal furrows (e.g. Fig. 7B).
63. *Fourth-sixth metasomal tergites of male*: 0 = simple; 1 = with submarginal lateral carinae (e.g. Fig. 7E).

Male genitalia

References: Tobias (1961, 1967); Quicke & van Achterberg, 1990); Belokobylskij (1987); Quicke (1996); Kistner *et al.* (2000).

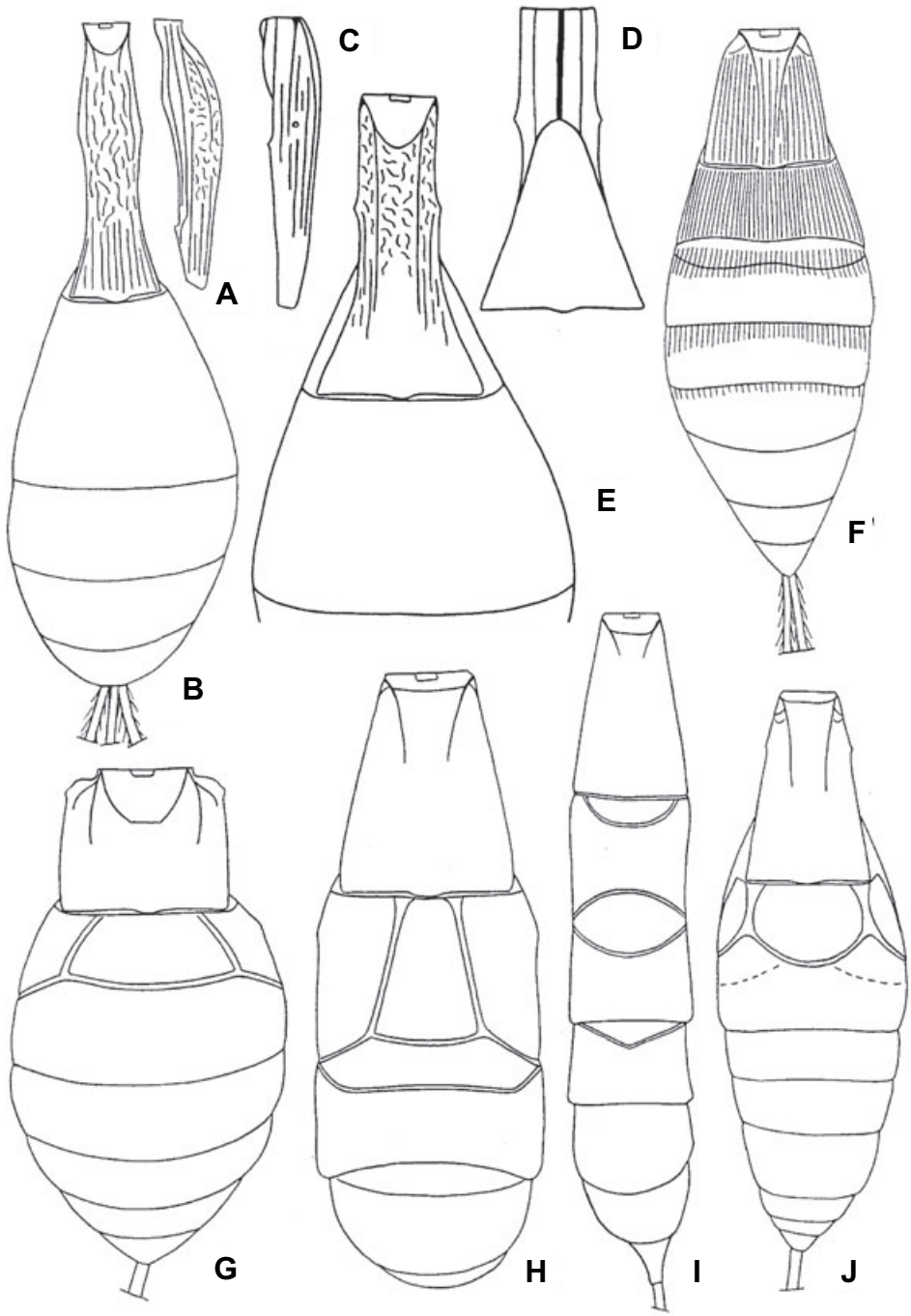

Figure 6. External morphological features in the Doryctinae. A, C, first metasomal tergite, lateral view; B, F–J, metasoma, dorsal view; D, first tergite, ventral view; E, first-third metasomal tergites, dorsal view. A, B, *Spathius wusheensis* Belokobylskij; C–E, *Fijibracon insularis* Belokobylskij; F, *Heterospilus hemitestaceus* Belokobylskij; G, *Liodoryctes australiensis* (Szépligeti); H, *Glyptocolastes rugulosus* (Cresson); I, *Bathycentor kraesselini* Saussure; J, *Siragra nitida* Cameron.

64. *Basal ring* (gonobase): 0 = short (e.g. Fig. 8C, D); 1 = medium sized (e.g. Fig. 8A); 2 = markedly elongated (e.g. Fig. 8H). See comment in character 28.
65. *Dorsal bridge of basal ring*: 0 = closed (e.g. Fig. 8A, B); 1 = open (e.g. Fig. 8D).
66. *Dorsal bridge of basal ring*: 0 = wide; 1 = very narrow (e.g. Fig. 8A, C).
67. *Basal lobe of basal ring*: 0 = absent (e.g. Fig. 8A, C); 1 = present (e.g. Fig. 7B, G).
68. *Parameres*: 0 = wide and roundly triangular;

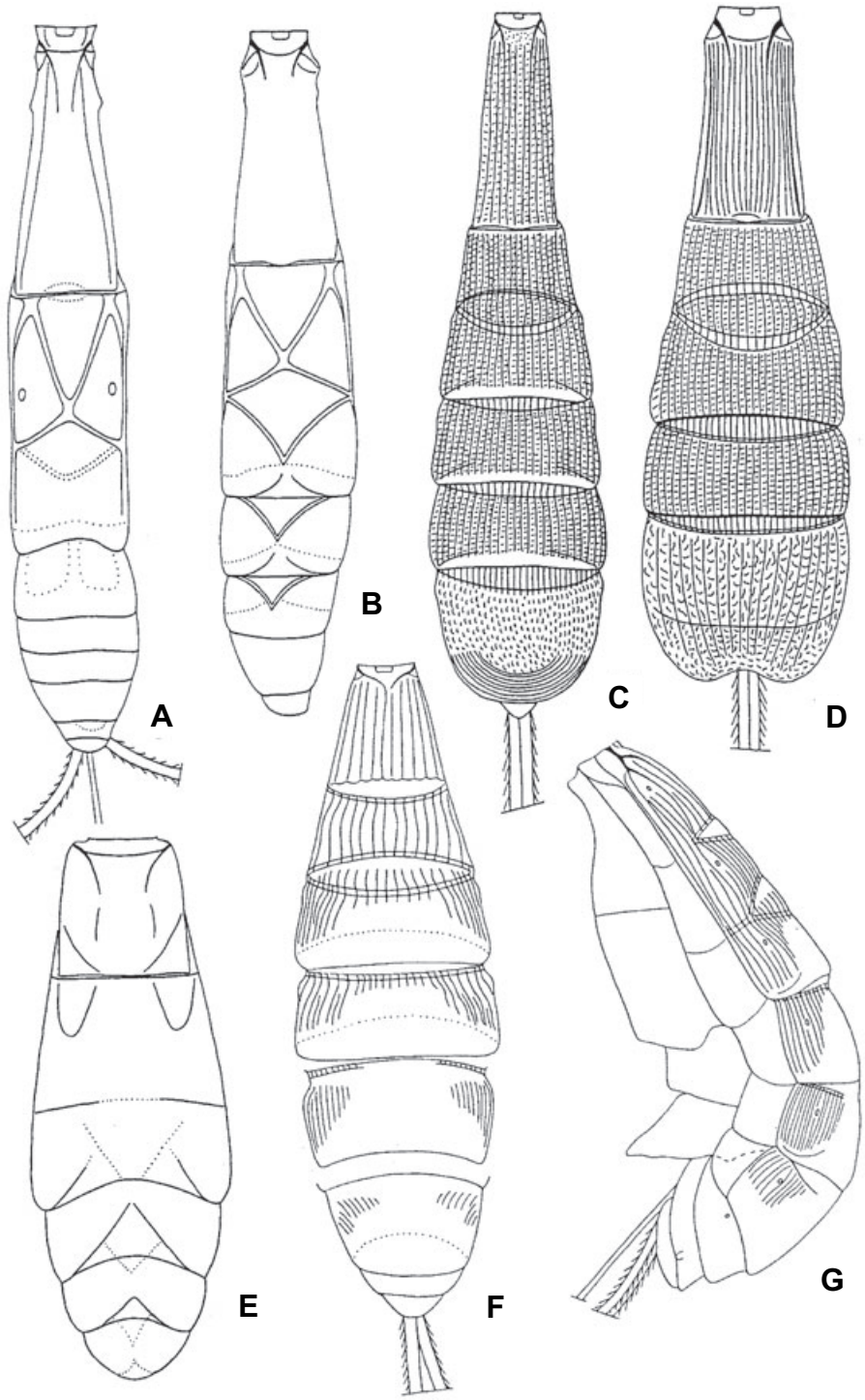

Figure 7. External morphological features in the Doryctinae. A, C, D, F, G, female; B, E, male. A–F, metasoma, dorsal view; G, metasoma, lateral view. A, B, *Halycaea rubata* Belokobylskij; C, *Rhaconotus ceylonicus* Belokobylskij; D, *R. excavatus* Belokobylskij; E, *Dendrosoter hartigii* (Ratzeburg); F, G, *Arhaconotus papuanus* Belokobylskij.

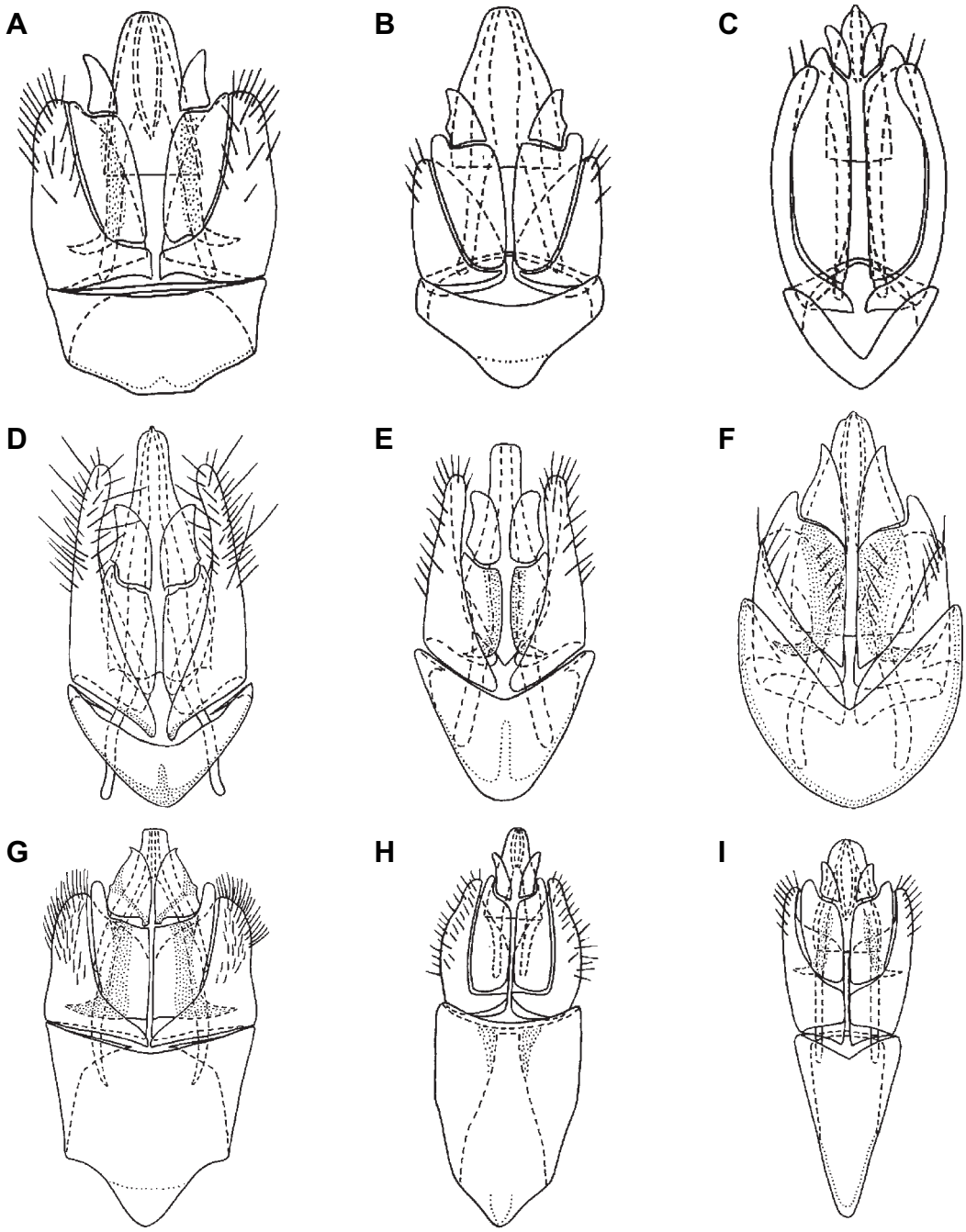

Figure 8. Male genitalia in the Doryctinae. A, *Doryctes striatellus* (Nees); B, *Hecabolus sulcatus* Curtis; C, *Euscelinus sarawacus* Westwood; D, *Monarea* sp.; E, *Zombrus bicolor* Enderlein; F, *Acanthodoryctes morleyi* (Froggatt); G, *Syngaster lepidus* Brullé; H, *Ecphylus silesiacus* (Ratzerburg); I, *Dendrosoter protuberans* Wesmael.

1 = partly narrowed distally (e.g. Fig. 8A, I); 2 = considerably narrowed along whole length (e.g. Fig. 8E). See comment of character 37.

69. *Parameres*: 0 = well developed (e.g. Fig. 8E); 1 = very short, not reaching the middle of digitus (e.g. Fig. 8I).
70. *Setosity of parameres*: 0 = dense (e.g. Fig. 8D); 1 = sparse (e.g. Fig. 8C).
71. *Volsellar apodemes*: 0 = present; 1 = absent. See character 32.
72. *Cuspis of volsella*: 0 = long; 1 = short. See comment of character 25.

Venom apparatus

References: Quicke & van Achterberg, 1990); Quicke *et al.* (1992c); Quicke (1996); Zaldivar-Riveron *et al.*, 2004).

73. *Venom reservoir*: 0 = undivided (e.g. Fig. 9B); 1 = divided (e.g. Fig. 9A).
74. *If venom reservoir divided*, *then comprising*: 0 = two parts (e.g. Fig. 9A); 1 = three parts.
75. *If reservoir undivided, then*: 0 = ovoid; 1 = tubular (e.g. Fig. 9B). Some genera of Holcobraconini and the two genera of Binareini have an elongated, more or less parallel-sided and finely sculptured venom reservoir (Quicke *et al.*, 1992c)
76. *Posterior of venom gland*: 0 = narrow; 1 = wide and hemispherical.
77. *Spiral sculpture of venom reservoir*: 0 = normal; 1 = posteriorly much courser than anteriorly.
78. *Base of secondary venom duct*: 0 = simple (e.g. Fig. 9C, D); 1 = swollen, horn-shaped (e.g. Fig. 9E).
79. *Number of separate insertions of the venom gland on to the reservoir or primary duct*: 0 = one (e.g. Fig. 9C); 1 = two (e.g. Fig. 9D, E) (1); 2 = more than two (Quicke *et al.*, 1992c: fig. 1a).
80. *Pair of blind-ended protuberances from the primary duct arising just posterior to the insertions of the venom glands:* 0 = absent (e.g. Fig. 9D); 1 = present.
81. *Primary venom duct and base of reservoir*: 0 = with spiral or 'hexagonal-like' sculpture; 1 = glandular, with simple ductules (e.g. Fig. 9F); 2 = glandular, with vase-shaped ductules. The primary duct and base of the reservoir of all doryctines and braconines lack spiral sculpture and instead is densely supplied with secretory ductules; however, whereas in all the braconines these ductules open into a vase-shaped chamber, in all the doryctines they are much simpler (Quicke *et al.*, 1992c).

Ovipositor system

References: Quicke, Ficken & Fitton (1992a); Quicke, Ingram & Fitton (1992b); Quicke, Fitton & Harris (1995); Quicke (1996); Rahman *et al.* (1998a, b).

82. *Ovipositor nodus*: 0 = single (e.g. Quicke *et al.*, 1992a: figs 9–11); 1 = double, with a second node weakly developed (e.g. Quicke *et al.*, 1992a: fig. 12); 2 = double, with both nodus well developed (e.g. Quicke *et al.*, 1992a: figs 1–8). A double nodus was suggested by Quicke *et al.* (1992a) as a uniquely derived, diagnostic feature for the Doryctinae, including *Ypsistocerus* Cushman, though it has been suggested that it was probably secondarily lost in some species of *Spathius* Nees and *Heterospilus* Haliday (Quicke & Marsh, 1992). It is also present in several xoridine ichneumonids, in the genus *Mesostoa*, and in few opiines (Quicke *et al.*, 1992a; Kimani-Njogu & Wharton, 2002).
83. *Number of valvilli*: 0 = two or more; 1 = one or zero (e.g. Rahman *et al.*, 1998b: fig. 1c, e).
84. *Ovipositor apex*: 0 = weakly or not sclerotized; 1 = heavily sclerotized and typically black (Quicke *et al.*, 1992a: figs 26–28). A sclerotized apex is found in virtually all members of the Doryctinae, including *Termitobracon* Brues (Quicke *et al.*, 1992a). It also occurs in New World members of the rogadine genus *Yelicones* (Quicke & Kruft, 1995).
85. *Valvillus of lower ovipositor valve*: 0 = present and well developed; 1 = reduced and very thin; 2 = absent.
86. *Position of the valvillar insertion*: 0 = medial; 1 = close to the dorsal edge of the egg canal (e.g. Rahman *et al.*, 1998b: fig. 2d, e).
87. *Bars posterior to valvillus or valvillar zone:* 0 = absent; 1 = present.
88. *Bars anterior to valvillus or valvillar zone*: 0 = absent; 1 = present. The presence of bars anterior to the valvillus has been found only in *Doryctes* and *Neodoryctes* and is a putative synapomorphy for them (Rahman *et al.*, 1998b).
89. *Tips of bars*: 0 = not forming spines; 1 = formed into spines (e.g. Rahman *et al.*, 1998b: fig. 2b).
90. *Ctenidia*: 0 = minor type only (e.g. Rahman *et al.*, 1998b: figs 1h, 3a–f); 1 = major type present (e.g. Rahman *et al.*, 1998b: fig. 4b–d). The egg canal of all the doryctines has ctenidia, two types of which are distinguished. In major ctenidia, the rows extend between dorsal and ventral edges of the egg canal, whereas in minor ctenidia the rows are shorter and there may be several separate ones within the width of the egg canal wall (Rahman *et al.*, 1998b).
91. *Broad-based, robust spines in egg canal, posterior to valvillar zone:* 0 = absent; 1 = present (e.g. Rahman *et al.*, 1998b: fig. 1h).
92. *Subctenidial setae*: 0 = simple (e.g. Rahman *et al.*, 1998b: fig. 3a); 1 = bifurcate (e.g. Rahman *et al.*, 1998b: fig. 3d); 2 = trifurcate or more divided (e.g. Rahman *et al.*, 1998b: fig. 3e).
93. *Subctenidial setae*: 0 = not or hardly flattened; 1 = distinctly flattened; 2 = strongly flattened. (e.g. Rahman *et al.*, 1998b: fig. 4a); 3 = formed into extremely thin, flattened leaflets. (e.g. Rahman *et al.*, 1998b: fig. 4b). In their study of the ovipositor internal microsculpture in several representative Doryctinae genera, Rahman *et al.* (1998b) found that the examined specimens

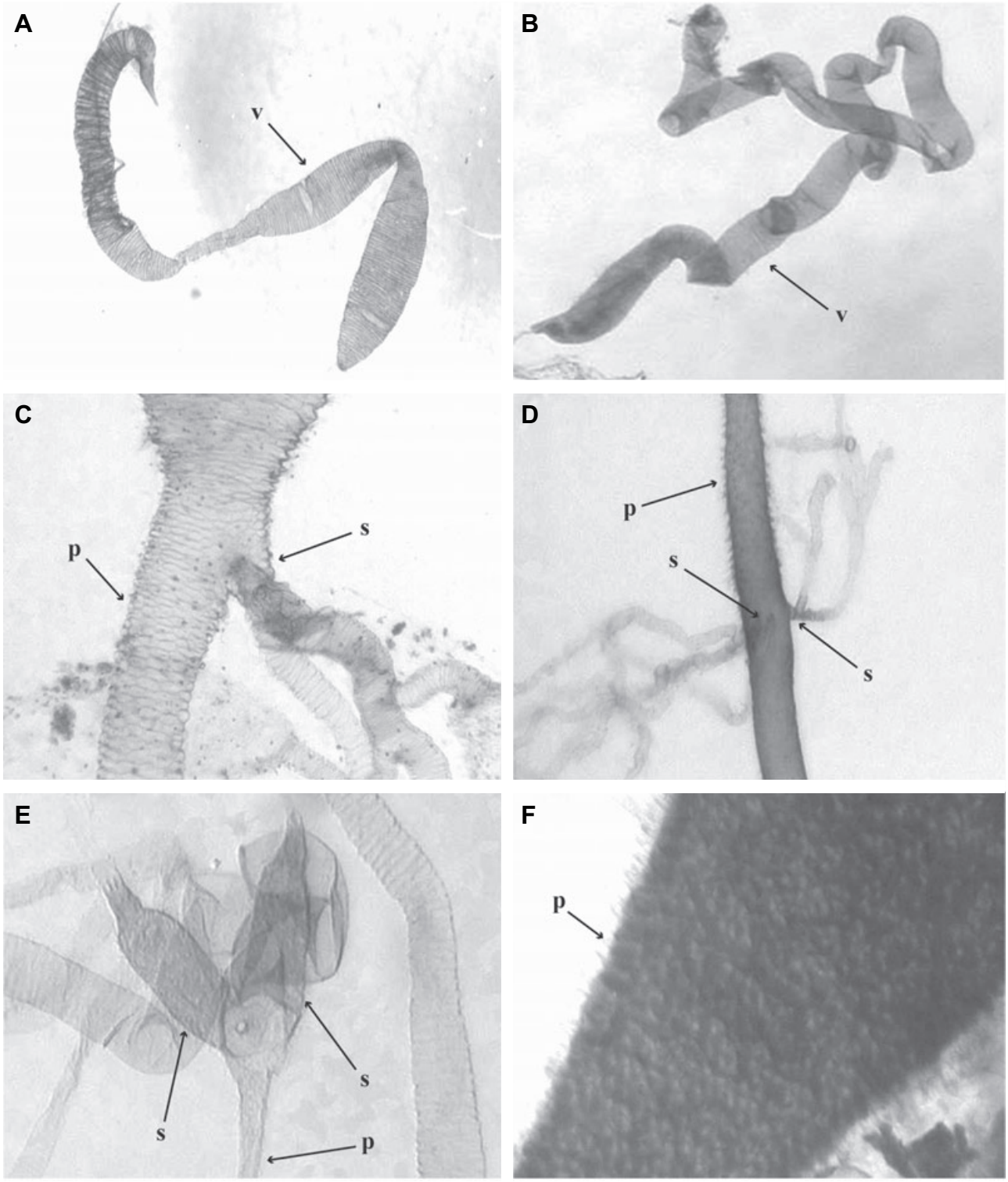

Figure 9. Selected features of the venom apparatus in the Doryctinae. A, *Megaloproctus* sp.; B, *Nervellius* sp.; C, *Aleiodes pulchripes* Wesmael; D, *Halycaea* sp.; E, *Hecabolus* sp.; F, *Syngaster* sp. v, venom reservoir; p, primary venom duct; s, secondary venom duct.

belonging to the Holcobraconini, Binareini and the genus *Monarea* have extremely flattened subctenidial setae, producing overlapping leaflet-like structures.

94. *Posterior ovipositor lower valve fans formed from groups of leaflets*: 0 = absent; 1 = present (e.g. Rahman *et al.*, 1998b: fig. 1a, b). Some doryctinae genera have very enlarged leaflets, which are erect and project into the egg canal lumen (Rahman *et al.*, 1998b).
95. *Basal most ovipositor lower valve setae*: 0 = small; 1 = larger than subsequent ones; 2 = modified into a pseudovalvillus.
96. *Single, large crescentic bar-like structure just distal to valvillus*: 0 = absent (e.g. Rahman *et al.*, 1998b: fig. 2c, f); 1 = present (e.g. Rahman *et al.*, 1998b: fig. 2e). Some genera possess a single, crescentic bar or abrupt excavation extending across the whole width of the egg canal just distal to the valvillus (Rahman *et al.*, 1998b)
97. *Transverse bars near valvillus*: 0 = straight, rather thin, not strongly raised; 1 = formed of thickened, curved and strongly raised arches.
98. *Pre-apical zone of the rachies*: 0 = without very dense and strong scale-like microsculpture; 1 = with very dense and strong scale-like microsculpture.
99. *One or more ancillary teeth near the tip of the ovipositor*: 0 = absent; 1 = present, not distinct and in the form of well developed distal grooves; 2 = very distinct present as isolated tooth-like processes. Ancillary teeth are present in the vast majority of doryctines and have been suggested as a synapomorphy for the subfamily (Quicke *et al.*, 1992a, 1995).

Larval cephalic structure

Reference: Capek, (1970).

100. *Epistoma of final larval instar head capsule*: 0 = present and complete (e.g. Capek, 1970: fig. 54); 1 = absent or reduced (e.g. Capek, 1970: fig. 55).

RESULTS

All unweighted analyses reached the computational limit of 30 000 most parsimonious trees, and the strict consensus trees for the four character sets are poorly resolved (Figs 10–12). Most of the clades recovered in these analyses are weakly supported as indicated by their bootstrap values, although these are potentially underestimated because it was not practicable to search each of the pseudoreplicates as thoroughly as we did to find the most parsimonious trees (see Gauthier *et al.*, 2000).

The different attributes and performance measures evaluated for the different data partitions are presented in Table 2. In general, the performance values for all the analyses are relatively low. The REPRODUCTIVE + LARVAL character set, which was the character set with the second highest proportion of missing entries, produced trees with the highest CI, RI and DD, while the two partitions with the lowest proportions of missing entries give trees with the lowest performance values. Whereas the ONLY EXTERNAL character set has the lowest CI, the >70% DATA has the lowest DD and RI. On the other hand, the character sets with the lowest proportions of informative characters (ONLY EXTERNAL and REPRODUCTIVE + LARVAL) yielded the highest performance values. Comparison between the external morphological and the remaining alternative character systems using the ILD test reveals that these data partitions are significantly incongruent ($P < 0.001$).

The QHS result for the ALL DATA character set gave an initial tree with length of 796 after 10 000 random additions. By repeatedly applying the various reweighting functions we finally yielded trees with length of 790, indicating that this is a particularly hard data set to search. The strict consensus of the most parsimonious trees from the ALL DATA character set is mostly unresolved but includes a number of small clades with from two to thirteen genera each (Fig. 10). The largest of these (clade 1) includes several members of the Hecabolini together with five previously unplaced genera (*Mimodoryctes* Belokobylskij, *Whartonius* Marsh, *Janzenia* Marsh, *Hemispathius* Belokobylskij & Quicke, and *Aphelopsia* Marsh). The Hecabolini components were also diverse, representing three of its four subtribes. The second largest clade (clade 2) contains all members of the Doryctiini subtribes Rhaconotina and Caenophanina together with *Platyspathius* Viereck of the Spathiina and *Chelonodoryctes* Belokobylskij & Quicke. The original description of the latter stated that it might belong to the Doryctini (Belokobylskij & Quicke, 2000). The third largest clade (clade 3) comprises the Holcobraconini and Binareini (except *Ivondrovia* Shenefelt & Marsh), but also includes *Monarea* Szépligeti [placed by Belokobylskij (1992a) in the Doryctina].

Among the most relevant smaller clades, one (clade 4) contains a subclade with the three members of the Ecphylini, but also *Pambolidea* of the Pambolideina and three previously unplaced genera (*Achterbergia* Marsh, *Masonius* Marsh, *Fritziella* Marsh). Another two (clades 7 and 9) comprise several members of the Doryctina, though one of them (clade 7) also contains the monotypic Trigonophasmina (*Trigonophasmus*

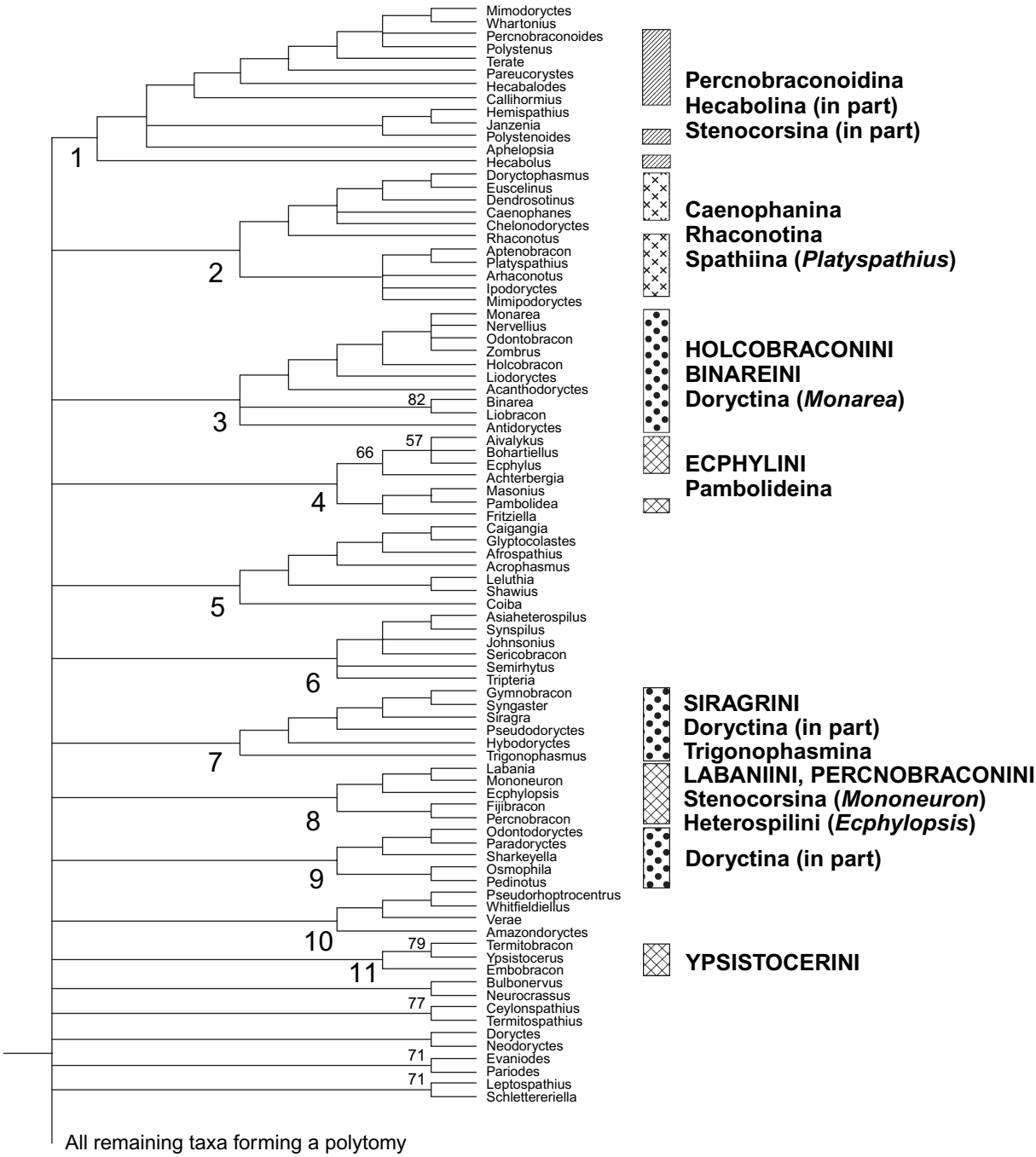

Figure 10. Strict consensus of 30 000 most parsimonious trees (length 790) produced by the QHS strategy using all the available information for all taxa (ALL DATA). Only resolved clades of Doryctinae are shown. Numbers above branches show bootstrap values ≥ 50. Numbers below branches refer to the major clades recovered (see text).

Enderlein) and Siragrini (*Siragra* Cameron). A fourth clade (clade 8) comprises both known genera of the Percnobraconini, which form a sister group of a subclade with *Ecphylopsis* Ashmead of the Heterospilini, *Mononeuron* Fischer of the Stenocorsina and *Labania* Hedqvist of the Labaniini. Finally, a small separate clade (clade 11) is formed by the three genera of the Ypsistocerini, *Ypsistocerus*, *Embobracon* and *Termitobracon*.

The topologies derived from the strict consensus of the most parsimonious trees obtained with the other partitions are largely unresolved (Fig. 11A–C).

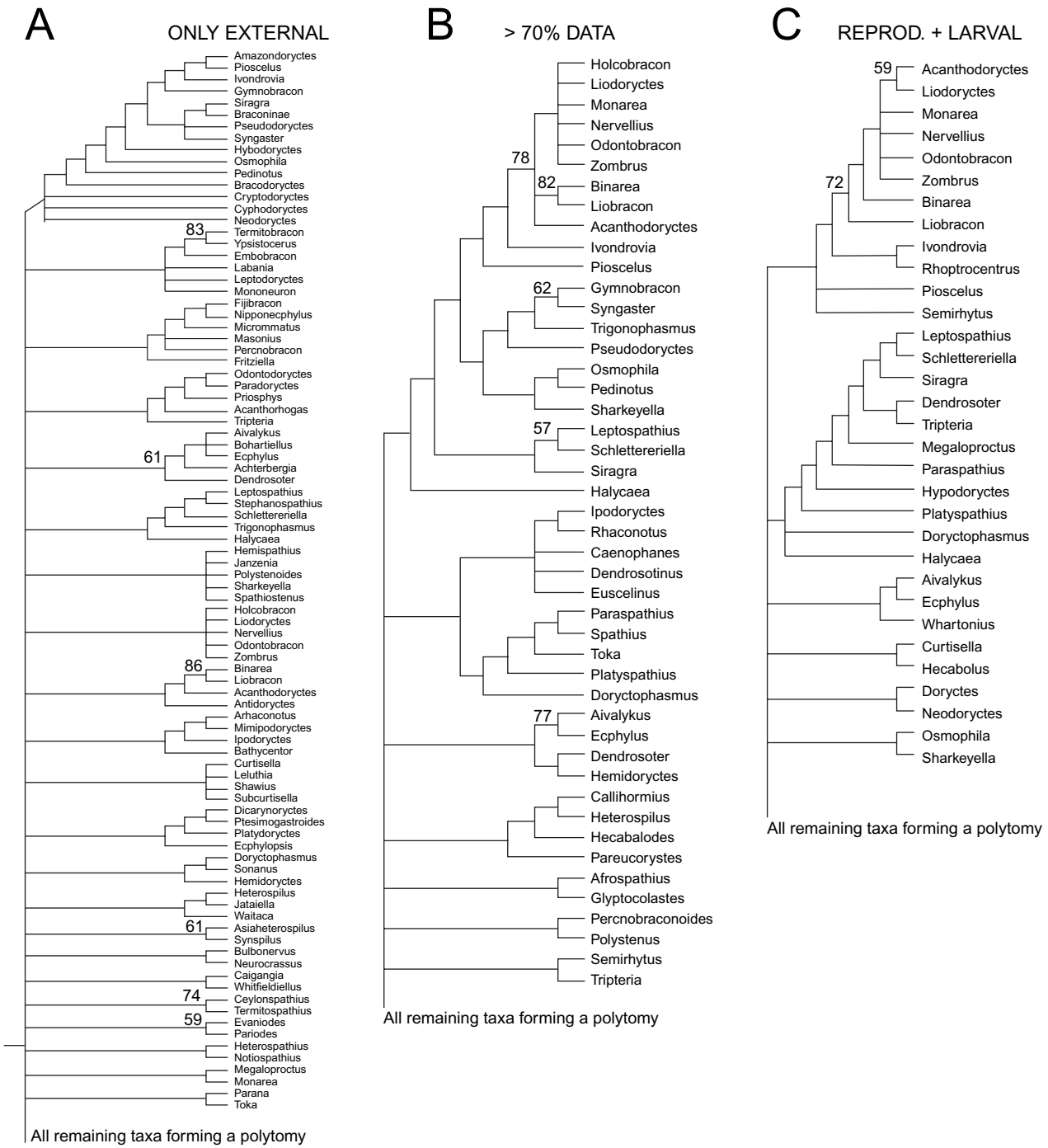

Figure 11. Strict consensus of the 30 000 most parsimonious trees obtained from each of three different character sets examined in this study following the QHS strategy. Numbers above branches show bootstrap values ≥ 50. A, strict consensus (length 502) including only the external characters for all taxa (ONLY EXTERNAL); B, strict consensus (length 556) including only taxa with ≥ 70% scored characters (> 70% DATA); C, strict consensus (length 180) including only characters systems others than external morphology and taxa with ≥ 50% of scored characters (REPRODUCTIVE + LARVAL).

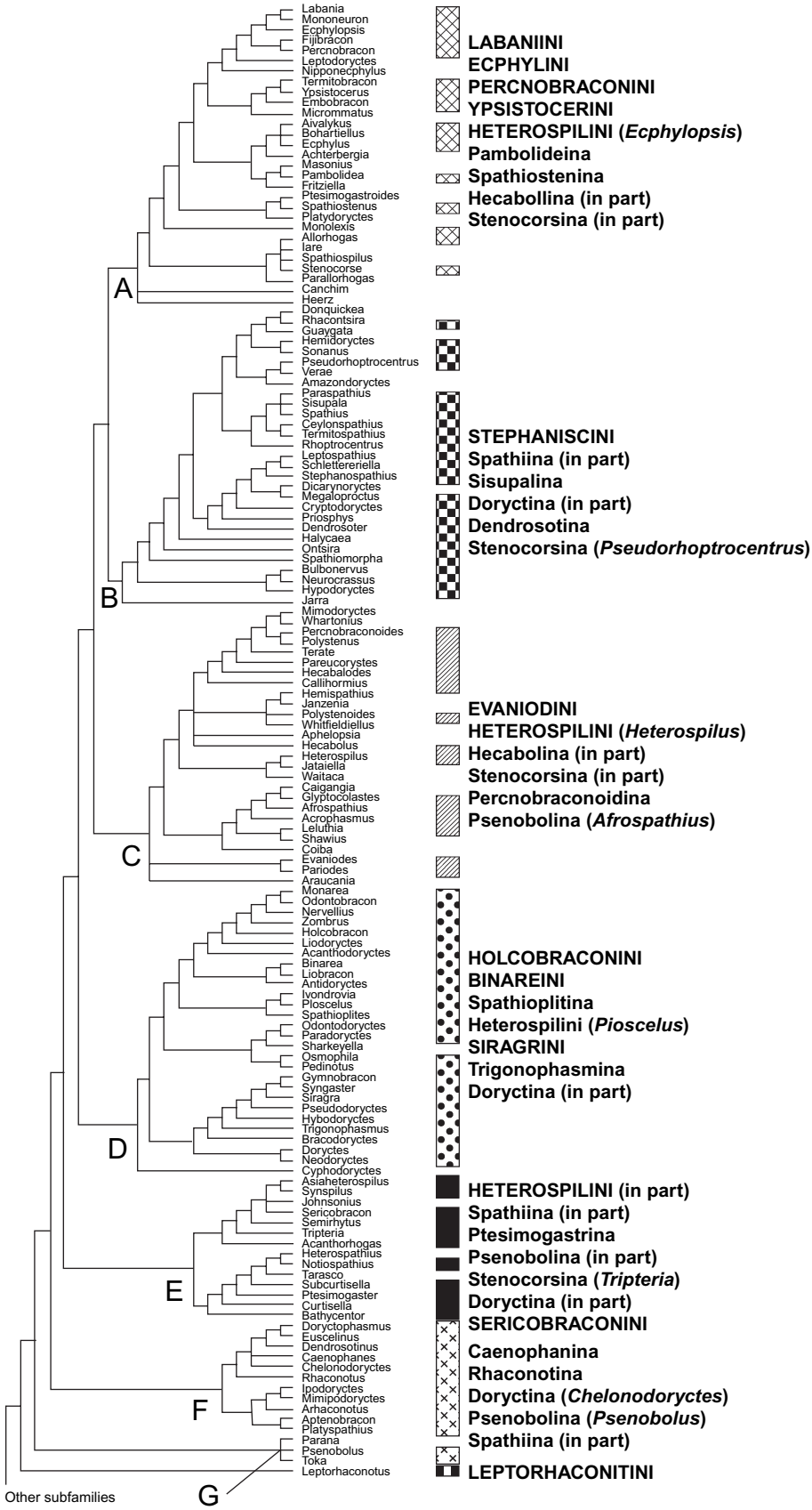
Labania
Mononeuron
Ecphylopsis
Fijibracon
Percnobracon
Leptodoryctes
Nipponecphylus
Termitobracon
Ypsistocerus
Embobracon
Micrommatus
Aivalykus
Bohartiellus
Ecphylus
Achterbergia
Masonius
Pambolidea
Fritziella
Ptesimogastroides
Spathiostenus
Platydoryctes
Monolexis
Allorhogas
Iare
Spathiospilus
Stenocorse
Parallorhogas
Canchim
Heerz
A
Donquickea
Rhacontsira
Guaygata
Hemidoryctes
Sonanus
Pseudorhoptrocentrus
Verae
Amazondoryctes
Paraspathius
Sisupala
Spathius
Ceylonspathius
Termitospathius
Rhoptrocentrus
Leptospathius
Schiettereriella
Stephanospathius
Dicarynoryctes
Megaloproctus
Cryptodoryctes
Priosphys
Dendrosoter
Halycaea
Ontsira
Spathiomorpha
Bulbonervus
Neurocrassus
Hypodoryctes
Jarra
B
Mimodoryctes
Whartonius
Percnobraconoides
Polystenus
Terate
Pareucorystes
Hecabalodes
Callihormius
Hemispathius
Janzenia
Polystenoides
Whitfieldiellus
Aphelopsia
Hecabolus
Heterospilus
Jataiella
Waitaca
Caigangia
Glyptoclastes
Afrospathius
Acrophasmus
Leluthia
Shawius
Coiba
C
Evaniodes
Pariodes
Araucania
Monarea
Odontobracon
Nervellius
Zombrus
Holcobracon
Liodoryctes
Acanthodoryctes
Binarea
Liobracon
Antidoryctes
Ivondrovia
Ploscelus
Spathioplites
Odontodoryctes
Paradoryctes
Sharkeyella
Osmophila
Pedinotus
Gymnobracon
Syngaster
Siragra
Pseudodoryctes
Hybodoryctes
Trigonophasmus
Bracodoryctes
Doryctes
Neodoryctes
D
Cyphodoryctes
Asiaheterospilus
Synspilus
Johnsonius
Sericobracon
Semirhytus
Tripteria
Acanthorhogas
Heterospathius
Notiospathius
Tarasco
Subcurtisella
Ptesimogaster
Curtisella
Bathycentor
E
Doryctophasmus
Euscelinus
Dendrosotinus
Caenophanes
Chelonodoryctes
Rhaconotus
Ipodoryctes
Mimipodoryctes
Arhaconotus
Aptenobracon
Platyspathius
F
Parana
Psenobolus
Toka
Leptorhaconotus
Other subfamilies
G
LABANIINI
ECPHYLINI
PERCNOBRACONINI
YPSISTOCERINI
HETEROSPILINI (*Ecphylopsis*)
Pambolideina
Spathiostenina
Hecabollina (in part)
Stenocorsina (in part)
STEPHANISCINI
Spathiina (in part)
Sisupalina
Doryctina (in part)
Dendrosotina
Stenocorsina (*Pseudorhoptrocentrus*)
EVANIODINI
HETEROSPILINI (*Heterospilus*)
Hecabolina (in part)
Stenocorsina (in part)
Percnobraconoidina
Psenobolina (*Afrospathius*)
HOLCOBRACONINI
BINAREINI
Spathioplitina
Heterospilini (*Pioscelus*)
SIRAGRINI
Trigonophasmina
Doryctina (in part)
HETEROSPILINI (in part)
Spathiina (in part)
Ptesimogastrina
Psenobolina (in part)
Stenocorsina (*Tripteria*)
Doryctina (in part)
SERICOBRACONINI
Caenophanina
Rhaconotina
Doryctina (*Chelonodoryctes*)
Psenobolina (*Psenobolus*)
Spathiina (in part)
LEPTORHACONITINI

Figure 12. Strict consensus of the 8438 most parsimonious trees produced by successive approximations weighting employing the minimum retention index, starting from the most parsimonious trees found with the QHS strategy using all available information for all taxa (ALL DATA). Only ingroup relationships are shown. Letters below branches refer to the major clades recovered (see text).

Table 2. Attributes and performance measures of the four character sets and their MPTs examined in this study

Character set	PIC	NIT	NIC	PMD	ITL	FTL	CI	RI	DD
ALL DATA	0.63	156	99	30.7	796	790	0.139	0.574	0.516
ONLY EXTERNAL	0.4	156	63	16.1	506	502	0.131	0.597	0.545
> 70% DATA	1.0	91	92	18.2	557	556	0.185	0.568	0.503
REPRODUCTIVE + LARVAL	0.43	84	36	20.7	181	180	0.238	0.697	0.685

PIC, proportion of informative characters with respect to number of included taxa; NIT, number of included taxa; NIC, number of informative characters; PMD, percentage of missing data (including polymorphic characters with all their states present); ITL, initial tree length (tree length obtained after 10 000 random replicates holding one tree from each addition); FTL, final tree length (tree length obtained after applying the QHS strategy); CI, consistency index; RI, retention index; DD, data decisiveness index. Specific features for each character set are mentioned in the text.

However, the > 70% DATA and the REPRODUCTIVE + LARVAL data sets also recover a clade comprising the Holcobraconini + Binareini. In addition, the ONLY EXTERNAL data partition also shows the Ypsistocerini and the Ecphylini as monophyletic.

The strict consensus trees of the SAW analyses for the ALL DATA character set employing MaRI and MiRI (lengths 386.52 and 386.19, respectively) applied separately are identical to one another and much better resolved (Fig. 12; relationships among members of the other subfamilies are not shown). The Doryctinae appears monophyletic with the exclusion of *Histeromeroides* Marsh, which comes out among the outgroups. Furthermore, *Monitoriella* is also nested with the outgroups, whereas the aberrant Madagascan *Leptorhaconotus* Granger appears at the base of the Doryctinae.

The topology recovered from the SAW analyses reveals seven larger clades (indicated in Fig. 12 by letter), which include most of the resolved assemblages present in the unweighted consensus tree (Fig. 10). Of these, however, clade F was the only one that was exactly the same in generic composition between the aforementioned topologies. The clades with the members of the Ecphylini and Ypsistocerini are recovered in the clade A, which also includes representatives of several of the smaller tribes and subtribes. Clade B contains a subclade composed by the members of the Stephaniscini, the single members of the Dendrosotina and Sisupalina, *Pseudorhoptocentrus* Granger of the Stenocorsina, and several genera of the Doryctina. Clade C comprises the same genera recovered in clade 1 of the unweighted analysis, together with additional genera of the Hecabolini, the only member of the Percnobraconoidina (*Percnobraconoides* Marsh), the two Evaniodini genera, *Heterospilus* of the Heterospilini, and six unplaced genera. The Holcobraconini + Binareini + *Monarea* clade is placed within a larger clade (clade D) that also includes *Ivondrovia*, 12 genera belonging to the Doryctina, the single members of the Trigonophasmina (*Trigonophasmus* Enderlein), Siragrini (*Siragra* Cameron) and Spathioplitina (*Spathioplites* Fischer), *Piocelus* Muesebeck & Walkley of the Heterospilini, and the unplaced *Cyphodoryctes* Marsh. Finally, the remaining two clades (clades E and G) are represented by a few genera belonging to various subtribes as well as some unplaced genera.

Most of the results of the Wilcoxon signed-ranks tests comparing the hypotheses obtained from the four data sets with the alternative hypotheses of monophyly constructed for the tribes Doryctini and Hecabolini *sensu* Belokobylskij (1992a) were not significant (Table 3). However, constraining the Doryctini to be monophyletic with the > 70% DATA and the INTERNAL + LARVAL data partitions resulted in significant differences ($P < 0.03$).

DISCUSSION

Relative performance of character partitions in analyses

Addition of taxa and/or characters with abundant missing data has been traditionally avoided in phylogenetic analyses because they are considered to be a nuisance factor that can lead to multiple shortest

Table 3. Results of the Wilcoxon signed-ranks tests comparing 100 randomly chosen trees from the analyses performed for the four different character partitions and those obtained from alternative hypotheses constraining the members of the Doryctini and Hecabolini (*sensu* Belokobylskij, 1992a) to be monophyletic

Alternative hypotheses and data sets	LT	*N*	*Z*	*P*
Doryctini monophyletic				
ALL DATA	824	63	–1.674 to –1.568	$P > 0.1$
> 70% DATA	623	43–44	–2.342 to –2.201	$P < 0.03$*
ONLY EXTERNAL	528	40–42	–1.319 to –1.259	$P > 0.2$
REPRODUCTIVE + LARVAL	206	24	–2.36	$P < 0.02$*
Hecabolini monophyletic				
ALL DATA	816	51–52	–1.295 to –1.256	$P > 0.1$
> 70% DATA	610	43–45	–1.458 to –1.352	$P > 0.1$
ONLY EXTERNAL	527	30–32	–0.215 to –0.206	$P > 0.2$
REPRODUCTIVE + LARVAL	191	18–20	–1.466 to –1.249	$P > 0.1$

LT, length of the 100 randomly chosen trees of the alternative hypotheses; *N*, number of positive differences; *Z*, normal approximation showed in the Wilcoxon signed-ranks test for $N = 25$

*Significant difference between the hypotheses obtained in this study and the alternative hypotheses with one-tailed probability.

trees and a poorly resolved consensus tree (see Wiens & Reeder, 1995; Wilkinson, 1995; Wiens, 1998 for reviews of this subject). However, based on computer simulations, Wiens (2003) demonstrated that it is not so much the presence of too many missing data cells, but rather the inclusion of few complete characters that lead to a reduction in accuracy in phylogenetic analyses. Therefore, he proposed that the level of completeness alone should not guide the exclusion of taxa. In this study we also observed that the incorporation of characters or taxa with a high proportion of missing data results in largely unresolved topologies; however, similar to the results obtained by Wiens (2003), we did not find an evident correlation between the proportion of missing data in the character sets and their analysis performances as measured by the CI, RI, or DD (Table 2). Instead, there was a negative correlation between the performance values of the data sets examined and the proportions of informative characters in them. This effect can be explained by the apparent extensive homoplasy contained in our data, which increases with the inclusion of more informative characters.

Several previous attempts at a tribal classification of the Doryctinae have argued that traditionally used external morphological characters are insufficient to resolve their higher level relationships in a clear way (e.g. Marsh, 1965; Shenefelt & Marsh, 1976; Fischer, 1981a; Belokobylskij, 1992a, 1993). On the other hand, reproductive, internal and larval character systems have often proved to be helpful for resolving higher level relationships within the Hymenoptera (e.g. Heraty, Wooley & Darling, 1994; Vilhelmsen, 2001, 2003) and indeed in most insect orders. The significant incongruence found in our study between the external morphological and the reproductive and larval character systems suggests that the same may apply to the Doryctinae, and it is not surprising therefore that their inclusion here has revealed previously unsuspected relationships. More extensive scoring of these internal features might therefore be expected to improve our understanding of the group, but unfortunately many genera are known from too few specimens to permit this at present.

Taxonomic implications

One of the principal reasons for the extensive confusion in the higher level classification of the Doryctinae is the procedure that numerous authors have followed in how they define genera. These have traditionally made use of combinations of characters or trends present in different tribes, mainly because of a lack of obvious autapomorphies (Marsh, 1993, 2002; Belokobylskij, 1998a; Barbalho & Penteado-Dias, 2000, 2002). For example, Barbalho *et al.* (1999) erected the genera *Heterospathius* Barbalho & Penteado-Dias and *Spathiospilus* Marsh (based on combined parts of the names *Spathius* and *Heterospilus*) to include some new species that do not possess any apparent uniquely derived feature, but instead present a mixture of features characteristic of the members of the Heterospilini (fore wing vein 2RS absent or not sclerotized) and Spathiini (metasoma petiolate). Thus, the characters used are not necessarily suitable for creating monophyletic groups or even for cladistic argumentation. Unfortunately, the high levels of homoplasy shown by many of the included characters

and the difficulty of measuring the nodal support in the different topologies do not allow us to propose a meaningful new higher level classification, even after formal analysis of all available morphological data. Nevertheless, there are several interesting relationships recovered by the different analyses performed, but only a few of these agree with the groups proposed by Belokobylskij, 1992a) higher classification of the subfamily.

Several authors have questioned the monophyly of the Doryctinae in the current sense. The traditional morphological characters used to define this subfamily (cubical head, complete occipital carina and a row of fore tibial pegs) have all been shown to be homoplastic and all are potentially symplesiomorphies (Quicke *et al.*, 1992a). Although a row of fore tibial pegs is one of the most reliable characters used, it is also found in several other cyclostome genera (*Yelicones* Cameron of the Rogadinae and some Braconinae and Rhyssalinae: Chishti & Quicke, 1995; van Achterberg, 1995; Quicke & Kruft, 1995) and in a recently described genus of the noncyclostome subfamily Orgilinae [*Doryctorgilus* Braet & van Achterberg (Braet & van Achterberg, 2003)], and these pegs are probably an adaptation to aid egress from a concealed pupation site (Eggleton, 1989; Quicke, 1997). Indeed, the cubical head of many doryctines probably reflects strong mandibular muscles and is therefore also associated with a need for the newly emerged adult to make its way out. More recently, in an attempt to find more reliable synapomorphies for the Doryctinae, Quicke *et al.* (1992a) identified three probable synapomorphies from the ovipositor system (presence of a heavily sclerotized ovipositor apex, a double nodus on the upper valve and a modified serration structure on the lower valve). However, even these were undoubtedly lost secondarily in some taxa (e.g. some *Spathius* Nees and *Heterospilus* species: Quicke & Marsh, 1992; Quicke *et al.*, 1992a). Our results suggest only one consistent putative synapomorphy for the Doryctinae (inclusive of Ypsistocerinae): the separate insertion of the two secondary venom gland ducts into the primary duct (character 79; RI = 1.0). This condition is present in all the doryctines for which venom apparatus has been investigated, but is not known in any other cyclostome taxon studied to date. Unfortunately, *Monitoriella* lacks venom glands and reservoir, as does *Mesostoa* (D. L. J. Quicke, unpubl. observ.), probably because both are primary gall formers (Infante, Hanson & Wharton, 1995; Dangerfield & Austin, 1998) and possibly gall formation is induced by larval secretion.

In the SAW analyses, *Histeromeroides* was recovered among the outgroup taxa despite the fact it possesses a row of spines on the outer surface of the fore tibia and has a double nodus on the dorsal valve of the ovipositor. This is probably because it is a morphologically very derived doryctine genus (although its name indicates convergent similarity to *Histeromerus* Wesmael, it is now known to be near the Rhyssalinae: Belshaw *et al.*, 1998; Dowton *et al.*, 2002), and its recovery with the outgroup reflects this. Moreover, *Leptorhaconotus*, which was recovered at the base of the Doryctinae, lacks the ovipositor characters proposed by Quicke *et al.* (1992a) as Doryctinae synapomorphies, except by having a well-developed accessory tooth on the lower valve. However, its ovipositor is highly modified, dorsoventrally depressed and strongly upcurved, thus clearly showing that this taxon does not attack wood-borer hosts. Additionally, this genus also lacks the glandular sculpture in the insertion of the secondary venom ducts (character 81), which is a condition observed in most of the rest of the Doryctinae; however, it does have two separate insertions of the secondary duct (fig. 10 in Quicke, 1996). *Leptorhaconotus* is also a highly morphologically aberrant genus, included by van Achterberg (1984) in a tribe of its own, and only tentatively placed within the Doryctinae. Whether this is because it really does not belong there or is just a consequence of its derived structure, will probably not be resolved using morphology alone.

The validities of the small doryctine tribes Ecphylini, Labaniini, Ypsistocerini, Percnobraconini, Leptorhaconotini and Stephaniscini need to be tested further, because in our trees most of them appear as derived taxa within more inclusive groups, rather than as separate, independent lineages. However, although they are supported by inconsistent synapomorphies (character numbers 8, 32, 63, 64, 66, 78, 84, 86), three of the four proposed genera of the Ecphylini were nested in a clade with *Achterbergia* Marsh at the base, suggesting the monophyly of this group. Of these synapomorphies, the presence of a markedly elongated basal ring in the male genitalia (RI = 0.48; e.g. Fig. 8I) appears to be the most reliable for its diagnosis. The Ypsistocerini also appears as monophyletic but its validity is still unclear because it is supported only by inconsistent synapomorphies (character numbers 17, 25, and 38). Moreover, these supposed synapomorphies involve reduction in wing venation and mesosoma sculpture, which probably are related to the termitophylic habits of at least some of the members of this tribe, and so could easily be products of convergent evolution.

All our analyses, except the one with the ONLY EXTERNAL data set, group the Holcobraconini and Binareini together along with *Monarea*, the latter having previously been included in the Doryctini (Belokobylskij, 1992a). The consistent synapomorphies that support this clade are found in the venom apparatus (venom reservoir tubular; character 75, state 1; RI = 0.89; e.g. Fig. 9B) and ovipositor struc-

ture (presence of a major type ctenidia; character 90, state 1; RI = 1.0); however, although most are large tropical species, they barely resemble one another in terms of external morphology. Therefore, it is not surprising that workers dealing only with external morphology have not suspected this grouping.

None of our analyses show any of the large doryctine tribes, namely Doryctini, Hecabolini or Spathiini, to be monophyletic [tribes defined both *sensu* Fischer (1981a) and *sensu* Belokobylskij (1992a)], and two of the four posterior statistical comparisons with the alternative most parsimonious hypotheses reject the monophyly of the Doryctini at the 5% level (Table 3). Fischer (1981a) defined the Doryctini as having the fifth tergite not well developed, smaller than the preceding one and with the sixth and the following ones not retracted under it (character 61). However, this condition is evidently a symplesiomorphy. On the other hand, the features used by Belokobylskij (1992a, 1993) to define the Doryctini consist only of four common trends and only one supposed synapomorphy, namely 'a trend' towards use of non-Coleoptera hosts, and it is not surprising therefore that they were not found to be monophyletic here.

Based on the SAW trees, the genera that comprise the subtribe Doryctina *sensu* Belokobylskij (1992a) do not form a monophyletic group but they do comprise two separate clusters that are each more related to other doryctine genera. One of these is placed within a larger clade together with the Holcobraconini + Binareini (clade D), whereas the second one is closer to members of the Spathiina (clade B). In Belokobylskij's (1992a) classification, the Doryctina were distinguished from the other Doryctini subtribes based on a single trend, i.e. the parallel vein (CU1a) originating from the posterior third to sixth of the brachial cell (character 31, state 2). However, this is also present in several other genera within the Doryctinae not included by Belokobylskij (1992a) in the Doryctini; therefore, failure to recover this subtribe is to be expected.

The various subtribes of the Hecabolini mostly appear not to be monophyletic; the Hecabolina (except *Monolexis* Foerster) is the only one whose members were largely recovered in a single clade. The clade containing the Hecabolina also comprises several members of the other Hecabolini subtribes and some members of the Heterospilini (including *Heterospilus* Haliday) and Spathiina, and the two members of the Evaniodini. However, there are no consistent synapomorphies supporting this grouping. A close relationship between the Hecabolini and Heterospilini was previously proposed based on four trends (Belokobylskij, 1993), one of which supported the aforementioned clade in our SAW analyses (hind wing of males with a stigma-like structure present in distal part of costal vein, with incurved marginal parts; character 39 state 1; RI = 0.81; e.g. Fig. 2J, K).

The non-monophyly of the Spathiini and its subtribes Spathiina and Psenobolina is probably also the consequence of erecting these taxa only on the basis of variable trends. The Spathiina were distinguished by having setose eyes, a malar suture present and fore wing brachial cell closed distally (Belokobylskij, 1993), the last two of these characters probably being symplesiomorphies. On the other hand, the only trait employed by Belokobylskij (1993) to differentiate the Psenobolina from the Spathiina was the brachial cell being open distally, a condition present in many other doryctine genera as well in the Braconidae as a whole.

CONCLUDING REMARKS

The present study represents the first attempt to investigate the evolutionary relationships among the doryctine genera following a strict phylogenetic reconstruction method. Unfortunately, we have shown that the currently available morphological data do not provide strong enough signals for resolving most of the relationships, and hence, we are not able, at this stage, to propose a meaningful higher classification of the group. However, our results do indicate that character systems others than the external morphology add valuable phylogenetic information, and their investigation in currently unscored genera could considerably improve the accuracy of the hypothesis obtained. Even so, it seems likely that the phylogenetic relationships among doryctine genera will be found to differ considerably from the current tribal and subtribal classification, which we suggest should be abandoned. The morphological hypothesis presented here will serve as a basis for further molecular phylogenetic studies within the group, which will help us to understand with more certainty not only the relationships amongst the doryctine genera, but also the evolution of their morphological characteristics and their life-history strategies.

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APPENDIX 1

List of valid doryctine genera and their synonyms. Generic composition of tribes and subtribes based on Belokobylskij's (1992a) classification and subsequent studies made by the same author. Does not include 12 genera recently described from Australia by Belokobylskij *et al*. (2004). Binaerini: Binareina (BB), Acanthodoryctina (BA); Doryctini: Caenophanina (BC), Dendrosotina (BDE), Doryctina (BDO), Rhaconotina (BR); Ecphylini (BE); Evaniodini (BEV); Hecabolini: Hecabolina (BHEC), Pambolideina (BP), Percnobraconoidina (BPE), Stenocorsina (BSN); Heterospilini (BHE); Holcobraconini: Holcobraconina (BH), Ivondrovina (BI), Odontobraconina (BO); Labanini (BL); Leptorhaconotini (BLE); Sericobraconini (BSE); Siragrini (BSIR); Spathiini: Psenobolina (BPS), Ptesimogastrina (BPT), Sisupalina (BSI), Spathiina (BS), Spathioplitina (BSA), Spathiostenina (BSO), Trigonophasmina (BT); Stephaniscini (BST); Percnobraconini (BPN). Generic composition of tribes and subtribes based on Fischer's (1981a) classification. Doryctini: Binareina (FB), Dendrosotina (FD), Doryctina (FDO), Heterospilina (FHE), Neoclinocentrina (FN), Pedinotina (FP), Stenocorsina (FST); Ecphylini (FE); Evaniodini (FEV); Hecabolini (FH); Odontobraconini (FO); Rhaconotini (FR); Spathiini (FS).

Acanthodoryctes Turner, 1918 (BA)†‡
Acanthorhogas Szépligeti, 1906 (BDO; FB)
Achterbergia Marsh, 1993
Acrophasmus Enderlein, 1912 (BSN; FP)†‡
=*Concurtisella* Roman, 1924
Afrospathius Belokobylskij & Quicke, 2000 (BPS)†‡
Aivalykus Nixon, 1938 (BE)†‡
=*Ecphyloides* Marsh, 1993
Allorhogas Gahan, 1912 (BSN; FST)†‡
=*Catolestes* Bréthes, 1922
Amazondoryctes Barbalho & Penteado-Dias, 1999
Angelica Marsh, 2002*
Antidoryctes Belokobylskij & Quicke, 2000 (BB)
Aphelopsia Marsh, 1993
Aptenobracon Marsh, 1965 (BR)
Araucania Marsh, 1993
Arhaconotus Belokobylskij, 2000 (BR)
Asiaheterospilus Belokobylskij & Konishi, 2001 (BHE)
Barbalhoa Marsh, 2002*
Bathycentor Saussure, 1892 (BDO)
Binarea Brullé, 1846 (BB; FB)†
Bohartiellus Marsh, 1983
Bracodoryctes Belokobylskij & Quicke, 2000 (BDO)
Bulbonervus Shenefelt, 1969 (BDO; FDO)
Caenophanes Foerster, 1862 (BC)†
=*Synodus* Ratzeburg, 1848
=*Eurybolus* Thomson, 1892
Caingangia Marsh, 1993
Callihormius Ashmead, 1900 (BSN; FN)†‡
Canchim Barbalho & Penteado-Dias, 1999
Cecidospathius Kieffer & Jorgensen, 1910*
Celereon Say, 1836*
Ceylonspathius Belokobylskij, 2002 (BS)
Chelonodoryctes Belokobylskij & Quicke, 2000
Coiba Marsh, 1993†‡
Cryptodoryctes Belokobylskij & Quicke, 2000 (BDO)
Curtisella Spinola, 1853 (BSN)†‡
=*Neorhyssa* Szépligeti, 1902
=*Lissophrymnus* Cameron, 1911
Curtiselloides Marsh, 2002*
Cyphodoryctes Marsh, 1997
=*Cyrtonion* Marsh, 1993†‡
Dapsilitas Braet, Barbalho & van Achterberg, 2003*
Dendrosoter Wesmael, 1838 (BDE; FD)†‡
=*Eurybolus* Ratzeburg, 1848
=*Caenopachys* Foerster, 1862
Dendrosotinus Telenga, 1941 (BC)†‡
=*Gildoria* Hedqvist, 1974
Dicarinoryctes Braet & van Achterberg, 2001
Donquickeia Marsh, 1997
=*Quickia* Marsh, 1993
Doryctes Haliday, 1836 (BDO; FDO)†‡
=*Ischiogonus* Wesmael, 1838
=*Udamolcus* Enderlein, 1920
=*Pristodoryctes* Kieffer, 1921
=*Plyctes* Fischer, 1980
Doryctophasmus Enderlein, 1912 (BS)†‡
Ecphylopsis Ashmead, 1900 (BHE)
Ecphylus Foerster, 1862 (BE; FE)†‡
=*Terenusa* Marshall, 1885
=*Paraecphylus* Ashmead, 1900
=*Sactopus* Ashmead, 1900
=*Sycosoter* Picard & Lichtenstein, 1917
Embobracon Achterberg, 1995
Esterella Pagliano & Scaramozzino, 1990 (BC)*
=*Prolatus* Sharma & Gupta, 1985
Euscelinus Westwood, 1882 (BC)†‡
=*Sbeitla* Wilkinson, 1934
Evaniodes Szépligeti, 1901 (BEV; FEV)†‡
Fijibracon Belokobylskij, 1995 (BPN)
Fritziella Marsh, 1993†‡
Glyptocolastes Ashmead, 1900 (BSN; FDO)†‡
=*Glyptodoryctes* Ashmead, 1900
=*Doryctinus* Roman, 1910
Guaygata Marsh, 1993
Gymnobracon Szépligeti, 1902 (BDO; FP)†‡
=*Rutheia* Szépligeti, 1908
=*Ipospathius* Enderlein, 1920
Halycaea Cameron, 1903 †‡ (BDO)
=*Cendebeus* Cameron, 1905
Hansonorum Marsh, 2002*
Hecabalodes Wilkinson, 1929 (BHEC)†‡
Hecabolus Curtis, 1834 (BHEC; FH)†‡
=*Anisopelma* Wesmael, 1838

Heerz Marsh, 1993
Hemidoryctes Belokobylskij, 1993 (BSN)†‡
=*Atopodoryctes* Marsh, 1993
Hemispathius Belokobylskij & Quicke, 2000
Heredius Marsh, 2002*
Heterospathius Barbalho & Penteado-Dias, 1999
Heterospilus Haliday, 1836 (BHE; FHE)†‡
=*Telebolus* Marshall, 1888
=*Kareba* Cameron, 1905
=*Anocatostigma* Enderlein, 1920
=*Harpagolaccus* Enderlein, 1920
Histeromeroides Marsh, 1993
Holcobracon Cameron, 1905 (BH)†
Hormiopius Blanchard, 1962*
Hybodoryctes Szépligeti, 1906 (BDO; FP)
Hypodoryctes Kokujev, 1900 (BDO; FDO)†‡
=*Mixtec* Marsh, 1993
Iare Barbalho & Penteado-Dias, 2002
Ipodoryctes Granger, 1949 (BR; FD)†‡
=*Epirhacon* Belokobylskij, 1990
Ivondrovia Shenefelt & Marsh, 1976 (BI)†‡
=*Lophogaster* Granger, 1949
Janzenia Marsh, 1993
Jarra Marsh & Austin, 1994†
Jataiella Barbalho & Penteado-Dias, 1999
Johnsonius Marsh, 1993
Labania Hedqvist, 1963 (BL)
Lamquetia Braet, Barbalho & van Achterberg, 2003 *
Leluthia Cameron, 1887 (BHEC)†‡
=*Doryctosoma* Picard, 1938
=*Russellia* Muesebeck, 1950
=*Russellella* Muesebeck & Walkley, 1951
=*Euhecabolodes* Tobias, 1962
=*Panama* Marsh, 1993 syn. nov.
Leptodoryctes Barbalho & Penteado-Dias, 1999 (BE)
Leptorhaconotus Granger, 1949 (BLE; FN)†‡
Leptospathius Szépligeti, 1902 (BST)†‡
=*Habnoba* Cameron, 1905
=*Rhoptrospathius* Cameron, 1910
Liobracon Szépligeti, 1901 (BB; FB)†‡
=*Parabinarea* Brues, 1912
=*Hyboderia* Enderlein, 1920
=*Triderodon* Enderlein, 1920
Liodoryctes Szépligeti, 1906 (BO)†‡
=*Neotrimoriodes* Strand, 1911
Lissodoryctes Marsh, 2002*
Lissopsius Marsh, 2002*
Masonius Marsh, 1993†‡
Megaloproctus Schulz, 1906 (BDO; FDO)†‡
=*Megaproctus* Brullé, 1846
=*Megistoproctus* Schulz, 1911
=*Ectetamenochir* Enderlein, 1912
=*Prosthiacantha* Enderlein, 1912
Micrommatus Marsh, 1993
Mimipodoryctes Belokobylskij, 2000 (BR)
Mimodoryctes Belokobylskij, 2001
Monarea Szépligeti, 1904 (BDO)†‡
Monolexis Foerster, 1862 (BHEC)†‡
Mononeuron Fischer, 1981 (BSN)
Neodoryctes Szépligeti, 1914 (BDO)†‡
Neostaphius Braet, Barbalho & van Achterberg, 2003*
Nervellius Roman, 1924 (BH)†‡
Neurocrassus Snoflak, 1945 (BDO)†‡
Nipponecphylus Belokobylskij & Konishi, 2001
Notiospathius Matthews & Marsh, 1973 (BPS)†‡
Odontobracon Cameron, 1887 (BO; FO)†‡
Odontodoryctes Granger, 1949 (BDO)
Ondigus Braet, Barbalho & van Achterberg, 2003*
Ontsira Cameron, 1900 (BDO; FDO)†‡
=*Wachsmannia* Szépligeti, 1900
=*Doryctodes* Hellen, 1927
Osmophila Szépligeti, 1902 (BDO)†‡
Pambolidea Ashmead, 1900 (BP)†‡
Pannuceus Marsh, 2002*
Paradoryctes Granger, 1949 (BDO)
Parallorhogas Marsh, 1993†‡
Parana Nixon, 1943 (BS)
Paraspathius Nixon, 1943 (BS)†‡
Pareucorystes Tobias, 1961 (BHEC)†‡
Pariodes Fischer, 1981 (BEV; FEV)
Pedinotus Szépligeti, 1902 (BDO; FP)†
=*Goniogmus* Enderlein, 1920
Percnobracon Kieffer, 1910 (BPN)†‡
Percnobraconoides Marsh, 1989 (BPE)†‡
Pioscelus Muesebeck & Walkley, 1951 (BHE; FHE)†‡
Platydoryctes Barbalho & Penteado-Dias, 2000
Platyspathius Viereck, 1911 (BS)†‡
=*Spathiohormius* Enderlein, 1912
Polystenoides Muesebeck, 1950 (BSN)
Polystenus Foerster, 1862 (BHEC)†‡
=*Corystes* Reinhard, 1865
=*Eucorystes* Marshall, 1888
=*Eucorystoides* Ashmead, 1900
Priosphys Enderlein, 1920 (BDO; FB)
Psenobolus Reinhard, 1885 (BPS)†‡
Pseudodoryctes Szépligeti, 1915 (BDO; FP)†‡
Pseudorhoptrocentrus Granger, 1949 (BSN; FN)†‡
=*Rhoptrocentroides* Marsh, 1993
Ptesimogaster Marsh, 1965 (BPT; FB)†‡
Ptesimogastroides Braet & van Achterberg, 2001
=*Sharkeyelloides* Marsh, 2002
Rhaconotus Ruthe, 1854 (BR; FR)†‡
=*Hedysomus* Foerster, 1862
=*Hormiopterus* Giraud, 1869
=*Rhadinogaster* Szépligeti, 1908
=*Euryphrymnus* Cameron, 1910
=*Rhaconotinus* Hedqvist, 1965
Rhacontsira Belokobylskij, 1998 (BDO)
Rhoptrocentrus Marshall, 1897 (BDO; FD)†‡
Rimacollus Marsh, 2002*
Schlettereriella Szépligeti, 1904 (BST)†‡
=*Stephaniscus* Kieffer, 1904

=*Biphymaphorus* Szépligeti, 1911
=*Ogmophasmus* Enderlein, 1912
=*Rhopalospathius* Cameron, 1912
Semirhytus Szépligeti, 1902 (BSN; FP)†‡
=*Neoclinocentrus* Szépligeti, 1906
=*Liparophleps* Enderlein, 1920
Sericobracon Shaw, 1985 (BSE)
Sharkeyella Marsh, 1993†‡
Shawius Marsh, 1993†‡
Siragra Cameron, 1907 (BSIR) †‡
Sisupala Nixon, 1943 (BSI)
Sonanus Belokobylskij & Konishi, 2001 (BDO)
Spathiomorpha Tobias, 1976 (BS)†‡
Spathioplites Fischer, 1962 (BSA)
Spathiospilus Marsh, 1999
Spathiostenus Belokobylskij, 1992 (BSO)
Spathius Nees, 1818 (BS; FS)†‡
=*Stenophasmus* Smith, 1859
=*Euspathius* Foerster, 1862
=*Rhacospathius* Cameron, 1905
=*Pseudospathius* Szépligeti, 1902
Stenocorse Marsh, 1968 (BSN; FST)†‡
Stephanospathius Belokobylskij, 1992 (BST)†‡
Subcurtisella Roman, 1924 (BPS)
Syngaster Brullé, 1846 (BDO; FB)†‡
=*Epitonychus* Szépligeti, 1902
Synspilus Belokobylskij & Quicke, 2000 (BHE)
Tarasco Marsh, 1993†‡
Terate Nixon, 1943 (BHEC)
Termitobracon Brues, 1923†‡
Termitospathius Belokobylskij, 2002 (BS)
Toka Nixon, 1943 (BS)†
Trigonophasmus Enderlein, 1912 (BT)†‡
Tripteria Enderlein, 1912 (BSN)†‡
Tripteroides Marsh, 2002*
Vanderentiellus Marsh, 2002*
Verae Marsh, 1993†‡
Waitaca Marsh, 1993
Whartonius Marsh, 1993†‡
Whitfieldiellus Marsh, 1997
=*Whitfieldia* Marsh, 1993
Ypsistocerus Cushman, 1923
Zombrus Marshall, 1897 (BO)†‡
=*Trimorus* Kriechbaumer, 1894
=*Neotrimorus* Dalla Torre, 1898
=*Acanthobracon* Szépligeti, 1902
=*Trichiobracon* Cameron, 1905
=*Trichodoryctes* Szépligeti, 1906

*Genera not included in the present study; †genera included in the >70% DATA partition; ‡genera included in the REPRODUCTIVE + LARVAL data partition.

APPENDIX 2

Morphological character states for the taxa analysed (polymorphic states added as: a = 0 1; b = 1 2; c = 1 3). See Methods for character descriptions.

Terminal taxa	10	20	30	40	50	60	70	80	90	100
Acanthodoryctes	00?0000000	0100100000	?01000?010	000001?00?	1011000000	0110100001	0101101011	010?11?010	1211011111	0131000000
Acanthorhogas	00?0000000	0000000000	?0100??010	00010000??	0011001000	01100??100	0?????????	??10?00010	12?1??????	??????????
Achterbergia	0100100100	001?000001	00101??000	100101?10?	?011000000	01000??01?	0?????????	??????????	??????????	??????????
Acrophasmus	00?0000000	001?000000	?0a0011010	?10100001a	001100100a	01110??001	0001000?1	0011?0a010	1211011000	000000001?
Afrospathius	00?0000000	001?001000	?010a12010	?101000011	1011001012	0110100000	0001011010	1011?0?010	1?1?011000	000000000?
Aivalykus	00?0101100	00a0000000	?a001??0a0	100101?10?	?011000000	01000??0a0	0012011?0	1011?00010	1211210000	001000000?
Allorhogas	00?0000000	0001000000	?00000?010	?10100000?	a01a001000	01100??000	000???????	??10?00010	1211011000	001000000?
Amazondoryctes	00?0000000	0000000000	?0100??1?0	?10100000??	0010000000	010010010a	0?????????	??????????	??????????	??????????
Antidoryctes	110000001a	0100100000	?01000?010	000000000?	1011000000	010011?000	000???????	??????????	??????????	??????????
Aphelopsia	00?0000000	0000010000	?0100??010	?10100000??	101100100a	01000??0a0	0?????????	??????????	??????????	??????????
Aptenobracon	00?00000?1	0001000000	?01???????	??????????	??11001010	01100??000	1?????????	??10?01010	1??1??????	??????????
Araucania	00?0000010	0000000000	?00000?010	0001000011	1011001000	01000??000	0001001021	00????????	??????????	??????????
Arhaconotus	00?0100000	000a000000	?00100?000	100100000?	0011001000	111111?000	1000012?1	01????????	??????????	??????????
Asiaheterospilus	0100000000	001?000000	?00100?1?0	?1011000??	0010001000	01100??100	0?????????	??????????	??????????	??????????
Bathycentor	00?0000001	0000000000	?0000??010	00000000??	0011001000	011111?000	0?????????	??????????	??????????	??????????
Binarea	00?1000010	0100100000	?1a0012010	000110000?	1011000000	0100a00a01	01011?10?0	010?11?010	1211001101	00c000002?
Bohartiellus	00?01011?0	0010000000	?0101??010	100101?10?	?011000000	01000??01?	0012010?0	11????????	??????????	??????????
Bracodoryctes	00?0000000	01000aa01a	001000?0a0	000000000?	0011001000	0110100001	0001010011	01????????	??????????	??????????
Bulbonervus	00?0000000	0000000000	?0000??1?0	2011000000?	1011000000	01100??000	000???????	??????????	??????????	??????????
Caenophanes	00?0000000	0001000000	?0a000?1?0	100100000?	a011001000	01000??01?	000???????	??????????	??1?010000	001000000?
Caingangia	10?0000000	001?000000	?0101??010	?101000011	0011001000	011010a100	000???????	??????????	??????????	??????????
Callihormius	00?000000a	0001010000	?0a000?010	?10100001a	101100100a	0111a1?000	000???????	??10?00010	1211011000	0000000001
Canchim	00?0000000	00a0000?00	?0001??1?0	010?00000?	1111001000	00?00??0??	000???????	??????????	??????????	??????????
Ceylonspathius	00?000110a	0000000010	?1a???????	??????????	??10101012	00?00??00?	0?????????	??????????	??????????	??????????
Chelonodoryctes	00?0000000	001?000000	?01000?000	10010000??	00110010a0	01000??000	0?????????	??????????	??????????	??????????
Coiba	00?0000000	001?000000	?0001??010	?101000011	1011001000	01100??000	0000000?1	0011?0?010	1????1???0	?????000??
Cryptodoryctes	00?0a00000	01000a0000	?01000?010	000100000?	0011000000	0100100001	0001011010	01????????	??????????	??????????
Curtisella	00?0000000	001?010000	?010011010	?10000000??	0011001000	01100??000	0?????????	??10?00010	1211111000	000010000?
Cyphodoryctes	00?0000000	0000000000	?01000?010	000100000?	0011001001	01000??001	0001000?1	00????????	??1?011000	000000000?
Dendrosoter	00?01a0001	10aa000000	?0a000?aa0	a000000010	0011000000	01000??01?	0012001110	0a11?11010	1211000000	0120000001
Dendrosotinus	00?0a0000a	0001000000	?01000?000	100100000?	0011000000	01000??0a0	0000000?1	aa11?0011a	1?1?010000	001011????
Dicarynoryctes	00?0100000	0000010000	?0001??010	10?1?00000?	1011100000	00??11?000	00????????	??????????	??????????	??????????
Donquickeia	00?0100000	0001000000	?00000?000	?10100000??	0011001000	01000??001	0?????????	??????????	??1?010100	000000000?
Doryctes	00?000000a	000a010000	?0a000?010	000a00000?	1011001000	01a0a0000a	0001001010	0110?0001a	1211001100	0000011000
Doryctophasmus	00?001000a	0001010000	?01000?0a0	1000000010	0011010011	01000??000	0001001021	1011?00110	1211010000	001000000?
Ecphylopsis	00?0102100	000000a00?	?0000??10?	?10?01?0??	0?1?00?000	00?00??01?	0?????????	??????????	?????1????	??????????
Ecphylus	00?01011?0	00a0000000	?0a01??010	100101?10?	?a11000000	00?00??0a0	0012010110	1110?00010	1211210000	0010000001
Embobracon	00?0001000	0000001000	?01100?010	010101?0??	110?000011	00?00??01?	0?????????	??????????	?????1????	??????????

APPENDIX 2 *Continued*

Terminal taxa	10	20	30	40	50	60	70	80	90	100
Euscelinus	00?0010000	001?000000	?0a000?000	100100000?	0011010000	01000??01?	0000001011	1010?00110	1211000000	000000002?
Evaniodes	00?0000000	0000000001	100001a010	00010000??	1011001012	01100??0a0	0?????????	??10?00010	0211011000	000000000?
Fijibracon	00?01001?0	0000000001	00001??1?1	110?01?1??	?110000011	00?00??01?	0?????????	??????????	??????????	??????????
Fritziella	00?0100000	00a0000000	?0101??0a0	?10100010?	?01100001a	01000??01?	0??1100?1	11????????	??1?011000	000000002?
Glyptocolastes	00?0000000	001?000000	?010012010	?10100001a	1011001000	0110100101	00a1000211	00????????	??1?011100	0000000?1
Guaygata	00?0000000	0001000000	?00000?0a0	20010000??	a010001000	01000??01?	0?????????	??11?01010	1??1?1????	??????????
Gymnobracon	00?010000a	0000000000	?a10010010	000000000?	0010000000	011010110a	0101001?0	0110?01010	1211001100	001000002?
Halycaea	00?000000a	00000a0000	?0100110a0	0?0a00000?	00a1001000	0100101000	0a0???????	??11?00110	1211010000	001000000?
Hecabalodes	00?0000000	0001010000	?0101??0a0	?101000011	1011001000	0110a0000a	000000010?1	1a11?00010	1211011000	00b000000?
Hecabolus	00?0000000	0000000000	?0101??010	?10a000011	101a001000	01100??000	0000000011	1110?00010	121?011000	0000100011
Heerz	00?0000000	0000000000	?0001??010	010?00000?	1011001000	0??00??000	000???????	??????????	??????????	??????????
Hemidoryctes	00?0a00000	0001000000	?01000?010	2000000010	0011000000	01000??00a	0?????????	??11?01010	121?210000	00000000??
Hemispathius	00?0000000	0000010000	?01000?010	20010000??	00110000a2	0110100000	0?????????	??????????	??????????	??????????
Heterospathius	00?0000000	001?000000	?01000?1?1	?1010a00??	0010000012	01000??01?	0?????????	??????????	??????????	??????????
Heterospilus	00?0a00000	00aa0a0000	?0a000?1?0	?101000011	aa1100100a	011a0??a00	0000001a11	1010?01010	1b11011000	0000000020
Histeromeroides	10?0000000	0000000000	?1000??010	?1010000??	1010000000	00?00??01?	0?????????	??????????	??????????	??????????
Holcobracon	00?0000010	0000010000	?01000?010	000000100?	1011000000	0110100001	00011?12?0	110?11?010	?2?1??????	????????0?
Hybodoryctes	00?0?00000	0000000000	?1a00??011	000000000?	0011001000	0110100101	0?????????	??????????	?2?1??????	????????2?
Hypodoryctes	00?000000a	0000000000	?00000?010	000100000?	1010001000	0110a01000	0a01001010	0011?01110	1211010000	001000000?
Iare	00?000???0	0001?00000	?00000?010	110?00000?	1011001000	1??00??000	0?????????	??????????	??????????	??????????
Ipodoryctes	00?000000a	00aa000000	?0a000?0a0	200100000?	a011001000	011aa1?a00	100???????	??10?00010	1?1?010000	001000002?
Ivondrovia	00?0100000	0100000000	?100010010	00010010??	1010000000	0110100a01	0?????????	??0?11?010	1211010000	000000000?
Janzenia	00?0000000	0001010000	?01000?000	?1010000??	001100000b	0111a00000	0?????????	??????????	??????????	??????????
Jarra	110000000a	000a000000	?00000?010	000100000?	a01a001000	011a0??000	000000001	0111?01010	1211011000	002000002?
Jataiella	00?0000000	0000000?00	?000012100	010?00001?	1011001000	0??00??0??	000???????	??????????	??????????	??????????
Johnsonius	00?00000?0	001?000000	?a000??010	?1010000??	0010001000	01100??00a	0?????????	??????????	??????????	??????????
Labania	00?0001100	0000000000	?0110??1?0	?1010001??	?111000000	01100??01?	0?????????	??????????	??????????	??????????
Leluthia	00?0000000	00aa010000	?010a0?010	?10000001a	1011001000	0110a0000a	00a1000ba1	0011?00010	0211011000	000000000?
Leptodoryctes	00?0000000	0000000?00	?0001??1?0	110?01?10?	1111000000	0??00??0??	000???????	??????????	??????????	??????????
Leptorhaconotus	00?0000000	0001000000	?01000?000	100100000?	000?000011	011a110000	00?10?0011	010?000010	001001????	??????????
Leptospathius	00?0100000	0000010001	001001?010	000110000?	1011000011	010011?000	00011?aa?0	1110?01010	1211210000	?12020010?
Liobracon	00?100001a	0100100000	?aa000?010	000010000?	1011000000	0100100a0a	01011?1b?0	0110?10010	1211011001	0030000020
Liodoryctes	00?0000011	0100011000	?01000?010	0000a0100?	1011000100	0110100001	000???????	??0?11?010	1211011111	003100000?
Masonius	00?0100000	001?000000	?0101??010	?10100010?	?111001011	01000??000	00010?01?1	1110?00010	1?1?0?1000	001000002?
Megaloproctus	00?0a00000	000001000a	01a000?010	000a00000?	1011000000	01000??10a	0001001?0	1111?01010	1211010000	111000000?
Micrommatus	00?0100000	00a0000000	?0101??010	110101?1??	?11000001a	00?00??01?	0?????????	??????????	??1?011000	000000002?
Mimipodoryctes	a0?000000a	001?000000	?00000?000	200100000?	0010001000	1111a1?000	1000001?21	01????????	??????????	??????????
Mimodoryctes	00?0000010	001?00a000	?0101??010	20010000??	1011001000	01100??001	0?????????	??????????	??????????	??????????

Monarea	00?00000a0	0000010000	?1100100010	000001?00?	1011000000	0100100000a	000011?200	0102112010	1211001001	0031?0002?
Monolexis	00?0100000	001?000000	?0a01??000	?101000000?	1011001000	01100??a01	000100011a	0110?00010	1211011100	0010000011
Mononeuron	00?0000?20	00a0000007	?000002?010	?102012a0?	111?000000	01100??012?	0??????????	??????????	??????????	??????????
Neodoryctes	00?0000000	0000000000	?000000?010	0001000000?	0011001000	01a01000a1	0101000171	01??????????	??1?001170	0000011002
Nervellius	00?0000011	0000010000	?01000?010	0001101000?	1011000000	0110a000001	000071127?0	000?112010	1211011111	0031?00002
Neurocrassus	00?0000000	000a000000	?000000?0a0	0011000000?	1011001000	01a00??a00	0001000071	0011?01110	1?1?010000	0000000007?
Nipponecphylus	00?01053?0	0000000000	?01011??1?0	1?0101?10?	?11a000000a	00?00??01?	000???????	??????????	??????????	??????????
Notiospathius	00?0000000	001?000000	?0100a101a	?101000000?	0010000011	01000??0a0	0001000071	1110?00010	1211011000	0000000007
Odontobracon	00?0a0001a	0000010000	?01000?010	0000001007	1011000100	0110100001	000???????	??0?112010	1211011101	0031000020
Odontodoryctes	00?0000?0	001?010000	?01007?010	000?000007?	0011000100	0110111?100	0??????????	??????????	??????????	??????????
Ontsira	00?0000000	0000000000	?000000?010	0001000007	101a001100a	0aa00??aa0	000a0012a1	0111?01010	1211010170	0000000002
Osmophila	00?0000000	0000000000	?0a0010010	000a000007	0011001000	0110010a100	00011?01?1	0111?10010	1211211000	0000000007
Pambolidea	00?0a0000a	001?000000	?0111??010	?101000007	1111000a0	01000??0a0	0??????????	??10?00010	1?????1000	0010000007
Paradoryctes	00?0000000	00a0010000	?0100??010	0001000007	1011000100	01101a0101	0??????????	??????????	??????????	??????????
Parallorhogas	00?0000000	00a0000000	?a0000?010	?101000007	a01a001000	01a00??a00	0001000071	1011?0?010	1?1?001000	0010000007
Parana	00?0107?70	0001000000	?0100??001	100?01?0??	0011000012	01100??017?	0??????????	??????????	??????????	??????????
Paraspathius	a1000000001	001?000000	?0a000?000	20010000a0	001a000012	01a00??017?	0??????????	??11?01110	1211010000	0110000007
Pareucorystes	00?0a00000	0001010000	?010a0?0a0	?101000011	a011000000	0110007?100	0001000011	1010?00010	1211011000	0010100007
Pariodes	?????70000	0000000001	11100??010	?a01000011	1a11001012	0110007?000	0??????????	??????????	??????????	??????????
Pedinotus	00?0000000	00000a0000	?0a0011010	000a000007?	0011001000	0110100101	0??????????	??????????	2211211000	0000000007
Percnobracon	10?0100100	001?000000a	0a001??011	?1010a010?	?111000001b	0110007?017	0??????????	??11?01010	1?1?011100	0010000007
Percnobraconoides	00?0000001	001?001000	?0101??010	?101000011	101100000a	0110007?0a1	0??????????	??10?01010	1?1?011100	0000000007
Piosselus	00?0100000	0001000000	?0100a0100	?101000007	0011000000	0110100?01	0??????????	??0?01?010	1?1?010000	0010000007
Platydoryctes	0000100000	001?001000	?000a0?010	110?01?000	0011000007	0?00?????0?	000?????0?	??????????	??????????	??????????
Platyspathius	00?0a0000a	0001000000	?0a000?000	1001000007	001a001011	0110007?000	0000001071	0010?01110	1211010000	0010000007
Polystenoides	00?0100000	0000010000	?0100??010	?101000011	0011001000	011010000a	0??????????	??????????	??????????	??????????
Polystenus	00?0000000	001?010000	?0101??010	?101000007	1a11000000	0110100001	0011000010	1110?00010	1211011000	0000000007
Priosphys	00?0100?70	0000010000	?0100111010	000?000007	0011000100	0110007?000	0??????????	??????????	??????????	??????????
Psenobolus	00?0100000	0000a00100	?a1000?010	?101000007	0011000012	0100007?0a0	0001000171	0010?00010	1211010000	0000010007
Pseudodoryctes	0110000001	0000000001	0aa001a010	0001000007	0011000000	0110100101	0011?00?71	1111?00011	1211001000	00b0000007
Pseudorhoptrocentrus	1100000071	0000000000	?000000?010	?101000007?	0010000000	0100007?000	0??????????	??10?01010	1?1?010000	1000000007
Ptesimogaster	00?0000000	001?000000	?0100??000	?100000007	0011001a001	0110117?000	000?????0?	??10?00010	1?1101110000	0000000007
Ptesimogastroides	00?0100010	0010010010	?0100?10?0	?1?1?11007	0011100010	00?0?0?7000	00?0?????0?	??????????	??????????	??????????
Rhaconotus	00?0a0000a	00aa000000	?0a00a1000	10010a0007	a011001000	011aa1?a007	a0000000011	1111?00010	1b11010000	0010000020
Rhacontsira	00?0100000a	00a1000000	?0010007010	2001000007	0010001000	0110007?100	0000000171	01??????????	??????????	??????????
Rhoptrocentrus	00?0000000	001?000000	?0a0007000	2001000007	001a000000	00?00??0000	0001171171	0107107010	1211010000	0010000000
Schletteriella	a0?0100000	10a0000001	0010011010	0000000007	0011000011	0100100001	0001171?0?0	0111?01010	1211210000	1210200107
Semirhytus	00?0000000	0000000000	?a0000?010	?101000007	0011001100a	0110007?10a	0001001071	1100017010	1211010000	0010000007
Sericobracon	00?0000000	001?000000	?000007010	0101000007	100?001000	0110117?100	0??????????	??????????	??????????	??????????
Sharkeyella	00?0100000	001?010000	?0100??010	1101000007?	0011000002	0110100101	0001171?1?	00??????????	??1?211000	0000000007?
Shawius	10?0000000	001?010000	?0100??010	?100000011	1011001000	0110007?000	0001000071	0011?01010	1?1?011000	0000000007?
Siragra	0110000001	0100000011	01000100a0	0000000007	0011000000	0100100a01	000117?0010	0111?01010	1211010000	0b200001??

APPENDIX 2 *Continued*

Terminal taxa	10	20	30	40	50	60	70	80	90	100
Sisupala	10?000000a	0100000000	?00000?000	200000000?	0010000011	01000??01?	0001??11?1	00????????	?2?1??????	????????0?
Sonanus	00?0a10000	0001000000	?01001?010	200100000?	0011010000	010010000[a]	000???????	??????????	??????????	??????????
Spathiomorpha	00?0000000	0000000000	?00000?010	000100000?	1011001002	01000??0a0	0001000110	0110?01010	1?1?000000	001000000??
Spathioplites	00?0000001	101?000000	?011010010	100100000?	1011000012	01100??0a1	000???????	??????????	?2?1??????	????????0?
Spathiospilus	00?0000000	0001000000	?00000?1?0	?10100000??	1010001012	01100??01?	0?????????	??????????	??????????	??????????
Spathiostenus	00?0100000	00a0010000	?0101??010	?10101?0??	00110000a1	0110101000	0?????????	??????????	??????????	??????????
Spathius	00?000000a	00aa0a0000	?00000?a00	b00100000?	a01a00a012	01a00??0a0	000100aa11	0011?01010	1b10010000	0220000000
Stenocorse	00?0000000	0001000000	?01000?010	?10100000?	10110010a0	01100??001	0001000?1	0010?00010	1211011000	001000000?
Stephanospathius	00?0100000	0000010001	001000?0a0	000000000?	0011000012	010011?01?	000???????	??11?00010	1?1?000000	10001000??
Subcurtisella	00?0000000	001?010000	?01000?010	?10001?0??	0011001011	01100??001	0?????????	??????????	??????????	??????????
Syngaster	1110a0000a	0000000000	?a1000?010	000000000?	0011000000	01101a010a	0011001?0	0111?01010	1211001110	101000002?
Synspilus	0100000000	001?000000	?00000?1?0	?10100000??	0010000000	01100??100	0?????????	??????????	??????????	??????????
Tarasco	00?0a00000	001?000000	?0101??010	?10100000??	0a11001012	01100??01?	0?????????	??10?00110	1?1?011000	011000000?
Terate	00?0000000	001?0a0000	?0101??010	?101000011	1011000000	0110a00000	000???????	??????????	??????????	??????????
Termitobracon	00?01032?0	0a00001110	?11000?000	?10?0a00??	111?000010	00?00??01?	0??10?0211	1110?00010	121100????	????????0?
Termitospathius	00?000110a	0000000000	?11000?000	200000000?	0011100012	00?00??00?	000???????	??????????	??????????	??????????
Toka	00?0100000	0001001000	?0100??010	10010000??	0011000011	01100??01?	0?????????	??????????	?211010000	011000000?
Trigonophasmus	00?010000a	0000010000	?01001a010	000000000?	0011001011	0110101002	00011?00?1	0110?00010	1211001000	01b000000?
Tripteria	00?0000001	0000000000	?01000?010	?10100000?	0010001000	01100??100	0?????????	??0?01?010	1211011000	0120000000
Verae	10?0000000	000a000000	?0101??010	?1010a00??	1010000001	01000??0a0	0001001 0?1	0111?00010	1?1?011000	000000000??
Waitaca	00?0000000	0000000000	?1000??000	?1000000??	1011001000	01100??000	0?????????	??????????	??????????	??????????
Whartonius	10?0000000	001?000000	?01000?010	?101000011	1011001000	01100??001	00110?01?0	10????????	??1?011000	001?0000??
Whitfieldiellus	1100000000	0000001000	?1100??010	?1010000??	0010001000	0111100000	0?????????	??????????	??????????	??????????
Ypsistocerus	00?00044?0	010000111?	?11000?1?0	?10?01?00?	111?000010	00?00??01?	0??10?0?11	??????????	??????????	??????????
Zombrus	00?0000010	0000010000	?01000?010	000000100?	1011000100	0110100001	00011?1200	010?11?010	1211011111	003100002?
Aleiodes	00?0a00000	00aa000000	?01000?010	00010a000?	100?000000	01000?0000	000???????	??a000?a00	0010?000??	???????000
Braconinae	aaa000110a	01aa00aa10	?1000aa010	a00001?00?	00a10000a0	0110aa10a0	0a0b0001aa	010?000020	2010000?0	000?0??000
Clinocentrus	00?0000000	0000000000	?00000?010	000?00000?	100?000000	00?00?0000	0000000 1?1	010?000000	0010000??	???0???000
Colastes	00?0000000	0000000000	?00000?010	000?01?00?	100?000000	00?00?0000	0001001011	0001000000	0000000??	???0???000
Dolopsidea	00?0000010	0000000000	?00000?010	0001000000	1010000000	00?00??01?	0001000000	00????????	??????00??	??????????
Hormius	00?0000010	00a0000000	?0a000?000	100100000?	100?000000	00?00?00a0	0000010211	110?00?000	0010?000??	???????000
Metaspathius	10?0000011	0000000000	?00???????	??????????	??11000001	00?00??01?	0?????????	??????????	??????????	??????????
Monitoriella	00?0001000	00010a00a0	?01000?000	1a0a000000?	000?000000	01100??000	0??1010011	0?????????	??????????	??????????
Phaenodus	00?0000000	00a0000000	?01000?010	0a0000000?	000?000000	01000?0010	000b0102?1	010?000000	0010000??	???????00?
Rhysipolis	00?0000000	00000a0000	?0a000?010	00000a000?	a00?000000	00?00?0000	0000010111	010?000000	0010000?0	00000??000
Rhyssalus	00?0000010	000a000000	?01000?0a0	000000000?	a0a1000000	0100000000	0000010201	000?000000	0000000?0	000?0??000
Stiropius	00?000000a	0001000000	?00a00?010	?1010a000?	000?000010	01100?0000	000???????	??0?000000	00100?00??	???0???00?
Doryctomorpha	10?0000000	0001000000	?00000?000	000101?00?	1010000000	0000000010	00000?????	??0?000000	0100000??	???????00?

APPENDIX 3

List of the species examined in this study from collection specimens and from literature. Abbreviations: H, holotype; L, lectotype; P, paratypes; PL, paralectotype; SP, nontype specimens examined; N, no specimens examined, scored from literature descriptions.

DORYCTINAE: *Acanthodoryctes* Turner: *Iphiaulax morleyi* Froggatt (L), *I. tomentosus* Szépligeti (H); *Acanthorhogas* Szépligeti: *A. setosus* Szépligeti (L); *Achterbergia* Marsh: *A. arawak* Marsh (P); *Afrospathius* Belokobylskij & Quicke: *A. dispar* Belokobylskij & Quicke (H); *Aivalykus* Nixon: *A. electus* Nixon (H) *Ecphyloides flavus* Marsh (H); *Amazondoryctes* Barbalho & Penteado Dias: *A. bicolor* Barbalho & Penteado Dias (N), *A. ater* Barbalho & Penteado Dias (N); *A. costaricensis* Marsh (P); *Antidoryctes* Belokobylskij & Quicke: *A. pronotalis* Belokobylskij & Quicke (H); *Acrophasmus* Enderlein: *A. amazonicus* Roman (H), *A. exilis* Enderlein (H), *A. maeandricus* Enderlein (H), *Concurtisella* Roman: *C. bidens* Roman (L); *Allorhogas* Gahan: *A. gallicola* Gahan (P); *Aphelopsia* Marsh: *A. annulicornis* Marsh (P); *Aptenobracon* Marsh: *A. formicoides* Marsh (H); *Araucania* Marsh: *A. penai* Marsh (H); *Arhaconotus* Belokobylskij: *A. papuanus* Belokobylskij (H); *Asiaheterospilus* Belokobylskij & Konishi: *A. kusegimati* Belokobylskij & Konishi (H); *Bathycentor* Saussure: *B. kraesselini* Saussure (L), *Ipodoryctes parallelus* Granger (L); *Binarea* Brullé: *B. spinicollis* Brullé (H), *B. pulchripes* Szépligeti (H), *B. nigridorsum* Enderlein (L); *Bohartiellus* Marsh: *B. cornutus* Marsh (N), *B. plaumanni* Marsh (N); *Bracodoryctes* Belokobylskij & Quicke: *B. tergalis* Belokobylskij & Quicke (H); *Bulbonervus* Shenefelt: *B. semilunaris* Shenefelt (H); *Caenophanes* Foerster: *Bracon incompletus* Ratzeburg (L), *Heterospilis asion* Nixon (H), *C. luculentus* Belokobylskij (H); *Caingangia* Marsh: *C. flavokolos* Marsh (H); *Callihormius* Ashmead: *Pambolus bifasciatus* Ashmead (L); *Canchim* Barbalho & Penteado Dias: *C. carinatus* Barbalho & Penteado Dias (N), *C. erugosus* Barbalho & Penteado Dias (N); *Ceylonspathius* Belokobylskij: *C. nixoni* Belokobylskij (H); *Chelonodoryctes* Belokobylskij & Quicke: *C. inopinatus*: Belokobylskij & Quicke (H); *Coiba* Marsh: *C. woldai* Marsh (H); *Cryptodoryctes* Belokobylskij & Quicke: *C. turneri* Belokobylskij & Quicke (H); *Curtisella* Spinola: *Neorhyssa nigra* Szépligeti (L); *Lissophrymnus annulicaudis* Cameron (H); *Cyphodoryctes* Marsh: *Cyrtonion brasiliense* Marsh (P); *Dendrosoter* Wesmael: *D. protuberans* (Nees) (SP), *D. middendorffi* (Ratzeburg) (SP), *D. hartigii* (Ratzeburg) (L); *Dendrosotinus* Telenga: *Dendrosoter ferrugineus* Marshall (L), *D. similis* Boucek, *Gildoria elegans* Hedqvist (H); *Dicarinoryctes* Braet & van Achterberg: *D. apicalis* Braet & van Achterberg (H); *Donquickeia* Marsh: *Quickia incompletus* Marsh (H); *Doryctes* Haliday: *D. striatellus* (Nees) (SP), *Hybodoryctes diversus* Szépligeti (H), *Udamolcus herero* Enderlein (H), and several species from Palaearctic and Oriental regions; *Doryctophasmus* Enderlein: *D. ferrugineiceps* Enderlein (H); *Ecphylopsis* Ashmead: *E. nigra* Ashmead (L), *E. swezeyi* Beardsley (N); *Ecphylus* Foerster: *E. silesiacus* (Ratzeburg) (SP), *E. caudatus* Ruschka (SP), *E. arephini* Belokobylskij (H); *Embobracon* van Achterberg: *E. brevistigmus* van Achterberg (N); *Evaniodes* Szépligeti: *E. areolatus* Szépligeti (H); *Euscelinus* Westwood: *E. sarawacus* Westwood (SP), *Sbeitla furax* Wilkinson (H); *Fijibracon* Belokobylskij: *F. insularis* Belokobylskij (H); *Fritziella* Marsh: *F. plaumanni* Marsh (H, P); *Glyptocolastes* Ashmead: *G. texanus* Ashmead (SP), *Glyptodoryctes caryae* (Ashmead) (SP), *Doryctes texanus* Ashmead (H); *Guaygata* Marsh: *G. howdeni* Marsh (P); *Gymnobracon* Szépligeti: *G. brasiliensis* Szépligeti (H), *Ipospathius denticoxa* Enderlein (H), *Rutheia superba* Szépligeti (H); *Halycaea* Cameron: *H. erythrocephala* Cameron (L), *Cendebeus filicornis* Cameron (L); *Hecabalodes* Wilkinson: *H. anthaxiae* Wilkinson (H), *H. radialis* Tobias (H), *H. tadzhicus* Tobias (H); *Hecabolus* Curtis: *H. sulcatus* Curtis (SP); *Heerz* Marsh: *H. tooya* Marsh (H); *Hemidoryctes* Belokobylskij: *H. soror* Belokobylskij (H), *Camptocentrus annulipes* Cameron (H); *Hemispathius* Belokobylskij & Quicke: *H. polystenoides* Belokobylskij & Quicke (H); *Heterospathius* Barbalho & Penteado Dias: *H. belokobylskiji* Barbalho & Penteado Dias (N), *H. petiolatus* Barbalho & Penteado Dias (N); *Heterospilus* Haliday: *Harpagolaccus pectinatus* Enderlein (H), *Anocatostigma paradoxum* Enderlein (H), and numerous species from Palaearctic and Oriental regions; *Histeromeroides* Marsh: *H. onkoterebrus* Marsh (H); *Holcobracon* Cameron: *H. fulvus* Cameron (H); *Hybodoryctes* Szépligeti: *Doryctes bicolor* Szépligeti (L), *Goniogmus ferrugineus* Enderlein (H); *Hypodoryctes* Kokujev: *H. sibiricus* Kokujev (H), *Mixtec whartoni* Marsh (H); *Janzenia* Marsh: *J. gauldi* Marsh (H); *Jataiella* Barbalho & Penteado Dias: *J. pilosa* Barbalho & Penteado Dias (N); *Johnsonius* Marsh: *J. xanthus* Marsh (H); *Ipodoryctes* Granger: *I. anticestriatus* Granger (H), *Epirhacon laetus* Belokobylskij (H), and several species from Afrotropical and Oriental regions; *Ivondrovia* Shenefelt & Marsh: *Lophogaster seyrigi* Granger (L); *Labania* Hedqvist: *L. straminea* Hedqvist (H); *Leluthia* Cameron: *L. mexicana* Cameron (H), *Doryctosoma paradoxum* (P), *Panama canalia* Marsh (H); *Leptodoryctes* Barbalho & Penteado Dias: *L. luizi* (N); *Leptorhaconotus* Granger: *L. brunneus* Granger (H); *Leptospathius* Szépligeti: *L. formosus* Szépligeti (L), *Rhoptrospathius striatus* Cameron (H), *Habnoba petiolata* Cameron

(L); *Liobracon* Szépligeti: *Hyboderia collare* Enderlein (L), *L. singularis* Szépligeti (H), *L. partitus* Enderlein (H), *Triderodon hoffmannsi* Enderlein (H); *Liodoryctes* Szépligeti: *Acanthodoryctes australiensis* Szépligeti (L), *Neotrimoriodes dentifer* Strand (H); *Masonius* Marsh: *M. fasciatus* Marsh (H, P); *Megaloproctus* Schulz: *Megaproctus nigridorsum* Enderlein (H), *M. didymus* Brullé (H), *M. brasiliensis* Szépligeti (H), *Ectetamenochir crinicornis* Enderlein (H), *Prosthiacantha harpactorina* Enderlein (H); *Micrommatus* Marsh: *M. brevicornis* Marsh (H, P); *Mimipodoryctes* Belokobylskij: *M. robustus* Belokobylskij (H); *Mimodoryctes* Belokobylskij: *M. proprius* Belokobylskij (H); *Monarea* Szépligeti: *M. fasciipennis* Szépligeti (H), *M. longicornis* Enderlein (H); *Monolexis* Foerster: *M. fuscicornis* Foerster (L), *M. atis* Nixon (H); *Mononeuron* Fischer: *M. duguetiae* Fischer (N); *Neodoryctes* Szépligeti*: N. thoracicus* Szépligeti (H); *Nervellius* Roman: *N. subdivisus* Roman (L); *Neurocrassus* Snoflak: *Ontsira rara* Belokobylskij (H), *N. tentorialis* Belokobylskij (H), *N. fabimaculatus* Belokobylskij (H); *Nipponecphylus* Belokobylskij & Konishi*; N. matsumurai* Belokobylskij & Konishi (H); *Notiospathius* Matthews & Marsh: *Psenobolus columbianus* Enderlein (H), *P. laucacrocera* Enderlein (H), *P. sculpturatus* Enderlein (H); *Odontobracon* Cameron: *O. nigriceps* Cameron (SP); *Odontodoryctes* Granger: *O. biannulatus* Granger (L); *Ontsira* Cameron: *O. reticulata* Cameron (H), *Clinocentrus anticus* Wollaston (L), *Wachsmannia maculipennis* Szépligeti (H); *Osmophila* Szépligeti: *O. hyalinipennis* Szépligeti (H); *Pambolidea* Ashmead: *P. yuma* Ashmead (H); *Paradoryctes* Granger: *P. coxalis* Granger (L); *Parallorhogas* Marsh: *P. pallidiceps* (Perkins); *Parana* Nixon: *P. clotho* Nixon (H); *Paraspathius* Nixon: *P. periparetus* Nixon (H); *Pareucorystes* Tobias*: P. varinervis* Tobias (H); *Pariodes* Fischer: *Evaniodes spathiiformis* Szépligeti (H); *Pedinotus* Szépligeti: *P. brasiliensis* Szépligeti (H), *P. columbianus* Enderlein (H); *Percnobracon* Kieffer: *P. secundus* Muesebeck (H); *Percnobraconoides* Marsh: *P. jojoba* Marsh (H); *Pioscelus* Muesebeck & Walkley: *Caenophanes borealis* Ashmead (H); *Platyspathius* Viereck: *P. bisignatus* (Walker) (SP), *P. dinoderi* (Gahan) (SP), *Spathiohormius ornatulus* Enderlein (L); *Polystenoides* Muesebeck: *P. lignicola* Muesebeck (H); *Polystenus* Foerster: *P. rugosus* Foerster (L), *Eucorystes aciculatus* Reinhard (H); *Priosphys* Enderlein: *P. denticulata* Enderlein (H); *Psenobolus* Reinhard: *P. pygmaeus* Reinhard (L); *Pseudodoryctes* Szépligeti: *P. annulicornis* Szépligeti (H); *Pseudorhoptrocentrus* Granger: *P. brunneus* Granger (L), *Rhoptrocentroides platyfemur* Marsh (P); *Ptesimogaster* Marsh: *P. parkeri* Marsh (H); *Ptesimogastroides* Braet & van Achterberg: *P. cerdai* Braet & van Achterberg (H); *Rhaconotus* Ruthe: *R. aciculatus* Ruthe (H), *Rhaconotinus caboverdensis* Hedqvist (H), and numerous species and types from Palaearctic, Oriental and Afrotropical regions; *Rhacontsira* Belokobylskij: *Ontsira heterospiloides* Belokobylskij (H), *R. sculpturator* Belokobylskij (H), *R. nana* Belokobylskij (H); *Rhoptrocentrus* Marshall: *R. piceus* Marshall (SP), *R. syrmiensis* Szépligeti (H); *Schlettereriella* Szépligeti: *Stenophasmus buettneri* Stadl (H), *Biphymaphorus rufithorax* Szépligeti (H), *Ogmophasmus flaviceps* Enderlein (H), *O. ingens* Enderlein (H); *Semirhytus* Szépligeti: *S. filicornis* Szépligeti (H), *Neoclinocentrus variegatus* Szépligeti (PL), *Liparophleps crassivena* Enderlein (H); *Sericobracon* Shaw: *S. armaensis* Shaw (H); *Sharkeyella* Marsh: *S. pilosus* Marsh (H); *Shawius* Marsh: *S. braziliensis* Marsh (H); *Siragra* Cameron: *S. nitida* Cameron (SP); *Sisupala* Nixon: *S. splendida* Nixon (H); *Sonanus* Belokobylskij & Konishi: *S. senzuensis* Belokobylskij & Konishi (H); *Spathiomorpha* Tobias: *S. varinervis* Tobias (H)*, S. brevipalpis* Belokobylskij (H); *Spathioplites* Fischer: *S. phreneticus* Fischer (H); *Spathiospilus* Marsh: *S. brasiliensis* Marsh (P); *Spathiostenus* Belokobylskij: *Eucorystes formosanus* Watanabe (H); *Spathius* Nees: *Spathius exarator* (Linneus) (SP), and type specimens of numerous species from Palaearctic, Oriental, and Afrotropical regions, *Pseudospathius tricolor* Szépligeti (H); *Stenocorse* Marsh: *Glyptocolastes bruchivorus* Crawford (H); *Stephanospathius* Belokobylskij: *Stenophasmus ornatipes* Kieffer (H); *Subcurtisella* Roman: *S. waterstoni* Roman (H); *Syngaster* Brullé: *S. lepidus* Brullé (L), *Epitonychus variegatus* Szépligeti (H); *Synspilus* Belokobylskij & Quicke: *S. nitidus* Belokobylskij & Quicke (H); *Tarasco* Marsh: *T. spathiiformis* Marsh (P); *Terate* Nixon: *T. menopon* Nixon (H); *Termitobracon* Brues: *T. emersoni* Brues (SP); *Termitospathius* Belokobylskij: *T. sumatranus* Belokobylskij (H); *Toka* Nixon: *T. glabrivena* Nixon (H); *Trigonophasmus* Enderlein: *T. schenklingi* Enderlein (H); *Tripteria* Enderlein: *T. crinicauda* Enderlein (H); *Verae* Marsh: *V. peculya* Marsh (H, P); *Waitaca* Marsh: *W. flavostigma* Marsh (H); *Whartonius* Marsh: *Clinocentrus rugulosus* Cameron (H); *Whitfieldiellus* Marsh: *Whitfieldia variegatus* Marsh (H); *Ypsistocerus* Cushman: *T. manni* Cushman (N); *Zombrus* Marshall: *Z. anisopus* Marshall (L), *Z. bicolor* Enderlein (H). OTHER SUBFAMILIES: RHYSSALINAE: *Metaspathius* Brues: *M. apterus* Brues (H). The remaining genera of the Rhyssalinae and those of the Exothecinae, Mesostoinae, Pambolinae, and Rogadinae and the Braconinae were scored from numerous specimens belonging to species particularly from the Palaearctic, Oriental, and Afrotropical regions.