

Phylogenetic analysis of the family Bostrichidae auct. at suprageneric levels

(Coleoptera: Bostrichidae)

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Abstract

A phylogenetic analysis of the beetle family Bostrichidae auct. was conducted based on 122 adult morphological characters (96 multistate) of 31 genera and species, including at least one genus and species from every currently accepted subfamily and tribe of Bostrichidae, and four outgroup taxa, two genera and species each of Anobiidae and Dermestidae. The most-parsimonious hypothesis suggests a distinctly different classification from those of previous workers on the family. The Lyctinae is divided into three tribes: Lyctini BILLBERG, 1820, Trogoxylini LESNE, 1921 **sensu novo** and Cephalotomini LIU, 2011 **tribus novus**. The Bostrichinae is divided further into four tribes: Bostrichini LATREILLE, 1802 **sensu novo**, Apatini JACQUELIN DU VAL, 1861 **sensu novo**, Sinoxylini LESNE, 1899 **sensu novo** and Xyloperthini LESNE, 1921. This is the first phylogenetic study at suprageneric level of Bostrichidae auct.. Because there are no previous phylogenetic studies for comparison, we discuss the most-parsimonious hypothesis in relation to morphological and biological information as well as the phylogenetic analysis.

Introduction

The Bostrichidae *auctorum* form one of four or five families included in the superfamily Bostrichoidea (LAWRENCE & NEWTON 1995; IVIE 2002; BOROWSKI & WĘGRZYNOWICZ 2007). If we consider those taxonomic groups included in the Bostrichidae in two of the most recent publications (IVIE 2002; BOROWSKI & WĘGRZYNOWICZ 2007), there is considerable variation in structure. However, most fall into one of two major morphological groups. Most Bostrichids have a hypognathous head which is not visible from above, but the head is prognathous in four subfamilies (Lyctinae, Psoinae, Polyaconinae, Dysidinae) (FISHER 1950; GERBERG 1957; IVIE 1985, 2002). In the hypognathous group, the pronotum is cowled and the anterior dorsal surface is rough and rasp-like, and may have curved horns or hooks at the anterior angles (FISHER 1950; IVIE 2002); the elytra are highly variable, usually coarsely punctate, often with a distinct apical declivity variously modified with spines or other processes (FISHER 1950). In the prognathous group, the pronotum is flat without rasp-like surface and the elytra are rather smooth without a distinct declivity. As will be shown below, these morphological differences are correlated with differences in life history and habits.

There have been many alterations in the classification of Bostrichidae in the past 200 years. Some bostrichid subfamilies have been even treated as members of other taxonomic groups, such as Ciidae, Cleridae, Colydiidae (LACORDAIRE & CHAPUIS 1854-1876; JEANNEL & PAULIAN 1944), which are no longer considered to be closely related to bostrichids. In his monograph of the family Bostrichidae, LESNE (1896, 1897, 1898a, 1901, 1906b, 1909) laid the basis of the modern classification, and his work is still the foundation of all more recent studies.

At first LESNE separated Lyctidae from Bostrichidae and did not include them in his monograph (LESNE 1896-1909), but later he included Lyctinae as a subfamily of Bostrichidae in his catalogue of the family (LESNE 1938). CROWSON (1955) separated Bostrichidae and Lyctidae, but he changed his decision later and treated Lyctinae as a subfamily of Bostrichidae (CROWSON 1968). LAWRENCE & NEWTON (1995) followed CROWSON (1961) in separating *Endecatomus* as a family (Endecatommidae).

IVIE (1985) constructed a phylogeny at the family level of the series Bostrichiformia based on the morphological characters of adults and larvae. He treated Anobiidae as a subfamily of Bostrichidae, but this

new status has not been widely accepted, and Anobiidae and Bostrichidae are treated as separate families in ‘American Beetles’ for example (IVIE 2002, PHILIPS 2002).

The first complete catalogue of Bostrichidae worldwide was given by LESNE (1938). The latest worldwide catalogue of Bostrichidae, including the distribution of each species, has been published by BOROWSKI & WĘGRZYNOWICZ (2007). This has been amended and corrected by IVIE (2010), and his corrections to nomenclature have been incorporated here.

Details of the classifications of LESNE (1938), CROWSON (1968) and LAWRENCE & NEWTON (1995), and the most recent classifications of IVIE (2002), and BOROWSKI & WĘGRZYNOWICZ (2007), together with that proposed in the present paper, are shown in Table 3. The changes have partly resulted from the discovery of new taxa, partly because different taxonomists have used different morphological characters in their classifications.

This study is the first attempt to resolve the confusion that has existed up to now in bostrichid classification using a phylogenetic analysis based on morphological characters, and using any previous available further information on biology and morphology of the relevant taxa.

Materials and Methods

Taxon sampling

Except for a few bostrichid pests of stored grains, bamboo and wood, most bostrichids are rare, so the materials for this study comprised mainly preserved dry pinned museum specimens. The specimens are deposited in the British Natural History Museum (BNHM); Deutsches Entomologisches Institut (DEI); Hungarian Natural History Museum (HNHM); collection of Dr. LIU LAN-YU (LLY); Naturhistorisches Museum Basel (NMB); New Zealand Arthropod Collection (NZAC); collection of Dr. Petr ZÁHRADNÍK (PZP); Staatliches Museum für Tierkunde, Dresden (SMTD); Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin (ZMHB); Zoologische Staatssammlung München (ZSM).

Thirty-one genera, including at least one genus from every currently accepted subfamily and tribe, have been examined, and are used as ingroups (Table 1). In seven of these genera showing considerable sexual dimorphism, both sexes have been examined and the male and female considered separately. The type genus of each subfamily and tribe are included, and the type species of each of these genera are the sample taxa for this study.

Outgroup selection

The selection of suitable outgroups for this analysis has caused some problems because of the uncertain relationship between the Bostrichidae and Anobiidae within the Bostrichoidea. It is possible that the similar habits of the Bostrichidae and Anobiidae, chiefly wood-boring and stored-grain feeding, have resulted in convergence. Traditionally, they have been treated as separate families (e.g. CROWSON 1955, 1968, LAWRENCE & NEWTON 1995). Based on a phylogenetic study of the Bostrichoidea using adult and larval morphological characters, IVIE (1985) suggested that the Anobiidae should be considered as a subfamily of the Bostrichidae. PHILIPS (2000) studied the phylogeny of Ptininae using four bostrichid taxa as outgroups, *Endecatomus* (treated by him as a separate family, Endecatomiidae, rather than as a genus within the Bostrichidae), *Prostephanus* (Dinoderinae), *Lyctus* (Lyctinae) and *Euderia* (Euderinae). The results indicate (Anobiidae s.s. + Ptininae) form a monophyletic clade, and the bostrichid outgroups also form a monophyletic clade. The families are treated as distinct in ‘American Beetles’ by IVIE (2002) and PHILIPS (2002) respectively. The classification of the Anobiidae has also been subject to change. LAWRENCE & NEWTON (1995) and PHILIPS (2000, 2002) included the Ptininae within the family. CROWSON (1955, 1968) and PHILIPS and FOSTER (2004) give the Ptinidae family rank. The most recent analysis based on molecular data (HUNT et al. 2007), separates the Ptinidae as a well-supported clade (support value 100) from a well-supported clade of Anobiid subfamilies (support value 100), ((Mesocoelopodinae + Ptilininae) + (Dorcatominae + Xyletinae) + Anobiinae) which form a sister-clade to the (((Bostrichinae + Dinoderinae) + Dryophilinae) + Lyctinae). This group is much less well-supported (support value 54) and includes one anobiid subfamily (Dryophilinae) as well as the three bostrichid subfamilies (ex nine) included in the analysis. The Dryophilinae, however, has never previously been associated with the family Bostrichidae, and in the species-based phylogeny of HUNT et al. (2007, Table S4), the sole species of Dryophilinae included (*Dryophilus pusillus* GYLLENHAL) lies

Table 1. Subfamily, tribe, genus, species, author& year and the abbreviations of the source of the materials used in the phylogenetic analysis.

Subfamily	Tribe	Genus	Species	Author&Year	Deposited (in abb.)
Lyctinae	Lyctini	<i>Lyctus</i> ¹	<i>linearis</i>	(GOEZE, 1777)	BNHM
		<i>Minthea</i>	<i>squamigera</i>	PASCOE, 1866	BNHM, HNHM
	Trogoxylini	<i>Cephalotoma</i>	<i>perdepressa</i>	LESNE, 1937	HNHM
<i>Trogoxylon</i> ¹		<i>parallelopipedum</i>	(MELSHEIMER, 1846)	BNHM	
Psoinae	Chileniini	<i>Chilenius</i> ¹	<i>spinicollis</i>	(FAIRM & GERM, 1861)	HNHM
	Psoini	<i>Psoa</i> ¹	<i>viennensis</i>	HERBST, 1797	ZSM, PZP
Polycaoninae		<i>Polycaon</i> ¹	<i>chilensis</i>	(ERICHSON, 1834)	SMTD, PZP
Euderiinae		<i>Euderia</i> [*]	<i>squamosa</i>	BROUN, 1880	NZAC, PZP
Dysidinae		<i>Dysides</i> ¹	<i>obscurus</i>	PERTY, 1830	ZSM, PZP
Endecatominae		<i>Endecatomus</i> ¹	<i>lanatus</i>	LESNE, 1934	DEI
Dinoderinae		<i>Dinoderus</i> ¹	<i>ocellaris</i>	STEPHENS, 1830	BNHM, LLY
		<i>Stephanopachys</i>	<i>substriatus</i>	(PAYKULL, 1800)	BNHM, SMTD
Bostrichinae	Bostrichini	<i>Bostrichus</i> ¹	<i>capucinus</i>	(LINNÆUS, 1758)	ZSM, PZP
		<i>Bostrychoplites</i> [*]	<i>cornutus</i>	(OLIVIER, 1790)	BNHM, PZP
		<i>Dolichobostrychus</i>	<i>angustus</i>	(STEINHEIL, 1873)	ZSM
		<i>Bostrychopsis</i> [*]	<i>parallela</i>	(LESNE, 1895)	BNHM, LLY
		<i>Lichenophanes</i>	<i>tristis</i>	(FÄHRAEUS, 1871)	BNHM
		<i>Sinoxylodes</i>	<i>curtulus</i>	(ERICHSON, 1847)	DEI, ZMHB
	Sinoxylini	<i>Sinocalon</i>	<i>vestitum</i>	(LESNE, 1895)	DEI, SMTD, ZMHB
		<i>Sinoxylon</i> ¹	<i>sexdentatum</i>	(OLIVIER, 1790)	PZP
	Xyloperthini	<i>Dendrobiella</i>	<i>sericans</i>	(LECONTE, 1858)	BNHM
		<i>Enneadesmus</i>	<i>trispinosus</i>	(OLIVER, 1795)	BNHM
		<i>Mesoxylion</i> [*]	<i>collaris</i>	(ERICHSON, 1842)	BNHM
		<i>Scobicia</i>	<i>chevrieri</i>	(VILLA & VILLA, 1835)	BNHM, PZP
		<i>Tetrapriocera</i>	<i>longicornis</i>	(OLIVIER, 1795)	ZSM
		<i>Xylobosca</i> [*]	<i>bispinosa</i>	(MACLEAY, 1872)	BNHM, HNHM
<i>Xylopertha</i> ¹		<i>retusa</i>	(OLIVIER, 1790)	PZP	
<i>Xylopsocus</i>		<i>capucinus</i>	(FABRICIUS, 1781)	LLY	
Apatinae	Apatini	<i>Apatē</i> [*]	<i>terebrans</i>	(PALLAS, 1772)	ZSM
	Diapatini	<i>Dinapate</i> ^{1*}	<i>wrightii</i>	HORN, 1886	DEI
(Anobiidae)		<i>Anobium</i> ¹	<i>punctatum</i>	DEGEER, 1774	ZSM
		<i>Lasioderma</i>	<i>serricorne</i>	(FABRICIUS, 1792)	ZSM
(Dermestidae)		<i>Dermestes</i> ¹	<i>undulatus</i>	BRAHM, 1790	ZSM
		<i>Attagenus</i>	<i>aurantiacus</i>	REITTER, 1900	ZSM

¹ type genus; * sexual dimorphism; outgroup in brackets

outside the clade including the six species of Bostrichidae in the analysis. It is evident that the relationships among the bostrichoid families and subfamilies still need further clarification.

Despite the problems mentioned above, but in agreement with almost all previous authors, we consider the Bostrichidae auct. to be a monophyletic group, based primarily on morphological characters. In this situation, we have followed the general rule to use an outgroup as closely related as possible to the taxon under investigation. This normally gives better results in rooting (MADDISON et al. 1984). We consider the Anobiidae and Ptinidae to be distinct families from the Bostrichidae, and have chosen the Anobiidae as the most closely related outgroup. However, to avoid any potential problems due to convergence, we selected a second taxon as an 'unequivocal' outgroup – Dermestidae. The Dermestidae form a well-supported monophyly within the Bostrichiformia (HUNT et al. 2007). The Dermestidae have a variety of habits, but most are scavengers, and none are wood-boring (KINGSOLVER 2002), so there should be no problem of convergence.

The following genera have been used as outgroups in the analysis: Anobiidae: *Anobium* (Anobiinae) and *Lasioderma* (Xyletininae); Dermestidae: *Dermestes* (Dermestinae) and *Attagenus* (Attageninae).

Character set

All characters used in this study are adult morphological characters. Larval and pupal characters were excluded due to lack of material and the associated problems with large numbers of missing data points (PLATNICK et al. 1991). The data matrix included 122 characters which can be divided into 3 categories: 29 measurement characters, 50 macro-structural characters, 43 micro-structural characters. The measurement and macro-structural characters were examined by light microscope, and the micro-structural characters by Environmental Scanning Electron Microscopes (ESEM, FEI: Inspect-S) and Scanning Electron Microscopes (SEM, LEO: 1430VP) using a low acceleration voltage to simulate the ESEM (cf. LIU et al. 2009).

Measurement and micro-structural characters are used here the first time to study bostrichid relationships. The arguments for and against the use of quantitative characters in phylogenetic studies have been discussed by ZELDITCH et al. (2000). They conclude that both quantitative and qualitative morphological data are useful in systematic analysis, because both aid in the detection of similarities and differences, and both can be used to make systematic inferences.

Measurement values as such are of little use as characters because they are closely correlated with the size of the beetles. To avoid this problem, we have converted these values into ratios and use the ratios as characters. Even though LESNE (1898b, 1906a), GERBERG (1957) and SANTORO (1969) examined the micro-sculptures on the elytra of bostrichids and used them as distinguishing characters for closely related species, they did not examine these structures by SEM, hence their information was limited. This study expanded the use of microstructural characters to include 43 characters from the frons, pronotum and elytra.

Coding

There are 96 multistate characters amongst the 122 characters. This study codes the state shared with the most outgroup taxa as '0', the state shared with the most ingroup taxa is coded as '1', the state shared with the next fewer taxa as '2', and so forth. The states of the continuous values of measurement characters were decided by the method of gap coding (SCHOLS et al. 2004; LIU 2009).

Because there is not enough information to show the possible sequence of evolution among these states, the states of each character are unordered (i.e. no polarity is given), (NIXON & CARPENTER 1993).

Phylogenetic analysis

Mesquites (version 2.5, W. MADDISON & D. MADDISON) was used for keying in the datamatrix and viewing the trees. All parsimony-based analyses were performed with PAUP* 4.0b (SWOFFORD 2002). Trees were estimated using heuristic searches with 10,000 random addition replicates and tree bisection-reconnection (TBR) branch swapping, and branches were collapsed if the minimum length was zero (CARPENTER 1988). Branch support in the resulting cladograms was assessed using bootstrap analysis (FELSENSTEIN 1985).

Because there is not enough information to show the possible sequence of evolution among these states, and some characters even show a division into two opposite extremes, the most-parsimonious analysis has no polarity (NIXON & CARPENTER 1993).

Even though bostrichids are known for their xylophagous way of life, the wood-dwelling part of the life cycle is not the same for every bostrichid. Many bostrichids bore into the wood as adults, and the whole life

cycle apart from a brief dispersal phase is spent within the wood. However, some bostrichids only live in the wood during the larval and pupal stages. The adults are free-living and do not tunnel into the wood. These differences in adult life style are correlated with differences in adult morphology. In some cases, the biological adaptations result in convergent morphologies which result in autapomorphies (CYMOREK 1968). Hence we included biological information when discussing our results of the parsimonious analyses.

Character description

As noted above, we divide the characters used into three categories: measurement ratios, macro-structural and micro-structural, and deal with each in turn. Within each category we begin with whole body characters, and then deal successively with characters of the head, pronotum, legs and abdomen.

Measurement characters

Twenty-eight measurements (Table 2) were made on each specimen under a binocular microscope fitted with a micrometer scale.

As noted above, because of the 'size effect' problem, we converted the values into ratios, and used the ratios as characters. There are 29 characters obtained from these 28 measurement values. The codes below (e.g. A/B) refer to Table 2.

Table 2. Measurements made.

Code	Measurement	Reference figure
A.	Width of body	figure 1
B.	Length of body	figure 1
C.	Width of pronotum	figure 1
D.	Length of elytra	figure 1
E.	Height of declivity	figure 2
F.	Length of declivity	figure 2
G.	Width of head	figure 3
H.	Width between eyes	figure 3
I.	Width of genae	figure 4
J.	Width of gula	figure 4
K.	Length of antenna	figure 4
L.	Length of antennal club	figure 4
M.	Width of prosternum	figure 5
N.	Width of prospinasternum	figure 5
O.	Width of mesosternum	figure 5
P.	Width of mesospinasternum	figure 5
Q.	Width of metasternum	figure 5
R.	Width of metaspinasternum	figure 5
S.	Length of metasternum	figure 5
T.	Width of profemur	
U.	Length of profemur	
V.	Width of mesofemur	
W.	Length of mesofemur	
X.	Width of metafemur	
Y.	Length of metafemur	
Z.	Width of 1 st visible sternite	figure 5
AA.	Length of 1 st visible sternite	figure 5
BB.	Length of abdomen	figure 5

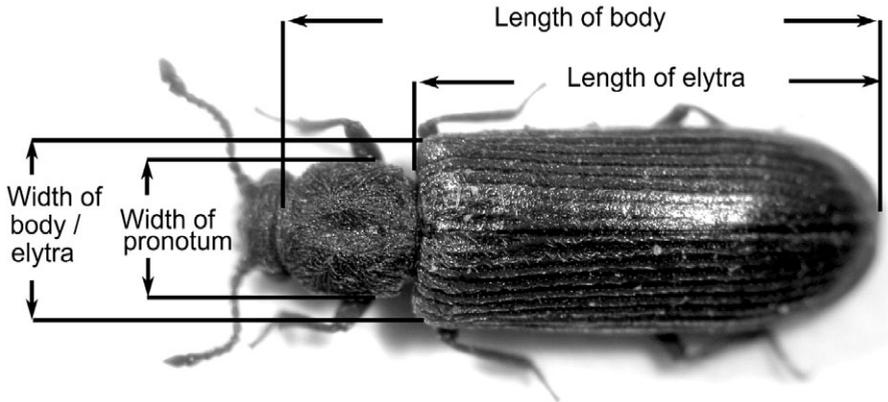


Figure 1. Dorsal view of *Lyctus linearis* to show the measurement of length and width of body, pronotum and elytra.

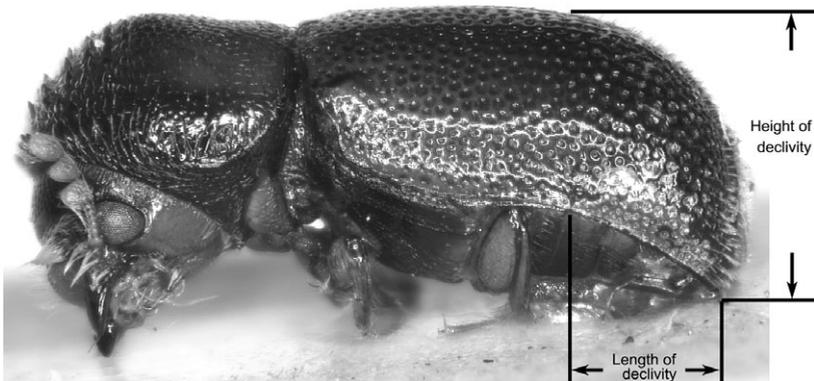


Figure 2. Lateral view of *Dinoderus ocellaris* to show the measurement of the height and length of the declivity.

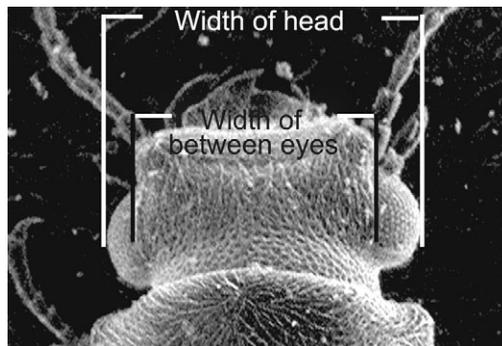


Figure 3. Dorsal view of head of *Trogoxylon parallelopedus* to show the measurement of the width of the head and the width between the eyes.

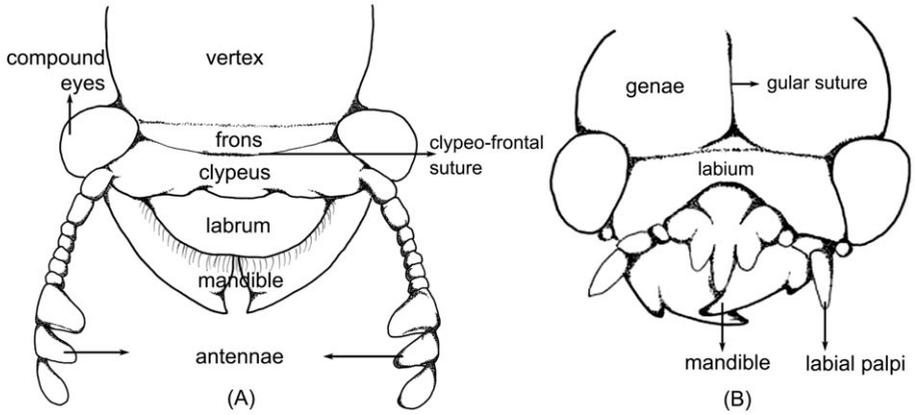


Figure 4. Head of *Rhyzopertha dominica*: (A). dorsal view; (B) ventral view.

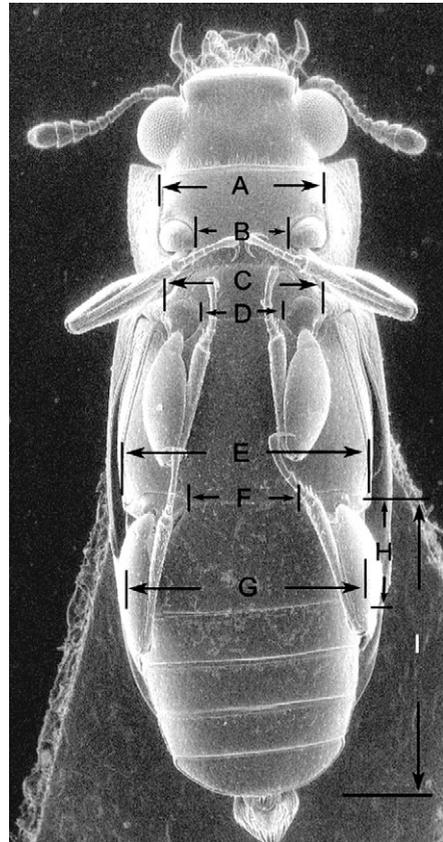


Figure 5. Ventral view of *Cephalotoma perdepressa* to show the measurements of

- width of prosternum (A)
- width of prospinasternum (B)
- width of mesosternum (C)
- width of mesospinasternum (D)
- width of metasternum (E)
- width of metaspinasternum (F)
- width of 1st visible sternite (G)
- length of 1st visible sternite (H)
- length of abdomen (I)

Measurement characters:

1. Ratio of width to length of body (A/B): (0) 0.260~0.350; (1) 0.355~0.375; (2) 0.390~0.450; (3) 0.175~0.255.
Bostrichidae have the pronotum narrower or equal in width to the elytra, and the elytra gradually narrow towards the apex. The width of the body was measured at the base of the elytra. Because the head is not visible in dorsal view in many Bostrichidae, the body length was measured in the midline from the apex of the pronotum to the apex of the elytra.
2. Ratio of width of pronotum to elytra (C/A): (0) >0.85; (1) 0.67~0.83; (2) <0.65.
3. Ratio of width to length of elytra (A/D): (0) 0.65~0.75; (1) 0.57~0.63; (2) 0.5~0.56; (3) 0.46~0.49; (4) 0.39~0.45; (5) 0.34~0.38; (6) 0.29~0.33.
4. Slope of declivity (E/F): (0) 0.7~1.4; (1) 1.5~1.7; (2) 1.8~1.9; (3) 2.0~2.2; (4) >3.0; (5) <0.2.
The elytral declivity in Bostrichidae varies from gently convex, to steep, truncate, and concave. The slope was calculated as the ratio between the height from the elytral margin to the upper margin of the declivity, and the length of the declivity from a point vertically below the upper margin to the elytral apex.
5. Ratio of length of declivity to length of elytra (F/D): (0) 0.15~0.24; (1) 0.25~0.35; (2) 0.36~0.44; (3) 0.45~0.50; (4) 0.14~0.10; (5) no distinct declivity.
6. Ratio of width of gula to width of genae (J/I): (0) 0; (1) 0.20~0.25; (2) 0.30~0.50; (3) 0.03~0.18 (no distinct gular suture).
The gula is a sclerite between the genae, separated from them by the gular sutures. Sometime the two sutures are joined on the median line so that the gula is no longer evident. The shape of the head affects the ratio. The flatter the head, the bigger the ratio value. Only the Lyctinae have a broad gula without distinct gular sutures, so all Lyctinae are coded as "State 3".
7. Ratio of width of eyes to width of head ((G-H)/G): (0) 0.150~0.230; (1) 0.240~0.320; (2) 0.325~0.395; (3) 0.405~0.430; (4) 0.450~0.500; (5) >0.550.
Bostrichid taxa have different sizes of eyes: some of them have very bulging eyes, e.g. *Cephalotoma*, others have rather flat eyes, e.g. Endecatominae. The size of the eyes is probably related to their habitat and biology.
8. Ratio of eye width to antenna length ((G-H)/2/K): (0) 0.150~0.180; (1) 0.100~0.140; (2) 0.190~0.200; (3) 0.205~0.225; (4) 0.230~0.300; (5) 0.070~0.090; (6) 0.350~0.600; (7) 0~0.030.
9. Ratio of length of antennal club to total length of antenna (L/K): (0) 0.40~0.49; (1) 0.50~0.55; (2) 0.57~0.63; (3) 0.66~0.72; (4) 0.30~0.38; (5) 0.75~0.80; (6) <0.30.
10. Ratio of total width with antennae extended laterally to body width ((2*K+G)/A): (0) 2.05~2.50; (1) 1.70~1.95; (2) 1.40~1.60; (3) 1.00~1.30; (4) 2.60~2.80; (5) 3.00~5.00; (6) 6.00~8.00.
11. Ratio of total width with antennae extended laterally to body length ((K+B)/B): (0) 1.20~1.30; (1) 1.10~1.19; (2) 1.32~1.39; (3) 1.40~1.50; (4) 1.60~1.70; (5) 1.80~2.20.
12. The activity space of the procoxae ((N-M)/2): (0) 0~1.0; (1) 1.2~1.6; (2) 2.0~3.5; (3) 3.8~5.0.
The activity space relates to the size of the coxae relative to the sternum. The sizes of the coxae (characters 12, 14 and 16) are affected by the habitat requirements, and they also limit the flexibility of movement of the beetle, especially in turning around. The ratio of the size of coxae to body length is related to the activity space and the ability of beetle to move (characters 13, 15 and 17).
13. Ratio of procoxal space to body length ((N-M)/2/A): (0) 0.235~0.280; (1) 0.285~0.320; (2) 0.200~0.230; (3) 0.320~0.350; (4) 0.170~0.200; (5) 0.150~0.170; (6) 0.350~0.500; (7) 0.100~0.150; (8) 0.500~0.750.
14. The activity space of the mesocoxae ((P-O)/2): (0) 0.005~0.060; (1) 0.065~0.080; (2) 0.090~0.100; (3) 0.120~0.150; (4) 0.160~0.250; (5) 0.300~0.350.
15. Ratio of mesocoxal space to body length ((P-O)/2/A): (0) 0.160~0.230; (1) 0.235~0.290; (2) 0.295~0.350; (3) 0.050~0.150; (4) 0.400~0.500; (5) 0.600~0.800.

16. The activity space of the metacoxae ((R-Q)/2): (0) 0.010~0.055; (1) 0.062~0.075; (2) 0.080~0.100; (3) 0.110~0.130; (4) 0.150~0.180; (5) 0.200~0.300; (6) 0.500~0.700.
17. Ratio of metacoxal space to body length ((R-Q)/2/A): (0) 0.350~0.400; (1) 0.235~0.345; (2) 0.170~0.230; (3) 0.430~0.480; (4) 0.500~0.570; (5) 0.100~0.120.
18. Ratio of length of 1st abdominal sternite to length of abdomen (AA/BB): (0) 0.45~0.90; (1) 0.95~1.40; (2) 0.20~0.40.
19. Ratio of width to length of 1st abdominal sternite (Z/AA): (0) 1.0~4.5; (1) 5.0~7.0; (2) <0.5.
20. Ratio of width to length of metasternum (Q/S): (0) 0.85~1.90; (1) 2.00~2.50; (2) 0.50~0.70; (3) 0.30~0.35.
21. Ratio of width to length of profemur (T/U): (0) 0.34~0.40; (1) 0.41~0.50; (2) 0.31~0.33; (3) 0.26~0.30; (4) 0.15~0.25; (5) 0.55~0.65.
22. Ratio of width to length of mesofemur (V/W): (0) 0.200~0.245; (1) 0.255~0.305; (2) 0.310~0.325; (3) 0.335~0.345; (4) 0.355~0.365; (5) 0.370~0.390; (6) 0.400~0.410; (7) 0.415~0.430; (8) 0.435~0.460.
23. Ratio of width to length of metafemur (X/Y): (0) 0.200~0.255; (1) 0.265~0.290; (2) 0.300~0.335; (3) 0.340~0.390; (4) 0.400~0.430; (5) 0.500~0.550.
24. Ratio of total width with profemora extended to body width ((M+2*U)/A): (0) 0.80~0.89; (1) 0.91~1.20; (2) 1.25~1.40; (3) 0.50~0.70; (4) 1.50~1.80.
These ratios (characters 24-26) relate to how much the femora can extend beyond the body. This is related to the flexibility of movement.
25. Ratio of total width with mesofemora extended to body width ((O+2*W)/A): (0) 0.70~1.20; (1) 1.25~1.55; (2) 1.60~1.80; (3) 2.10~2.30; (4) 0.50~0.60.
26. Ratio of total width with metafemora extended to body width ((Q+2*Y)/A): (0) 0.80~1.45; (1) 0.40~0.75; (2) 1.50~2.00.
27. Ratio of width of pro-sternum intercoxal process (or prospinasternum) to body width (M/A): (0) open cavity; (1) 0.010~0.020; (2) 0.030~0.060; (3) 0.070~0.100; (4) 0.125~0.150; (5) 0.175~0.200; (6) 0.340~0.360.
These ratios (characters 27-29) relate to the type of spinasternum (Fig. 1). This is related to the type of coxal cavity which may be closed or open, and the degree of openness.
28. Ratio of width of meso-sternum intercoxal process over body width (O/A): (0) 0.020~0.950; (1) 0.105~0.130; (2) 0; (3) 0.160~0.180; (4) 0.320~0.340.
29. Ratio of width of meta-sternum intercoxal process over body width (Q/A): (0) 0.040~0.080; (1) 0.010~0.035; (2) 0.081~0.115; (3) 0.120~0.140; (4) 0; (5) 0.175~0.200; (6) 0.250~0.320; (7) 0.440~0.460.

Macro-structural characters

Fifty characters were observed on each specimen under a binocular microscope.

30. Sexual dimorphism: (0) no; (1) yes.
31. Head prognathous or hypognathous: (0) hypognathous; (1) prognathous.
The bostrichids with prognathous head show the head clearly from the dorsal view; in the hypognathous form the head is concealed under the pronotum, and not visible from the dorsal view.
32. Clypeo-frontal suture: (0) distinct groove; (1) obsolescent; (2) none; (3) ridge.
The clypeus is always transverse and separated from the frons by a more or less marked suture (Fig. 4) in bostrichids (LESNE 1924). The suture varies from a distinct groove to a ridge.
33. Front margin of clypeus: (0) convex; (1) straight; (2) concave; (3) sinuate.
The labrum is more or less covered by the clypeus in Bostrichidae, so the front margin is also the front

end of the clypeus (Fig. 4). The margin may be curved in the middle towards the front (convex anteriorly), or straight, or concave anteriorly, or with a sinuate margin.

34. Angle between frons and clypeus: (0) 0; (1) $<45^\circ$; (2) $>60^\circ$.
35. Labrum emarginated: (0) yes, (1) no.
36. Apex of mandible: (0) pointed tip; (1) pachygnathous; (2) forceplike; (3) toothed; (4) asymmetrical.
The mandibles show important characters useful in classification. The mandibles with pointed tip are pointed in both front and lateral view and usually overlap at the tips. The pachygnathous mandibles (LESNE 1924) are very short and thick, and end in a sort of gouge, the free margin of which fits exactly into that of the opposite side when closed. The forceplike mandibles are pointed in front view but rounded at the tip in lateral view and do not overlap at the tips. The toothed mandibles are short and thick and have one to three teeth at the tip rather than a gouge. The asymmetrical mandibles have a different type of apex on each side.
37. Mandible fringed with hairs on outer side: (0) yes; (1) no.
38. Mandible toothed on inner side: (0) 2; (1) 1; (2) 0.
39. Mandibular apices crossing: (0) no; (1) yes.
40. Number of antennal segments: (0) 11; (1) 10; (2) 9.
41. Number of antennal club segments: (0) 3; (1) 2; (2) 4; (3) >4 .
42. Relative lengths of scape and 2nd segment of antenna: (0) scape longer than 2nd segment; (1) scape equal to 2nd segment.
43. Relative lengths of antennal club and funicle: (0) club 3 times or more longer than funicle; (1) club less than 3 times longer than funicle; (2) club equal to funicle; (3) club shorter than funicle.
44. Elevation of eyes from surface of head: (0) none; (1) weakly raised; (2) distinctly raised.
45. Apical horns: (0) no; (1) yes.
Most members of Bostrichini and a very few Xyloperthini have a pair of apical horns on the front of the pronotum at the anterior angles (Fig. 6), especially well-developed in the male. These apical horns can be useful characters to distinguish the sexes.
46. Shape of apical horns: (0) flat triangular process; (1) spines; (2) hook, uncus.
47. Size of apical horns (Fig. 6): (0) none; (1) very small; (2) small; (3) large.
48. Teeth on anterior slope of pronotum (Fig. 7): (0) no; (1) yes.
49. Anterior angles of pronotum: (0) no; (1) indistinct; (2) distinct.
50. Special structures on pronotal disc: (0) none; (1) yes.
A few bostrichids have special structures, such as spines, ridges and tubercles on the disc of pronotum
51. Number of special structures on pronotal disc: (0) 0; (1) 1; (2) 2; (3) 3.
52. Posterior angles of pronotum: (0) smoothly rounded; (1) vague; (2) distinct.
53. Lateral margin of pronotum: (0) distinct; (1) vague; (2) obsolete.
54. Scutellum elevated: (0) yes; (1) no.
55. Length of epipleura: (0) 1/3 of meta thorax; (1) 1/2 of metathorax; (2) 2/3 of meta thorax; (3) to the end of metathorax; (4) whole elytra.
The more cylindrical the body, the longer the epipleura in Bostrichidae. This character compares the length of the epipleura to the length of the metathorax and elytra.
56. Striae on elytra: (0) no; (1) yes.
57. Number of striae: (0) 0; (1) <5 ; (2) 6–8; (3) >9 .

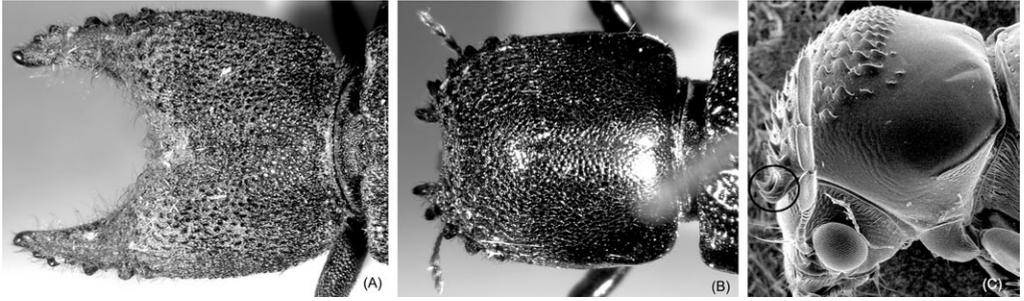


Figure 6. Dorsal view and lateral view of the pronotum. (A) *Bostrychoplites cornutus* male has a pair of large apical horns; (B) *Bostrychopsis parallela* male has a pair of small apical horns; (C) *Xylothrips flavipes* has a pair of very small uncinuate apical horns (marked by a circle).

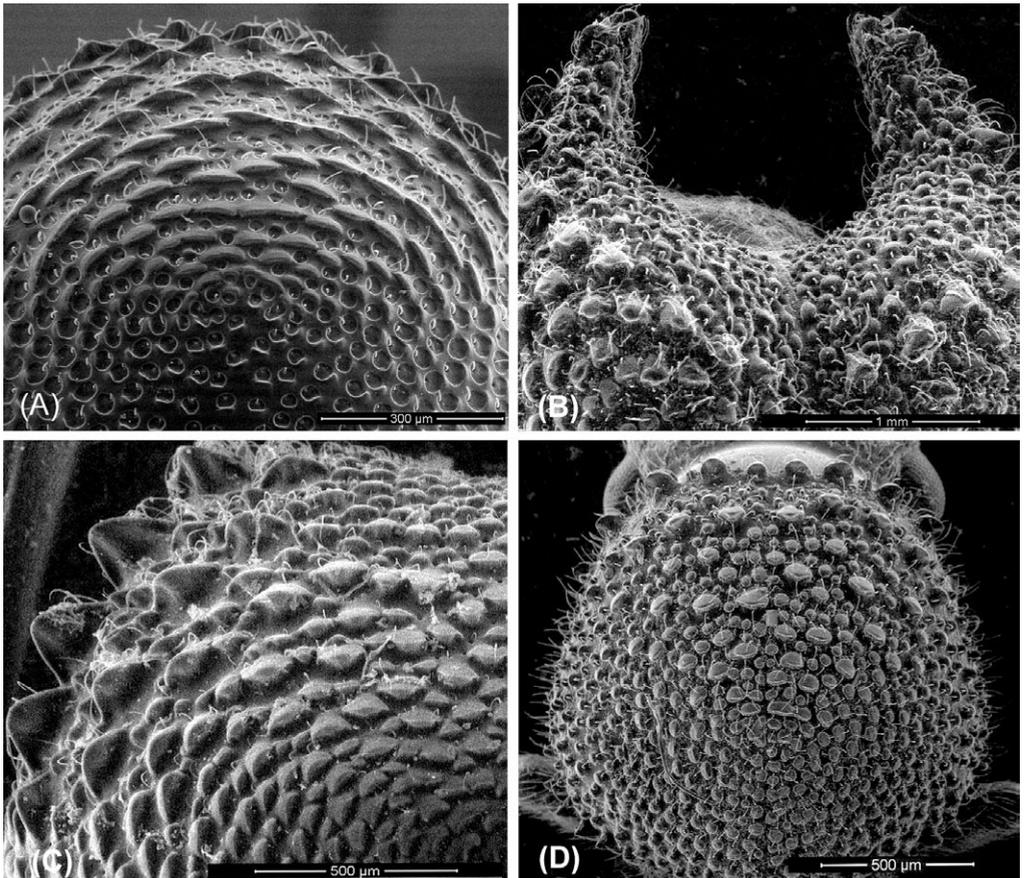


Figure 7. Dorsal view of the anterior part of the pronotum. (A) *Dinoderus minutus* has teeth arranged into few concentric semicircle lines on the anterior part of pronotum; (B) *Bostrychoplites cornutus* male has very dense teeth on the anterior part of pronotum; (C) *Bostrychopsis parallela* male has dense teeth on the anterior part of pronotum; (D) *Stephanopachys substriatus* has dense tubercles on the pronotum.

58. Elytral disc suture marginated: (0) yes; (1) no.
59. Ridges on disc of elytra: (0) no; (1) yes.
60. Uniformity of ridges on disc of elytra: (0) no ridge; (1) variable; (2) uniform.
61. Presence of hairs on ridges on elytral disc: (0) no; (1) yes.
62. Presence of elytral declivity: (0) yes; (1) no.
63. Special structures such as tubercles, teeth, costae or carinae on lateral margin of elytral declivity: (0) no; (1) yes.
64. Special structures such as tubercles, teeth or a elongate swelling on suture of elytral declivity: (0) no; (1) yes.
65. Special structures such as tubercles or teeth on disc of elytral declivity: (0) no; (1) yes.
66. Form of procoxal cavity: (0) closed; (1) open.
67. Tibial length relative to tarsus: (0) all longer than tarsus; (1) all equal to tarsus, except for protibia which is longer than tarsus; (2) all equal to tarsus, except for mesotibia which is longer than tarsus; (3) all equal to tarsus, except for metatibia which is longer than tarsus; (4) all equal to tarsus; (5) all shorter than tarsus, except for protibia which is equal to tarsus; (6) all shorter than tarsus; (7) all longer than tarsus, except for mesotibia which is shorter than tarsus.
68. Protibial apical spines (4 different sizes of spines: s, m, l, xl): (0) s*2; (1) s*1+m*1; (2) s*1+l*1; (3) s*1+xl*1; (4) m*2; (5) s*3; (6) s*1; (7) m*1; (8) l*1; (9) none.
Characters 39-41 deal with the apical spines of the tibiae - both the size of the apical spine(s) and the number of spines on the apex of the tibia. The states show the size (abbreviated as: small-s; medium-m; large-l; very large-xl), and number of the spines.
69. Mesotibial apical spines (3 different sizes of spines: s, m, l): (0) s*2; (1) s*1+m*1; (2) s*1+l*1; (3) m*2; (4) s*3; (5) s*1; (6) m*1; (7) none.
70. Metatibial apical spines (4 different sizes of spines: s, m, l, xl): (0) s*2; (1) s*1+m*1; (2) s*1+l*1; (3) s*1+xl*1; (4) s*3; (5) s*1; (6) none.
71. Teeth on outer side of protibia: (0) no; (1) yes, 1; (2) yes, 2; (3) yes, 3.
Characters 42-44 deal with both the presence of teeth (yes/no) and the density of teeth. The density states are shown as numbers: 1-few, 2-dense, 3-very dense.
72. Teeth on outer side of mesotibia: (0) no; (1) yes, 1; (2) yes, 2; (3) yes, 3.
73. Teeth on outer side of metatibia: (0) no; (1) yes, 1; (2) yes, 2; (3) yes, 3..
74. Hair fringe on outer side of protibia: (0) no; (1) yes, 1; (2) yes, 2; (3) yes, 3.
Characters 45-47 deal with both the presence of a hair fringe (yes/no) and the density of hairs. The density states are shown as numbers: 1-few, 2-dense, 3-very dense.
75. Hair fringe on outer side of mesotibia: (0) no; (1) yes, 1; (2) yes, 2; (3) yes, 3.
76. Hair fringe on outer side of metatibia: (0) no; (1) yes, 1; (2) yes, 2; (3) yes, 3.
The tarsi have five segments in the bostrichids, but the first segment of some bostrichids is greatly reduced, not obvious, rarely fused to the second (LESNE 1924). Characters 48-50 deal with the type of tarsi of the three pairs of legs. There are 6 tarsal types: 1) the first segment is extremely small; 2) every segment is equal except for the last segment; 3) the second segment is extremely long; 4) the first segment is the longest of all segments; 5) the fourth segment is extremely small; 6) the second segment is extremely small.
77. Protarsal type: (0) type 1; (1) type 2; (2) type 3; (3) type 4; (4) type 5; (5) type 6.
78. Mesotarsal type: (0) type 1; (1) type 2; (2) type 3; (3) type 4; (4) type 5; (5) type 6.
79. Metatarsal type: (0) type 1; (1) type 2; (2) type 3; (3) type 4; (4) type 5; (5) type 6.

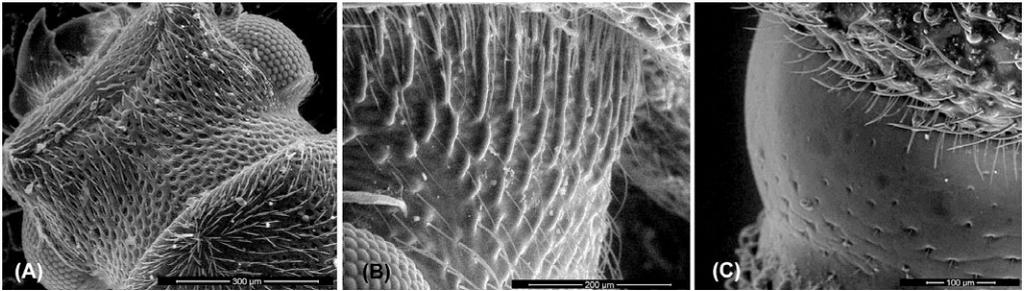


Figure 8. Dorsal view and lateral view of the bostrichids vertex. (A) *Trogoxylon parallelopipedus* has dense punctures on vertex; (B) *Amphicerus bicaudatus* has dense grooves on vertex; (C) *Stephanopachys substriatus* has smooth vertex.

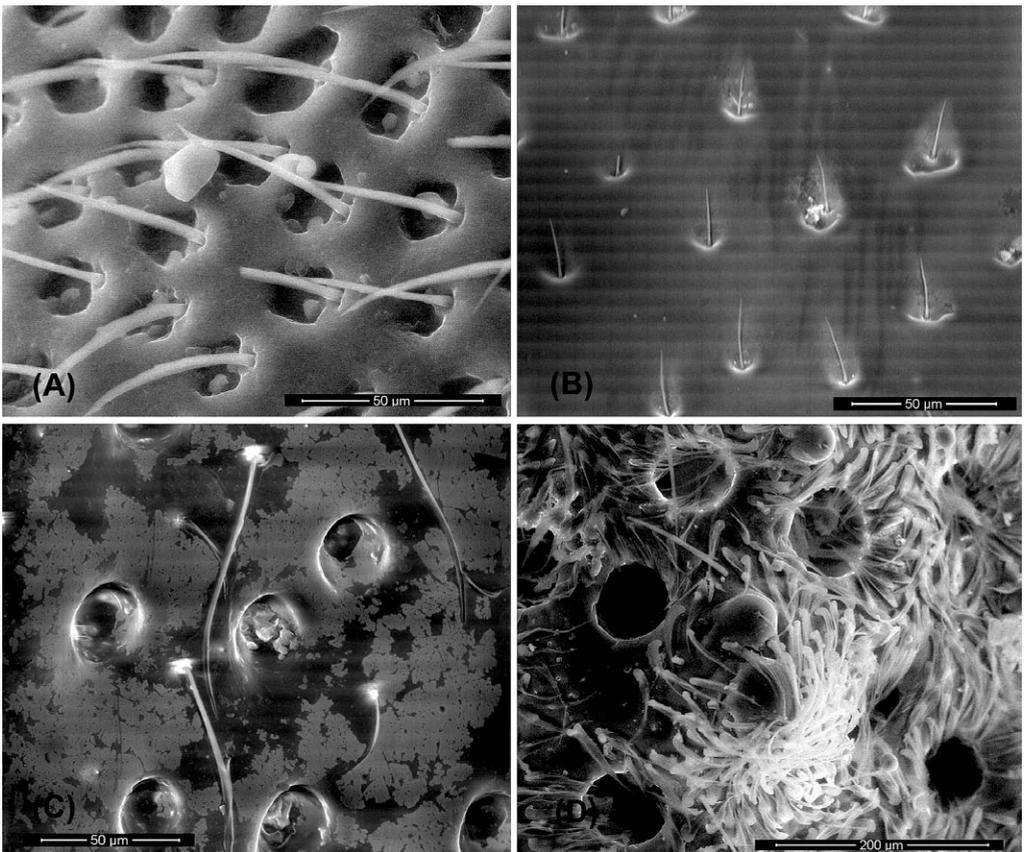


Figure 9. The dorsal view of pronotum disc. (A) *Trogoxylon praeustum* has the vestiture inserted next to punctures; (B) *Xylobosca bispinosa* has the vestiture inserted in punctures; (C) *Scobicia chevrieri* has the vestiture inserted away from punctures; (D) *Lichenophanes caudatus* has the vestiture inserted at three different locations related to punctures and tubercles.

Micro-structural characters

Forty-three characters were observed on each specimen under Environmental Scanning Electron Microscopes and Scanning Electron Microscopes using a low acceleration voltage to simulate the ESEM.

80. Vertex surface (Fig. 8): (0) punctures; (1) tubercles; (2) grooves; (3) smooth.
81. Density of micro-structures on vertex: (0) dense; (1) less dense; (2) sparse; (3) very dense; (4) none.
82. Presence of vestiture on vertex: (0) yes; (1) no.
83. Density of vestiture on vertex: (0) less dense; (1) dense; (2) very dense; (3) none.
84. Hair insertion on vertex (Fig. 9): (0) in punctures; (1) next to punctures; (2) away from punctures; (3) none.
85. Frons surface: (0) punctures; (1) tubercles; (2) punctures+tubercles; (3) smooth.
86. Density of micro-structures on frons: (0) dense; (1) less dense; (2) sparse; (3) very dense; (4) none.
87. Presence of vestiture on frons: (0) yes; (1) no.
88. Density of vestiture on frons: (0) dense; (1) less dense; (2) sparse; (3) very dense; (4) none.
89. Hair insertion on frons (Fig. 8): (0) in punctures; (1) next to punctures; (2) away from punctures; (3) 2 types; (4) 3 types; (5) none.
90. Sense area location on antennal club: (0) whole; no special area; (1) anterior side of first two club segments, all over the rest; (2) anterior side of first two club segments, middle of the rest; (3) anterior side of first two club segments, tip of the rest; (4) anterior of all club segments; (5) middle part of both sides; (6) anterior of first club segment, middle of second, posterior of the rest; (7) tip of club only.
The sensillae on the club of bostrichids are sometimes regularly distributed over the surface, sometimes concentrated in depressions of various shapes, forming good characters for generic separation (LESNE 1924). The antenna is the major sensory receptor in bostrichids. There are special sensory areas which can be observed very well on the club of the antenna using the ESEM (Fig. 10).
91. Presence of hairs on funicle: (0) yes; (1) no.
92. Density of hairs on funicle: (0) dense; (1) less dense; (2) sparse; (3) very dense.
93. Number of types of sensory hairs on antenna (Fig. 11): (0) 2; (1) 3.
94. Pronotum surface: (0) smooth; (1) punctures + tubercles; (2) punctures; (3) tubercles; (4) punctures + teeth; (5) imbricate scales; (6) teeth.
95. Density of microstructures on apical horns surface: (0) none; (1) sparse punctures; (2) very dense punctures; (3) very dense tubercles.
96. Density of vestiture on apical horns surface: (0) none; (1) dense; (2) very dense.
97. Density of teeth on apical part of pronotum: (0) none; (1) sparse; (2) dense; (3) very dense.
98. Uniformity of microstructures on apical part of the pronotum: (0) none; (1) variable; (2) uniform.
99. Pronotum disc surface: (0) smooth; (1) punctures+tubercles; (2) punctures; (3) tubercles; (4) punctures+tubercles+teeth; (5) imbricate scales; (6) teeth.
100. Density of microstructures on pronotum disc: (0) none; (1) sparse; (2) less dense; (3) dense; (4) very dense.
101. Uniformity of microstructures on pronotum disc: (0) none; (1) variable; (2) one type of microstructure uniform, another type variable; (3) uniform.
102. Number of types of vestiture on pronotum disc: (0) 1; (1) 2; (2) 0.
103. Hair insertion on pronotum disc (Fig. 8): (0) in punctures; (1) next to punctures; (2) away from punctures; (3) 2 types; (4) 3 types; (5) none.

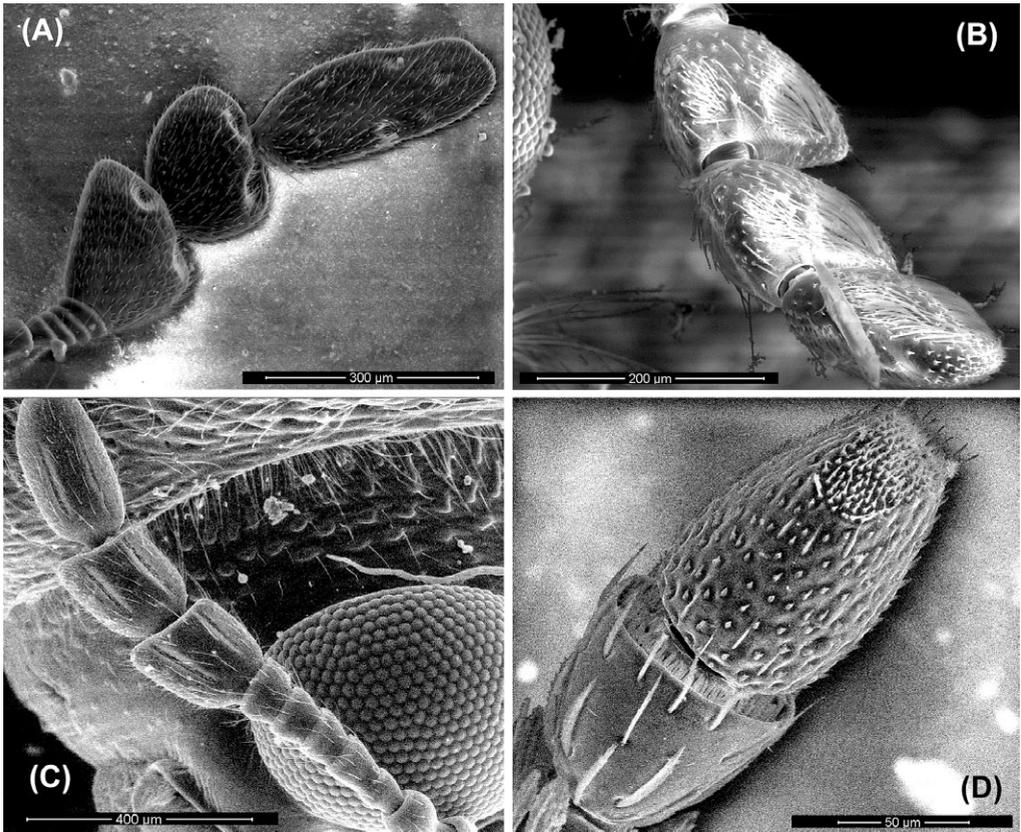


Figure 10. The antennal club of bostrichids. (A) *Scobicia chevrieri* has the sensory areas distributed on the anterior sides of the first two club segments, and in the middle of the last club segment; (B) *Micrapate brasiliensis* has the sensory areas distributed on the anterior side of first two club segments, and at the anterior sides of the last club; (C) *Amphicerus bicaudatus* has the sensory areas distributed in the middle of both sides of club segments; (D) *Lyctoxylon dentatum* has the sensory areas distributed at the tip of the last segment.

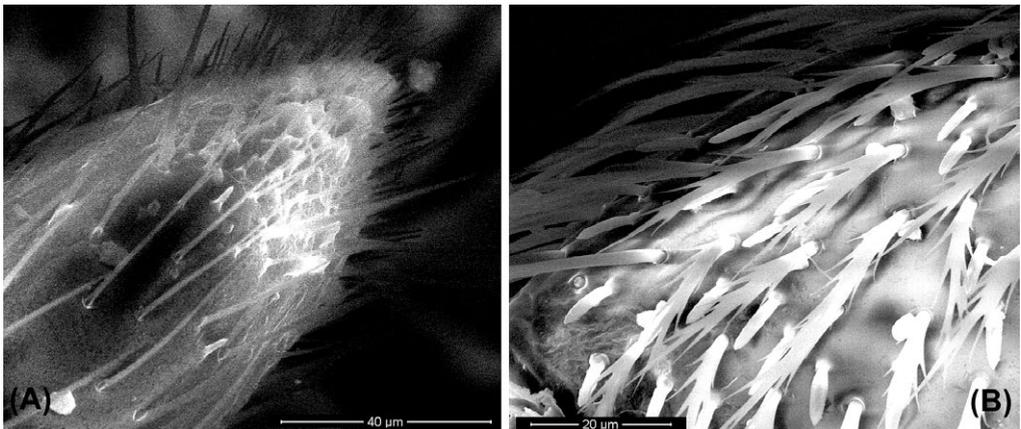


Figure 11. The antennal club of bostrichids. (A) *Trogoxylon impressum* has two types of sensory hairs on antenna; (B) *Dinoderus minutus* has three types of sensory hairs on antenna.

104. Pronotum base surface: (0) smooth; (1) punctures+tubercles; (2) punctures; (3) tubercles; (4) imbricate scales; (5) teeth.
105. Density of microstructures on pronotum base: (0) none; (1) sparse; (2) less dense; (3) dense; (4) very dense.
106. Uniformity of microstructures on pronotum base: (0) none; (1) variable; (2) one type of microstructure uniform, another type variable; (3) uniform.
107. Scutellum surface: (0) with microstructures; (1) smooth.
108. Scutellum vestiture: (0) yes; (1) none.
109. Density of vestiture on scutellum: (0) very dense; (1) dense; (2) less dense; (3) sparse; (4) none. Elytral disc surface: (0) smooth; (1) punctures; (2) punctures+tubercles; (3) tubercles.
110. Density of microstructures on elytral disc: (0) none; (1) sparse; (2) less dense; (3) dense; (4) very dense.
111. Uniformity of microstructures on elytral disc: (0) uniform; (1) variable.
112. Hair in microstructures on elytral disc: (0) no; (1) some yes, others no; (2) yes.
113. Number of types of vestiture on elytral disc: (0) 1; (1) 2; (2) none.
114. Hair insertion on elytral disc (Fig. 9): (0) in punctures; (1) next to punctures; (2) in and next to punctures; (3) away from punctures; (4) next to and away from punctures; (5) none.
115. Declivity surface: (0) punctures; (1) punctures+tubercles; (2) tubercles.
116. Density of microstructures on declivity: (0) sparse; (1) less dense; (2) dense; (3) very dense.
117. Uniformity of microstructures on declivity: (0) uniform; (1) variable.
118. Hair in microstructures on declivity: (0) no; (1) some yes, others no; (2) yes.
119. Number of types of vestiture on declivity: (0) 1; (1) none; (2) 2.
120. Density of vestiture on declivity: (0) very dense; (1) dense; (2) less dense; (3) sparse; (4) extremely sparse.
121. Hair insertion on declivity (Fig. 8): (0) in punctures; (1) next to punctures; (2) in and next to punctures; (3) away from punctures; (4) next to and away from punctures; (5) 3 types.

Results

Parsimony analyses

The results from the parsimony analysis are shown in Figure 12. Thirty-one most-parsimonious trees of 1155 steps (CI: 0.3411, RI: 0.5202) were recorded. One hundred and twenty-one characters were parsimony-informative. One cladogram was obtained by successive character reweighting (*a posteriori* weighting) (FARRIS 1969; CARPENTER 1988). Nine characters were weighted 1, the other 114 characters were weighted other than 1. The reweighted tree with a length of 218.92559 steps (CI: 0.4083, RI: 0.5917) is presented in Figure 13.

The strict consensus yields a well-resolved tree that contains few polytomies and divides the Bostrichidae auct. into three major clades (Fig. 12) : 1. Euderiinae, 2. Polycanoninae, Lyctinae, Dysidinae and Endecatomininae, 3. Psoinae, Dinoderinae and Bostrichinae (including Apatinae) (we are using the subfamily divisions here according to the classification of BOROWSKI & WĘGRZYNOWICZ 2007). The outgroup taxa are divided into two groups, *Anobium* is the sister to all other taxa as the pure outgroup, and the other three outgroup taxa form a polytomous group in-between the Psoinae-Dinoderinae-Bostrichinae polytomies and other taxa.

After reweighting (Fig. 13), the outgroup taxa are still divided between two groups which are respectively the cluster of (Dinoderinae+Bostrichinae) and the clusters of all other taxa. The clade (*Polycaon* + *Psoa* + *Chilenius*) becomes the sister of the other taxa except for *Euderia* and *Anobium* after reweighting.

Besides *Euderia*, the subfamilies Lyctinae, Dysidinae, Endecatomininae, Polycaninae and Psolinae of previous authors form the sister to the outgroup and the remaining Bostrichidae in our hypothesis. The Apatinae auct. combines with *Bostrychopsis* into a clade as a part of the polyphyletic Bostrichinae. The three tribes of Bostrichinae, Bostrichini, Sinoxylini and Xyloperthini, are all shown as polyphyletic groups. Both sexes of the seven sexually dimorphic genera form well-supported (the branch support values all above 90) monophylies in the most-parsimonious hypothesis.

Even though the branch support values are low, the fact that three of the outgroup taxa form an ingroup in the most-parsimonious results suggests a reorganisation of the classification of Bostrichidae is needed. A modified classification resulting from the phylogenetic hypothesis (Fig. 12) is shown in Table 3, and the main clades of the hypothesis are discussed in turn.

It may be noted here that the Anobiidae, one outgroup family, shows a polyphyletic relationship in the most-parsimonious hypothesis (Fig. 12). Even though we are not concerned with the Anobiidae in this paper, this shows the necessity for further study of the phylogeny of the family.

The performance of the characters

The *ci* and *ri* of each character used in this study, arranged in the order of the data matrix, are composed in an electronic appendix which is available by e-mail (liulysky@gmail.com) on request.

Measurement and micro-structural characters are both newly used in this study to examine the phylogeny of the Bostrichidae auct. Measurement characters are mainly synapomorphies and most micro-structural characters are autapomorphies at generic level. They are both useful sets of characters and usually good for distinguishing different ranks of taxa within the bostrichids.

Because of the controversy regarding the use of measurement characters in phylogenetic studies (see above), the effect of their exclusion on the phylogeny, analysed by PAUP using the remaining 93 characters, is shown in Figure 14. The 4 outgroup taxa are separated as a single group from the ingroup taxa. The latter are clustered into (Euderinae+Dysidinae), Endecatomininae, Lyctinae, (Psolinae+Polycaninae), Dinoderinae and Bostrichinae (including Apatinae). The taxa of 3 tribes of Bostrichinae (Bostrichini, Sinoxylini and Xyloperthini) and Apatinae all appear polyphyletic. This shows that the measurement characters contribute very little to clarify the relationships among Bostrichinae and other subfamilies of Bostrichidae, and between outgroup and ingroup. However, the measurement characters do contribute to clarify the relationships among the tribes of Bostrichinae and Apatinae.

The performance of micro- structural characters is better in *ri* (17 characters with *ri*<0.5) than in *ci* (34 characters with *ci*<0.5), also better on the vertex, pronotum and elytral disc, especially the characters relating to the hair insertion (eg. characters 36, 41, 54, 55, 64, 75, 93, 104, 105) and the uniformity of microstructures on the surface of the beetles (eg. characters 32, 59, 63, 67, 68, 70, 76, 78, 81, 88, 90, 102).

The influence of outgroup

To show the influence of rooting with different outgroups, we compare the effects of using different combinations of outgroup taxa on the phylogeny. The results are shown in Figures 15 to 18 and summarized in Table 4.

The results show that Anobiidae is a problematic family which appears polyphyletic when both outgroup genera are included (see Figs 12, 13 and 15). The classification of Euderinae will be discussed further below, because the subfamily Euderinae always forms a clade with *Anobium*. On the other hand, the Dermestidae forms a more reliable outgroup (see Figs 12-14, 16), so further discussion of the classification of the bostrichid subfamilies should mainly be based on the topology rooted using Dermestidae (Fig. 16).

Within the subfamily Bostrichinae, when Dermestidae are used as an outgroup, the tribe Bostrichini (*sensu* BOROWSKI & WĘGRZYNOWICZ) forms a polyphyletic assemblage in which *Bostrychopsis* (tribe Bostrichini) always forms a clade with the Apatinae, and *Sinoxylodes* (tribe Bostrichini) forms a clade with *Sinocalon* (tribe Sinoxylini), and *Sinoxylon* (tribe Sinoxylini) forms a clade with Xyloperthini. When Anobiidae is used as an outgroup, *Sinoxylodes* (tribe Bostrichini) forms a clade with (*Bostrychopsis*+Apatinae), and *Sinoxylon* (tribe Sinoxylini) forms a clade with *Dendrobiella* (tribe Xyloperthini) and *Sinocalon* (tribe Sinoxylini) form a monophyly with *Lichenophanes* (tribe Bostrichini) in the polyphyletic bostrichine

assemblage. These differences from the current classification suggest the classification of Bostrichinae needs further consideration.

The subfamily Lyctinae is currently composed of two tribes, Lyctini and Trogoxylini. The topology of the Lyctinae in Figures 12 to 18 remains constant: (Lyctini+*Trogoxylon*)+*Cephalotoma*. The Trogoxylini forms a paraphyletic clade and its classification needs further consideration.

Discussion

The situation of Euderinae

Euderia BROUN is currently a monotypic genus and the only genus of Euderinae (BOROWSKI & WĘGRZYNOWICZ 2007). It is confined to New Zealand. In the phylogenetic hypothesis of this study (Fig. 12), and in the topology of figures 15 and 17, *Euderia* always forms a clade with *Anobium*, and appears as a sister-group to all the other bostrichid taxa and outgroups. This suggests that the Euderinae should be separated from Bostrichidae.

BROUN (1880) described the monotypic genus from one pair of specimens, one male and one female. He thought it a remarkable insect which should be placed 'at the end of' the Anobiidae. It was transferred to Bostrichidae by LESNE (1934) and placed in a new subfamily Euderitae [sic].

CROWSON (1961) described *Euderia* as the most anobiid-like bostrichid because of the shape of its hind coxae and the type of larval spiracles. He thought it highly probable that *Euderia* is a relict survival of a group from which the Bostrichidae were derived, and that the Anobiidae probably evolved from bostrichid-like ancestors akin to *Euderia* (CROWSON 1961).

IVIE (1985) suggested the Anobiidae should be placed as a subfamily under Bostrichidae because the sister-group relationship of the anobiines and euderines seemed well established in his study. But *Euderia* and anobiids (*Anobium* and *Lasioderma*) are polyphyletic in the results of our study in disagreement with IVIE's suggestion.

The sexually dimorphic antenna (Fig. 19B, C), the trapezoidal labrum, the shape of the pronotum (Fig. 19A), and the broad squamous setae (Fig. 19D) covering almost all of the body except for the tibiae and tarsi are all autapomorphies of *Euderia*.

The body shape of most bostrichids is rather stout with stout legs and teeth on the external side of the tibiae as adaptations to a wood-boring life (CYMOREK 1968). *Euderia* is elongate and slim, the legs are quite slender, the tibiae almost linear without any teeth, the tarsi a little longer than the tibiae (Fig. 19A, B). All these characters suggest that the *Euderia* adult is not adapted to a wood-boring life. However, it has the hypognathous head typical of the wood-boring bostrichids. The actual habits of the species remain unknown.

According to table 4, Anobiidae is a problematic family which needs further study to clarify the classification, and because *Euderia* and anobiids (*Anobium* and *Lasioderma*) are polyphyletic in Figs 12, 13 and 15, *Euderia* does not fit happily into the Bostrichidae. However, it needs further analysis of the phylogeny of Anobiidae to determine if it should be transferred back to Anobiidae, where originally placed, or made a separate family. Even though we feel it should be a separate family, we retain the position of Euderinae here pending further studies.

The situation of Psolinae and Polyaoninae

Besides Lyctinae, Psolinae and Polyaoninae are the only two prognathous bostrichid subfamilies. There are six genera and thirteen species currently recognized in the Psolinae, and two genera (*Melalgus* DEJEAN, *Polycaon* CASTELNAU) with 24 species and four species respectively, currently included in the Polyaoninae (BOROWSKI & WĘGRZYNOWICZ 2007).

LESNE (1921) treated *Chilenius* as a monogeneric subfamily, and treated both Psoini and Polyaonini under Bostrichinae in the same paper, but later he treated Chileniini, Psoini and Polyaonini as three tribes under Bostrichinae (LESNE 1938). BÖVING & CRAIGHEAD (1931), and JEANNEL & PAULIAN (1944) treated Psolinae as an independent family based on the larval characters, and abdominal and genital characters respectively. Since CROWSON's studies (1955, 1968), this group has been treated as a subfamily of Bostrichidae, even though CROWSON (1968) mentioned that the Psolinae are clerid-like insects with the first tarsal segment completely obliterated so that the tarsi are 4-segmented. IVIE (2002) also mentioned the Psolinae are atypical bostrichids that resemble clerids more than other bostrichids, and transferred *Chilenius* into Apatini from Psolinae (IVIE 1985) which action was ignored by BOROWSKI & WĘGRZYNOWICZ (2007).

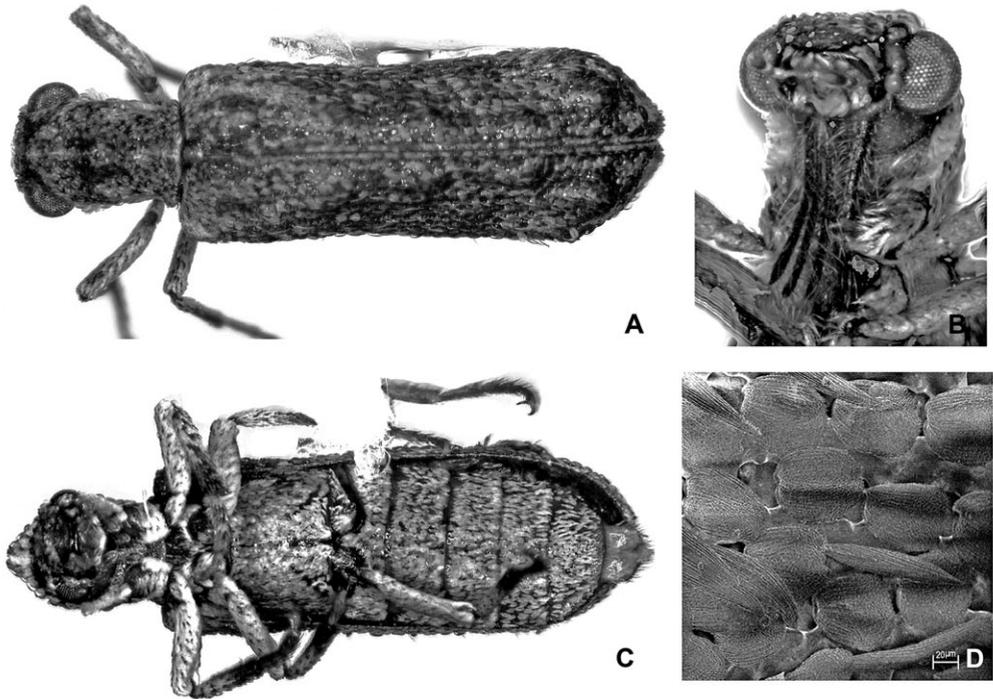


Figure 19. *Euderia squamosa* BROUN 1880. (A) Dorsal view (male); (B) ventral view of head (male); (C) ventral view (female); (D) broad squamous setae (SEM). Figs 12-18 see pages 126-129).

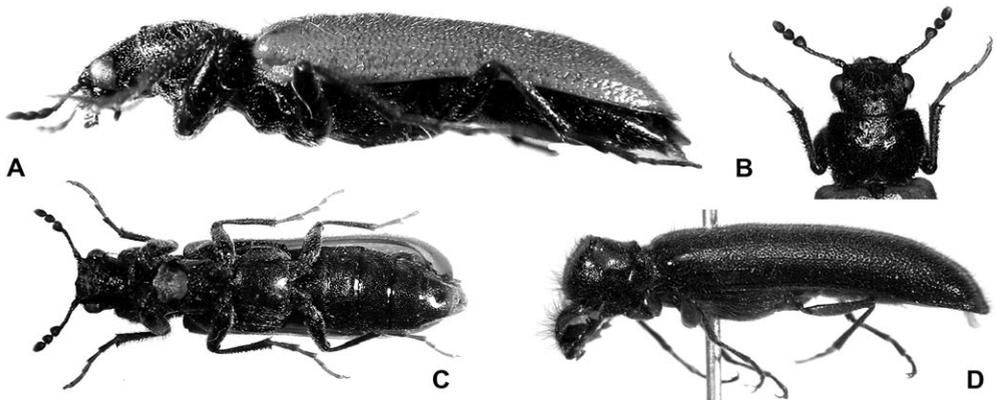


Figure 20. A-C. *Psoa viennensis* HERBST 1797, lateral view (A), dorsal view of head (B), ventral view (C); (D) *Chilenius spinicollis* (FAIRM & GERM 1861), lateral view.

The Polyaoninae have been included in the Psocinae by most anglophone authors, including LÉCONTE (1861), HORN (1878), LÉCONTE & HORN (1883), BÖVING & CRAIGHEAD (1931) and CROWSON (1981), but LESNE (1938) and VRYDAGH (1960a, b) treated polyaonines at the same tribal taxonomic level as the psocines. IVIE (1985) treated the polyaonines as a separate subfamily from the psocines.

Laboratory observations (TILDEN 1953) indicate that the psocine adults do not bore into the wood. The remarkably extensible ovipositor allows gravid females to oviposit either in cracks in the bark or in the axils

of small branches (TILDEN 1953). However, the psoine larvae are obviously adapted to boring. Based on the larval characters, BÖVING & CRAIGHEAD (1931) treated Psoinae as an independent family, and included within it the Dinoderinae, a group which has always been considered a separate subfamily when based on adult characters. Because the larvae of both Psoinae and Dinoderinae are adapted for boring, it is possible that more symplesiomorphic characters have been retained in both groups.

Studies of their biology (SOLERVICENS & VIVAR 1976; SOLOMON 1995; ZALOM et al. 2009), suggest that polycanonine larvae are well-adapted to a xylophagous life, but polycanonine adults do not bore into wood. Adult polycanonine females move to recently broken or pruned branches and deposit their eggs in cracks and crevices (SOLOMON 1995), or bore small, round holes at the base of buds or axils of twigs injured by sunburn to oviposit (ZALOM et al. 2009).

The subpediculate head (Fig. 20B), the narrow anterior part of the body, the cleroid-like elytra (Fig. 20A), the lack of differentiation of the elytral declivity (Fig. 20A, D), the rather conical coxae, the raised metacoxae, and lack of postcoxal carinae, and the concealed intercoxal process of the first visible abdominal sternite (Fig. 20C), less dense micro-structures and vestiture on head, pronotum and elytra – all these characters are autapomorphies of psaines (LESNE 1935a; IVIE 1985; this study). The prognathous head which is prominent from above (Fig. 21A), as well as the wide intercoxal process of the first visible abdominal sternite (Fig. 21B) and the nontuberculate pronotum (Fig. 21A) are all autapomorphies of Polycanonidae (IVIE 1985; this study).

IVIE (1985) supposed the special relationship of the Psoinae and Polycanoninae to be based on symplesiomorphies that result in a similar facies. However, the autapomorphies of each subfamily – the longer epipleura (Fig. 21C), the harder elytra and more distinct declivity (Fig. 21C), the wider intercoxal process of the first visible abdominal sternite (Fig. 21B), the flatter meso- and meta-coxae (Fig. 21B), and the stouter femora (Fig. 21B) and the denser micro-structures and vestiture on the pronotum and elytra of polycanonines – all suggest the polycanonines have evolved further towards boring habits than the psaines. These characters also suggest that the polycanonine adult, like the psoine adult, is not a typical wood-boring beetle.

In the phylogenetic hypothesis of this study (Fig. 12), the clade (*Chilenius*, *Psoa*) and *Polycaon* are shown as part of a polytomy, which includes the outgroups. In the topology of figures 16 and 18, the clade (*Chilenius*, *Psoa*) and *Polycaon* are parts of a polytomy in Bostrichidae. *Chilenius* and *Psoa* form a monophyly in Figs 12, 16 and 18, and the assemblage is paraphyletic to *Polycaon*. So we retain the classification of the two subfamilies here.

The situation of Lyctinae

FORBES (1926), BÖVING & CRAIGHEAD (1931), and JEANNEL & PAULIAN (1944) treated Lyctinae as a family based on the characters of wing venation, larvae, and abdomen and genitalia respectively. CROWSON (1955) also treated Lyctidae as a family, but later (CROWSON 1968) reduced them to subfamily status. IVIE (1985) retained Lyctinae as a subfamily in order not to raise too many groups included in the Bostrichidae to family status using the monophyletic family concept. In the phylogenetic hypothesis of this study (Fig. 12), the clade Lyctinae is a well-supported monophyly. The lyctine clade is also shown as part of a polytomy, which includes the outgroups, and in the topology of figures 16 and 18, the clade Lyctinae forms part of a polytomy in Bostrichidae.

The lyctine female does not make galleries in the wood for oviposition but lays her eggs in the big pores of the xylem vessels in the sapwood of hardwoods and bamboo (LIU et al. 2008a). The female may use broken surfaces or fissures in the wood, to the bottom of which she inserts her long and very mobile ovipositor (ALSTON 1923). The male and female lyctines court and mate on the surface of wood (LIU et al. 2008b). These biological observations make it clear that the lyctine adults are not adapted to a wood-boring life.

The prognathous head, very flat body form without an elytral declivity (Fig. 22), two-segmented antennal club (except for *Cephalotoma* and *Lyctoderma* with three segments), the denser microstructures (punctures, tubercles) on the pronotum and elytral disc, rather elevated scutellum, elytral disc suture not marginated (Fig. 22), closed procoxal cavities (Fig. 23), round procoxae which do not project and the very long first visible abdominal sternite (Fig. 23) are all autapomorphies of Lyctinae.

Cephalotoma and *Lyctoderma* are the only two taxa in Lyctinae with three antennal club segments and the widest and flattest members of the Lyctinae (Fig. 22D). A pair of very bulging eyes, no clear gular sutures but the gular area in between the genae distinct and the widest in lyctines, a rather transverse pronotum with distinctly angled anterior and posterior corners (Fig. 22D) are all autapomorphies of *Cephalotoma*. The Lyctinae in general all have an evident clypeo-frontal suture and the frons is not in the same plane as the

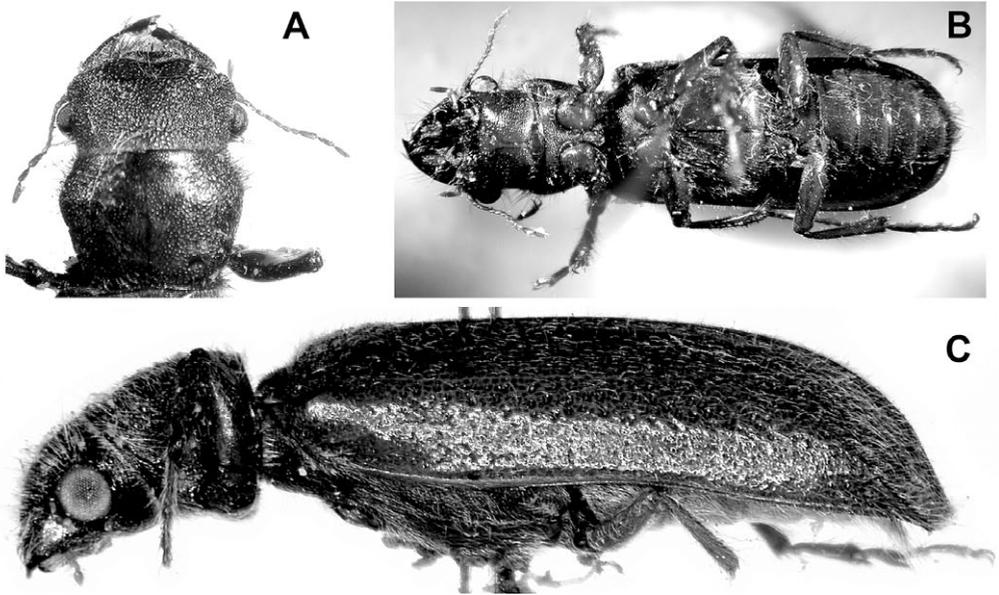


Figure 21. A-B. *Polyscaon chilensis* (ERICHSON 1834), dorsal view of head and pronotum (A), ventral view (B); (C) *Melalgus subdepressum* (LESNE 1897) female, lateral view.

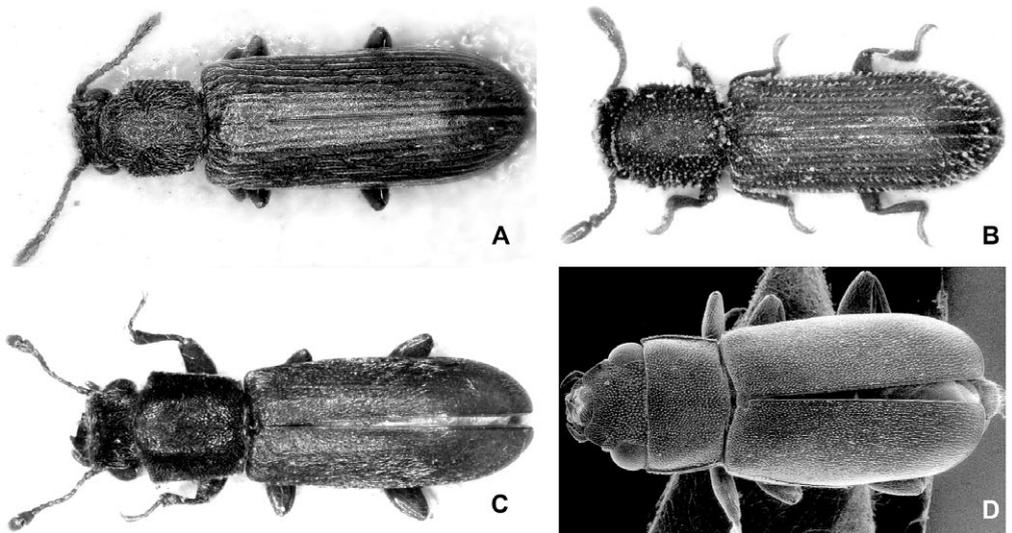


Figure 22. Dorsal view of lyctids. (A) *Lyctus linearis* (GOEZE 1777); (B) *Minthea squamigera* PASCOE 1866; (C) *Trogoxylon parallelipipedum* (MELSHEIMER 1846); (D) *Cephalotoma perdepressa* LESNE 1937.

clypeus, but *Cephalotoma* only has an obsolescent clypeo-frontal suture and the clypeus and frons lie in almost the same plane (Fig. 22D). Compared to other lyctines, *Cephalotoma* also has a rather flattened, round and small coxal cavity, and the coxae are more globular and project less than the rather conical coxae of other lyctines (Fig. 23).

The micro-structural characters also differ between *Cephalotoma* and *Trogoxylon* (Fig. 24). There are distinct differences in the shape and type of vestiture on the frons and pronotum. In *Cephalotoma*, there are two types of vestiture on the frons (Fig. 24B). One consists of flattened, stout and short setae with a rounded tip, the other one of longer, narrower setae with a more pointed tip. There are also two different types of setae on the pronotum of *Cephalotoma*, one is short and stout with a rounded point, the other is much longer and plumose in the upper half gradually tapering to a pointed end. There are only slender setae with a pointed end on the frons and pronotum of *Trogoxylon* (Fig. 24A).

In the phylogenetic hypothesis of this study (Fig. 12) and also in the topology of figures 14 to 18, *Cephalotoma* is the sister group of the clade (*Lyctus*, *Minthea*, *Trogoxylon*). This means that the Trogoxylini sensu BOROWSKI & WĘGRZYNOWICZ (2007) becomes paraphyletic.

The body form of *Cephalotoma* and the closely related genus *Lyctoderma* LESNE are rather different from the other genera currently placed in the Trogoxylini. The body is strongly depressed and flattened. The base of the mandibles is expanded and leaflike. The pronotum has the margins reflexed and grooved. So far as is known, all the species are inquilines - commensals in the galleries of other bostrichids (LESNE 1932; LIU *pers. obs.*). The flattened body is an adaptation to the narrow space between the underside of the host bostrichid and the gallery wall (LESNE 1932). LESNE (1932) noted that the normally very active beetles became quiescent when beneath the body of the host bostrichid. They are also able to move through the woody debris in the bostrichid gallery, and appear to feed on this material (LESNE 1932; LIU *pers. obs.*), and perhaps also on fungal hyphae growing on it. The mandibles are not adapted to boring into wood. Members of certain other genera of Lyctinae have occasionally been found in the galleries of other bostrichids (LESNE 1932), and it seems likely that the inquiline habit and morphological adaptations of *Cephalotoma* and *Lyctoderma* have evolved from a genus like *Lyctopsis* LESNE which is morphologically closer to *Trogoxylon*, but which also appear to live in the galleries of other bostrichids (LESNE 1932).

Based on the results of the phylogenetic analyses, the special commensal lifestyle of *Cephalotoma* and *Lyctoderma*, and the distinguishing characters discussed above, a new tribe, Cephalotomini is separated from the Trogoxylini as a distinct tribe of Lyctinae.

Cephalotomini tribus novus

Type genus: *Cephalotoma* LESNE, 1911. Other genus included: *Lyctoderma* LESNE, 1911.

Diagnosis

Body very flattened, less elongate than other lyctines.

Eyes large and strongly projecting occupying about 40% of total head width. Clypeus lobed or dentate and its anterior angles, emarginated in front. Clypeo-frontal suture obsolescent, and clypeus and frons lie in almost the same plane unlike other lyctines. Labrum bilobate, fringed with fine and long hairs. Gular suture indistinct with a wide and impunctate gular area. Antenna 11 segmented, club 3 segmented (except for African species with 2 segmented club).

Pronotum more transverse than other lyctines, with distinct lateral margins, anterior and posterior angles distinct.

Elytra flat, more or less parallel, without declivity and epipleura, without striae.

Legs moderately long, stout. First tarsomere very small, fifth tarsomere almost as long as all preceding segments combined. Coxae widely separated, pro- and meso-coxae rounded, and weakly projecting. Intercostal process of first visible abdominal sternite broadly truncate anteriorly.

The situation of Dysidinae

The Dysidinae is a small group comprising two genera in which the first tarsal segment is longer than the second, and which have a strikingly discontinuous geographical distribution, bitypic *Dysides* distributed in South America, monotypic *Apoleon* distributed in Southeast Asia and some of the Indonesian islands (BOROWSKI & WĘGRZYNOWICZ 2007). This taxon has remained in its present form since LESNE (1894) revised it under the generic name *Dysides*.

The Dysidinae have a rather depressed body form. The female dysidines can evert a very long membranous ovipositor (LESNE 1894) like the female lyctines, psocines and polycanines. At present, we know very little about the biology of dysidines, but the very long ovipositor and the flattened body form probably imply that the female dysidines have similar oviposition habits to the other female prognathous bostrichids, and differ from the groups which are entirely xylophagous as adults.

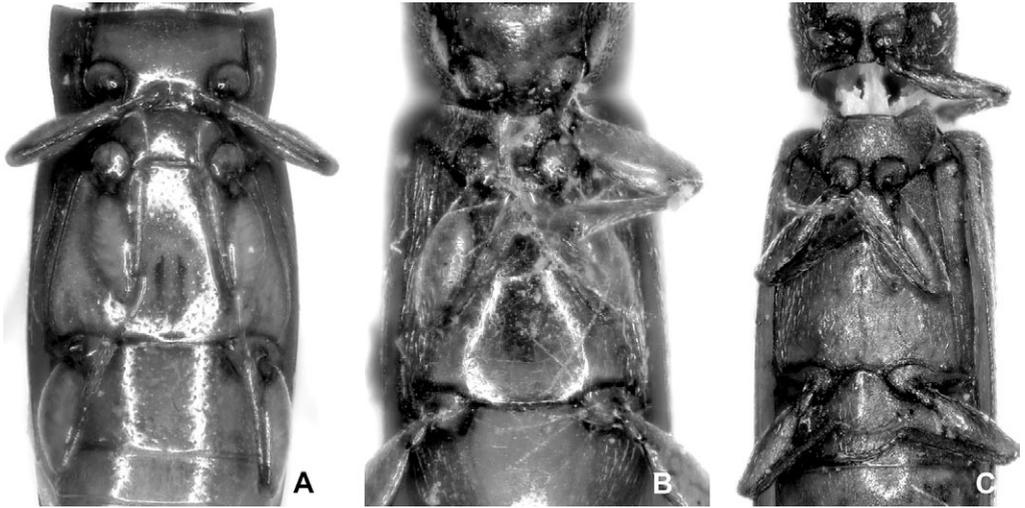


Figure 23. The ventral view of *Cephalotoma perdepressa* (A), *Trogoxylon parallelipedus* (B) and *Lyctus linearis* (C) to show the three pairs of coxae and sternum intercoxal process.

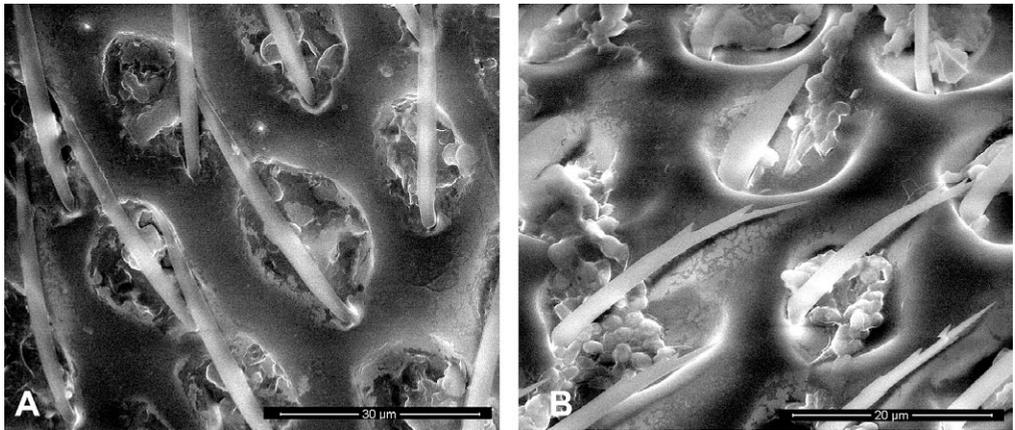


Figure 24. The vestiture on the pronotum of *Trogoxylon parallelipedus* (A) and *Cephalotoma perdepressa* (B).

The prognathous head (Fig. 25A), the reduced elytral declivity and the wide intercoxal process on the first visible abdominal sternite (Fig. 25B), and the bilobate labrum (Fig. 25A) are all autapomorphies of the monophyletic Dysidinae. Dysidinae have dense vestiture on pronotum and elytra, and the density and shape of the setae are similar to those of *Lyctus* and *Minthea*.

In the phylogenetic hypothesis of this study (Fig. 12), *Dysides* is the sister-group to Lyctinae, and a part of the polytomy which includes Lyctinae in Figs 16 to 18. This suggests that the subfamily Dysidinae is most closely related to the Lyctinae.

IVIE (1985) suggested that the Dysidinae may be a primitive group within the Bostrichidae. If that is so, and bostrichids are derived from a lyctine-like ancestor, because the fossils suggest the below-bark habitat should be the original habitat of beetles (PONOMARENKO 2003), then it appears that either the dysidines have retained more of the characters of the lyctines, or that the Bostrichidae evolved from a Lyctine ancestor akin to Dysidinae.

The situation of Endecatominæ

The Endecatominæ is a monogeneric group and the relationships of this taxon have been uncertain for a long time. The characters of the genus were studied very comprehensively by LESNE (1935b). CROWSON (1961) confirmed the position of the genus in the family Bostrichidae on the basis of a study of the larvae. However, LAWRENCE & NEWTON (1995) established a separate family for the Endecatominæ in the superfamily Bostrichoidea (ZAHRADNIK 2006). IVIE (1985) also treated it as a separate family, but later he changed his mind and reduced its rank to subfamily (IVIE 2002).

The distribution of the Endecatominæ is limited to the Palearctic and Nearctic areas derived from Laurasia. The group also has a very distinctive host amongst Bostrichoids, hard polypore fungi (*Phellinus*, *Polyporus*) growing on the dead logs of birch, oak (*Betula*, *Quercus*), and other hardwood trees (LIU et al. 2008b). It seems possible that the group evolved from primitive xylophagous bostrichids that bred in birch or other hosts of hard polypore fungi, and then evolved mycophagous habits.

The rather short antennae and antennal club (Fig. 26B), the uniformly sized tubercles on pronotum and elytra (Fig. 26A), very short legs and very stout femora (Fig. 26B), pentamerous tarsi with a very small first segment, the microcalcars on the tibial corbels of the mid and hind tibiae are all autapomorphies of Endecatominæ.

In the phylogenetic hypothesis of this study (Fig. 12), *Endecatomus* is shown as part of a polytomy, which includes the outgroups, and as a sister-group to the Bostrichinae *sensu stricto*. In Figs 15 to 18, Endecatominæ is a part of the polytomy which includes Lyctinae and Dysidinae.

The situation of Dinoderinae

Compared to all bostrichid subfamilies, Dinoderinae is the most stable one. Its classification has not changed since LESNE (1938). The representatives of Dinoderinae, *Dinoderus* and *Stephanopachys*, in this study form a stable monophyly in Figs 12 to 18, and sister group to the Bostrichinae assemblage.

The situation of Bostrichinae and Apatini, Sinoxylini, Xyloperthini

In the most recently published classification (BOROWSKI & WĘGRZYNOWICZ 2007), the subfamily Bostrichinae includes three tribes (i.e. Bostrichini, Sinoxylini and Xyloperthini), and the Apatinae auct. is treated as a subfamily of Bostrichidae. According to this study (Figs 12, 15 to 18), Bostrichinae is comprised of Bostrichini, Sinoxylini, Xyloperthini and Apatinae auct.. Within the Bostrichinae, only Apatini (*Bostrychopsis*, *Apate*, *Dinapate*) is a well-supported monophyly. This suggests the relationships within Bostrichinae are poorly resolved. The currently accepted bostrichine tribes (Bostrichini, Sinoxylini, Xyloperthini) are not well supported in Fig. 12 and all are polyphyletic in Figs 15 to 18.

LESNE (1909, 1938) included subtribes Dinapatina and Apatina in the tribe Bostrichini; BEESON & BHATIA (1937) included Apatini in the subfamily Bostrichinae. CROWSON (1968) included Dinapatini and Apatini in the Bostrichinae, and they kept this classificatory rank until BOROWSKI & WĘGRZYNOWICZ (2007) raised them together into a subfamily of Bostrichidae without discussion or nomenclatural notice.

Their large size is one character which distinguishes Apatini from other bostrichids. The rather large body size, sexual dimorphism, rather short antennae and clubs, hairs inserted in the punctures on the frons, denser teeth on the outer side of the tibiae, sparse vestiture on the elytral declivity and less dense microstructures on the pronotum base and elytral declivity are all autapomorphies of the clade (*Bostrychopsis*, (*Apate*, *Dinapate*)) in this study.

Apatinae auct., currently including only *Apate* and *Dinapate*, are here reduced to the status of a tribe of Bostrichinae, Apatini. Because *Bostrychopsis* forms a monophyletic clade with *Apate* and *Dinapate* in the polyphyletic clade Bostrichinae (Figs 12, 15-18), it is here transferred to Apatini from Bostrichini.

In the present analysis (Table 4), the Bostrichini form a polyphyletic group. When Dermestidae are the outgroup, *Sinoxyloides* (Bostrichini) forms a clade with *Sinocalon* (Sinoxylini), and *Sinoxylon* (Sinoxylini) forms a clade with Xyloperthini. When Anobiidae are the outgroup, *Sinoxyloides* (Bostrichini) forms a clade with Apatini, and *Sinoxylon* (Sinoxylini) forms a clade with *Dendrobiella* (Xyloperthini). The relationships of these tribes and genera need to be examined further.

The Sinoxylini consists of six genera and 77 species (BOROWSKI & WĘGRZYNOWICZ 2007). *Sinoxylon* is the biggest genus with 52 species and the type genus of this group. LESNE (1898a) raised the subtribe Sinoxylina under Bostrichini based on the broad and very short mandibles which are symmetrical and meet with their cutting edges against each other in the midline (pachygnathous mandibles in LESNE 1901). In the



Figure 25. *Dysides obscurus* PERTY 1830, dorsal view of head and pronotum (A), ventral view (B).

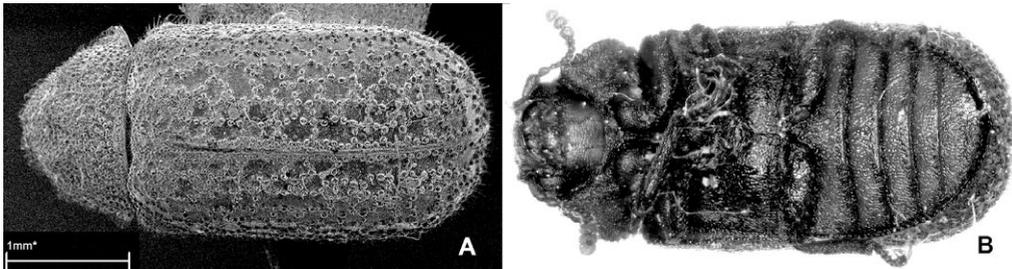


Figure 26. *Endecatamus lanatus* LESNE 1934, dorsal view (A), ventral view (B).

phylogenetic analyses, the genus *Sinoxyloides*, which is currently placed in the Bostrichini, usually forms a monophyletic clade with the genus *Sinocalon* (Fig. 16, 18), currently placed in the Sinoxylini. *Sinoxyloides* has the flabellate antennal club and pachygnathous mandible of the Sinoxylini. The surface of the vertex with mixed tubercles and grooves differs from the tuberculate vertex of Bostrichini (except for *Lichenophanes*). The lack of pronotal hooks and the indistinct anterior angles of pronotum are also sinoxylini characters. Accordingly, *Sinoxyloides* LESNE and its single included species, *S. curtulus* (ERICHSON), are here transferred to the Sinoxylini.

Conclusion

This first attempt to examine the taxonomic characters of bostrichid genera in all currently accepted subfamilies and tribes in a cladistic framework is successful at subfamily level, but does not resolve the relationships between tribes of Bostrichinae. The results of the study identified morphological characters which support monophyletic groups, and suggest some taxonomic changes. The new classification is shown in Table 3. The Cephalotomini is erected as a new tribe of Lyctinae. *Bostrychopsis* is transferred to Apatini from Bostrichini, and *Sinoxyloides* is transferred to Sinoxylini from Bostrichini. Further possible changes, such as the erection of a new family for the Euderinae must await additional studies.

This study shows that measurement and micro-structural characters are both useful in studies of the phylogeny of the Bostrichidae auct. The micro-structural characters can sometimes contribute more to the distinction between closely related and morphologically similar species than macro-structural characters (LIU et al. 2009). For practical reasons, the micro-structural characters may not contribute greatly to the diagnosis of different genera, but their study can contribute to our knowledge of the phylogeny of the bostrichid taxa.

Because there were potential problems to using the Anobiidae as an outgroup, this study also used genera from the Dermestidae, and studied the effects of using all the genera together, or one or both genera in each family separately as outgroup for the phylogenetic analysis. Figs 12, 14-18 show how different the results can be depending on the outgroup chosen. However, each result does provide information and suggest alternative hypotheses.

The two anobiid genera used as outgroup (*Anobium* and *Lasioderma*) belong to the Anobiinae and Xyletininae respectively. These subfamilies are paraphyletic in the phylogenetic study based on molecular data (HUNT et al. 2007). In the results of this study (Figs 12, 13 and 15), the two genera are polyphyletic, too. *Lasioderma* is monophyletic with the dermestid outgroups genera in several analyses, whilst *Anobium* usually groups with *Euderia*. This indicates that further studies of the relationships between the subfamilies of Anobiidae, and of their relationship to the Euderinae and other bostrichid subfamilies are needed.

Further phylogenetic studies within the Bostrichidae should concentrate on the relationships between tribes. In addition, the incidence of character convergence at different taxonomic levels requires further study. Further progress may be made by the inclusion of further morphological characters, especially micro-structural characters, but may also depend primarily on the availability of DNA data for the genera. This may prove difficult to acquire because many of the genera are rare, and old museum specimens are generally not suitable for DNA studies. Because of the widespread distribution of the group, collecting efforts and the preservation of specimens using modern techniques will be necessary in all the regions of the world.

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Zusammenfassung

Die Käferfamilie der Bostrichidae wurde phylogenetisch untersucht. Dazu wurden 122 morphologische Merkmale der adulten Käfer (96 davon in mehr als zwei Ausprägungen) von 31 Gattungen und Arten untersucht. Von jeder Unterfamilie und jeder Tribus, die bisher anerkannt werden, wurde mindestens eine repräsentative Art untersucht. Außerdem wurden vier Außengruppentaxa untersucht, je zwei Gattungen und Arten der Anobiidae und der Dermestidae. Das vorgestellte Kladogramm (most parsimonious hypothesis) begründet eine deutlich andere Klassifikation der Bostrichidae als die bisher publizierten Systeme.

Die Lyctinae gliedern sich in drei Triben: Lyctini BILLBERG, 1820, Trogoxylini LESNE, 1921 **sensu novo** und Cephalotomini LIU, 2011 **tribus novus**. Die Bostrichinae werden in folgende vier Triben gegliedert: Bostrichini LATREILLE, 1802 **sensu novo**, Apatini JACQUELIN DU VAL, 1861 **sensu novo**, Sinoxylini LESNE, 1899 **sensu novo** und Xyloperthini LESNE, 1921.

Die vorliegende Arbeit ist die erste phylogenetische Analyse der Bostrichidae auct. (Coleoptera) oberhalb der Gattungen. Die Ergebnisse werden in Bezug und ihrer Bedeutung zu früheren morphologischen und biologischen Erkenntnissen diskutiert.

LESNE 1938A	CROWSON 1968	LAWRENCE & NEWTON 1995	IVIE 2002	BOROWSKI & WĘGRZYNOWICZ (2007)	PRESENT STUDY (LIU & SCHÖNITZER)
<p>Lycetinae Lycetini Trogoxylini</p> <p>Dysidinae Euderinae Endecatomininae Dinoderinae Bostrychinae Bostrychini Bostrychina Xyloperthina Apatina Dinapatina</p> <p>Psoini Chileniini</p> <p>Polycaonini</p>	<p>Lycetinae</p> <p>Dysidinae Euderinae Endecatomininae Dinoderinae Bostrychinae</p> <p>Psoinae</p> <p>Polycaoninae</p>	<p>Lycetinae</p> <p>Dysidinae Euderinae Endecatomininae Dinoderinae Bostrychinae</p> <p>Psoinae</p> <p>Polycaoninae</p>	<p>Lycetinae Lycetini Trogoxylini</p> <p>Dysidinae Euderinae Endecatomininae Dinoderinae Bostrychinae Bostrychini Sinoxylini Xyloperthini Apatini Dinapatini</p> <p>Psoinae</p> <p>Polycaoninae</p>	<p>Lycetinae Lycetini Trogoxylini</p> <p>Dysidinae Euderinae Endecatomininae Dinoderinae Bostrychinae Bostrychini Sinoxylonini Xyloperthini Apatinae Apatini Dinapatini Psoinae Chileniini Psoini</p> <p>Polycaoninae</p>	<p>Lycetinae sensu novo Lycetini Trogoxylini sensu novo Cephalotomini tribe novo Dysidinae Euderinae Endecatomininae Dinoderinae Bostrychinae Bostrychini sensu novo Sinoxylini sensu novo Xyloperthini Apatini sensu novo</p> <p>Psoinae Chileniini Psoini Polycaoninae</p>

Table 3. The different classifications of Bostrychidae (taxonomic changes in the present classification are indicated in bold italics).

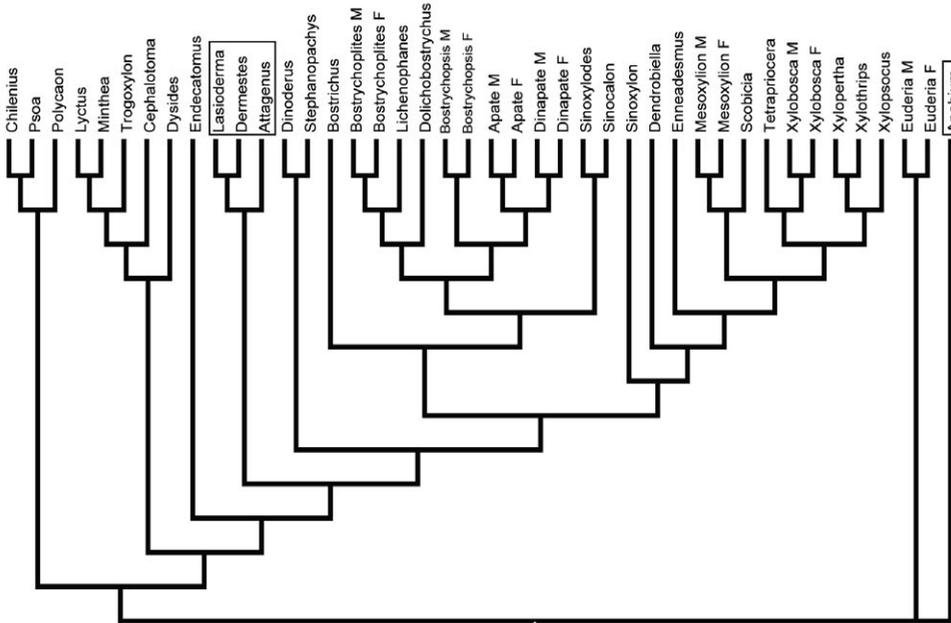


Figure 13. Strict consensus of one most-parsimonious tree of 218.92559 steps after reweighting. (The outgroups were boxed.)

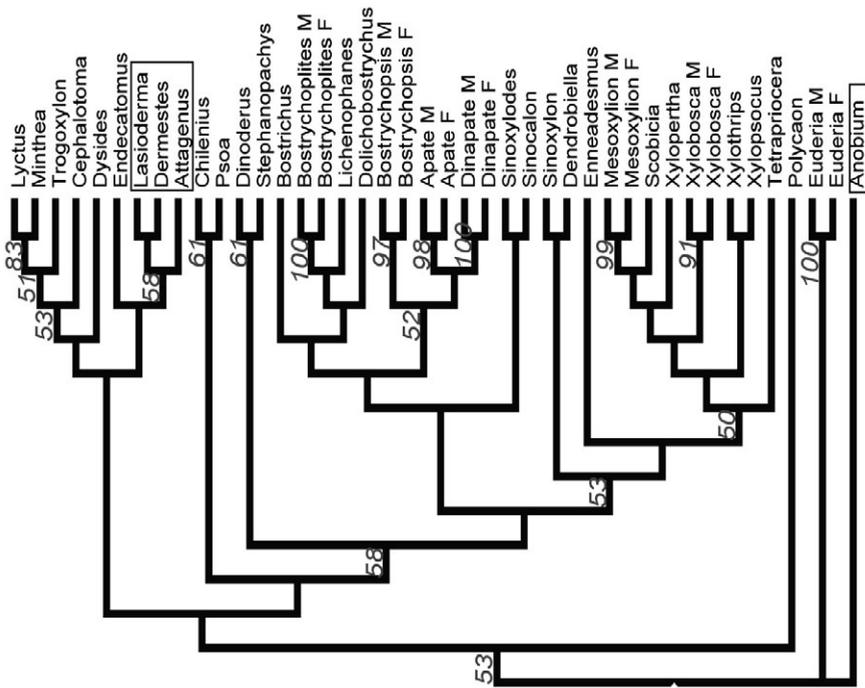


Figure 12. Phylogenetic hypothesis for Bostrichidae and the families derived from Bostrichidae auct. resulting from parsimony analysis. Strict consensus of 31 most-parsimonious tree of 1155 steps (CI=0.3411, RI=0.5202). The number above branches represent bootstrap value > 50%. (The outgroups were boxed.)

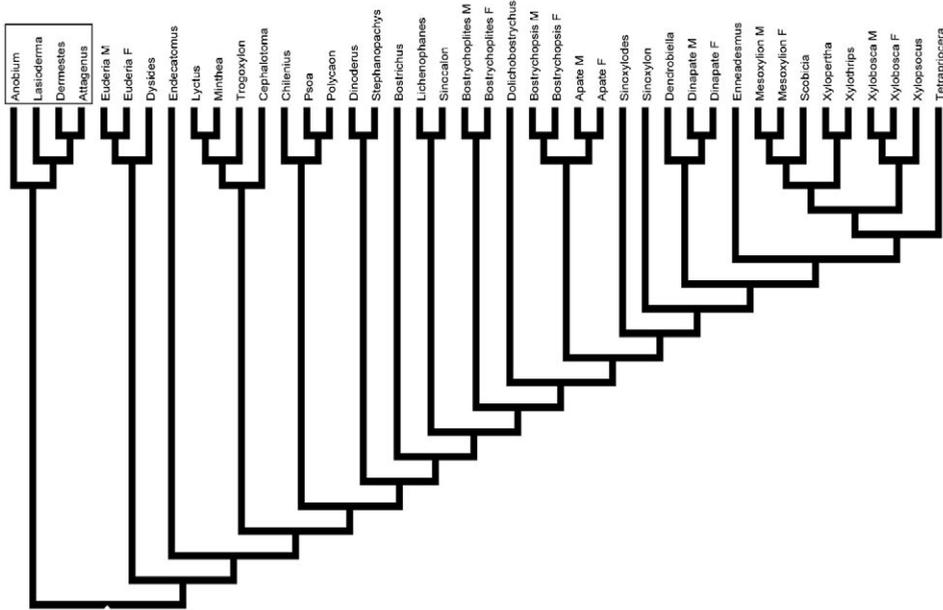


Figure 14. Phylogenetic hypothesis for Bostrichidae and the families derived from Bostrichidae auct. resulting from parsimony analysis excluding 29 measurement characters. (The outgroups were boxed.)

Fig. 15 (outgroup: 2. anobiid taxa)

(**Anobium**+Euderinae)+(Dysidinae+(**Lasioderma**+(Endecatominae+(Lycitinae+(Psoinae, Polycaninae)+(Dinoderinae+Bostrichinae))))))

The cluster of Bostrichinae: (*Bostrichini*,**Sinocalon**)+((**Sinoxylon**+Dendrobiella)+((*Sinoxylodes*+(*Bostrychopsis*+Apatinae))+ Xyloperthini))

The cluster of Lycitinae: (Lycitini+*Trogoxylon*)+*Cephalotoma*

Fig. 16 (outgroup: 2. dermestid taxa)

Outgroups+((Lycitinae+Dysidinae), Endecatominae, Psoinae, Polycaninae, Euderinae)+(Dinoderinae+Bostrichinae))

The cluster of Bostrichinae: (*Bostrichini*+(*Bostrychopsis*+Apatinae)))+((*Sinoxylodes*+**Sinocalon**)+(Dendrobiella+(**Sinoxylon**+ Xyloperthini))

The cluster of Lycitinae: (Lycitini+*Trogoxylon*)+*Cephalotoma*

Fig. 17 (outgroup: *Anobium*)

(**Anobium**+Euderinae)+(Polycaninae+(Psoinae+(Lycitinae+Dysidinae)+Endecatominae)+(Dinoderinae+Bostrichinae))

The cluster of Bostrichinae: (*Bostrichini*,**Sinocalon**)+((**Sinoxylon**+Dendrobiella)+((*Sinoxylodes*+(*Bostrychopsis*+Apatinae))+ Xyloperthini))

The cluster of Lycitinae: (Lycitini+*Trogoxylon*)+*Cephalotoma*

Fig. 18 (outgroup: *Dermestes*)

Dermestes+(Lycitinae, Dysidinae, Endecatominae)+(Psoinae, Polycaninae, Euderinae)+(Dinoderinae+Bostrichinae))

The cluster of Bostrichinae: (*Bostrichini*+(*Bostrychopsis*+Apatinae)))+((*Sinoxylodes*+**Sinocalon**)+(Dendrobiella+(**Sinoxylon**+Xyloperthini))

The cluster of Lycitinae: (Lycitini+*Trogoxylon*)+*Cephalotoma*

* Names in **Bold** and type refer to the outgroup taxa in the whole topology and the *Sinoxylini* taxa in the cluster of Bostrichinae.

* Names in *Italic* type refer to the Bostrichini taxa in the cluster of Bostrichinae.

* Names underlined refer to Xyloperthini taxa in the cluster of Bostrichinae

Table 4. The topology of Figs 15 – 18.

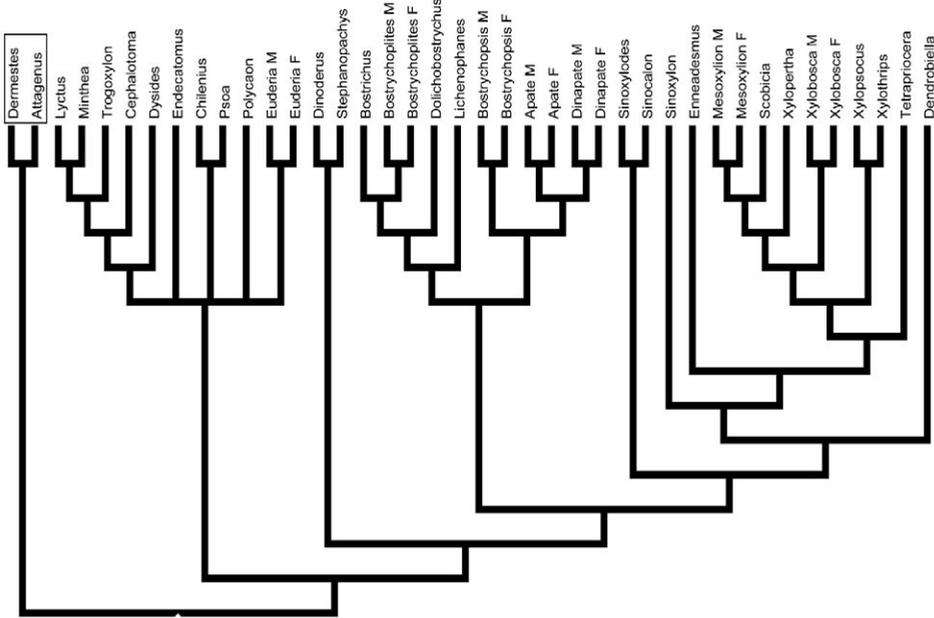


Figure 16. Phylogenetic hypothesis for Bostrichidae and the families derived from Bostrichidae auct. resulting from parsimony analysis with two Dermestid taxa as outgroup only. (The outgroups were boxed.)

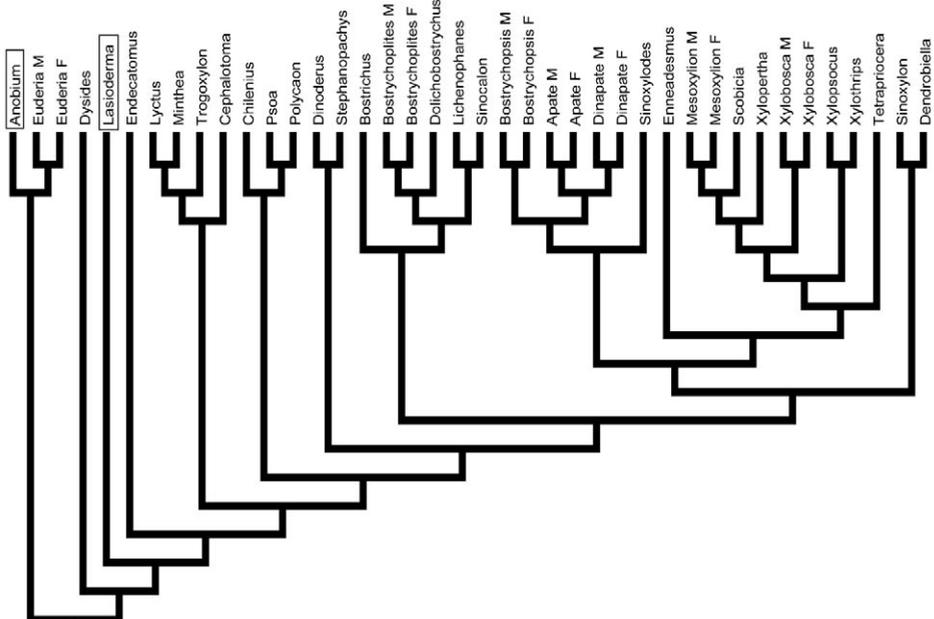


Figure 15. Phylogenetic hypothesis for Bostrichidae and the families derived from Bostrichidae auct. resulting from parsimony analysis with two Anobiid taxa as outgroup only. (The outgroups were boxed.)

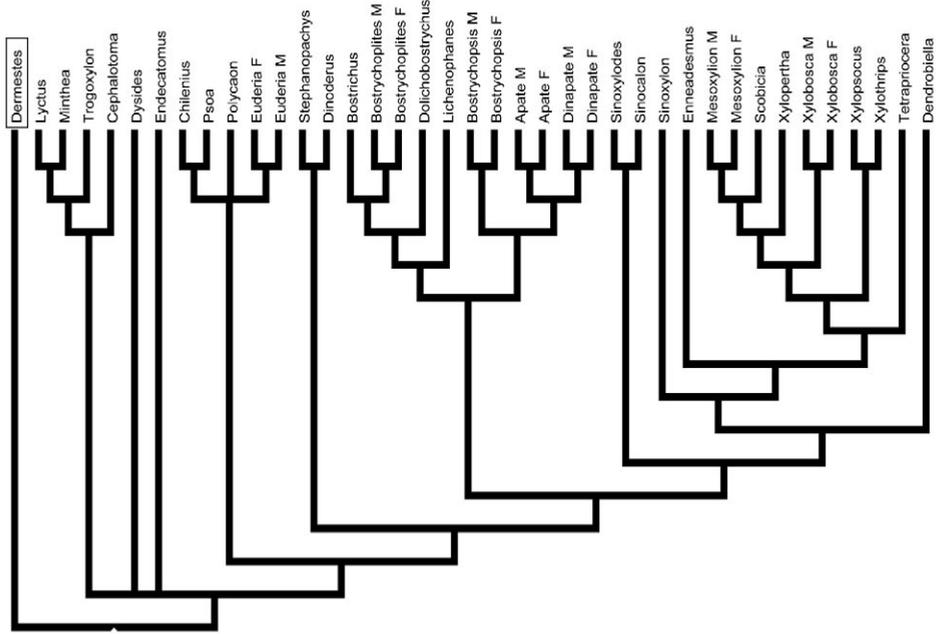


Figure 18. Phylogenetic hypothesis for Bostrichidae and the families derived from Bostrichidae auct. resulting from parsimony analysis with *Dermestes* as outgroup only. (The outgroup was boxed.)

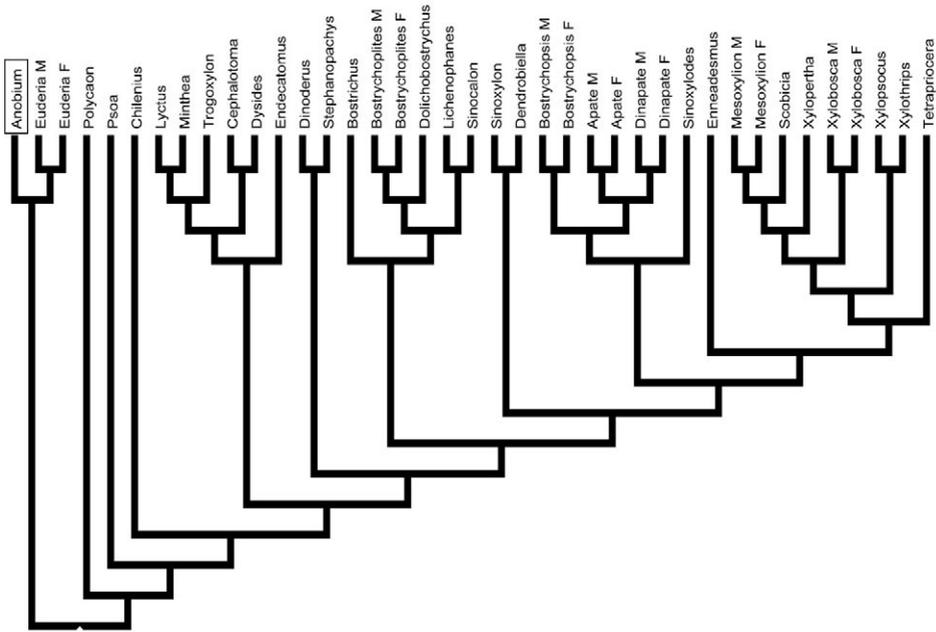


Figure 17. Phylogenetic hypothesis for Bostrichidae and the families derived from Bostrichidae auct. resulting from parsimony analysis with *Anobium* as outgroup only. (The outgroup was boxed.)

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