

Cladistic review of generic taxonomic characters in Xyleborina (Coleoptera: Curculionidae: Scolytinae)

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Abstract. A cladistic analysis of morphological characters of the subtribe Xyleborina (Curculionidae, Scolytinae) is presented. An examination of individual characters revealed little phylogenetic information in many characters currently used for delimiting genera. Phylogenetically stable characters were used for the evaluation of the contemporary generic concept. The following genera have been recovered as monophyletic: *Cnestus*, *Dryocoetoides*, *Eccoptopterus*, *Xylosandrus*, *Schedlia*, *Sampsonius* and *Taurodemus*. The following genera have been found to be polyphyletic: *Amasa*, *Ambrosiodmus*, *Arixyleborus*, *Coptoborus*, *Coptodryas*, *Cryptoxyleborus*, *Cyclorhipidion*, *Euwallacea*, *Leptoxyleborus*, *Taphrodasus*, *Theoborus*, *Webbia*, *Xyleborinus* and *Xyleborus*. The analysis permitted the resurrection of four genera: *Anisandrus*, *Microperus*, *Pseudowebbia* and *Streptocranus*. A number of new combinations at specific level are given: *Anisandrus cornutus* (Schaufuss, 1891), *A. dispar* (Fabricius, 1792), *A. eggersi* (Beeson, 1930), *A. improbus* (Sampson, 1913), *A. longidens* (Eggers, 1930), *A. maiche* Stark, 1936, *A. obesus* (LeConte, 1868), *A. sayi* Hopkins, 1915, *A. apicalis* (Blandford, 1894), *A. hirtus* (Hagedorn, 1904), *Microperus myristicae* (Schedl, 1939), *M. eucalypticus* (Schedl, 1938), *M. huangi* (Browne, 1983), *M. intermedius* (Eggers, 1923), *M. kadoyamaensis* (Murayama, 1934), *Pseudowebbia armifer* (Schedl, 1942), *P. seriata* Browne, 1963, *P. squamatilis* (Schedl, 1955), *P. trepanicauda* (Eggers, 1923), *P. curvatus* (Browne, 1986), *Streptocranus bicolor* Browne, 1949, *S. bicuspis* (Eggers, 1940), *S. capucinulus* (Schedl, 1942), *S. forficatus* (Schedl, 1957), *S. fragilis* Browne, 1949, *S. longicauda* Browne, 1960, *S. longispinis* Browne, 1986, *S. mirabilis* Schedl, 1939, *S. usagaricus* (Eggers, 1922), *S. sexdentatus* (Eggers, 1940). The characters most useful for generic-level taxonomy of Xyleborina were identified and their states refined and illustrated. An accompanying illustrated multiple-entry electronic key for the updated xyleborine classification has been published on-line at www.scolytid.msu.edu.

Introduction

Stephen L. Wood's 'Reclassification of the genera of Scolytidae' (Wood, 1986) was the first publication to place the chaotic classification of bark and ambrosia beetles (Coleoptera, Curculionidae, Scolytinae) within an evolu-

tionary framework. This publication synthesized scattered generic descriptions, redefined generic boundaries and attempted to infer taxonomic relationships. Unfortunately, a reclassification of subtribe Xyleborina, one of the most diverse and economically important groups of scolytids, was exceptionally problematic. Wood's (1986) introduction to the tribe was foreboding and stated, in part, that the generic classification of the subtribe was tentative and flawed.

Females of Xyleborina can be distinguished from other scolytines by the circular, dorsoventrally flattened antennal club with the first segment often conspicuously sclerotized, by the depressed submentum, by arcuate and flattened

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meso- and metatibiae armed with six or more denticles (unless secondarily reduced), and by a pronotum strongly convex anterodorsally, armed with asperities on the anterior slope. Biologically, this group is clearly defined by the combination of a haplodiploid genetic system in which haploid males are flightless and often dwarfed, and show extreme inbreeding, and obligate nutritional symbiosis with xylophagous fungi (the ambrosial habit, or 'fungus gardening'; Francke-Grosmann, 1967; Beaver, 1989; Jordal *et al.*, 2000; Farrell *et al.*, 2001). Although these biological features are found elsewhere in Scolytinae, their combined occurrence in Xyleborina is unique. These biological features are also hypothesized to be the cause of a rapid radiation that has produced nearly 1400 species since the early Oligocene (Jordal *et al.*, 2000). Both the rapid diversification and the inbreeding are probable causes of unclear species limits and a relative lack of clearly definable morphological characters.

Contemporary systematics recognizes monophyletic groups of organisms as evolutionary entities, which form the basis of taxonomy and nomenclature (Hennig, 1966). Monophyletic groups are defined by synapomorphic characters, which are shared by an ancestor and all its descendants. However, taxonomic groups are often not defined by synapomorphies, and only unique combinations of homoplasies define clades. Numerous morphological attributes have been proposed to define the genera of Xyleborina (Hopkins, 1915; Wood, 1980, 1983, 1986; Maiti & Saha, 2004), but it is untested if these characters represent synapomorphies. This study examined the utility of morphological characters to define monophyletic groups of Xyleborina species and the association of these groups with current generic nomenclature (Wood & Bright, 1992; Bright & Skidmore, 1997, 2002). Trees resulting from a cladistic analysis of 193 species using 39 characters allowed evaluation of the monophyly of genera and the relative phylogenetic information of the characters. Identification of several monophyletic groups allowed a partial revision of the current classification.

Since the inclusion of the family Scolytidae into the family Curculionidae as a subfamily (Marvaldi, 1997; Kuschel *et al.*, 2000), previous scolytine tribes (e.g. Xyleborini sensu Wood & Bright, 1992) are currently treated as subtribes (Xyleborina; Arnett *et al.*, 2002; Rabaglia *et al.*, 2006). This classification is followed in this paper.

Methods

The cladistic analysis was based on 39 morphological characters in 193 species of Xyleborina. Species of Xyleborina were sampled evenly from currently valid genera. For most genera, we scored 25% of species. Only the most speciose genus, *Xyleborus* Eichhoff (534 species) was represented by less than 10% of species. In *Hadrodemius* Wood, only one species was available. Two species of *Premnobius* Eichhoff were selected as outgroups, as *Premnobius* was previously considered a genus of Xyleborina (Wood, 1986), and because *Premnobius* belongs among the groups most

closely related to Xyleborina (e.g. Farrell *et al.*, 2001; Cognato, unpubl.).

The analysis presented was based on female morphology. Males, which are cryptic and rare, most often occur within maternal galleries in very low numbers, and are unknown for most species. Type species of all xyleborine genera were examined, except for *Amasa*, *Sampsonius* and *Taurodemus*, for which only nontype species were available at the time of the study.

The set of characters for this study was compiled from the literature (Hagedorn, 1912; Hopkins, 1915; Wood, 1986; Maiti & Saha, 2004) and from our own studies. All the characters extracted from the literature fell into one of three groups (Table 1):

1. characters included in the analysis (Table 1);
2. characters excluded from the analysis due to ambiguous definition of their states (Table 2);
3. characters that were impossible to use because they were damaged or inaccessible in many examined specimens (Table 2). For example, the majority of scolytid type specimens in Schedl's collection in the Natural History Museum, Vienna, are glued to mounting boards, which precludes the use of many ventral characters.

The character matrix is provided as on-line supplementary material.

The independence of several characters in the analysis is suspect. For example, pronotum types (characters 8, 15) include the pronotal length/width ratio (character 2), and antenna type (character 6) is composed of characters 23 (central portion of the apical margin of the first club segment), 17 (extent of the first club segment) and 14 (posterior face of the antennal club). Developmentally or otherwise correlated characters should not be used in cladistic analyses, as they function as nonindependent pseudoreplications (Kluge, 1985) and could potentially skew the resulting tree. However, in this study, analysis of the phylogenetic correlation of all available characters was a higher priority than the finalization of the relationships among taxa.

The phylogenetic analysis was performed using TNT software (Goloboff *et al.*, 2003). The driven search employed all four search modules [sectorial search (RSS and CSS), ratchet, drifting and tree fusing]. Default settings were used except that trees were fused globally after every hit and the search continued until the minimal length tree was found ten times. Random seed was set to 1. Tree bisection and reconnection swapping was performed on the resulting trees to search for more nonduplicate maximum parsimony (MP) trees holding a maximum of 10 000 trees. Trees were filtered for duplicates. The islandic structure of the distribution of MP trees in tree space was not examined. The distribution of characters among taxa was examined using randomly selected MP trees, relationships between taxa were inferred from the strict consensus tree (Fig. 1). Bootstrap analysis of branch support was performed with WINCLADA (Nixon, 1999).

The cladistic analysis provided us with a measure of phylogenetic information content for each character.

Table 1. Characters used in the analysis, references to literature, retention index (RI) and character states.

No.	Character	RI	Reference	State 1	State 2	State 3	State 4	State 5
1	Enlarged metatibia and metatarsus	100	Wood (1986)	Normal size	Exceedingly large metatibiae and metatarsi	Third third of the range		
2	Pronotum length/width ratio	80	This study	First third of the range	Second third of the range			
3	Second club segment posteriorly	75	This study	Corneous	Soft or undecided	Not visible		
4	Scutellum	75	Wood (1986)	Flush	Invisible or visible only on the slope of the elytral base	Process-like		
5	Pronotal mycangial tuft	74	This study	Absent	Present			
6	Antennal club type (see Fig. 2)	74	This study	Truncated, circle closed anterior	Circle closed posterior	Not truncated, first segment convex, second prominent	First segment anterior smaller than second, both convex	Sutures merged
7	Antennal club profile	72	Wood (1986)	Truncate	Unclear	Whole		
8	Pronotum type – dorsal (see Fig. 4)	69	This study	See Fig. 4 for character states				
9	Elytral mycangial tuft, hair on mesonotum/elytra associated with mycangium	69	This study	No tuft	Tuft present			
10	Costa of first club segment	68	Wood (1986)	Weak, obsolete, obscured by hair	Continuous			
11	Elytra length/width ratio	67	This study	First fifth of the range	Second fifth of the range	Third fifth of the range	Fourth fifth of the range	Fifth fifth of the range
12	Extent of pronotal asperities/pronotal summit position	66	This study	Asperities/summit extending to posterior half, or unclear	Asperities/summit confined to the anterior half			
13	Second club segment anteriorly	66	Maiti & Saha (2004); Wood (1986)	Corneous, glabrous	Soft, unclear	Hardly or not visible		
14	Posterior face of antennal club	64	Wood (1986)	Posterior face covered by first segment	Comb of overreaching pubescence visible from back	One segment visible on the posterior side	Two segments visible on the posterior side	Segments merged
15	Pronotum type – lateral (see Fig. 3)	63	This study	See Fig. 3 for character states				
16	Pronotal disc surface/asperities	63	Wood (1986)	Shining, puncturation may be present	Dull, fine reticulation	Asperities of approximately the same size as on the frontal slope		
17	Extent of apex of the first club segment	63	Wood (1986)	Less than one-third of club height	Approximately one-third	More than one-third		
18	Pronotal lateral subacute elevation/costa (not carina)	60	Wood (1986)	None or short, pronotum generally rounded	Long costa (elevated rim), exceeding two-thirds of length			
19	Posterolateral costa of elytral declivity	59	Maiti & Saha (2004); Wood (1986)	No elevated costa	Costa not reaching beyond seventh interstriae	Costa reaching over seventh interstriae, or encircling the whole declivity		

Table 1. Continued.

No.	Character	RI	Reference	State 1	State 2	State 3	State 4	State 5
20	Declivity surface – teeth, outward structures	59	This study	No prominent outward structures	Prominent teeth or other structures			
21	Pronotal anterior edge serration	58	Wood (1986)	None, first row of asperities distant from edge, or serration does not differ from pronotal asperities	Two conspicuous teeth	Conspicuous row of more or less equal teeth		
22	Elytral end shape	58	Wood (1986)	Rounded or unclear	Attenuated	Emarginate	Truncated	Angulate
23	Central portion of the apical margin of the first club segment	57	Wood (1986)	Convex	Straight or unclear	Concave		
24	Protibia secondary tubercles	57	Wood (1986)	Absent	Present			
25	Pronotum anterolateral angle from sideview	56	This study	Less than 90°	More than 90°, bulging	Unclear, approximately 90°		
26	Geographical distribution	56	Wood (1986)	Eurasia, Australasia	Africa, Madagascar	Americas		
27	Protibia type	53	Wood (1986)	Rounded	Triangular	Stick-like, inflated, or otherwise modified		
28	Vestiture inside declivity	51	Wood (1986)	Declivity bald or almost so	Few setae	Long and/or dense setae		Scales, flattened setae
29	Declivity surface – rugged surface	51	This study	Surface flat, smooth (may have tubercles or teeth)	Densely rugged surface			
30	Pronotal lateral edge emargination	50	Wood (1986)	Convex	Straight or unclear	Concave, emarginate		
31	Declivity extent seen from above	48	Wood (1986)	Reaching beyond posterior half of elytra	Confined to posterior half	Only structures (ridges, rugosities) extended anterior		
32	Declivity surface – furrows and ridges	45	Wood (1986)	Surface flat	Ridges, furrows			
33	Pronotum bulging, quadrate	45	This study	Normal	Unclear, bulging at sides, semiquadrate	Bulging frontally		
34	Gular–pregular sutures joint	44	Wood (1986)	Impressed	Flat			
35	Procoxae	43	Wood (1986)	Contiguous	Narrowly separated	Widely separated, gap wider than scapus		
36	Punctures on elytral disc	41	Wood (1986)	Punctures seriate	Punctures confused			
37	Pronotal lateral acute carina	38	Wood (1986)	No carina	Short carina	Long carina exceeds two-thirds of pronotum width		
38	Second segment of funnicle	12	Hopkins (1915)	Shorter than first	Same length or longer than first			
39	Elytral horizon anterior to declivity/elytral disc horizon	11	This study	Flat or convex	concave, saddle-shaped			

Dark grey, antennal characters; light grey, elytral characters; black, pronotal characters.

Table 2. Characters used by other authors but not used in the present analysis.

No.	Character	Author	Reason
41	Mesocoxal distance	Wood (1986)	Most specimens in Schedl's collection have been glued on the ventral side, thus preventing the analysis of ventral characters.
42	Antennal funicle segments number	Wood (1986)	Unobservable in many museum specimens, but should be used in future analyses.
43	Basal segment of labial palpus cylindrical, same size as second segment	Wood (1986)	Required damage to specimens.
44	Ornamental setae on labial palpus	Wood (1986)	Required damage to specimens.
45	Prolonged labium	Hagedorn (1912)	Required damage to specimens.
46	Small oval ligula	Hagedorn (1912)	Required damage to specimens.
47	Relative size of the segments of labial palpi	Hagedorn (1912)	Required damage to specimens.
48	Maxilla's mala attenuate towards apex	Hagedorn (1912)	Required damage to specimens.
49	Shapes of segments of labial palps	Hagedorn (1912)	Required damage to specimens.
50	Ventral margin of metafemur angulate, rounded or flat	Wood (1986)	Character states gradually change across species and are difficult to score without making arbitrary decisions.
51	Metatibial groove for reception of tarsus	Wood (1986)	Character states, as defined by the author, are not observed in most species.
52	Number of denticles on protibia	Wood (1986)	Character states are variable within some species. Moreover, it is unclear whether it is a continuous, meristic, or discrete character and it is difficult to determine homology of individual denticles.
53	Number of denticles on metatibia	Wood (1986)	See reason for character 52.
54	Denticles on protibia confined to less than half/more than three-quarters	Wood (1986)	Character states, as defined by the author, are not observed in most species. May be used in future analyses after re-evaluation.
55	Declivity broad, flat	Wood (1986)	Character states gradually change across species and are difficult to score without making arbitrary decisions.
56	Spaces between striae – dull or shining	Wood (1986)	Character states gradually change across species and are difficult to score without making arbitrary decisions. In some species, both surface types occur on various parts of the elytra of a single specimen.
57	Eye emargination	Wood (1986)	Character states gradually change across species and are difficult to score without making arbitrary decisions.

Homoplasy for each character was measured with the retention index (RI) (Farris, 1989). Two continuous characters were used (length/width ratio of pronotum and elytra). Both have a gradual distribution, which hampers the division into discrete states. Thus, the optimal number of states used for these continuous characters was determined by maximizing the consistency of the assigned states with a phylogenetic hypothesis based on all characters. The scales of both characters were divided into thirds, fourths, fifths and sixths and each of these segments was assigned a discrete state. The rescaled characters were treated as additive. Separate analyses were performed with the datasets each containing one of the rescaled continuous characters and the discrete characters, and RI was calculated for the character in question. Differences among the RIs of the differently rescaled continuous characters were minor; however, the highest indices were found in the character

'pronotum length/width ratio' when divided into thirds, and in the character 'elytra length/width ratio' when divided into fifths. These two-character codings were used for the final analysis.

For the purpose of consistent coding and feasibility of communication between taxonomists, states of the most useful characters have been formalized. Dorsal and lateral types of the pronotum (characters 8 and 15, respectively) have been assembled by recording every distinct shape of pronotum encountered. The five types of antennal club (character 8, Fig. 2) are combinations of several characters typically evolving together: longitudinal profile (character 7), accentuation of the costa of the first club segment (character 10), curvation of the suture of the first segment (character 23), size of the first and second segments (character 17) and the number of segments visible on the posterior face of the antennal club (character 14).

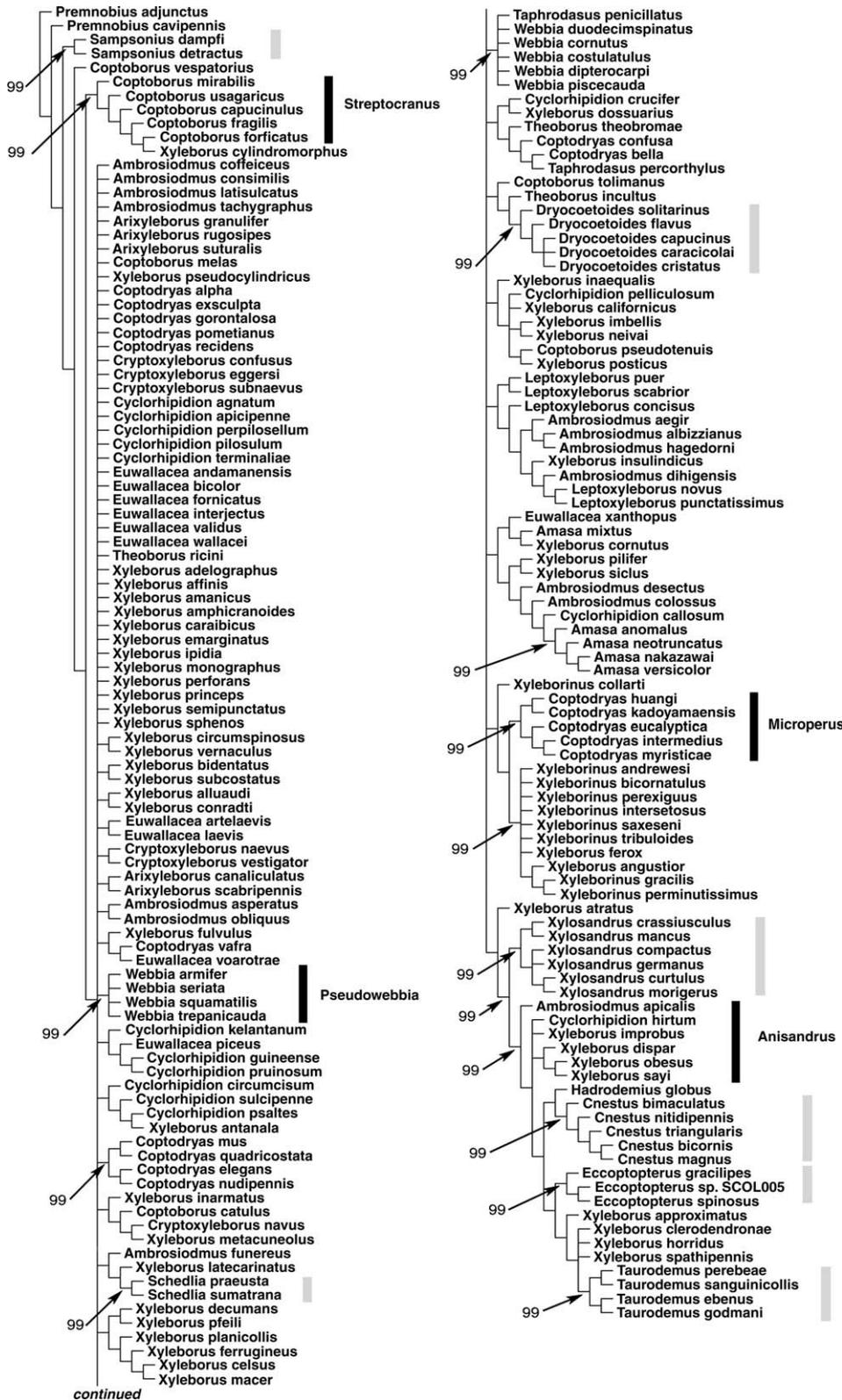


Fig. 1. Strict consensus of the 10 000 maximum parsimony trees, 1045 steps long. Monophyletic genera are marked with grey and resurrected genera are marked with black. The numbers are bootstrap values of the clades discussed in the text.

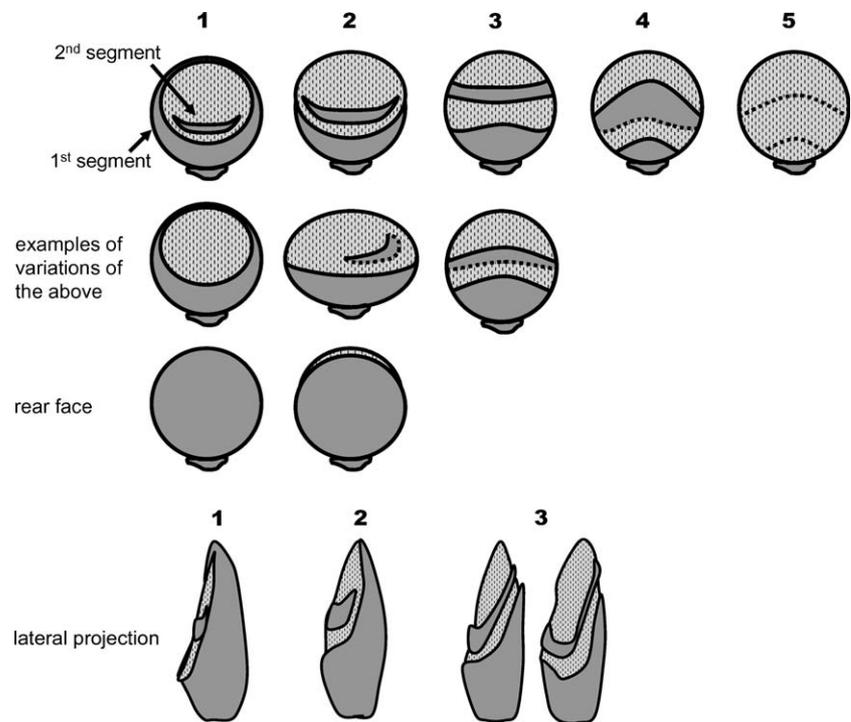


Fig. 2. Types of antennal club in Xyleborina. Upper row, five basic types; second row, variations in types 1–3; third row, posterior face of the club of types 1 and 2; fourth row, lateral view of types 1–3.

Results and discussion

Trees

We found 10 000+ equally parsimonious trees [1045 steps, consistency index = 0.06, RI = 0.46]. The strict consensus tree was mostly unresolved (Fig. 1). However, all nodes of the consensus tree were recovered in more than 50% of replications in the bootstrap analysis. The large number of spurious groups was probably caused by the unfavourable ratio of the number of taxa vs. the number of characters, by the substantial degree of homoplasy among characters, and perhaps by missing or ambiguous coding in a number of instances (4% of cells in the matrix). The weak support and lack of resolution indicate that the hitherto used set of characters was insufficient for a complete revision of Xyleborina genera. Hence, the addition of alternative characters is essential for the development of a stable generic concept.

Characters

Characters were ranked according to RI (Table 1). Generally, only characters with RI = 0.6 and higher were phylogenetically informative and are discussed further. The most stable character was the enlarged metatibia and metatarsus in *Eccoptyterus* Motschulsky (RI = 1, character 1).

Three groups of characters are highlighted in the table: characters associated with pronotum shape, antennal club and elytra. Apparently characters from the former two

groups often have high RIs, whereas elytral characters often have the lowest RIs. Thus, most discussion pertains to pronotal and antennal characters, along with other informative characters.

States of the most useful characters have been formalized: antennal club type (Fig. 2), lateral aspect of pronotum shape (Fig. 3), and dorsal aspect of pronotum shape (Fig. 4). The evolution of the antennal club probably progressed from the type 4 found in the outgroup and in *Sampsonius* Eggers, through type 3. Type 3 is the basal state of all the rest of Xyleborina. Derived antennal club types include type 2, which is most common among Xyleborina, and type 1, which is found mostly in *Xyleborinus* Reitter and in the clade that contains *Xylosandrus* Reitter and related genera. Type 5 is found only rarely, typically in *Amasa* Lea, and in a clade of a few species that represent the genus *Notoxyleborus* Schedl, a genus currently synonymized with *Xyleborus*.

The standard types of pronotum shape can be understood as a pattern of hypothetical diversification of the pronotum shape. The most common type of the lateral aspect of the pronotum (Fig. 3) is type 0, from which the pronotum was either prolonged (types 7 to b) or shortened (types 2–5), or assumed other rarer shapes (1, 6). The prolonged types of the pronotum can be further distinguished by the extent to which the summit of the pronotum remained approximately median (7, a) or moved anteriorly, causing the anterior end of the pronotum to bulge anteriorly and laterally (8 and especially b). (The forms of pronotum ‘a’ and ‘b’ are not given numbers 10 and 11, as would be expected logically. We decided to choose single-character names that can be readily

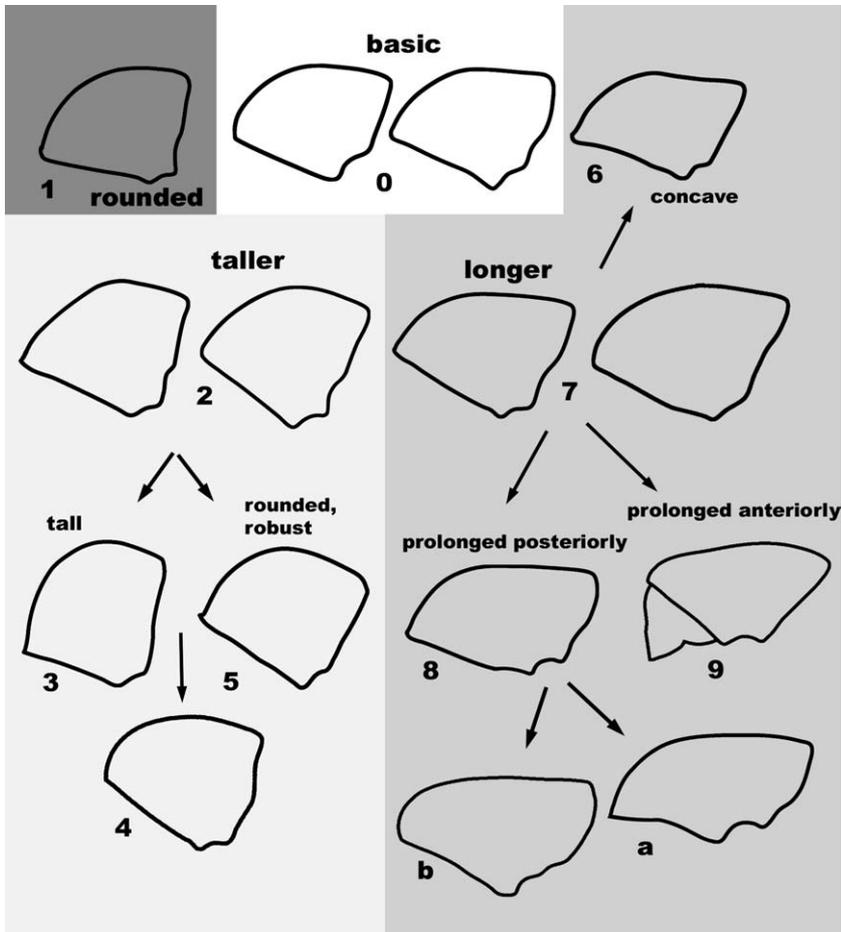


Fig. 3. Types of pronotum in Xyleborina, lateral aspect. The types are modifications of the basic shape (0) and are modified into relatively taller shapes (left side) or relatively longer shapes (right side).

used in cladistic software, where the utility of two-character numbers is limited).

The diversity of the topical aspects of the pronotum can be expressed as a combination of an increase in length/width ratio and the tendency of the anterolateral sides to bulge (Fig. 4). The latter represents a gradual change from almost triangular to quadrangular shapes.

Another important phylogenetically informative character is the scutellum (character 4), even though highly consistent state definitions need further elaboration in the future. For example, we suspect that a number of species are currently included in *Coptodryas* Hopkins because of their lack of an externally visible scutellum. However, some of these species possess a cone-shaped scutellum (state 3) concealed under the elytra. Unfortunately, this is impossible to examine without damage to the specimens. The cone-shaped scutellum and absence of a visible scutellum in many species may be linked to the presence of elytral mycangia (Beaver, 1975).

Although not used in any taxonomic analysis known to us, the presence and type of mycangia proved to be a reliable character. Xyleborine mycangia are conserved structures, as compared with other bark and ambrosia beetles (for exam-

ple, Platypodidae), where the presence and type of the mycangium varies between related species (Wood, 1993). Four types of mycangium are known to occur in Xyleborina: mandibular, prothoracic, mesothoracic and elytral (Francke-Grosmann, 1967; Beaver, 1989; Goto, 1998). Only the pronotal type is easy to recognize externally by the presence of a tuft of setae on the medioposterior edge of the pronotum. This mycangium is typical for the group of apparently related genera *Cnestus* Sampson, *Eccoctopterus*, *Hadrodemius*, *Xylosandrus* and the 'Anisandrus' group of species. The setae presumably collect fungal spores from tunnel walls. It must be emphasized that in the present work the tuft has been scored, not the presence/absence of the mycangium. The tuft may often be absent even though the mycangium is present, which is perhaps the case in some species of *Cnestus*. Conversely, several species have posterior pronotal vestiture resembling the mycangial tuft, although the presence of a pronotal mycangium has not been proved. Thus, the character 'pronotal mycangial tuft' may be more homoplastic than the actual presence/absence of mycangia, which may be scored only after the dissection of specimens.

The tufts of setae occurring on the mesonotum and on the anterior margin of the elytra (character 9) are presumably

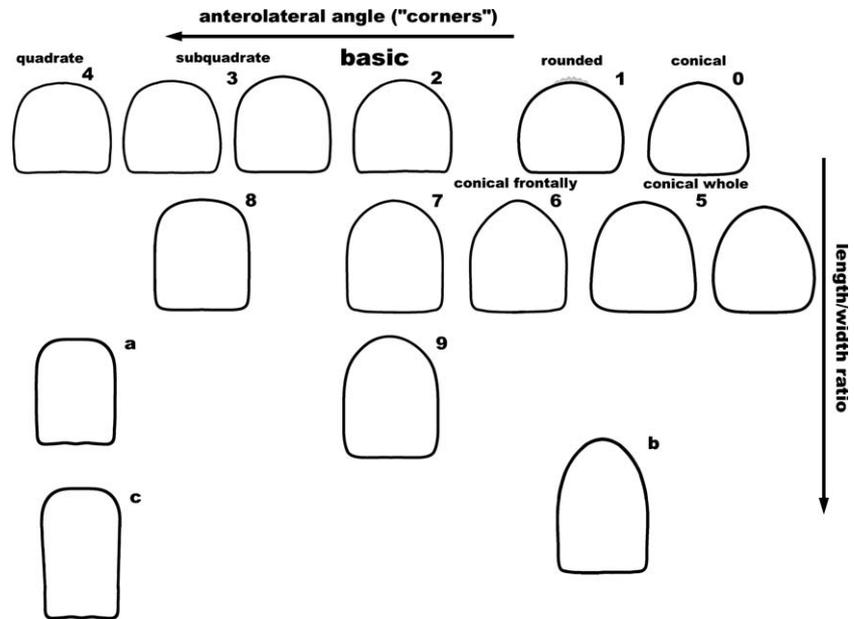


Fig. 4. Types of pronotum in Xyleborina, dorsal aspect. The types are modified by the length/width ratio and the lateral expansion of the anterior portion of the pronotum.

also associated with mycangia. However, it is sometimes unclear whether the mycangium is of the mesothoracic or elytral type. It is also unclear whether the mycangia in some *Cryptoxyleborus* Schedl that have openings on the outer surface of the elytra are homologous to the general elytral mycangia, or represent yet another type. Mycangial characters will probably be more informative following future study, and will be especially helpful for resolution within and between the genera *Cryptoxyleborus*, *Coptodryas*, *Pseudowebbia* Browne, *Schedlia* Browne, *Taphrodasus* Wood and *Xyleborinus*.

Character 11 'elytral length/width ratio' is the only elytra-associated character appearing relatively consistent. Rather than an elytral feature, this ratio describes the shape of the whole abdomen. It is probably for that reason that it is phylogenetically more stable than other elytral characters.

The third state of character 16 'pronotal disc surface/asperities' (asperities covering most of the pronotal surface) is mentioned in most keys as diagnostic for *Ambrosiodmus* Hopkins (Wood, 1986; Maiti & Saha, 2004). Wood (1986) and Beaver (2004) mentioned several species of *Ambrosiodmus* that have the asperities confined only to the anterior parts of the pronotum, as in other Xyleborine species (e.g. *A. apicalis* (Blandford), *A. funereus* (Lea)). These species share characters with other genera of Xyleborina. This finding suggests the removal of these species from *Ambrosiodmus*, but, with the exception of *A. apicalis*, this is not undertaken here pending further investigations.

In character 19 'posterolateral costa of elytral declivity' it seems that states 1 (no costa) and 2 (small costa present) are not consistent across Xyleborina, but state 3 (costa reaching beyond the seventh interstria, often encircling the whole elytral declivity) has arisen only a few times. There are problems with coding this third state, however, because it is

unclear whether costa, carina, and elevated row of teeth/serrations are all homologous traits. Presently, only costa and carina have been scored as the third state, which causes inconsistency in some groups, for example *Webbia* Hopkins s.str.

Of the three states of character 21 'pronotal anterior edge serration', only the third (two prominent teeth on the front edge of the pronotum) seems to be phylogenetically informative. It is a typical feature of *Sampsonius*, and of the group of the four closely related genera *Cnestus*, *Eccoptopterus*, *Hadrodemius* and *Xylosandrus*, only rarely appearing elsewhere.

According to the distribution of character states for character 22 'elytral end shape' on the tree, the plesiomorphic state is apparently a rounded end. The derivations are abundant and often inconsistent with other characters, but within some groups, derived character states are often stable and diagnostic. This is the case for *Cryptoxyleborus*, which has attenuated elytra, *Streptocranus* Schedl with emarginate elytra, *Amasa* Lea, *Pseudowebbia* and *Webbia* with truncated elytra, and *Dryocoetoides* Hopkins with angulate elytra. It may be noted here that Schedl appears to have based his classification of Xyleborina to a large extent on the shape and sculpture of the elytral declivity (Schedl, 1963, 1977). However, characters associated with the elytral declivity are the least phylogenetically informative for generic-level relationships.

Character 26 'geographical distribution' was included in the analysis even though it is not genetically heritable and its phylogenetic utility may be questioned. However, the history of the distribution of taxa and the centres of speciation, both of which provide continuity of lineages through space and time, are often of great value for a systematist, especially in groups for which history has been shorter than that of continents. Geography was also

one of the crucial features used by Wood to delimit the contemporary genera of xyleborines. Our analysis showed that geography is among the less decisive characters for generic-level phylogeny.

Most of the original descriptions of Xyleborina genera and species were published in the prephylogenetic era of taxonomy, and as such often lack sufficient information on the descriptive characters (e.g. Lea, 1893; Sampson, 1911; Hopkins, 1915). Contemporary authors usually provide extensive discussion of characters, but the definitions of characters and especially their states may not be comparable between authors. We suggest that future descriptions of species of Xyleborina should refer to the set of phylogenetically most informative characters identified in the presented analysis, namely the pronotum shape types (Figs 2, 3), antennal club types (Fig. 4), scutellum and mycangial tufts. To assure consistency between descriptions, we suggest use of the formalized states presented here. Adoption of such a set of characters, and descriptions of their states, will increase the clarity of descriptions and provide greater justification for taxonomic changes within this group.

Taxonomy

The majority of characters used hitherto in the classification of Xyleborina do not support the generic concepts as defined by Wood & Bright (1992). Several monophyletic or stable paraphyletic groups were recovered in the present analysis. The following genera are supported: *Cnestus*, *Dryocoetoides*, *Eccoptopterus*, *Xylosandrus*, *Schedlia*, *Sampsonius* and *Taurodemus* Wood. *Hadrodemius* would probably be supported as well, but unfortunately only one species was available for the analysis. Genera that appear not to be monophyletic are *Amasa*, *Ambrosiodmus*, *Arixyleborus* Hopkins, *Coptoborus* Hopkins, *Coptodryas*, *Cryptoxyleborus*, *Cyclorhipidion* Hagedorn, *Euwallacea* Hopkins, *Leptoxyleborus* Wood, *Taphrodasus*, *Theoborus* Hopkins, *Webbia*, *Xyleborinus* and *Xyleborus*. Monophyletic subgroups of the following genera were consistently recovered: *Amasa anomalous* group, *Coptoborus mirabilis* group, *Coptodryas eucalyptica* group, *Coptodryas elegans* group, *Webbia trepanicauda* group and *Webbia dipteroearpi* group (Fig. 1). We now discuss some of the monophyletic genera and species groups, and put forward taxonomic changes based on these discussions. It should be noted that in making generic transfers of species, we cite the current name of the species as given by Wood & Bright (1992) in their catalogue, and not the original genus in which the species was described. The latter information can be obtained from the catalogue.

Xyleborinus Reitter, 1913

The apparent nonmonophyly of *Xyleborinus* in the present analysis is caused by the ambiguous positions of *Xyleborinus collarti* (Eggers), *Xyleborus angustior* Eggers and *Xyleborus ferox* Blandford. The holotype of *Xyleborinus*

collarti (in the USNM) does not possess the cone-shaped scutellum and elytral mycangia, which define *Xyleborinus* uniquely, and evidently is incorrectly placed by Wood & Bright (1992). The holotype of *Xyleborus angustior* (in the USNM), on the other hand, does have the *Xyleborinus* type of scutellum and therefore is transferred here to that genus. *Xyleborus ferox* was placed by Wood (1982) in a new subgenus (*Neoxyleborus*), but the four species included in the subgenus by Wood (1982) are listed in Wood & Bright (1992) under *Xyleborus*. The position of *Xyleborus ferox* within *Xyleborinus* requires further examination. Its position within the *Xyleborinus* clade is difficult to explain as it lacks most diagnostic characters of this genus. Except for these three species, *Xyleborinus* is a rather uniform genus and future revision will probably preserve its monophyly.

Nomenclatural changes resulting from the examination of type material.

Xyleborinus angustior (Eggers) **comb.nov.** for *Xyleborus angustior* Eggers, 1925.

Xyleborus collarti Eggers is returned here to its original genus from its current placing (Wood & Bright, 1992) in *Xyleborinus*.

Cnestus Sampson, 1911 and related genera

A stable group containing *Cnestus*, *Eccoptopterus*, *Hadrodemius*, *Xylosandrus* and a group of species currently placed in *Ambrosiodmus*, *Cyclorhipidion* and *Xyleborus* has been recovered (Fig. 1). We propose to restore the genus *Anisandrus* Ferrari for the latter group of species (indicated by the heavy black line at the lower right hand side of Fig. 1). Species in this group of genera are defined by the short, stout body, antennal club shape (generally type 1 and very flat) and, most importantly, by the presence of a pronotal mycangium. In the present analysis, this assemblage is paraphyletic with respect to a morphologically uniform group of species of *Taurodemus* and a few other similar *Xyleborus* species. These species are very similar to the previously mentioned paraphyletic group of genera, except that the mycangium has not been observed.

Anisandrus Ferrari, 1867

Anisandrus represents a paraphyletic, but diagnosable, assemblage of species within the clade above. These species share the pronotal mycangial tuft, antennal features (antenna type 1, flattened), the shape of the tibia, conspicuous tibial denticles and overall body shape. The group shares many features with *Xylosandrus*, but unlike *Xylosandrus*, the procoxae of *Anisandrus* are contiguous. Although on the morphological evidence the group is paraphyletic with respect to the rest of the clade, a preliminary molecular phylogeny reconstructed using rDNA 28S data showed *Anisandrus* to be monophyletic (Cognato *et al.*,

unpubl.), and thus the genus *Anisandrus* is resurrected here. An overview of the synapomorphies is given in Table 3.

Diagnosis. Body dark brown or black, up to 3.7 mm long, rather bulky, length/width ratio 2.0–2.3. Antennal club of type 1 – truncated, margin of segment 1 elevated into circular costa on the anterior face, no sutures on the posterior face; segment 2 visible on the anterior face, glabrous or soft; segment 3 normally unapparent; scape and funicle long and slender. Pronotum moderately short to very short, stout, robust, sometimes tall (types 0, 3, mostly 5); its anterior edge bearing either two conspicuous teeth, a row of equally sized teeth, or without teeth; disc dull, not shining, without asperities, with a median tuft of mycangial setae posteriorly; lateral margin convex, sometimes with a short carina. Scutellum triangular, flush with elytra. Elytra seriate-punctate, vestiture sparse and inconspicuous in most species, rarely long and dense; declivity rounded, without outstanding sculpture apart from small interstrial tubercles; declivital costa never reaching beyond seventh interstriae, never conspicuously elevated, sometimes absent. Legs relatively long, slender, often with denticles held in enlarged sockets. Procoxae contiguous.

Type species. *Anisandrus dispar* (Fabricius, 1792) (Fig. 5). The type species was described first in *Apate* Fab., but this genus belongs in the family Bostrichidae. It was designated the type species of the genus *Anisandrus* by Ferrari (1867), but subsequently has usually been considered as a member of the genus *Xyleborus*.

Nomenclatural changes associated with the resurrection of *Anisandrus* (asterisks mark species of which the holotype or a paratype was examined). The following species listed under *Xyleborus* by Wood & Bright (1992) are here transferred to *Anisandrus*:

- A. cornutus* (Schaufuss, 1891)* **comb.nov.** [Lectotype (USNM) examined but not included in the analysis];
A. dispar (Fabricius, 1792)*;
A. eggersi (Beeson, 1930) **comb.nov.** (specimen examined but not included in the analysis);
A. improbus (Sampson, 1913)* **comb.nov.**;
A. longidens (Eggers, 1930) **comb.nov.** (specimens examined but not included in the analysis);
A. maiche Stark, 1936 (specimens examined but not included in the analysis);
A. obesus (LeConte, 1868)* **comb.nov.**;
A. sayi Hopkins (1915)*.

The following species listed under *Ambrosiodmus* by Wood & Bright (1992) is here transferred to *Anisandrus*:

- A. apicalis* (Blandford, 1894)* **comb.nov.**

The following species listed under *Cyclorhipidion* by Wood & Bright (1992) is here transferred to *Anisandrus*:

- Anisandrus hirtus* (Hagedorn, 1904) **comb.nov.**

Table 3. Synapomorphies of *Anisandrus* and a comparison with other genera.

	<i>Xyleborus</i>	<i>Xylosandrus</i>	<i>Ambrosiodmus</i>
First segment of antennal club	Variable	Forming circular costa mostly visible on the anterior face 1, 2	Not forming circular costa on the anterior side 2, 3
Antennal club type	Variable	Segments 2 and 3 not visible, segment 1 covering the whole face	Segment 2 always visible, segment 3 mostly visible on the posterior face of antennal club
Posterior face of antennal club	Variable	Mostly present	Absent
Pronotal mycangial tuft	Absent	More or less apart	Adjacent
Procoxae	Adjacent	1, 2	Variable
Pronotum type, dorsal profile	Variable	0, 1, 5	Variable, mostly 4, 7
Pronotum type, lateral profile	Variable	Mostly rounded, but often truncated or other shapes	Variable
Elytral end shape	Variable		



Fig. 5. *Anisandrus dispar* (Fabricius), 3.25 mm. Type species of *Anisandrus* Ferrari.

Coptodryas Hopkins, 1915

In the present analysis, *Coptodryas* is polyphyletic. However, two distinct monophyletic groups have emerged. The first is comprised of the species *Coptodryas elegans* (Sampson), *C. mus* (Eggers), *C. nudipennis* (Schedl) and *C. quadricostata* (Schedl). Although this group and the type species, *C. confusa*, do not form a monophyletic group on the cladogram, they share all but a few minor characters, such as pronotal anterior serrations, the shape of the costa of the first antennal club segment and overall habitus. These species should thus remain in a single genus until a more thorough analysis is performed.

Diagnosis. Body proportions variable, length/width ratio 1.6–2.8. Antennal club variable, but never of type 1, ranging from obliquely truncate with segment 1 dominant on both anterior and posterior faces, with elevated and continuous costa, to not truncate with segment 1 smaller than segment 2 anteriorly; marginal costa of first segment usually procurved, sometimes straight; weak or obscured by setae in some species; second segment usually corneous on the anterior side, sometimes soft, always visible on the posterior face, where sometimes also corneous. Pronotum of variable shape, most often slightly shorter and taller than the basic type, rarely longer or more robust, rounded; never of extreme shape, nor bulging conspicuously anterolaterally; rounded laterally, sometimes with elevated blunt costa, but no carina; serrations on anterior edge of pronotum variable; usually with a dense tuft of setae at the base of the pronotum, and always with a distinct tuft of setae on the mesonotum and/or at bases of elytra. Scutellum conical, normally invisible, rarely visible as a pointed process almost hidden under the bases of elytra. Elytral bases typically costate or carinate, sometimes procurved; striae and interstriae sometimes forming ridges and furrows; declivital costa absent or short and inconspicuous; declivital sculpture normally consisting only of tubercles; elytral apex usually rounded, rarely truncate or slightly angulate; declivital vestiture variable, from almost none to

dense, long hair. Legs of usual xyleborine type, procoxae almost always contiguous, except in several species with narrow separation. This variable genus is characterized by the scutellum concealed beneath the elytra, and by the usually conspicuous vestiture on the mesonotum and elytral bases, associated with elytral mycangia. Such tufts of setae can also be found in *Pseudowebbia*, which can be distinguished by the truncate elytra, and in *Microperus*, but the latter genus has type 1 antennae, whereas *Coptodryas* has type 2, 3 or 4.

Type species. *Coptodryas confusa* Hopkins, 1915.

Microperus Wood, 1980

A second monophyletic subgroup of species currently placed by Wood & Bright (1992) in *Coptodryas* is represented in our analysis by *C. huangi* (Browne), *C. intermedia* (Eggers), *C. eucalyptica* (Schedl), *C. myristicae* (Schedl) and *Xyleborus kadoyamaensis* Murayama. These species differ from the type species *Coptodryas confusa* in many characters (Table 4), especially antennal characters and prolonged body shape. The species share characters and general appearance with *Xyleborinus*, but the small, conical scutellum is concealed by the elytra, and the elytral bases are not or very slightly incurved on either side of the scutellum. *C. myristicae* includes as one of its synonyms *Xyleborus theae* Eggers (Wood, 1989). The latter species was designated the type species of the genus *Microperus* Wood (Wood, 1980). Therefore, this genus name is resurrected to include the species listed above in the second monophyletic group.

Diagnosis. Small with elongate body, 1.5–2 mm long and 0.5–0.7 mm wide. Antennal club of type 1, marginal costa of segment 1 continuous, segment 1 often covering most of the anterior face of the club, always completely covering the posterior face, which lacks sutures; segment 2 on the anterior side soft or barely distinguishable; segment 3 barely or not visible. Pronotum of the basic shape (type 0), slightly prolonged anteroventrally, especially if seen from dorsal aspect; anterior margin almost never with a distinct row of serrations; lateral margin with a blunt elevated costa, but no carina; disc dull or shining; mycangial tuft never present, mesonotal or elytral mycangial tuft always present. Scutellum cone-shaped but normally hidden beneath the elytra. Elytral bases sometimes procurved, often costate; disc seriate-punctate, but punctures sometimes confused on declivity; declivity with elevated costa or carina laterally; the costa never extending beyond seventh interstriae, surface not strongly sculptured, but almost always coarse and matt, contrasting with smooth, shining elytral disc; declivital vestiture variable from almost absent to distinct, long and dense. Legs of the usual type, not inflated; procoxae contiguous. The genus is very similar to some small *Coptodryas*, the main difference being the form of the antennal club, which is of type 1 in *Microperus*, but type 3 or 4 in *Coptodryas* (see Table 4). *Microperus* is also closely

Table 4. Characters distinguishing *Microperus* from *Coptodryas*. *Coptodryas confusa* is the type species of *Coptodryas* and is thus used for the comparison.

	<i>Coptodryas confusa</i>	Majority of other <i>Coptodryas</i>	<i>Microperus</i>
Antennal club type (Fig. 3)	4	3, 4	1
Pronotum shape type (Fig. 1)	2	Varied, mostly 0	0 (7 in <i>M. kadoyamaensis</i>)
Antennal club profile	Rounded	Rounded (truncated in <i>C. gorontalonus</i>)	Truncated
Extent of the first segment of antennal club anteriorly	Less than one-third of the club height	Less than one-third, rarely approximately one-third or more	Exceeding one-third of the club height
Central portion of the apical margin of the first club segment anteriorly	Convex	Convex or straight	Concave, straight in <i>M. eucalyptica</i>
Costa of the first antennal segment	Weakly defined or obscured	Varied	Pronounced
Second club segment anteriorly	Corneous	Mostly corneous	Soft or hardly distinguishable
Second club segment posteriorly	Corneous	Varied, mostly soft	Not visible
Posterior face of antennal club	Second and third segments visible	Varied	Covered by first segment
Pronotal vestiture resembling mycangial tuft	Present	Varied	Absent
Vestiture on elytral declivity	Sparse	Mostly sparse	Often rich, either dense setae or scales, except sparse in <i>M. eucalyptica</i>
Body shape	Short, robust	Varied	Never conspicuously robust

related to *Xyleborinus*, but in *Microperus* the cone-shaped scutellum typical of *Xyleborinus* is hidden under the elytra, the elytral bases tend to be costate, and the elytral declivital costa is more developed than in most *Xyleborinus*.

Type species. *Xyleborus theae* Eggers (synonym of *Xyleborus myristicae* Schedl; Fig. 6).

Nomenclatural changes associated with the resurrection of Microperus. The following species listed under *Coptodryas* by Wood & Bright (1992) are here transferred to *Microperus*:

Microperus myristicae (Schedl, 1939)* **comb.nov.**;
M. eucalypticus (Schedl, 1938)* **comb.nov.**;
M. huangi (Browne, 1983)* **comb. nov.**;
M. intermedius (Eggers, 1923)* **comb.nov.**

The following species listed under *Xyleborus* by Wood & Bright (1992) is here transferred to *Microperus*:

Microperus kadoyamaensis (Murayama, 1934) **comb.nov.**

According to a preliminary study of characters not used in this analysis (absolute size, details of elytral punctuation, details of scutellum) and according to the similarity of general appearance, a number of smaller *Coptodryas* species will probably be eventually transferred to *Microperus*.

Pseudowebbia Browne, 1961

Species placed in the genus *Webbia* by Wood & Bright (1992) fall into two distinct, stable groups, which we consider represent two genera, *Webbia* and *Pseudowebbia* Browne. Wood (1983) synonymized *Pseudowebbia* with *Webbia* because the two type species, *W. dipterocarpi* Hopkins and *P. trepanicauda* Browne belonged to the same 'species group', but no characters were given to support this suggestion. In our opinion, *Pseudowebbia* shares more characters with some species of *Coptodryas* than with



Fig. 6. *Microperus myristicae* (Eggers), 1.55 mm. Type species of *Microperus* Wood.

Webbia s.str. (e.g. the shape of the pronotum, antennal club, body vestiture, especially the tuft, which is probably associated with an elytral mycangium; see Table 5). The main characters shared by *Webbia* and *Prowebbia* are the concealed scutellum and the truncate elytral declivity. The former character is also characteristic of *Coptodryas* species, and the shape of the elytral declivity is a character with little phylogenetic information. Thus, *Pseudowebbia* is resurrected for the clade that includes *W. trepanicauda* and three other species.

Diagnosis. Body somewhat variable in proportions, up to 3.3 mm long, length/width ratio 2.1–2.7, generally covered with sparse vestiture, never glabrous. Antennae of type 3 or 4, not truncate, costa of segment 1 often discontinuous, obscured by hair, procurved (convex) on the anterior face of the club; segment 2 corneous and glabrous on the anterior side or both sides of the club, segment 3 visible on both sides. Pronotum dorsally of type 7, rarely 2 or 3, never bulging or conspicuously quadrate or prolonged; laterally costate or rounded, without a carina; anterior margin of pronotum without a distinct row of serrations; surface of pronotal disc dull; mesonotum and bases of elytra of most species with a tuft of setae, possibly associated with a mycangium; in rare cases vestiture resembling mycangial tuft also present on posterior end of pronotal disc. Scutellum invisible externally. Elytra always sharply truncate; declivity encircled by declivital costa, sometimes armed with prominent teeth, declivital surface often rugose; declivital setae often transformed to flattened scales, vestiture sometimes rather sparse. Legs of the usual type, flattened; procoxae contiguous. The genus is characterized by the antennal club of type 3 (type 4 in *P. squamatilis*), the slightly prolonged shape of the pronotum (type 7 both laterally and dorsally, in *P. trepanicauda* the pronotum may be shorter, resembling types 2 or 3); scutellum not visible externally and truncate elytra. A tuft of setae associated with the mycan-

gium is usually present. The genus is superficially similar to *Webbia*, differing mainly in antennal characters, protibiae and pronotum shape (Table 5).

Type species. *Xyleborus trepanicauda* Eggers, 1923 (Fig. 7).

Nomenclatural changes associated with the resurrection of *Pseudowebbia*. The following species listed under *Webbia* in Wood & Bright (1992) are here transferred to *Pseudowebbia* (asterisks mark species for which the holotype or paratype was examined):

P. armifer (Schedl, 1942)* **comb.nov.**;
P. seriata Browne, 1963*;
P. squamatilis (Schedl, 1955)* **comb.nov.**;
P. trepanicauda (Eggers, 1923).

The following species listed under *Xyleborus* in Wood & Bright (1992) is here transferred to *Pseudowebbia*:

P. curvatus (Browne, 1986)* **comb.nov.** (species examined but not included into the analysis).

Webbia Hopkins, 1915

Diagnosis. Body cylindrical, usually with abruptly truncate elytra; very little or no vestiture. Length/width ratio 2.4–3.1. Antennae rather short, antennal club often wider than long; costa of first segment pronounced and continuous; segment 2 anteriorly mostly corneous, rarely soft; posterior side largely covered by corneous segment 1 with soft segment 2 visible above the edge of segment 1. Pronotum of a very characteristic shape – prolonged, quadrate from dorsal view, slightly bulging frontally and frontolaterally; no distinct row of serrations on the frontal margin; laterally with long costa, sometimes transformed to sharp carina;

Table 5. Comparison of characters of *Pseudowebbia* and *Webbia*.

	<i>Pseudowebbia</i>	<i>Webbia</i>
Antennal club type	3 or 4	2 or 1
Protibia	Normal, flattened	Stick-like, rounded
Pronotum type lateral aspect	2, 7	Very distinct, autapomorphic pronotum type b
Pronotum type dorsal aspect	2, 7	Distinctly prolonged, quadrangular, type a, c
Antennal club profile	Not truncated, oval	Truncated
Anterior costa of the first segment of antennal club	Convex	Concave or straight
Costa of the first segment of antennal club	Sometimes obscured by hair laterally or posteriorly, discontinuous, merged to the soft parts	Distinct costa running at both posterior and anterior faces, sometimes almost entirely on the anterior face
Posterior face of antennal club	Segments 2 and 3 visible	At most segment 2 visible, often completely covered by corneous segment 1
Pronotal summit, reach of pronotal asperities	Asperities cover more than the anterior half of the pronotum, summit in typical position	Asperities confined to the anterodorsal half of pronotum, summit pushed anteriorly
Vestiture inside declivity	Most often scale-like flattened setae	Sparse hair-like setae



Fig. 7. *Pseudowebbia trepanicauda* (Eggers), 2.50 mm. Type species of *Pseudowebbia* Browne.

disc and sides uniformly chagrinata; no vestiture. Scutellum invisible externally or visible only as pressed to the anterior slope of elytral bases. No vestiture associated with mycangia. Elytra of most species abruptly truncate, sometimes obliquely truncate or rounded or even angulate; elytral disc with seriate or confused punctures; declivity usually armed with prominent teeth, or conspicuous rugosities, or ridges and furrows; declivital costa from blunt or unapparent, to long, encircling the whole declivity; vestiture sparse or absent. Protibiae not flattened, but stick-like; procoxae contiguous. The genus is characterized by the antennal club of type 1 or 2, the elongate, quadrate, densely chagrinata pronotum of type a (both dorsal and lateral views) strongly bulging frontally and frontolaterally, truncate elytra, and stick-like protibiae. Distinguishing characters from *Pseudowebbia* are given in Table 5.

The *Webbia* s.str. clade also contains *Taphrodasus penicillatus* (Fig. 1). *Taphrodasus* is represented by only two species in our analysis, but these two species were never recovered as a monophyletic group. Although *T. percorthylus* is affiliated with *Coptodryas*, *T. penicillatus* always appears within *Webbia*. The most important characters shared between *T. penicillatus* and *Webbia* species are the antennal club type 2 and prolonged quadrangular pronotum bulging anteriorly and laterally. Additional characters and further analyses are needed to evaluate the taxonomic status of *Taphrodasus*.

***Streptocranus* Schedl, 1939**

Species placed in the genus *Coptoborus* by Wood & Bright (1992) appear scattered throughout the cladogram, with the exception of a group of extremely elongate African and Asian species. This group is distinct from the remaining *Coptoborus* species, which are mostly shorter species, and of American origin. Wood (1980, 1986) synonymized the genus *Streptocranus* with *Coptoborus* without giving any reason for his action. In the present analysis, the type species of *Coptoborus* (*C. vespatorius* (Schedl)), and the other New World species have not been recovered within the highly

autapomorphic group of the Old World species (Fig. 1). Because this group includes the type species of *Streptocranus* (*S. mirabilis* Schedl 1939), the genus *Streptocranus* is resurrected.

Diagnosis. Extremely elongate species, with length/width ratio 3.8–4.1. Antennae always obliquely truncate, types 1 or 2, with segment 1 dominant on both sides; costa of segment 1 always clearly formed, generally enclosing the club on its anterior face, its anterior part usually recurved (concave); segment 2 mostly soft, sometimes corneous on the anterior face, barely or not visible on the posterior face. Pronotum always extremely long, types a (lateral) and b (dorsal view); anterolateral margin sometimes bulging, making pronotum almost rectangular; laterally always emarginate, concave, in rare cases with a long sharp carina; anterior margin without conspicuous serrations; dorsally glabrous, shining; pronotum without any vestiture associated with mycangia. Elytra always long, declivity deeply emarginate, emargination sometimes extending into the anterior half of elytra; declivital costa none to very long, encircling the whole declivity; margins of declivity often armed with teeth; surface of declivity smooth, with few setae. Protibiae typically slender, stick-like; procoxae contiguous.

Type species. *Streptocranus mirabilis* Schedl, 1939 (Fig. 8).

Nomenclatural changes associated with the resurrection of *Streptocranus*. The following species included in *Coptoborus* by Wood & Bright (1992) are here transferred to *Streptocranus*:

Streptocranus bicolor Browne, 1949*;
S. bicuspis (Eggers, 1940)* (holotype of synonym, *S. recurvus* Browne, 1949, examined);
S. capucinulus Schedl, 1942* (holotype of synonym, *S. penangensis* Browne, 1950, examined);
S. forficatus (Schedl, 1957)* **comb.nov.**;
S. fragilis Browne, 1949*;
S. longicauda Browne, 1960*;
S. longispinis Browne, 1986*;



Fig. 8. *Streptocranus longispinis* Browne, 2.15 mm. A characteristic member of *Streptocranus* Schedl.

S. mirabilis Schedl, 1939*;
S. usagarius (Eggers, 1922) **comb.nov.**

The following species included in *Ambrosiodmus* by Wood & Bright (1992) is here transferred to *Streptocranus*:

Streptocranus sexdentatus (Eggers, 1940)* **comb.nov.** (type examined but not included in the analysis).

Coptoborus Hopkins, 1915

Diagnosis. Medium-sized, often elongate species from the New World tropics, almost always light brown or yellowish, length/width ratio 2.8–3.5. Antennal club of types 2 or 3, almost always obliquely truncate, with segment 1 dominant on both sides and its costa elevated; segment 1 is smaller than segment 2 in some species, its costa less pronounced; posterior side always with segment 2 visible, sometimes also segment 3. Pronotum prolonged but never extremely long, types 7 or 8, its dorsal side sometimes slightly concave (type 6); anterior edge almost always with inconspicuous or lacking serration; lateral sides often concave, emarginate from lateral view, sometimes with a short or long carina. Scutellum flush with elytra, no vestiture associated with mycangium. Elytra usually slightly elongate, their apices attenuated or emarginate, rarely rounded; declivital costa mostly inconspicuous, but sometimes long and elevated forming an emarginate declivity; prominent teeth or other structures absent, declivital surface may be densely rugose; vestiture mostly sparse. Legs of usual xyleborine shape, very rarely thinner. Procoxae contiguous. Characters that distinguish the genus from *Streptocranus* are given in Table 6.

The position of *Coptoborus melas* (Eggers, 1927) from the Philippines is yet to be investigated in detail. Although only a damaged specimen was available, the species probably belongs in *Xyleborus*. Although the *Streptocranus* clade contains *Xyleborus cylindromorphus*, this species lacks the important diagnostic character, a slender protibia, and thus is not included in *Streptocranus*.

Conclusion

This study is the first to examine xyleborine taxonomic characters in a cladistic framework. Although many generic relationships were unresolved, this analysis identified morphological characters that supported monophyletic species groups, which guided revision and resurrection of some genera. An obvious solution for the resolution of generic relationships is the inclusion of additional morphological (those unsampled, Table 2) and DNA data. Current research is underway to identify cladistically informative nucleotide characters sampled from nuclear and mitochondrial genomes (Cognato *et al.*, unpubl.). Past and preliminary data (Jordal *et al.*, 2000; Jordal, 2002) suggest that these data will aid this effort. Current attempts to reconstruct the phylogeny using molecular DNA sequences of several genes lend support for groups defined by the presence and type of mycangia (e.g. the group of *Anisandrus* and related genera; Cognato *et al.*, unpubl.).

The data matrix used for the analysis was implemented in an on-line, multiple-entry illustrated electronic key at www.scolytid.msu.edu.

Table 6. Comparison of characters of *Coptoborus* and *Streptocranus*.

	<i>Streptocranus</i>	<i>Coptoborus</i>
Antennal club type	1, 2 (3 seen in a dried-out specimen of <i>S. usagarius</i>)	Mostly 3; 2 in <i>C. vespatorius</i>
Protibia	Stick-like or inflated	Normal, flattened
Pronotum type lateral aspect	Type 14, conspicuously prolonged	Types 9 or 11 – mildly prolonged
Pronotum type dorsal aspect	b, c – conspicuously prolonged, often quadrangular frontally	2, 7, 8, 9
Costa of the first segment of antennal club	Concave or flat	Convex or flat
Second segment of antennal club on the posterior face	Almost never visible	Almost always visible
Posterior face of antennal club	Mostly only comb of pubescence visible reaching over the otherwise fully corneous first segment, rarely second segment visible	Mostly second and third segments, sometimes only second segment visible
Pronotum bulging	Pronotum frontolaterally bulging except in <i>S. forficatus</i>	Pronotum not bulging frontally
Surface on pronotal disc	Always shining	Mostly opaque, shining in <i>C. tolimanus</i>
Reach of pronotal asperities (position of pronotal summit)	Asperities reaching less than one-half of pronotal length	Asperities reaching beyond one-half of pronotal length (unclear in <i>C. catulus</i>)
Elytral declivity shape	Always emarginate	Ranging from angulate to emarginate
Elytra length/width ratio	2.15–2.4	1.65–2.07
Pronotum length/width ratio	1.42–1.92	1.11–1.33

Supplementary material

The following material is available at <http://www.blackwell-synergy.com> under DOI reference doi: 10.1111/j.1365-3113.2007.00386.x.

S1. Data matrix.

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