PHYLOGENETIC STUDIES IN THE BOSTRICHIFORMIA (COLEOPTERA)

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

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* * * * *

The Ohio State University
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3. Apomorphic Character States of Bostrichid subfamilies.........................91
This study began rather naively as a revision of the bostrichid subfamily Psoinae sensu Fisher (1950) and Crowson (1961). Being interested in phylogenetic studies and zoogeography, I chose to deal with the world fauna of approximately 40 described species. After becoming suitably ensnared in the project, and still unable to polarize characters in any informative way, or even characterize the subfamily adequately, I realized it was based entirely upon symplesiomorphies. In an attempt to delimit monophyletic lineages within the psoines, I attempted to investigate the bostrichid subfamilies' relationships, using Anobiidae as the sister-group. An analogous situation soon developed, with polarizations yielding nonsensical non-patterns. In frustration, I went to the superfamily level, using Dermestoidea as my out-group, and began to see something was wrong when the Anobiidae came out within the bostrichid cladogram. Because the nosodendrids were difficult to place, I decided to look at the whole Bostrichiformia, using whatever beetles I could for an out-group. It was clear by then that existing classifications were not based on a monophyletic taxon concept, so I examined the literature
for polarizable characters useful at the highest taxonomic levels in the Coleoptera - the suborders, series, and superfamilies. I used these characters to build a provisional cladogram upon which my work in the Bostrichiformia could be based.

By this time I had almost forgotten what a psoine looked like. What follows is a reorganization of the families formerly included in Crowson's (1981) Bostrichiformia, the subfamilies formerly included in his Bostrichoidea, and a rather uneven treatment of tribes, genera, and/or species of the various subfamilies in his Bostrichidae.

The taxonomic changes proposed may seem radical, but I hope my reasons are put forth in an understandable and testable manner. I do not expect my phylogenetic hypotheses to stand unchallenged for long, but I hope it will be found to be an advance, albeit a small one, in the knowledge of beetle evolution.
INTRODUCTION

With nearly a half-million named species, and a very large number yet to be described, the beetles are the largest and most diverse order of animals documented. Although in progress well over 200 years, the documentation of this group has more recently been aimed at providing information on the evolution and phylogeny of the beetles, in addition to merely providing names and a classification. Attempts to bring to the classification information on phylogenetic descent are ongoing, and the subject of great interest to coleopterists (Ivie and Stribling, 1984).

Perhaps the first major attempt at achieving an evolutionary-based classification of beetles, and the last to revise the world genera of beetles, was that of Lacordaire (1854-1872). The impact of this monumental work, which predated Wallace and Darwin's discovery of evolutionary mechanisms, is still seen today. No doubt the excellence of this series greatly contributed to the excellence of French coleopterists that followed, including the first and only great bostrichidologist, Pierre Lesne (1871 - 1949) whose contributions made this work possible.
Modern attempts at phylogenetic beetle classification must be dated from the work of Böving and Craighead (1931) and its subsequent reexamination by Peyerimhoff (1933). It was from this starting point that the first truly comprehensive phylogenetic classificatory effort was made, by Roy Crowson, published in 1955. Although Crowson has without doubt contributed more to our knowledge of the evolutionary history of the Coleoptera than any other, his framework and subsequent refinements are more a starting point than an end in the search for the phylogeny of the Coleoptera.

With the availability of Hennig's techniques for discovering phylogeny, and the rapid improvement of these techniques, we can expect considerable progress in this search. However, even with these tools, the best we can hope for is steady improvement. Any hypothesized phylogeny, especially the one proposed here, must be considered merely provisional, subject to rigorous examination and testing, and in need of further refinement.

The order Coleoptera was divided by Crowson (1981) into 4 suborders. The group under study, the Bostrichiformia belongs to the largest of the suborders, the Polyphaga. With more than 90% of the beetle species, (Lawrence and Newton, 1982), this is a huge assemblage, which contains more species than all the non-arthropod
phyla of animals together (Villee, Walker and Barnes, 1978; Lawrence and Newton, 1982). I can claim no more than a passing knowledge of this group, and rely heavily upon the work of Crowson (1955 et esqq.), Lawrence (1982), and others cited in the text for information on character-states present in the majority of the coleopteran lineages. The group under study, the Bostrichiformia of Crowson, is a paraphyletic group, whose various lineages are among the most basal in the Polyphaga.

There are two conflicting evolutionary trends seen throughout the Coleoptera: reduction and adaptive novelty. Reduction is by far the more common, and least informative. Some structures, such as certain wing veins, are lost independently in virtually every major beetle lineage. The operative pathway for redundant reduction is obvious: if a morphological (or other) feature is not necessary for maximal reproductive success, the genetic accidents that result in its loss are not detrimental, assuming the character is not tied developmentally or otherwise to an advantageous one. Since the loss is not detrimental, it immediately becomes advantageous, since construction has an energetic cost, and it is one less structure to serve as a source of mortality, be it as a predator-handle, site of pathogenic attack, or opportunity for detrimental developmental accident. Convergent loss or reduction would
be predicted to occur more among species that share ecologic guilds, habitats or strategies than in phyletic lines. This would predict that loss or reduction would be a poor indicator of phylogeny. This is exactly the case, with loss of wing veins being most evident in small beetles, loss of eyes in litter and cave beetles, etc. Additionally, the systematist seeking phylogenetic information from character distribution must constantly be concerned about reversals of developmental mutations that caused the loss of expression of a character, but not the genetic information to construct it.

Adaptive novelties, on the other hand, are evolutionarily risky, and therefore rare in comparison. However, when an adaptive novelty is successfully obtained, it tends to be a very good indicator of phylogeny, as the advantage it imparts leads to evolutionary success, almost by definition. Examples of such adaptive novelties are the elytron for the entire Coleoptera, cryptonephridism in the higher Polyphaga, or pygidial defense glands in the Adephaga. These characters tend to be highly conservative; for example, the elytron has been totally lost in beetles that attain the adult condition in only a handful of cases: one dermestid and a few members of the Cantharoidea. Cryptonephridy has been lost several times, and in the way reductions are predicted: in species adapted to a common
situation, in this case they are aquatic or feed on material with unusually high water content.

These concepts should be kept in mind in the following discussions, as I have relied heavily upon them when making polarity and homology decisions.
MATERIALS AND METHODS

The materials utilized consisted mainly of preserved museum specimens, with live materials used when needed and available. Sources of material are listed in Appendix A. I have examined over half the species, and most of the genera of the bostrichids (sensu Crowson), and those directly relevant to the discussions that follow will be indicated at that time. I examined far fewer species of the other groups and these will be discussed where relevant.

Methodology of modern phylogenetics is well covered elsewhere (see for instance Wiley, 1981), and will not be reviewed here. My work is based on Hennig's principle that groups of common phylogeny can only be recognized by the presence of shared derived characters (synapomorphies), and that shared primitive characters (synaplesiomorphies) are uninformative for this purpose. Characters were polarized using out-group analysis, with an appreciation of the limitations of this method. Characters that indicate homoplasy were reexamined for homology problems in a simplified method derived from Michevich's (1982) useful, but unduly onerous and circular methods. These characters
were either resolved or discarded from the phylogenetic reconstruction. All such characters were dealt with under the operational assumptions described below, and each is discussed in the pertinent character discussions. Characters supporting hypothesized clades were actively sought, each then being examined as a test of preliminary hypotheses. The characters were weighted under the guidelines outlined below, and the resulting phylogenetic hypothesis was arrived at via a hand-fit procedure that incorporated admittedly a priori aspects. As far as possible, all sources of bias on my part will be discussed in the character discussions.

Although strict avoidance of a priori weighting of characters and final appeal to best-fit parsimony is regarded as the most scientific approach to phylogenetic reconstruction by many, I feel ts use at high levels is restricted to those who wish to construct a dendogram that most closely reflects character distribution, not evolutionary history.

To clarify the characters deemed phylogenetically informative, only those considered synapomorphic will be shown on the cladograms, with homoplasy indicated in the tabular data, and discussed, including the assumptions applied, in the character discussions.
Nomenclatorial decisions are based on two criteria: 1 – only groups which are hypothesized to meet the criteria of monophyly (*sensu* Haeckel) are suitable for formal taxonomic names; and, 2 – within the confines of 1 above and the International Code of Zoological Nomenclature (ICZN), the changes that will cause the least perturbation of the existing system, i.e. contribute most to nomenclatorial stability, are the most desirable.

Two operational assumptions are applied to decision-making in several areas of this paper, they are stated here for examination, and cited by number in the text below.

Operational assumption #1. When a character is generally distributed in its complex form throughout the Coleoptera or other higher groups, reduction is considered derived. However, reductions that occur widely, and in a step-wise sequence (such as loss of segments or wing veins) are over-ridden as synapomorphic and assumed convergent in a given case when in conflict with a novelty character. This is an extrapolation of, and special case of the out-group method.

Operational assumption #2. When examining homoplasy for character reevaluation, if a character-state known or hypothesized to be habitat-adaptive, especially if it is expressed in a reduction or in a variable manner, conflicts
with a structural novelty, the novelty will be considered homologous and the adaptive one convergent.
NOTE ON THE SPELLING, AUTHORSHIP, AND USAGE OF **BOSTRICHUS**.

The genus-group name **Bostrichus** is generally credited to Geoffroy (1762), a work rejected by the ICZN for not consistently using binomial nomenclature (Hemming, 1958). Sifverberg (1978) discussed the situation, and corrected the authorship of **Bostrichus** to Muller (1764). He found that validation of the genus (by first inclusion of a described species) was by Fabricius (1775), and the type species (**Dermestes capucinus** Linneaus) was designated by Latreille (1810), not Thomson (1859), as stated by Fisher (1950).

Anyone who delves into the literature on the bostrichids will very soon encounter differences in spelling of this genus-group name upon which the family name is based. **Bostrichus** Geoffroy contains an economically important species commonly spread in commerce, and has a large body of literature. This name has been used extensively in an emended form (**Bostrychus** Zoufal), which is an unjustified emendation under Article 33 of the ICZN. However, several authors, especially Europeans, continue to use the incorrect name. This is not a severe problem, as the two names are immediately recognizable synonyms,
however, the emended name has resulted in competitive spellings of the family-group name, although Article 29 of the ICZN is quite clear that Bostrichidae is the correct spelling. A glance through the literature section of this paper will reveal the scope of the problem.

I will use the correct spellings for both the generic, and the family-group names. A further problem comes with the name of the series. This taxonomic level is not bound by the proviso of Article 29 of the ICZN, and its first use by Crowson (1955) is with the spelling Bostrychiformia. It would appear that on the basis of priority, this spelling should be used for the series name. However, in the tradition of bostrichidology, and for the sake of consistency, I will use the series name spelled in agreement with the genus name.

Further, the emended name has been incorporated into the names of other genera by latter authors, and in those names, the "emended" form is the valid one, by original spelling.
ON THE ORIGIN OF THE BOSTRICHOIDEA (=BOSTRICHIFORMIA)

In order to examine the origin of the
Bostrichiformia, and clarify the phylogenetic relationships
of its member groups, a general understanding is needed of
the relationships of this series to the rest of the
Coleoptera. Crowson has repeatedly stated that his
Bostrichiformia is paraphyletic, suggesting that it
contained the ancestor of the cucujiform lineage (Crowson,
1959). The bostrichiforms contain member taxa that are
highly generalized, and retain pleiomorphic characters
lost in nearly all Polyphaga. An extensive overview of
beetle phylogeny is thus required for polarization
decisions, and constructing the resulting hypotheses of
phylogeny.

The relationships of Coleoptera suborders, series and
superfamilies have never been extensively examined and
published using Hennigian phylogenetic methods. Table 1
includes repolarized characters traditionally used in the
higher classification of the beetles. In nearly all cases,
these characters are reversed somewhere in the groups they
define, usually through reduction, and the cladogram that
results from these characters (fig. 2) cannot be considered
Table 1. Apomorphic Character States of Coleopteran Suborders and Series.

<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>Hind coxa fused to metasternum</td>
</tr>
<tr>
<td>2</td>
<td>Pygidial defense glands present</td>
</tr>
<tr>
<td>3</td>
<td>Larvae with mandibular mola</td>
</tr>
<tr>
<td>4</td>
<td>Loss of oblongum cell</td>
</tr>
<tr>
<td>5</td>
<td>Larva with 3-segmented antenna</td>
</tr>
<tr>
<td>6</td>
<td>Cryptopleuron movable, fused to trochantin</td>
</tr>
<tr>
<td>7</td>
<td>Loss of cubital hinge</td>
</tr>
<tr>
<td>8</td>
<td>Abdominal ganglia fused</td>
</tr>
<tr>
<td>9</td>
<td>Acrotrrophic ovaries</td>
</tr>
<tr>
<td>10</td>
<td>Five-segmented larval leg</td>
</tr>
<tr>
<td>11</td>
<td>Loss of notopleural suture</td>
</tr>
<tr>
<td>12</td>
<td>Loss of articulated urogomphi</td>
</tr>
<tr>
<td>13</td>
<td>Dermestoid male genitalia</td>
</tr>
<tr>
<td>13'</td>
<td>Cucujoid male genitalia</td>
</tr>
<tr>
<td>14</td>
<td>Hylecoetoid metendosternite</td>
</tr>
<tr>
<td>15</td>
<td>Cryptonephridism</td>
</tr>
<tr>
<td>16</td>
<td>Fused rhabdom</td>
</tr>
<tr>
<td>17</td>
<td>Nonexcavate metacoxa</td>
</tr>
<tr>
<td>18</td>
<td>Loss of spiracles on abdominal segment VIII</td>
</tr>
<tr>
<td>19</td>
<td>Apical portion of metathoracic wing rolled</td>
</tr>
<tr>
<td>20</td>
<td>Mandible with articulated preapical tooth</td>
</tr>
<tr>
<td>21</td>
<td>Maxilla lacking distinct galea</td>
</tr>
<tr>
<td>22</td>
<td>Obtec pupa</td>
</tr>
<tr>
<td>23</td>
<td>Pleurites IX confluent anterior to tergite</td>
</tr>
<tr>
<td>24</td>
<td>Paired ocelli on elevations adjacent to eyes</td>
</tr>
<tr>
<td>25</td>
<td>Derodontoid metendosternite</td>
</tr>
<tr>
<td>26</td>
<td>Modified cryptonephridism</td>
</tr>
</tbody>
</table>
Figure 1. Phylogenetic Hypothesis of Coleopteran Relationships. Numbers refer to characters in Table 1.
more than very preliminary. This cladogram is given to form a basis for my polarization of characters within the Bostrichiformia, and to clarify my decisions on placement of groups removed from it. Most of the information was extracted from the literature, and polarized by the criteria described below. I hope that the repeatability of the conclusions outlined below will make objective evaluation of my hypotheses easier, and encourage further research to be conducted and communicated in phylogenetic terms with a monophyletic taxon concept.

Whenever possible, out-group analysis was the basis of polarization. This was almost exclusively used within the Polyphaga, but was not always immediately possible at the higher levels. In these cases, if the distribution of the character in the Megaloptera is known (to me), the Megaloptera were used as out-group. In theory, the Strepsiptera should be used, as they constitute the hypothesized sister-group of the beetles (Kinzelbach, in press), but in virtually every character system they are so highly derived that they are very nearly uninformative for polarization decisions. The Neuroptera (sens. lat.) were chosen as out-group because they contain primoformic taxa, which seem to retain many Holometabola groundplan features (Hennig, 1981). Whether or not they are the sister-group of the Strepsiptera-Coleoptera is beyond the scope of this
study.

If the character is unique to the Coleoptera (as most are), a character state that involved reduction was considered derived. Once some order began to appear in the cladogram, based on those characters polarizable by out-group comparison with the Megaloptera, the very useful progressive restriction out-group analysis of Watrous and Wheeler (1981) was used. Characters that had been initially polarized by other criteria were reexamined in this way.

The major departure from previous hypotheses of phylogeny are in the branching sequence of the suborders. The resolution of these 4 taxa was necessary for polarization of wing, head, and other characters in the bostrichiforms, as the use of existing concepts led to very high levels of homoplasy when applied to bostrichiform character distributions.

By using the methods outlined above, I obtained a hypothesis of phylogeny that suggests the Adepaga are the sister-group of the other modern Coleoptera, with the Polyphaga the sister-group of the Archostemata + Myxophaga.

The choice between opposing opinions, such as the membership in the groups defined by the first clade, has sometimes been influenced by biological scenario. For instance, Crowson (1976, 1981) felt that the primitive
beetle was a subcortical fungivore, and the predatory habits of the Adephaga derived. This led him to hypothesize this habit for the Permian Arche coleoptera, and to state (1976: 52) that the essential separation of the Arche coleoptera from the modern Archostemata was the adoption of wood-boring habits. As far as I can see this is totally unsupported by any knowledge of the habits of the larvae or adults of the Arche coleoptera, or even a single larval character (described larvae of Arche coleoptera are unknown). It also ignored some possible synapomorphies of the modern suborders that preclude an origin of the Archostemata within the Arche coleoptera, and that indicate that wood boring is a derived habit in the Archostemata. All similarities of the Arche coleoptera and Archostemata are obvious symplesiomorphies, and thus useless for phylogenetic statements.

I find that the predacious habits of the Neuroptera (sens. lat.) and the aquatic habitat of the Megaloptera support the possibility of the riparian predatory Adephagan habit being plesiomorphic, with the subcortical fungivory-xylophagy of the Archostemata and Polyphaga apomorphic, and possibly synapomorphic.

The early "beetle" fossils (Permian) have been placed by some workers with the modern suborder Archostemata on the basis of elytral similarity. Kukalova (1969) has moved
several of these forms (Lower Permian) to another order, the Protelytroptera (=Protocoleoptera in part of Crowson, 1976, not of authors). Crowson (1976) erected the suborder Arche coleoptera for the Upper Permian fossil "beetles", concluding that there was no evidence to place any of them in modern suborders. As the characters I will use below are not available in the Permian fossils, I will not be able to discuss the placement of the fossil groups. I accept Kukalova's and Crowson's removal of these forms from a Recent Coleoptera that I will propose, as a working hypothesis, is monophyletic. For the purpose of phylogenetic analyses, I consider the Archostemata to include only the extant taxa.

The fossil record of extant families of Archostemata extends only to the Triassic (Lawrence and Newton, 1982, and Crowson, 1976, citing Ponomarenko, 1970). The earliest known fossils attributed to the Adephaga are members of the Triaplidae, Trachypacheidae (Lawrence and Newton, 1982), and Carabidae [Umko masia depressa Zeuner, (Hennig, 1981)] from the Middle Triassic. Ponomarenko (1970, cited by Crowson 1976) suggested that the Triassic Ademosynidae, formally placed in the Archostemata, could belong instead to the Polyphaga, while obvious members of the Polyphaga [Pelt osynidae, Elateroidea, Curculionoidea (Lawrence and Newton, 1982) and a species attributed to the Silphidae
[Pseudosilphites natalensis] Zeuner (Hennig, 1981)] are reported from the Middle Triassic. The Triassic Schizophoridae and Catiniidae, currently in the Archostemata, may represent Myxophaga (Lawrence and Newton, 1982).

Therefore no fossil evidence exists that would preclude various interpretations of the basal clades of the modern suborders of Coleoptera. It is often implied that the large numbers of archostematan fossils relative to others is evidence for that group's placement at the base of the Coleoptera. It is obvious that this is of no consequence, as the sister-group of the Archostemata must have been first present at the same time as the first archostematan, if the Archostemata are monophyletic. Further, the presence in the Triassic of all 4 suborders, including members of extant families for 3 of them, precludes ordination based on fossil evidence.

The question then is what is the basal clade of the modern Coleoptera? Few workers have dealt with this question from a monophyletic group definition. Crowson's view has changed from an Archostemata-Adephaga vs. Myxophaga-Polyphaga split (1976) to an unresolved trichotomy of Archostemata/Adephaga/Polyphaga + Myxophaga (1981). Ponomarenko (1973) suggests the Archostemata and Adephaga form a natural group, based on 3 supposedly
derived characters of the wing. Two of the 3 are reduction characters: the absence of a recurrent vein on the Rs, which is a common occurrence throughout the Coleoptera; and loss of fold B, which is replaced in a totally different manner in the 2 groups, suggesting nonhomology.

Ponomarenko's third character: presence of only 2 branches of the first anal vein, is the plesiomorphic condition in the Megaloptera (Glorioso, 1981), and therefore should be considered symplesiomorphic in the Coleoptera. Additionally, the three branched 1A condition in the Polyphaga exists as at least 2 non-homologous characters: the third branch arising on the 1A₁ [as in Cebrio (Cebrionidae)], or on the 1A₂ [as in Attagenyus (Dermestidae)]. (Terminology of wing venation follows Ponomarenko, 1973.)

Lawrence and Newton (1982) discussed the problem of suborder relationships, but offered no solution. Other classifications that have placed the Adephaga and Archostemata together also rely on symplesiomorphies, such as the 6 segmented larval leg, presence of the oblongum cell in the hind wing, and presence of the notopleural suture.

Larval similarity between the Adephaga and Megaloptera-Neuroptera suggested reexamination of larval characters. The adephagan lineage has been defined by the
loss of the mandibular mola in the larvae. However, the megalopteran larvae, and in fact all neuropteran (sens. lat.) larvae that I am aware of, lack this character. Changing the polarization of this character would link the Archostemata and Myxophaga with the Polyphaga, on the basis of the synapomorphy of the mandibular mola in the larvae.

With the Adephaga hypothesized as the sister-group of the rest of the modern Coleoptera, I turned my attention to the next clade. Two characters often employed at this level that exhibit no clear pattern are number of larval leg segments and the presence of articulated urogomphi. For the first, it seems that the 6 segmented condition in the Adephaga and Archostemata has always been considered the primitive condition, and its presence in the Megaloptera confirms this polarization. However, it seems likely that the reduced number of leg segments in the Polyphaga and Myxophaga may be nonhomologous, and due to convergence. Evidence for this tendency toward independent reduction is found in the 5 segmented leg of the last instar larva of Cupes (Crowson, 1962), and the various conditions found in the Micromalthus heteromorphic larvae. The small size of the modern species of Myxophaga lends itself to reductions, and there seems no way to link the Myxophaga with the Polyphaga to the exclusion of the other suborders, except by this character, which would impose
reversals in other places. In general, the habitus of the nonadephagan groups' larvae agree, and the 3 suborders seem well supported as monophyletic groups. Therefore, I do not consider reduction in the number of larval leg segments informative as a synapomorphy above the subordinal level (assumption #1).

The other character that required examination at the subbasal clade of the Coleoptera is the presence of articulated urogomphi in the larvae. This character is present in the Megaloptera, the Adephtag, Myxophaga, and Staphyliniformia, and is undoubtedly plesiomorphic. Crowson's suggestion (1959) that the articulated urogomphi of the Staphyliniformia may be a secondary novelty seems based only on convenience. It is absent in the Archostemata and the non-staphyliniform Polyphaga. Again ecological factors enter my analysis in suggesting nonhomology of reduction. The known larvae of the Archostemata are wood-borers. The larval form is remarkably similar to wood-borers in other groups, and lacks complex terminal structures. Other wood-boring taxa belonging to groups that have urogomphi, such as the Rhysodidae (Adephtag), lack these structures. Even in the non-staphyliniform Polyphaga, where non-articulated urogomphi are common, the norm is for wood boring groups to lack them. This loss even occurs within families, such as
the zopherids, elaterids, and cerambycids. It therefore seems logical that the articulated urogomphi are plesiomorphic for the Coleoptera, and that they have been lost independently several times. This reduction is hypothesized to be synapomorphic for the Archostemata, although the case is rather weak.

The placement of the Myxophaga is also a problem. Reichardt (1973a) gave by far the best account of this group, which is defined by the synapomorphies of an obtect pupa, the maxillae lacking a galea, and the mandible with an articulated preapical tooth. These characters are associated with the aquatic habitat and/or with algal feeding common to the Myxophaga. The larvae have a mandibular mola, and thus are placed in the Archostemata-Polyphaga lineage. If the rolled apex of the wing is taken as derived, the Myxophaga would be considered the sister-group of the Archostemata. Here the Upper Permian beetle wing illustrated by Ponomarenko (1973) is useful for polarization. This wing fossil shows no sign of a rolled apical portion, and also lacks the special features of the Adephagan wing (although its folding pattern seems to me to be most like the adephagan pattern). It seems reasonable that the rolled wing is synapomorphic [rolled wings do occur in the Polyphaga (R. S. Miller, pers. com.) but not necessarily of the same type] for the 2 suborders. The
smooth elytra and round body form of the Myxophaga is a great deal different from the form of the Archostemata, but this is obviously adaptive for a group of beetles that lives in water, especially those groups that live in fast running water (Reichardt, 1973).

A character that may oppose this scheme is the form of the testes. I can find no information on the testes of the Megaloptera, and Lawrence and Newton (1982) throw doubt on the type exhibited in the Archostemata, but Crowson (1955) reports tubular testes link the Archostemata and Adephaga. Although this character seems unique to the Coleoptera (Chapman, 1969), in the Adephaga at least it seems to be a reduction of follicle numbers to 1 (Chapman, 1982), and so falls under assumption #1. However, this character is poorly studied outside the Adephaga, and deserves further examination.

It is not the purpose of the cladogram presented to resolve all clades. I fully expect that the cucujiforms that have lost the functional VIII spiracle and the trichotomy in the lower Polyphaga are resolvable. However, it is beyond the needs of the present study to introduce my views on these subjects.

The clade that defines the higher Polyphaga remains weakly supported. Although it is accepted by most students of beetle evolution, I can find no polarizable,
nontransformed character to support it. The fact that this lineage includes over 90 families and more than half the described beetles, made it impossible for me to seek new data to resolve the clade during this study. However, a hypothesis of monophyly, based on the opinions of Crowson (1959), Lawrence and Newton (1982), and others, was used as an initial hypothesis for the lineage. Based on Crowson's (1955, 1959) suggestion that the cucujoid aedeagus could be derived from the dermestoid condition, and noticing the paraphyletic distribution of the dermestoid external genitalia (sensu Tandon, 1970), I suggest that a homologous transformation series of dermestoid to cucujoid states exists. This would make the character synapomorphic for the higher Polyphaga, with the transformed cucujid state synapomorphic for the 5 apical superfamilies.

The recognition of the Derodontoidea was first put forth by Crowson (1944), although he later (1955, 1959, 1981) abandoned it in favor of an admittedly paraphyletic Dermestoidea. Lawrence and Newton (1982), seeking a classification based on monophyletic taxa, have recently revived the Derodontoidea, as suggested by Lawrence and Hlavac (1979). They included the Dermestidae in the Bostrichoidea, which is implied to have an undefined special relationship with the Derodontoidea (=Bostrichiformia of Crowson).
I hypothesize a sister-group relationship between the Derodontidae and the group I will informally call the cryptonephridiformia. The synapomorphy for the latter group is the development of cryptonephridy. This condition does occur in other groups, including lepidopteran larvae, scarabs, and buprestids. However, Saini (1964) showed these other types to be significantly different in structure from that of the cryptonephridiformia, and I consider these others nonhomologous (assumption #2).

Thus the special relationship of the Derodontoida and Bostrichoidea is based on symplesiomorphies. This renders the Bostrichiformia of Crowson paraphyletic, necessitating a change in the composition of series.

The urge to reduce the number of names suggests that all of what I call the higher Polyphaga be called Cucujiformia, but to do so would not only submerge the very well-supported Cucujiformia of current usage, but would give formal status to a group with no un-transformed synapomorphy. The next most reductionist choice would be to recognize the single family series Derodontiformia and recognize what I call the cryptonephridiformia as Series Cucujiformia. This may be the best choice in the long run, although it is still less well supported by synapomorphies than the current Cucujiformia. I have chosen to recognize 3 series in the higher Polyphaga - Derodontiformia,
Bostrichiformia, and Cucujiformia. This is done mainly because it causes the least nomenclatorial change (one new series vs. one new, one synonymized) while maintaining groups defined by synapomorphies.

In the discussion below, the names Bostrichiformia (=Bostrichoidea mihi), Bostrichoidea [Bostrichoidea plus Dermestoidea of Crowson (1981), minus Derodontidae and Jacobsoniidae], and Bostrichidae (former Anobiidae, Ptinidae, Lyctidae, Psoidae, and Bostrichidae, minus the Endecatomidae) are used in the new sense (evidence for the combination of groups included in the Bostrichidae will be presented under that family). Dermestidae is used in the sense of Lawrence (1982) to include Thorictidae and Thylodriidae, but the Orphilinae are moved to the Nosodendridae. The "bostrichid lineage" is meant to include the Endecatomidae and Bostrichidae mihi, and the "dermestid lineage" includes the Dermestidae and Nosodendridae. Derodontiformia (=Derodontoidea mihi) is limited to the Derodontidae.

Lawrence and Newton (1982) placed 3 families in their Derodontiformia - Derodontidae, Jacobsoniidae, and Nosodendridae. The Jacobsoniidae are moved to the Cucujiformia because of the hylocetoid metendosternite (Crowson 1959), having been placed in the Derodontoidea on the basis of functional spiracles on the VIII sternite and
the dermestoid aedeagus, both sympleiomorphies. The loss
of functional spiracles on VII separates the rest of the
Cucujiformia as the hypothesized sister-group of the
Jacobsoniidae. This necessitates recognizing the family as
a superfamily, to maintain taxa hypothesized as
monophyletic. The final placement of the Jacobsoniidae is
far from settled, as I have seen no specimens, and the
condition of the malpighian tubules and rhabdom is unknown.
I will predict, however, based on the published
information, that the malpighian tubules will be found to
exhibit unmodified cryptonephridism, and that the eye will
have fused rhabdoms. The Jacobsonoidea is placed in the
cladogram as if these predictions were the case, to avoid
indicating that they are known to be absent. I expecte
that the possibility of proving me wrong will be more
motivating to those with access to living specimens of
these taxa than it would be to simply move the character as
I suggest.

The Nosodendridae are moved to the Bostrichoidea, as
I consider the character used to place it in the
Derodontoidea of Lawrence and Newton (1982) (free
malpighian tubules) to be convergence. I will discuss the
relationships of the nosodendrids more fully in the
discussion of bostrichoid phylogeny.

This leaves only the Derodontidae in the
series/superfamily. The most evident synapomorphy for the group is the placement of the paired ocelli on elevations adjacent to the eyes. The presence of the ocelli themselves is probably plesiomorphic, as ocelli occur in other Coleoptera both above and below the derodontiform clade, but the placement is unique, and undoubtedly homologous. Other possible synapomorphies — short abdomen, reduced wing venation, and peculiar wing folding — are all reduction characters, difficult to homologize with any certainty.

Lawrence and Hlavac (1979) discuss the ground plan of the family, and the problems of polarizing characters within the family, proposing 3 alternative hypotheses of phylogeny for derodontid genera (cladograms A, B, C, pg 394). Based upon the polarizations drawn from my cladogram, I feel Lawrence and Hlavac understate support for their cladogram C (their preferred choice).

First, I disagree that the concealed antennal insertions of *Pelastica* are autapomorphic. The degree of development may well be so, but the presence of this character in the Cupedidae, Adephaga, lower Polyphaga, and cryptonephridiformia suggests it is primitive. In the Bostrichiformia, its presence is the rule in the bostrichid lineage. Given this type of polarization choice, I feel independent loss more likely than multiple independent
origin of a novelty character (assumption #1). Thus the exposed condition of the other 3 genera can be considered synapomorphic.

Lawrence and Hlavac's assertion that cladogram C requires independent origin of head canals in *Derodontus* and *Nothoderodontus* is inconsistent with the presence of homologous head pores on *Laricobius*. It is easily conceivable that *Laricobius* has lost the canals and bridges as an apomorphy, possibly due to its adoption of surface habitats. The degree of differentiation in the expression of the character in the 3 genera results in transformed states being autapomorphic for each of the genera, but this is not inconsistent with the degree of overall change between the lineages, and in no way supports the hypothesis of nonhomology for these structures. The other suggested convergences were apparently not examined for evidence of being secondarily reversed synapomorphies.
PHYLOGENY OF THE BOSTRICHIFORMIA

Crowson (1981) dated the origin of the
Bostrichiformia to the upper Triassic, moved back from the
beginning of the lower Jurassic in his 1976 paper. He gave
no examples of fossil bostrichiforms older than the
Oligocene, although he indicated both dermestid and
bostrichid lineage forms from that period. Larsson (1978)
lists members of the Dinoderinae, Anobiinae, and Ptinini
from Danish Amber, and implied a bostrichine from the same.
Bachofen-Echt (1949) shows a photo of a bostrichine in
amber, presumably Baltic in origin. These ambers date from
the Eo-Oligocene boundary (Larrson, 1978). Dunstan (1923)
described 2 genera and 5 species of dermestids from the
Mesozoic of Queensland. Thus the bostrichid subfamilies
were well differentiated in the Tertiary, and the
dermestid-bostrichid split was complete in the Mesozoic.

Lawrence and Blavac (1979) stated that Ponomarenko
(1973) implied the existence of fossil derodontids from the
early Jurassic. If the derodontids are monophyletic, their
sister-clade, the cryptonephridiformia, must have been
present during that period. Crowson (1976) dated the rich
cucujiform fossils of the Kara Tau to the beginning of the
early Cretaceous (considered Jurassic by Ponomarenko),
which would give a minimum age for the sister-clade Bostrichiformia. Although I see no strong evidence to tie the origin of the bostrichiforms to any particular epoch, neither do I see any data refuting Crowson's hypothesis. Suffice it to say that the Bostrichiformia must have been evolving independently before the Cretaceous, and possibly as early as the Triassic. Occurrence of native members of 3 of the 4 bostrichiform families on all major pieces of Pangaea (except Greenland and Antarctica) supports the dating of the lineage to the Triassic-Jurassic interface, or earlier.

The general characters of the most recent common ancestor of the Bostrichiformia can be hypothesized by a compilation of the plesiomorphic characters as polarized for use in the phylogenetic reconstruction of the member-groups of the Bostrichiformia. The ancestor was most likely descended from a species similar to the general characters of the Derodontidae, although all extant genera of derodontids are highly derived, and none can be considered to approximate the bostrichiform ancestor.

Based on my analysis, I suggest that the ground plan for the series included the following features: Head - hypognathus; antenna 11-segmented with a 3-segmented club. Thorax - tarsi 5-5-5; tibia slender, with spurs; procoxa transverse and approximate, possibly with exposed
trochantins; pleurosternal suture present; procoxal cavity open externally behind; prosternum with a very short intercoxal process; pronotum with complete, possibly denticulate, lateral margin; mesocoxa large and broadly open laterally, meeting mesepimeron and metepisternum; elytron with a scutellary striole; relatively complex wing venation of the dascilloid type; medial and transverse sutures of metasternum present; excavate hind coxa. Abdomen - abdomen with sclerotized remnant of sternite II; abdomen with functional spiracles on VIII; abdominal segment IX with complete sternite and divided tergite; abdominal segment X present; male genitalia of dermestoid type; modified cryptonephridiform malpighian tubules, with all 6 attached on one side, in bundles of 2 and 4, with the crytonephridic sac displaced to one side of the gut for most of its length, and not reassociliated with the ascending hind gut. Larva - campodeiform; mandible with accessory ventral process, tuberculate mola and prosthoea; maxilla with distinct galea and lacinia; epipharyngeal, cibarial, and hypopharyngeal armature well developed; tarsungulus with 2 setae; spiracles with closing apparatus; tenth segment well developed.

Evolution of the Bostrichiform families.

From a natural history point of view, the major evolutionary development in the Polyphaga between the
derodontiform clade and the bostrichiform clade was the development of cryptonephridism. This synapomorphy allowed the cryptonephridiforms to exploit drier food sources and habitats.

The modified cryptonephridism that unites the Bostrichoidea (hypothesized to be secondarily lost in the Nosodendridae) seems tied to very efficient utilization of water (Saini 1964), and is hypothesized to have predisposed the ancestral bostrichiform to exploiting very dry food resources.

My hypothesis of phylogenetic relationships between the major groups of bostrichiforms can be see in the cladogram in fig. 2. This cladogram is based on the characters and polarizations in Table 2. Specific characters, and incidences of homoplasy and their resolution are discussed in the character discussions and under specific taxa.

I hypothesize the bostrichiform ancestor was a fungal-feeding, subcortical or surface active grazer. The major novelty of the bostrichid lineage involved the change from the plesiomorphic externally feeding campodeiform larvae to an internally feeding scarabaeiform one, and the changes in adult structure that correlate with this.

The fungivorous *Endecatomus*, whose larvae feed internally on woody fungi, seem to represent an early
Table 2. Apomorphic Character States of Bostrichiform Families.

| 1. Modified cryptonephridism |
| 2. Head hypognathous |
| 3. Single median ocellus |
| 4. Antennal fossa on hypomeron |
| 5. Internal sternal plates on abdominal segments III & IV |
| 6. Prolegs with tibia anterior in repose |
| 7. Procoxal plates posterior to trochanter |
| 8. Procoxa conical |
| 9. Metacoxa shorter than femur |
| 10. Modified larval setae |
| 11. Abdomin with margining carina |
| 12. Head reflexed, with excavate procoxae |
| 13. Body ventrally flattened |
| 14. Antennomere 3 very long |
| 15. Abdominal sterna with tarsal grooves |
| 16. Mentum expanded and plate-like |
| 17. Prosternum without intercoxal piece |
| 18. Head prognathous |
| 19. Pleurosternal suture obsolete |
| 20. Bostrichoid metendosternite |
| 21. Metacoxa compressed |
| 22. Larva C-shaped |
| 23. Procoxal cavities rounded externally |
| 24. Elytra with setose tubercles, recticulate |
| 25. Lateral margin of pronotum with projecting setae |
| 26. Larval mandible transversely tridentate |
| 27. Larval head retracted (transformed) |
| 28. Larva unable to walk on surface |
Figure 2. Phylogenetic Hypothesis of Bostrichiformi Relationships. Numbers refer to Characters in Table 2.
stage of evolution on the bostrichid lineage. They retain the ancestral ability to leave the host and crawl on the substrate. As far as I know, no bostrichid larva can crawl in the open, the internal feeding C-shaped adaptation being total. From the habitat of *Endecatomus* to true wood boring in the basal bostrichids, and on into utilization of seeds, plant detritus, and even back to fungi in the anobiines seems a logical, tidy, scenario, and similar to the situation in the Scolytidae.

The dermestid lineage as a whole remains more primoformic, the major adaptive apomorphies being discovered at the family-level clade.

The move from surface or subcortical fungal grazing to feeding on fungi associated with dead animal matter seems a likely scenario for the dermestids. The inexact knowledge of the larval habits of the orphiline nosodendrids hinders the understanding of this lineage, as all that is apparently known is that the larvae have been found in an oak log in Algeria (Paulian, 1943). The very highly modified larvae of nosodendrines in relation to the more generalized orphelines indicate to me that the sap flow habitat of nosodendrines is not the ancestral one.

**Key to the families of Bostrichiformia**

(Adults of the dermestid genera *Thylodrias* and *Thorictes* will key imperfectly below. To make the key work for these
genera, numerous exceptions would be needed that would greatly increase the length of the couplets. It is unlikely that anyone would recognize adults of either of these genera as bostrichiforms, except by recognition of the genera themselves. Characters for recognizing these genera are presented in the discussion under the Dermestidae below.)

Adults

1. Hypomeron variously excavate to receive antennal club in repose; pleurosternal suture present, with a notch where this suture joins procoxal cavity; antenna with a somewhat rounded, compact 1-3 segmented club; metacoxa excavate; metatrochanter slightly to very obliquely attached to mesofemur..............................2

1'. Hypomeron without excavations to receive antennal club in repose; pleurosternal suture obsolete, procoxal cavities rounded antero-laterally; antennal club usually loose, asymmetrical, with 3-4 segments, if with a 2-3 segmented compact, symmetrical club, metacoxa flat, if metacoxa excavate, metatrochanters squarely attached to femur.................................3

2. Metacoxa subequal in length to femur, reaching, or very nearly reaching elytral edge; antennal club covered by proleg in retracted position; proleg with tibia anterior to femur in retracted position; all Malpighian
tubules free; abdominal sternite III and IV with internal plates at junction; procoxae very transverse

..................................................Nosodendridae

2'. Metacoxa shorter than femur, separated from elytra by mesepisternum, which reaches abdomen; antennal club not covered by leg in retracted position; proleg with tibia posterior to femur in fully retracted position; Malphigian tubules modified cryptonephridic; abdominal sternites III and IV without internal plates......................................Dermestidae

3. Pronotum with explanate lateral margins, with row of projecting straight or recurved setae; elytra with unisteose microtubercles arranged in an irregular, rectiulate pattern with smooth areas between..........

..................................................Endecatomidae

3'. Pronotum with or without distinct lateral margins, but margin not explanate; elytra smooth, tuberculate, punctate, or rugose, not as above...........Bostrichidae

Larvae

1. C-shaped and grublike (scarabaeiform).................2

1'. Elongate, more or less dorso-ventrally parallel (campodeiform)........................................3

2. Head fully exserted; maxillary palpus 4 segmented; antenna 3 segmented; mandible scoop-shaped, with 3 apical teeth transversely arraigned........Endecatomidae
2'. Head retracted, or if fully exerted, maxillary palpus 2 or 3 segmented* and antenna 1 or 2 segmented; mandible not as above..........................Bostrichidae
3. Setae simple....................................Nosodendridae
3'. At least some setae modified, clubed, spear-shaped, spatulate, etc..........................Dermestidae

Character discussion.

Some characters used in the phylogenetic hypothesis are self explanatory; others, discussed below, are more complicated, and require comment.

HEAD and PROTHORAX. The plesiomorphic position of the bostrichiform head is difficult to ascertain. There is so much plasticity in this character within the Coleoptera that out-group analysis is useless. Looking at primoformic taxa, I suggest that the hypognathous condition of Dermestes and Endecatominus is perhaps plesiomorphic. The somewhat deflexed head in these groups is relatively non-specialized, and yet could easily give rise to the deflexed head of the other dermestids, anobiines and Orphiilinae, the rigidly hypognathous head of the bostrichines and dinoferines, and the prognathous condition of the

* Lawrence (1982) reported occasional anobiine larvae with 4 segmented maxillary palpi, but I have seen no specific report of this.
nosodendrines, dysidines and others. This character is not used extensively in my analyses because of the apparent convergence problems.

Similarly, the form of the prothorax is not extensively used. Crowson (1955) coined the name bostrichoid prothorax for the hood-like prothorax of his Bostrichoidea. I prefer to use this term for the thorax with the pleurosternal suture obsolete, feeling it is better defined, and lessens the problems of interpreting convergence of pronotal form. There is a certain gestalt-based similarity to the bostrichiform prothorax, but nothing that I can define as a character. Therefore this condition will not be used, although others might consider it a synapomorphy for the Bostrichiformia.

A deflexed head has originated several times in the series, taking 2 broad forms: a rigidly deflexed head as in the bostrichines and dinoderines, and a flexible form, as in the Euderini, Anobiinae, Dermestidae, and Orphilineae.

The rigidly deflexed head and associated cowled pronotal form of the Bostrichinae and Dinoderinae are deceivingly similar. The similarity is considered convergence. Several characters of the wing, leg, and larva support this conclusion. Perhaps the deflexed head in these groups is associated with modification of the oviposition site by the adult female. Several bostrichines
are known to chew holes for oviposition, the most famous being the lead cable borer (*Scobicia declivus* LeConte). *Apate* spp. construct a gallery in a branch, then oviposit in it. The weakened branch breaks in the wind, providing dying wood for the developing larvae (Wolcott, 1951). I am unaware of any similar behavior in the Dinoderinae, but it seems possible.

It may also be that the rigidly deflexed head allows better pressure to be brought to bear when biting wood while inside the gallery. It is most interesting that the sister-group pairs Bostrichinae-Polycaoninae and Dinoderinae-Lyctinae each have one member with widely separate procoxae and the other with a deflexed head and cowled pronotum. It is possible that these nonhomologous adaptations all serve the same function.

The flexibly deflexed head is apparently involved in protection of the mouthparts and antennae in a contractile habitus. Since the general contractile condition involves several associated characters of the head and prothorax, they will be discussed together.

In the nosodendrids, dermestids, and anobiines, the tendency has been toward a tightly contractile form. All primoformic bostrichoids are somewhat retractile in form, and the degree of development in these 3 groups merely involves extremes of the ancestral condition. In all 3
cases, this has resulted in protection of the legs, antennae and mouthparts, yet although the results have been similar, all 3 groups have achieved them via different pathways, as evidenced by several fundamental differences in the ways in which this protection was achieved.

The dermestids and nosodendrids can be separated from the anobiines by the presence of excavations for the anteninal club on the hypomera. In the higher anobiines, the antennae are protected by the relexed head, but in these cases the club is held in a space between the mouthparts and procoxae, not in hypomeral excavations.

Within the dermestid lineage, the retractile forms are of two sorts. The plesiomorphic condition is retained by the Dermestinae, with the legs and sterna not greatly modified. The dermestis that are highly contractile, such as the Anthreninae, retain the pleisomorphic position of the prolegs in retraction (tibia posterior to femur) (fig. 3), and the mouthparts are protected by an expansion of the prosternum. The antennae are received in margined, but externally exposed fossae.

In the Nosodendridae, the same general facies occurs, but in a totally different manner (fig. 4). The plesiomorphic condition of the prolegs in repose is with the tibia posterior to the femur (fig. 4), the apomorphic with the tibia anterior to the femur (fig. 3). The
Figure 3. *Attagenius* sp. (Deremestidae), ventral view.
Figure 4. *Nosodendron* sp. (Nosodendridae), ventral view.
nosodendrids exhibit this latter condition as a synapomorphy, with the prolegs protecting the antennal club lying in the hypomeral excavations.

The nosodendrid mouthparts are protected in two different ways, neither homologous to the expanded prosternum of the dermestids. The problem to be solved appears to be how to keep the antennal club covered by the prolegs, and at the same time, protect the mouthparts. In the nosodendrines the submentum is enlarged and plate-like, covering the mouthparts below the mandibles. In the orphelines, the head is flexibly deflexed but unlike the dermestids where it is in contact with the prosternum, the orphiline head is directly in contact with the procoxae, which are excavate to receive it.

In the anobiines that are highly retractile, the mouthparts cover the procoxae and the antennae either pass posteriorly between them, or are held in excavations on the under side of the head and prosternum, immediatly before the procoxae.

The post-trochanteral plates of the nosodendrid procoxae are synapomorphic, but seem tied to the anterior rotation of the retracted prolegs. These plates are extensions of the coxae, posterior to the trochanter and medial to the base of the femur. They form a flattened plate postero-medial to the trochanter-femur junction (fig.
3). These plates are of remarkably similar form in the two subfamilies. Other beetles that exhibit the tibia-anterior retractile condition are variable in the presence of analagous plates: they are absent in the Monommidae, but present in the Chelonariidae.

The plesiomorphic condition of the procoxa is strongly transverse, with the narrowed ovoid dermestid procoxa and the narrowed, triangularly conical bostichid lineage procoxa differing in form and relation to the shape of the procoxal cavities. These two conditions, although further modified in the higher bostrichids, are not considered homologous.

The shape of the procoxal cavities differ as a result of the presence of the pleurosternal suture in the dermestid lineage, the plesiomorphic condition, as opposed to its synapomorphic obsolescence in the bostrichid lineage. In the dermestid lineage, there is a notch where this suture joins the procoxal cavity, while in the bostrichid lineage the cavity is rounded at that point.

OCELLUS. A pair of ocelli is apparently plesiomorphic for the Polyphaga, being found in the staphyliniforms and derodontiforms. Crowson (1955) suggests that the single median ocellus in the dermestid lineage originated from the fusion of the pair retained in the derodontids. The problem with this scenerio is, do I treat the single
ocellus, which is definitely a derived state, as a synapomorphy for the bostrichiforms, which is then lost in the bostrichid lineage, or as a synapomorphy for the 2 families in the dermestid lineage? To choose the first is to indicate a level of knowledge which cannot be tested, and for which no informational support exists. To choose the latter requires that I either consider the ocellus a de novo synapomorphy, or homologize it with the derodontid ocelli. Because ocelli are unknown in the sister-clade of the Bostrichiformia, and because a single median ocellus is exclusive to the dermestid lineage, I choose to consider lack of ocelli plesiomorphic within the series, and the median ocellus a de novo synapomorphy. The other choice requires hypothesizing a crytponephridiform ancestor with a pair of ocelli, which are independently lost in the bostrichid and cucujiform lineages, and fused in the dermestid lineage, with no taxon retaining the plesiomorphic condition. This seems to me to be just too much scenario for the evidence.

The median ocellus has been lost several times in the dermestid lineage, in the Nosodendrinae, Dermestinae, Thorictinae, and in some very small species of other dermestid subfamilies. These occurrences all seem independent, based on character correlation (assumption #1).
ANTENNA. The number of antennomeres varies from 3 to 11 in the bostrichid lineage, the minimum exhibited by myrmecophilous ptinine anobiines. Eleven is considered pleisiomorphic in all lineages at the subfamily level and higher.

Many genera exhibit variability in this character, with Polycacoon and Melalgus both having 9, 10, and 11 segmented member species. Some Xyloperthini (Bostrichinae) have been seen that have a different number of antennomeres on the left and right sides of the same specimen. Thus, number of antennal segments is considered a weak character.

The number of segments in the club also varies within this group. The pleisiomorphic number is 3, with 4 occurring independently in the Bostrichinae and Psoinae, 2 in most lyctines, and nearly all possibilities in the Anobiinae. This is also considered a plastic character system, and is not widely used in my reconstruction.

The micromorphology of the sensory structures on the antennal club undoubtedly hold characters of great phylogenetic interest, but must await accumulation of enough expendable material and dollars, so that the SEM work needed for both survey and documentation work can be accomplished.
PRONOTUM. Complete lateral margins on the pronotum are considered plesiomorphic. This condition occurs in the Derodontidae, all the non-bostrichid bostrichoids, the Dascilloidea, and Lymexylonoidea. No matter which is used as the out-group, this polarization results. Some type of lateral margins is indicated in at least some members of the Bostrichinae, Dinoderinae, Psoinae, Lyctinae, and Anobiinae. The Dysidinae, the majority of the Psoinae and most Bostrichinae have lost all trace of lateral margins.

The plesiomorphic prothorax was probably narrowed anteriorly, with the widest point at, or near, the base. This is the condition of nearly all the out-group possibilities, as well as the Endecatomidae, Dermestidae and Nosdendridae.

PROSTERNUM. To interpret prosternal structures in the bostrichid lineage, it is necessary to understand the origin of the various structures. I will use the terminology of Doyen (1966) in the following discussion. The endecatomid-type prosternum is considered plesiomorphic. It has the procoxal cavities closed internally by the connection of the internal postcoxal closures with the sternellum, the coxae approximate, and a short, acute prosternal process arising from the basisternum and free at the tip. No matter if the out-group is the Dermestidae, Dascilloidea, or Lymexylonoidea,
this polarization is supported. This condition is found in the majority of the genera of bostrichids in a remarkably uniform state.

From this primitive condition there are two directions taken in the bostrichids, which externally look alike. One is the lengthening of the prosternal process, seen in Coccographis (Psoinae), and to a greater extent in the Polycaoninae, where it reaches the mesosternum, and is slightly expanded. In these cases, the process is free at the tip from the internal postcoxal closures and the sternellum. The other direction is the loss of this process altogether, with a resulting exposure of the sternellum as a wide concave area behind a more or less obvious transverse carina running at the anterior level of the procoxae. This carina is all that is left of the prosternal process in Chilenius (Psoinae) and Euderia (Euderiiinae). The wide intercoxal process of the Lyctinae is homologous with this condition, as the process is derived from the sternellum, is continuous with it for its entire length, and is attached to the internal closures.

Most of these modifications are associated with a widening of the distance between the procoxae. In Polycaon, Melalgus, and Lyctus, it appears associated with a general widening of the prothorax, perhaps for greater strength in obtaining purchase in the tunnel, increasing
biting ability. This condition does not appear in the wood-boring groups with a deflexed head, where other mechanisms to achieve the same end may occur.

In Euderia this width between the coxae is associated with the antennae passing between the procoxae when the deflexible head is in repose. This is analogous with, and perhaps homologous with, the same condition in some anobiines.

In Chilenius the procoxae are approximate, and with no knowledge of the biology of the genus, I can make no guess as to the functional significance of the loss of the prosternal process.

ELYTRA. Synapomorphies in the elytra appear limited to the subfamily groups, and are of less use in grouping subfamilies. Endecatomidae is tightly held together by the microtuberculate elytra.

Lateral margins on the apical declivity and associated ornamentation of the elytra occur in the Bostrichinae, Dinoderinae, and Polycaroninae. In all these groups there are genera that lack these structures, and ones where they appear only in males. Analogous structures occur in other wood-boring groups, notably the Platypodidae and Scolytidae. It appears that these structures have arisen at least 3 times independently in the bostrichid lineage. Perhaps there is a predisposition to its development, as in
most cases at least the lateral margin appears in a relatively constant position.

METACOXAE. The excavate hind coxae of Anobiinae are considered autapomorphic, and not homologous with those of the dermestid lineage. In the dermestid lineage the coxal carina continues across the trochanteral insertion to the medial edge of the coxa. This carina, which follows the caudo-dorsal edge in the derodontids, dermestids and nosodendrids either as a flange in the last 2 or as a simple carina in the derodontids, is homologous with a similarly located carina in the Endecatomidae, Dysidinae, Euderiiinae, etc.

It seems best to consider the completely carinate and excavate coxa as plesiomorphic for the Bostrichoidea, with the coxa then synapomorphically compressed in the bostrichid lineage. The flange in the excavate anobiine coxa starts laterad of the trochanteral insertion. This seems easier to derive from the carina on the compressed, flattened coxa of *Euderia* than the flange that extends across the trochanteral insertion in the dermestid lineage. In the anobiines the trochanteral insertion ends the flange, with a notch above the insertion. The coxae are also shaped like the normal bostrichid coxa. The next character supports this view of nonhomology between dermestid lineage and anobiine excavate coxae.
METATROCHANTER. In bostrichoidea, the normal condition is the hind trochanters oblique to the femur. This state, also present in the derodontids, dermestids and nosodendrids, is considered plesiomorphic. The anobiines and euderiiines have the trochanters square to the femur, and long, a state considered synapomorphic.

HIND WING. Wing venation has turned out to be one of the most useful characters discovered in this phylogenetic reconstruction. It has also been one of the hardest to polarize. *Apoleon edax* (Dysidinae) shows the most complete venation in the bostrichid lineage, although *Dysides* has some plesiomorphic states not present in *Apoleon*. These wings show characters that necessitated considerable investigation to polarize. The out-groups used included the Cupedidae, Dascillidae, Lymexyloidae, Tenebrionoidea, Cleroidea, and Adephaga. In the following discussion, the venation homologies of Ponomarenko (1972) are followed.

In *Apoleon* (fig 5) the Cu2+1A1 reaches the Cul, the M1 is unbroken, the M is spurred with a r-m, the cul-cu2 is present, as are the W and R cells. The crossvein between the 1A1 and 1A2 placed beyond the W cell is considered plesiomorphic, being exhibited in the Lymexyloidae (*Hylecoetus*), the heteromera (*Alleculinae, Mycetophagidae*), and Cleroidea (*Ostomidae*). This is considered homologous to the crossvein beyond the W cell in the Cupedidae.
Figure 5. *Apoleon edax*, metathoracic wing.
(Cupes). In the Adephaga this crossvein is located at the W cell, and this condition occurs in most Bostrichidae where it is present. It also occurs at this level in the Dascillidae and Dermestidae, but in the examples available in both these groups, considerable fusion has occurred in the anal area, analogous but independent of the same situation in the Bostrichidae. In these groups the direct Cul - Cu2 connection is lost, as is the M1 in the Dermestidae.

Because virtually all beetle taxa have members with reduced venation, because there is a limited number of veins that apparently can be lost without sacrificing functionality of flight wings, and because there appears to be tremendous convergence between members of various superfamilies, I consider the most complete venation in the bostrichoids pleisiomorphic, with reductions within the families apomorphistic at those levels.

CRYPTONEPHRIDISM. The modified cryptonephridial system of the Bostrichoidea has been the subject of considerable discussion (Crowson, 1961; Lawrence and Hlavac, 1979). Examining the data available from a phylogenetic standpoint, I have drawn some hypothetical conclusions. Cryptonephridism is known in all the Cucujiformia, the Bostrichiformia, Scarabaeoidea and Buprestoidea (Saini, 1964; Poll, 1932; Stammer, 1934). [The condition exhibited
in the Dryopoidea is not true cryptonephridism (Saini, 1964).]

Saini (1964) shows the cryptonephridism of the scarabs to be nonhomologous with that of the higher Polyphaga, and the Buprestidae have not been critically studied beyond gross morphology. Thus, cryptonephridism appears to be the defining synapomorphy of the bostrichiform-cucujiform lineage. The noncryptonephridic members of this lineage are all aquatic or utilize wet fungi for food - *Donacia* (Chrysomelidae), *Noturis* (Curculionidae: Erirrhininae), *Platypus* (Platypodidae) and *Nosodendron* (Nosodendridae).

Saini (1964) and Poll (1932) both point out the relationship between moisture content of food sources and the degree of development of cryptonephridism. Poll (1932) was the first to suggest that the lack of cryptonephridism in aquatic cucujiforms was secondary. Since the system seems firmly tied to water conservation (Saini, 1964), mutations that result in its secondary loss would hardly be detrimental to aquatic beetles, which have the opposite problem of getting rid of water.

The modified cryptonephridism (mc) of the bostrichoids is a highly specialized system characterized by all the malpigian tubules (m.t.s) joining the hind gut on one side, and the perinephric sac displaced to one side of the gut,
supported by a sclerotized rod, running elliptically around
the gut.

Saini (1964) concluded that the mc arrangement is
simply a modification of the radial type found widely in
the Cucujiformia. Although the condition of only a few
species of bostrichiforms have been reported in the
literature, due mainly to the perceived need to work from
fresh or specially fixed material, I have found that the
rod is visible even in very old dried material, and can be
seen in cleared preparations of the hind gut. As such, it
can be inferred that those species with the rod exhibit mc.
It occurs in the Endecatomidae, and all subfamilies of the
Bostrichidae, as well as in the Dermestidae and is the
defining synapomorphy of the Bostrichiformia. It does,
however also occur in Typhaea (Mycetophagidae), and
Sitophilus (Curculionidae), both stored product pests, and
I consider it convergence in these cases.

One aspect of the mc system that requires further
comment is the tendency for the descending rectum to become
reassociated with the mc sac in a looped fashion. This
occurs in the dermestids, and bostrichids, but with
important differences. In Dermestes the gut contents of
the reassociated portions run in the same direction, but in
the bostrichids reported to have the gut so looped, the
contents of the reassociated portions run in opposite
directions (counter current). The gut is not so looped in *Endecatomus rugosus* (pers. obs.), but exhibits the normal mc condition of the rod.

In *Endecatomus* as well as *Bostrichus* and *Rhyzopertha*, the m.t.s reassociate in groups of 2 and 4, which then join. In all other reported Bostrichidae the m.t.s all reassociate in a single bundle. Since the 2+4 condition is common in the Cucujiformia (Crowson, 1981), this is considered plesiomorphic, with the single bundle apomorphic. Unfortunately, fresh or fixed material is needed to examine this condition, and therefore cannot be used here due to lack of critical taxa.

In *Dermestes*, *Endecatomus* and *Bostrichus* the upper portion of the reassociated m.t.s run completely around the hind gut, the displaced portion posterior to this ring. In the other described bostrichoids it is completely displaced. In all cases observed, the rod runs completely around the gut.

Use of these variations for phylogenetic purposes is dangerous, as Saini (1964) found in the Chrysomelidae, Curculionidae and Tenebrionidae that variation was closely tied to moisture content in the normal food of a given species, and much less to phylogenetic lineages. With the exception of a synapomorphy for the Ptilini and Anobiinae, discussed under that subfamily, this variation is not used
for the phylogenetic analysis.

**Dermestidae Latreille NEW SENSE**

Dermestidae of Mroczkowski, 1968, minus Orphilineae.

This taxon corresponds to Dermestidae of all recent major authors, minus the genus *Orphilus*, which is transferred to the Nosodendridae.

The Dermestidae, from the standpoint of the insect systematist, contains some of the most important pestiferous insects known. It is a family recognized by taxonomic workers involved with any insect group that is stored dry, and is virtually universally despised for its depredations.

The Dermestidae can be recognized by the combination of the metacoxa shorter than the femur, and separated from the edge of the elytron by the metepisternum, the exposed antennal excavations on the hypomeron, and the prolegs with the tibia held posterior to the femur in repose. The larvae are campodeiform, and distinguished by the presence of modified setae. These setae take a variety of forms, some rather fancifully spear-pointed, and others more simply scale-like. Studies of dermestid larvae include important works by Hinton (1945), Rees (1943), and Anderson (1949).

The exclusion of the Orphilinae allows a much simpler diagnosis of this family, as the characters used previously
to include it involved such symplesiomorphies as presence of a median ocellus and other reversed characters. These characters are discussed more fully under the Nosodendridae and in the character discussions.

If the exclusion of the Orphilinae is seen as intolerable to familial recognition, the other choice within the confines of the monophyletic taxon concept is to place the Nosodendrinae as a subfamily of the Dermestidae.

This course was not taken for 2 reasons. First, recognition of the 2 families requires changing the placement of only 6 extant and one fossil species. Moving Nosodendron, with nearly 50 described species, would change the status of far more taxa, and eliminate a well known family name. Besides the stability aspect, a combined Dermestidae-Nosodendridae would be difficult to diagnose on untransformed synapomorphies.

The adults of the aberrant genera Thylodrias and Thorictes require separate diagnosis. Female Thylodrias lack elytra and metathoracic wings and have a single median ocellus, while males can be recognized by the 4 long filiform segments where the antennal club would normally be, the malacoderm facies and presence of a single median ocellus. Both sexes have the pleurosternal suture obsolete, but it would be very unlikely that anyone would mistake them with the bostrichid lineage. In both sexes
the metacoxae are narrowed, the malpighian tubules exhibit modified cryptonephridism, and in the male the external genetilia are dermestoid.

The adult Thorictes is so unlike any other bostrichiform that it is easiest to recognize it totally on habitus (Anderson, 1949, fig. 9). It could be keyed imperfectly in my key by the compact anten nal club, hypomeral excavations for the anten nal club, and the narrow metacoxae. The genitalia of the male are obviously dermestoid. The larva is also difficult, as all setae on the body are simple except 1 pair on each of abdominal segments I-VIII. These setae are short and clubbed. I have seen no specimens of Thorictes, and base my statements totally on Anderson's (1949) treatment. The condition of the malpighian tubules is unknown, but given the dry foodstuff habitat, I predict that modified cryptonephridy will be found in this genus.

The nearly 900 described species are rather unevenly distributed among 9 subfamilies and 43 genera. Some 650 of these species are placed in only 6 genera, with 3 genera containing almost exactly half the species. At the other end of the spectrum, half the genera (22) contain only 1 or 2 species. This family would benefit greatly from a modern generic level phylogenetic analysis.
Subfamilies of Dermestidae, after Mroczkowski (1968).

[Numbers in parentheses are numbers of included genera/species, (*) indicates taxa examined.]

Marioutinae (1/2)
Egidyellinae (1/1)
*Dermestinae (2/74)
*Attageninae (4/181)
*Megatominae (27/489)
*Anthreninae (2/89)
Trinodinae (4/31)
*Thyloptrinodinae (1/1)
*Thaumaphrastinae (1/4)

Nosodendridae Erichson NEW SENSE


The Nosodendridae have been placed in many areas of the Coleoptera classification, most recently in the Derodontidea by Lawrence and Newton (1982). Formerly including only Nosodendron, they were usually placed near the Byrrhidae until the work of Crowson (1955), when they were included in the Dermestoeidea. Their placement in the Derodontidae was based on the free malpighian tubules and similarity of larval mouthparts. The first is a reversal shared with the orphiline, and Lawrence and Hlavác (1979) stated that the latter is a combination of symplesiomorphies and convergence associated with similar habitats. Thus, Nosodendron shares no special similarity of a derived type with Derodontidae.
The Nosodendridae is placed in the Bostrichoidea on the basis of the form of the metendosternite, and synapomorphies of the Dermestidae and Nosodendridae (fig. 2). Further, synapomorphies of the Orphilinae and Nosodendrinae strengthen this placement, as there is little doubt that the orphelines, formerly placed in the Dermestidae, share an ancestry with that family. However, the similarities of the orphelines and dermestids are definitely symplesiomorphic when compared with the Nosodendrinae.

The defining synapomorphies of the Nosodendridae mihi are the loss of cryptonephridy; presence of internal plates at the junction of sternites III and IV (and sometimes others); the prolegs held forward, over the antennal club in repose; and the resulting form of the procoxa. The dermestids have been repeatedly diagnosed as having the malpighian tubules crytonephridic (see Lawrence, 1982, etc), yet Orphilus has specifically been included in that family. Paulian (1943), Hinton (1945), and Crowson (1961) have all called attention to the special nature of Orphilus, and Anderson (1949) went so far as to insinuate a problem with it being included in the Dermestidae. After discovering several apparent synapomorphies with the nosodendrines, and others for the dermestids that excluded the Orphilinae, I checked for the presence of the
scleritized rod indicative of modified cryptonephridy. There is no indication of this rod on the hind gut of Orphilus, and its presence is known in every confirmed instance of modified cryptonephridy. Therefore, I consider it reasonably certain that Orphilus lacks the modified cryptonephridial character, and that its absence is another synapomorphy with Nosodendron.

Diagnostic plesiomorphies include extremely transverse procoxae, metacoxae as long as the femur, and simple setae on the campodeiform larva.

The two subfamilies, each with a single genus, are well supported as monophyletic. The Nosodendrinae have the head prognathous, with the mouthparts protected by the enlarged, plate-like mentum; tarsal grooves on the abdominal sternites; antennal segment 3 very long, subequal to length of the club; the internal sternal plates greatly enlarged, and the ventral surface flattened, in part by longitudinal corrugation of the abdomen. The larvae were discussed by Crowson (1959), and the adults treated by Reichardt (1976), who reviewed the world literature. Biological studies of this group have recently been reported by Kulhavy, et al. (1982 and citations).

The Orphilinae have the abdomen ventrally margined by a complex carina and associated groove, running from coxa to coxa. This carina is preceded on the last visible
sternite by a complex depression, and forms a false pygidium on the same sternite, which is not covered by the elytra. The head is deflexed against the procoxae in the retracted position with the procoxae excavate on the anterior face; and there is no visible intercoxal piece on the prosternum. The larva of one species is described (Paulian, 1943), having been found in an oak log. Unfortunately, neither the actual food of the larva, nor the moisture conditions of the larval habitat were reported, so the ecological correlation of lost cryptonephridy and wet conditions remains untested in this group.

Subfamilies and genera of Nosodendridae

Nosodendrinae NEW SENSE.

Nosodendron Latreille. 48 described species (Reichardt, 1976), (1 undescribed known from Peru, FMNH).
Orphilus Erichson. 5 described extant species, 1 from Miocene of Colorado. (Mroczkowski, 1968). TRANSFERED FROM DERMESTIDAE.

Key to the Subfamilies of Nosodendridae.

1. Head with a median ocellus; venter of body convex; abdominal sternites without tarsal grooves; head reflexed against procoxae, which are excavate on vertical face; procoxae approximate; third antennal
segment short, subequal to segments 4 and 5; antennal insertions on top of head; mentum normal, not expanded; abdomen ventrally margined with a sharp marginal carina and associated groove running from coxa to coxa, setting off a false pygidium on last visible sternite...............Orphilinae

1'. Head without ocellus; venter of body flat; abdominal sternites with tarsal grooves; head prognathous; procoxae distinctly separated by procoxal piece; third antennal segment long, as long as club; antennal insertions concealed by ridge that runs around margin of head from eye to eye; mentum expanded and plate-like, covering mouthparts in retracted position; abdomen without marginal carina.........Nosodendrinae

Endecatomidae LeConte

Endecatomini LeConte, 1861. Horn, 1878. LeConte and J.LHorn, 1883.
Hendecatomini Kiesenwetter, 1877.
Hendecatomidae Lesne, 1921; 1934; 1935.
The single genus included here was originally placed in the Ciidae, and some authors have persisted in this placement into the recent past (Arnol'di 1965; Benick, 1952). The 4 included species were originally described in genera now placed in such diverse groups as Anobiinae, Mycetophagidae, Ciidae, and Bostrichidae.

Jacquelin du Val (1861) and LeConte (1861) first placed this genus near the bostrichids, and Lesne (1921, 1935) established this relationship beyond reasonable doubt. Descriptions of larvae of two species by Crowson (1961) and Kompantsev (1978) ended any doubt that could have remained.

This family is unique in the Bostrichoidea due to the explanate lateral margins of the pronotum, which are margined with projecting setae. The combination of very slightly excavate hind coxae, setose tubercles on the pronotum and elytra, 3 segmented antennal club, and unique habitus will further distinguish the group.

The larvae are easily identified from other bostrichoids by the combination of lightly sclerotized, C-shaped body; exerted head; 3 segmented antennae; 4 segmented maxillary and 2 segmented labial palpi, and the scoop-shaped mandible with 3 apical teeth.

The ranking of taxa, except for a requirement of monophyly, is subjective, and for a variety of reasons,
this group is recognized as a family whose sister-group is hypothesized to be the Bostrichidae. The bostrichids and endecatomids share the synapomorphies of C-shaped larvae and reduced, nonexcavate hind coxae (the last reversed in the anobiines). The bostrichids are supported as a monophyletic lineage by the totally internal feeding larvae, which are unable to walk upon the substrate, and have the head retracted (reversed in the anobiines). This may be correlated with a move from fungivory to xylophagy.

The endecatomids have as synapomorphies setose tubercles in the adult for holding encrustations (Lawrence and Hlavac, 1979), explanate pronotal margins, and a 3-toothed, scoop-shaped mandible in the larvae. If, as seems to be the case from examination of specimens, a secretion is involved with cementing the encrustations, such secretions may be sympleisiomorph with defense secretions in derodontids and encrustation secretions in the derodontids and jacobsoniids, making their absence synapomorphic in the bostrichids.

The fungivorous endecatomid larvae retain the ability to walk on the substrate, on the outside of their host. This observation, originally reported for *E. lanatus* by Kompantsev (1978), has been repeated by me for *E. rugosus* with material supplied by Karl Stephan from Red Oak,
Oklahoma. This is, to my knowledge, unique among the C-shaped bostrichoid larvae.

The endecatomid lineage is probably very old, and is tightly tied to woody fungi, possibly the ancestral habit. I suspect the most recent common ancestor of the 4 extant species was not, however, so far removed from the present. The Holarctic distribution seems to be one predicted by Pleistocene disjunction of a Laurasian or Beringian species. Perhaps this is an example of a temperate-adapted genus, holding out relictually against younger lineages, such as the anobiines, which have replaced them in the tropics. If a winter active adult is characteristic of all 4 species, this strategy could explain the continued success of this ancient group in a narrow ecological niche.

This scenario would predict endecatomids in south temperate faunas, yet only Euderia shows such a distribution among bostrichoids. Euderia seems well associated with the anobiines, and no support for any relationship with endecatomids was found. It is possible that Southern Hemisphere endecatomids will be discovered, probably in association with woody fungi in temperate forests.
Endecatomus Mellière


Dictylotus Redtenbacher 1847 (type species Anobium reticulatum Herbst, by monotypy).


For more complete references, see Lesne (1938) and Fisher (1950). The latter gives a description for the genus and discusses its nomenclatorial history. The emendation of Endecatomus Mellière to Hendecatomus Schaum is considered unjustified under Article 33 of the ICZN. This taxon is redundant with Endecatomidae, and the discussion above relates directly here.

All 4 species of Endecatomus are rare in collections. The apparent rarity is evidently the result of the adult activity period being mainly during the winter, when collecting effort among coleopterists is at its lowest. Adults are present on host fungus from late fall to early spring, with larvae also present during winter.

The only collection date I have for the European E. reticulatus is "2-4-04" on a French specimen. Kompantsev (1978) records larvae of the Asian E. lanatus present in
June, with adults emerging in late July and early August. Lesne's data on this species includes a collection date in early May and one from June.

Karl Stephan regularly collected both the American species in series during the winter months (K. Stephan, pers. com.). Although museum records for these two species include all months, over 90% (154 of 169) of specimens examined were collected in the months September through May. Only one adult was seen from July and, judging from the condition of the specimen, may have been found dead. Seven each were seen from June and August. Most of these summer specimens were from north of 45 degrees lat. where seasonal extension would be expected. Highest numbers were from February (32) and September (29), although these are relatively inactive months for collectors.

Matthewman and Pielou (1971), working north of Ottawa in Quebec, report *E. rugosus* emergence from July to January, with the peak in August and September. Material from their study was included in mine, and these data are included in my summations.

One indication that the species may indeed be rare in the field is further data from Matthewman and Pielou's (1971) study. *Endecatomus* emerged from only 10 *Fomes* fruiting bodies of 1448 collected. However, in the Red Oak
material, the larvae were in fungal filled areas in bark, which correlates with the specimens recorded by Crowson (1961) and Kompantsev (1978), indicating occupation of the sporophores may not be the preferred habitat.

Another possibility, supported by the presence of adults and medium-sized larvae in the Red Oak material, is a 2 or more year life cycle. Matthewman and Pielou (1971) did not hold hosts long enough to exclude this possibility, but did record that sporophores yielding *Endecatomus* were all 2–4 years old.

Host data are insufficient to make well-supported statements about host specificity, but some trends are indicated. All known hosts of the 4 species of *Endecatomus* are rather hard members of the Polyporaceae. The European *E. reticulatus* is recorded to be associated with *Polyporus betulinus* (Crowson, 1961), yet *E. rugosus* was not found to feed on this fungus in Quebec, even though the fungus was abundant, and the beetle present on other fungi in the same forest (Pielou, 1966; Matthewman and Pielou, 1971). *Endecatomus rugosus* does feed on other *Polyporus* species, as well as *Fomes* and *Sterium*. The Asian *E. lanatus* is recorded from *Fomes* (*Phellinus*) (Kompantsev, 1978), and *E. dorsalis* is commonly collected from a *Poria* in Oklahoma. The only place that I know of *E. dorsalis* and *E. rugosus* occurring sympatrically is in Latimer Co., Oklahoma, and
they apparently are never found there on the same species of fungi (K. Stephan, pers. com.).

Interestingly, only the larva of the European species is still unknown. Crowson (1961) and Kompantsev (1978) described the larvae of \textit{E. rugosus} and \textit{E. lanatus} respectively, and I have a specimens associated with \textit{E. dorsalis} (unfortunately, this specimen is very small, probably an early instar, and not well preserved).

Key to the species of \textit{Endecatomus}

1. Curved setae on caudal portion of elytral disk without spurs, tips at 90 degree angle from elytral surface, not even close to surface. Soviet Far East and Japan

\hspace{1cm} \textit{E. lanatus}

1'. Curved setae on caudal portion of elytral disk recurved, with tips touching elytra, usually short spurs

\hspace{1cm} \textit{E. rugosus}

2. Dorsal face of mandible smooth, with a longitudinal groove

\hspace{1cm} \textit{E. dorsalis}

2'. Dorsal face of mandible imbricate, without a longitudinal groove. North America

3. Setae projecting from pronotal margin straight, stout; both these setae and recurved setae on elytral disk without a spur. Southeastern North America

\hspace{1cm} \textit{E. dorsalis}
Setae projecting from pronotal margin curved at a right angle; both these setae and those on elytral disk with a spur at point of curve. Europe........ *E. reticulatus*

**Endecatomus lanatus** Lesne

*Hendecatomus reticulatus* (not Herbst) von Heyden, 1886.


Lesne (1934) described this species from 7 specimens from the Soviet Far East, and 4 specimens in the Lewis collection, thought to be from Japan. I have examined 6 of these specimens, housed in the MNHN and BMNH, and here designate as Lectotype the specimen in the MNHN labeled "Amour; Kotzel/ Museum Paris; coll. St. Claire-;Deville 1932/ TYPE/ Hendecatomus; lanatus Lesne; P. Lesne vide/

with my Lectotype label. Two additional specimens in the MNHN are designated paralectotypes: 1 labeled "Nicolajevsk, Amur Kaltze"; and 1 - "G. Lewis". Two paralectotypes are found in the BMNH labeled "G. Lewis; 1910-248/ co-type". All these latter specimens bear my paralectotype labels. 5 additional paralectotypes from Amour (4) and Nicolajevsk (1) should be found in the Eberswalde collection.
This species is described by Lesne (1934) and Chůjó (1957), illustrated by Chůjó (1957; 1958), and Lesne (1934). The larva is described and illustrated by Kompantsev (1978).

**Endecatomus lanatus** can be recognized by the lack of spurs on the curved setae on the posterior area of the elytral disk. Unfortunately, the condition of the dorsal surface of the mandible is unknown, due to lack of material. A phylogenetic analysis of this genus must await the arrival of promised material of this species from Paris.

**DISTRIBUTION:** Recorded from the Soviet Far East and Japan. Records include: RSFSR: Khabarovsk Kray -- Nikolayevsk-na-Amur (mouth of Amur River), Khabarovsk (confluence Amur and Ussuri Rivers); Amur Oblast' -- Kundur-Khabarovshiy, Khingan National Park (on Amur River, at confluence of Uril and Khingan Rivers); Primorskk Kray -- Anuchino (= 150 km NE Vladivostok) 5 May 1929; Yevreysk Autonomous Oblast'; Raddevka [near Radde ?], Lesne (1935a) says 1000 km from mouth of the Amur River]; locality unknown -- Sikoba-Alyn, June (?). JAPAN: Honshu; Tokyo Pref. -- Nippara.

All the Soviet records are near the Ussuri and lower Amur Rivers, which each form portions of the border with China. This species undoubtedly occurs in China, and perhaps Korea as well.
BIOLOGY: Kompantsev (1978) records the larvae under bark of *Quercus mongolica* Fisch. in late June, feeding on resupinate *Fomes* (*Phellinus*) sp. Fungivory was confirmed by gut analysis, and the larvae were observed walking on the surface of the fungus. Adults emerged in late July and early August. Lesne (1934) records an adult collected in May and one in June.

*Endecatomus reticulatus* (Herbst)

*Anobium reticulatum* Herbst 1793.


Cymorek, 1969.


This list of citations is not nearly complete, but includes the important citations since 1938. For citations prior of 1938, see Lesne (1938). *Endecatomus reticulatus* is illustrated by Dominik (1958), Cymorek (1969), and Arnol'di (1965). The adult morphology of this species is treated by Lesne (1935a). This is the only species of the family whose larva remains unknown.

A specimen in the MNHB is designated Lectotype. It is labeled "53100" and with my lectotype label. This specimen stands first in a series of 6 specimens following a label that reads "Hendecatomus/ Mellië", and another, with a
black border reading "Recticulatum; Ht - Pz * Fab.;
Austria". In the Museum log under the number 53100 is the
notation "Hendecatomus reticulatus Hbst, 7 - Austria". The
use of an * on such labels in German collections signifies
the curators belief that either the specimen(s) that follow
the label bearing it is/are the type or type series (M.
Uhlig, pers. com.). The next 5 specimens are designated
paralectotypes, and each bears my paralectotype label. The
seventh specimen following the label may also be a
paralectotype, but is labeled differently (Aust.), and is
not designated as such.

This species can be recognized by the setation on the
lateral margin of the pronotum only slightly recurved at
the tip, and at a right angle to the base. At the point
where the tip of the seta curves from the base, there is a
short spur extending forward from the junction. *E.
reticulatus* most resembles *E. rugosus* from North America,
but can immediately be distinguished from it by the smooth
dorsal surface of the mandible and the longitudinal groove
on the same surface. From *E. lanatus*, *E. reticulatus* can
be distinguished by the curved setae on the posterior
portion of the elytral disk having a spur, and being
recurved to the point that the tips of the setae contact
the elytra.
DISTRIBUTION. The full distribution of this species within Europe is somewhat unclear. A paper by Lesne (1935b) on distribution and biology is unavailable. Cymorek (1969) states that the species may no longer occur in Germany and Austria. I have seen no recently collected material, although the only specimen with a date would appear to be from 1904. Judging from the few specimens I have seen and faunal treatments that include the species, it appears that the species occurs or did occur in the European U.S.S.R., Poland, Germany, Austria, Czechoslovakia, Hungary, France, and would thus be expected in such neighboring countries as Switzerland, Italy, Yugoslavia, and Romania. I have not made an exhaustive search of the various European faunal lists, so the recorded distribution may indeed exceed this area.

This species does not occur in North America. Its listing from there arises from confusion over the application of the names of the American species, and an account of the problem will be found under R. rugosus below.

BIOLOGY. The paper by Lesne (1935b) on this subject has been unavailable. Crowson (1961) says this species is particularly associated with Polyporus betulinus on dead beech, yet E. reticulatus is not included in the 102 beetle species recorded from this fungus by Benick (1952) in his extensive review. Lesne (1935) says it is associated with polypores on beech and birch.

**Endecatomus rugosus** (Randall)

*Triphyllus rugosus* Randall 1838.


**Endecatomus reticulatus** (not Herbst); Melshimer 1853.

LeConte 1865. Horn 1878. LeConte and Horn, 1883.

**Endecatomus reticulatus;** Lesne, 1934 (part), 1935a (part), 1938 (part).

For a description of the adult and complete bibliography of references prior to 1950 see Fisher (1950). Crowson (1961) describes and figures the larva.

This species was described from Maine, and the type, like most of Randall's types, is lost. Although the description is worthless for recognition of this species, because only one species of **Endecatomus** is known from the New England area, it seems relatively certain which of the
two North American species is involved. For this reason, it is may not be necessary to designate a neotype for this species. However, because the application of this name to Endecatomus could be questioned from the description, which could belong to any number of things, and because of the consistent misapplication of the name by early workers, a neotype will be designated as soon as I can find a Maine specimen.

There has, however, in the past been confusion as to the correct name for this species. Derivation of this name from the nomen nudum Cis rugosus of Dejean, as was done by Fisher (1950), is totally unjustified, as there is no indication of such in Randall's paper. Melshimer (1853) listed this species under the name Cis rugosus, also listing Endecatomus reticulatus and E. dorsalis as occurring in the U.S.A. LeConte (1865b) synonymized rugosus and dorsalis, and continued to list reticulatus as North American. Horn (1878) misapplied the European species name to the Endecatomus occurring in the northern U.S., and used rugosus (including dorsalis Mellis) for the southern species, in spite of the Maine type locality of rugosus. This status was continued by LeConte and Horn (1883). Lesne had a high regard for the opinions of LeConte (Lesne, 1935a), and accepted the North American records of E. reticulatus, considering the other North American species
before him *E. rugosus*, since it was not the same as the European species. In fact, Lesne apparently never saw a specimen of *E. dorsalis*, and applied the name *rugosus* correctly by mistake. Thus, *reticulatus* of Horn and LeConte is *rugosus* of Randall, while *rugosus* of Lesne is indeed Randall's species. Further, *rugosus* of Horn and LeConte is *dorsalis* of Mellis.

The imbrications on the dorsal surface of the mandible in *E. rugosus* will immediately distinguish it from both *E. reticulatus* and *E. dorsalis*. The condition of the dorsal surface of the mandible in *E. lanatus* is unknown to me, but the lack of spurs on the curved setae on the posterior portion of the elytral disk will serve to separate it. *Endecatomus rugosus* can be further distinguished by the tightly recurved marginal setae on the lateral edges of the pronotum. They curl completely back, to come into contact with the margin at their tips. In the European species, they curve only 90 degrees, while in the narrowly sympatric *E. dorsalis*, they are straight, and very stout. *Endecatomus rugosus* is also noticeably more broad than *E. dorsalis*, but insufficient material of the latter is available to test the significance of this difference numerically.
DISTRIBUTION. This species occurs from Maine to Manitoba, south to Texas and Florida. I have seen no records for the Gulf coastal plain, with the exception of one specimen from Florida's Gulf coast. Records or specimens exist for the following political divisions - Canada: Manitoba, Ontario, Quebec. United States: Minnesota, Iowa, Michigan, New York, Maine, Massachusetts, Rhode Island, New Jersey, Delaware, Maryland, Pennsylvania, Ohio, Indiana, Illinois, Kansas, Oklahoma, Texas, Missouri, Tennessee, Virginia, North Carolina, Florida. I see no reason to assume that it does not occur throughout the birch belt from Manitoba to Alaska, as well as in the Maritime Provinces.


Lab., 21 May 1922, bracket fungus on red oak (CNCI); 4
(OSUC); 1 - Philadelphia Co., July, 1920, H. Wenzel (OSUC);
3 - Mt. Alto 19 February, J. N. Knuth (OSUC); 1 - Allegheny
(CASC). New Jersey: 7 - Newark (OSUC); 1 - Orange Mt. Ohio;
8 - Franklin Co., 16 December 1948, E. Sleeper (OSUC); 10 -
ibid. 25 March 1950 (OSUC); 1 - Perry Co., 29 March 1915,
D. M. DeLong (OSUC); 24 - Clinton Co., 15 February 1961, F.
J. Moore (OSUC); 1 - ibid. 15 July 1961, F. J. Moore [may
be mislabeled member of previous series, i.e. II-15 vs.
VII-15]; 1 - Adams Co., 13 April 1963, F. J. Moore (OSUC);
3 - Warren Co. 19 May 1963, F. J. Moore (OSUC); 1 - Scioto
Co., 11 May 1963, F. J. Moore (OSUC); 1 - Wooster, 12 June,
1959, C. A. Triplehorn, at light [?]; 1 - Fairfield Co., 28
February, D. J. & J. N. Knuth (OSUC); 1 - Athens Co.,
Warren Twp. 24 October 1946, W. C. Stehr (MAIC); New York:
1 - Hewlett, Long Island, 15 November 1925, Quirsfeld
(CNCI); 1 - Rochester, 15 June 1940, W. B. St. John (MAIC);
Buffalo, February, 1880, E. P. Van Duzee, (UCBC). Michigan:
1 - Macomb Co., E. of Memphis, 7 May 1971, Brivio (MAIC); 1
- Livingston Co. E. S. George Reserve, 13 October 1962,
Brivio (MAIC). Maryland: 1 - 3 mi S Colesville, 24 October
1950, G. H. Nelson, crevice oak bark (MAIC); 1 - Baltimore,
25 May, Howden (HABC). Oklahoma: 30 - Latimer Co., Red Oak,
September - March, 1976, 1976, 1983, R. Stephan (KSC,
MAIC). North Carolina: 1 - Morrison (BMNH); 2 - Faison, 23

BIOLOGY. This species has the widest known host range of any Eucratomus. Most host records are vague, such as "woody fungus under bark" and "maple sap in spring" (Blatchley, 1910), or ex fungus and ex basidiomycete. With the exception of Blatchley's maple sap record, all the records seem to be associated with woody fungi on trees. All generic or specific records are for the Polyporaceae. Records include Polyporus gilvus (Fisher, 1950; FSCA), Fomes fomentarius (Matthewman and Pielou, 1971 and references), Sterium oestrae (MAIC, KSC). Although the larvae do feed in the sporophores of Fomes fomentarius (Matthewman and Pielou, 1971), they are rare there. Live material sent to me by Karl Stephan from Latimer Co., Oklahoma was in the portions of fungus (Sterium oestrae) growing intersitially and within bark of a dead sycamore. Larvae were reasonably common in this habitat, but less so
than anobiine larvae. These larvae maintained a hole to the outside, usually at the lowest point of connection between the bark and the small, thin, cup-shaped sporophore. Frass was pushed out this hole, and presence of a larva could be predicted by the resulting pile of frass. Records of Crowson (1961) and Blatchley (1910), as well as label data from Maryland indicate the corticolous habitat may be preferred. The apparent rarity of larval specimens may be a result of the similarity of habitus and habitat with anobiines, leading collectors to pass over these "common" specimens.

Of note is the apparent absenence of *E. rugosus* in sporophytes of *Polyporus betulinus* in Gatineau Park, Quebec (Pielou, 1966; Pielou and Verma, 1968), where it was present in *Fomes fomentarius*. *Endecatomus reticulatus* is said (Crowson, 1961) to be particularly associated with *P. betulinus* in Europe, yet its congener seems to not utilize this very common and widely distributed resource in North America.

Matthewman and Pielou (1971) report that *E. rugosus* larvae mainly tunnel the pore surfaces and margins of the current years growth of *F. fomentarius* sporophytes, not penetrating deeply into the interior. These tunnels lack an outer wall. Chambers, possibly for pupation, are constructed 5 – 9 mm below the surface. Nine out of 10
sporophytes that yielded adult E. rugosus in this study were 2 - 4 years old.

Endecatomus dorsalis Mellie

(Fig. 6)

Endecatomus rugosus (not Randall); LeConte, 1865b. Horn, 1878. LeConte and Horn, 1883.

For a description of this species, see Fisher (1950). A discussion of nomenclatorial confusion of this species and rugosus is discussed above, under that species. Described from Texas, the type of this species does not exist in the MNHN or MCZC, and is presumed lost. From Mellie's paper, it would seem the type was to be returned to the collector, whose collection was mostly destroyed, the few remnants being in the MCZC. Because there has been confusion in the names of North American Endecatomus, and because E. rugosus is also known from Texas, I will designate as Neotype a specimen in the CNCI labeled "Kerrville, TEX.; April 13 1959; Becker and Howden/ beating oak; (Quercus sp.)." This specimen conforms to the description of this species by Mellie (1848) and Fisher (1950). The provisions of Article 75 of the ICZN are intended to be met by the above discussion and designation, combined with the diagnosis below.
Figure 6. *Endecatomus dorsalis*, Nellie.
**Endecatomus dorsalis** can be recognized by the form of the arcuate setae on the elytral disk. These setae are recurred, have their tips in contact with the surface of the elytra, and lack a distinct spur. From the sympatric *E. rugosus*, it can be distinguished by the smooth dorsal surface of the mandible, which bears a longitudinal groove, and the straight, stout setae fringing the lateral margin of the prothorax. *Endecatomus dorsalis* appears to be considerably more slender than the other species of the genus, but insufficient material was available to test this numerically.


**BIOLOGY.** This species is commonly collected in winter, between the laminations of rotting oak in Oklahoma (K. Stephan, pers. com.). A single small larvae was removed in January, 1985 from the very hard sporophyte of *Poria* in
rotted Black Jack Oak from Latimer Co., Oklahoma.

**Bostrichidae**

Secondary references in Lesne (1938) are not repeated. A few papers of note since then are listed below.

The hypothesis of phylogeny for the subfamilies of Bostrichidae presented in fig. 7, based on the characters in table 3, should be considered preliminary. It is based on relatively few characters, due to the extensive time spent in resolving higher clades. It is hoped this weakness will be offset by the phylogenetic framework developed for the Bostrichiformia, which will hopefully allow much better polarization in the further studies planned on this group.

The Dysidinae seem well established as the basal clade in the Bostrichidae, and the Dinoderinae-Lyctine, Euderinae-Anobiinae, and Polycaoninae-Bostrichinae sister-group relationships seem quite secure, but the placement of the Psoinae is based mainly on character reduction. The problem is the rarity of the basal taxa in the Psoinae; for instance *Psoidia* is known only from the unique holotype of the type species.

More specific considerations are discussed under the various subfamilies below, and the character discussions above.
Table 3. Apomorphic Character States of Bostrichid

<table>
<thead>
<tr>
<th>Subfamilies</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Last abdominal spiracle of larva enlarged</td>
</tr>
<tr>
<td>2. Gular sutures fused</td>
</tr>
<tr>
<td>3. Procoxa constricted by cavity</td>
</tr>
<tr>
<td>4. Abdominal intercoxal process lamiform or absent</td>
</tr>
<tr>
<td>5. Metacoxa semi-excavate</td>
</tr>
<tr>
<td>6. Metacoxa excavate</td>
</tr>
<tr>
<td>7. Larva with 2-segmented antenna</td>
</tr>
<tr>
<td>8. Antennae received in groove between procoxae</td>
</tr>
<tr>
<td>9. Segments of antennal club as long (wide) as antenna</td>
</tr>
<tr>
<td>10. Intercostal process long, free</td>
</tr>
<tr>
<td>11. Bostrichoid (hood-like) prothorax</td>
</tr>
<tr>
<td>12. Cu2+1A1 - 1A2 crossvein lost, 1A2 fused to Cu2+1A1</td>
</tr>
<tr>
<td>13. Cu2+1A1 free from 1A2</td>
</tr>
<tr>
<td>14. Cu2+1A1 - 1A2 free (wish bone type)</td>
</tr>
<tr>
<td>15. No W cell</td>
</tr>
<tr>
<td>16. No R cell</td>
</tr>
<tr>
<td>17. Long, squarely attached metatrochaters</td>
</tr>
<tr>
<td>18. Larval head exerted</td>
</tr>
<tr>
<td>19. Protibia with single spur</td>
</tr>
<tr>
<td>20. Pronotum dorsally tuberculate</td>
</tr>
<tr>
<td>21. Pronotum narrowed posteriorly</td>
</tr>
<tr>
<td>22. Head with &quot;neck&quot;</td>
</tr>
<tr>
<td>23. Cryptosternum exposed, procoxal cavities closed behind</td>
</tr>
<tr>
<td>24. Body dorso-ventrally flattened</td>
</tr>
<tr>
<td>25. Tarsomere 1 distinctly longer than others</td>
</tr>
<tr>
<td>26. Pronotum with conical tubercle medially</td>
</tr>
<tr>
<td>27. Heteromorphic males</td>
</tr>
<tr>
<td>28. Head strongly prognathous</td>
</tr>
<tr>
<td>29. No leptophragma in m.c. system</td>
</tr>
</tbody>
</table>
Figure 7. Phylogenetic Hypothesis of Bostrichid Subfamilies. Numbers refer to characters in Table 3.
Key to the subfamilies of Bostrichidae

1. Gular sutures confluent..........................2

1'. Gular sutures separate, sometimes narrowly so........4

2. Head easily visible from above, prosternal process
   long, reaching mesosternum and slightly expanded at
   apex; antennae 9-11 (usually 11) segmented...........
   ......................................................Polycaoninae

2'. Head more or less covered by pronotum; prosternal
   process short, acute, not extending between procoxae,
   antennae 8-10 (usually 10) segmented..................3

3. Protibia with 1 apical spine; prothorax in dorsal view
   evenly rounded in front, first tarsomere subequal to
   second; prothorax, in lateral view, without a vertical
   front, never with a flat or excavate front...........
   ......................................................Dinoderinae

3'. Protibia with 2 apical spines; prothorax in dorsal view
   flattened or excavate in front; first tarsomere very
   much shorter than second; prothorax in lateral view
   with a flat or excavate front......................Bostrichinae

4. Hind trochanter attached squarely to femur; first
   tarsomere almost always longer than second............5

4'. Hind trochanter obliquely attached to femur; first
   tarsomere shorter than second, or tarsi 4 segmented...
   ..........................................................6
5. Hind coxa usually excavate to receive hind femur, if not, antennal insertions approximate and antennae without pectinate 3 segmented club. World wide..............................Anobiinae

5'. Hind coxa conical at trochantal insertions, not excavate to receive hind femur; antennae 11 segmented with a 3 segmented pectinate club, each ramus longer than antenna. New Zealand...............Euderiniinae

6. Pronotum with complete lateral margins; antennae 11 segmented, usually with a 2, rarely with segmented club; first tarsomere subequal to second; procoxae widely separated, procoxal cavities open or closed externally.................................Lyctinae

6'. Pronotum without lateral margins, or with only basal portion margined; antennae with 11 or less segments, club with 3 or 4 segments; first tarsomere subequal, longer, or shorter than second; procoxal cavities open externally.................................7

7. First visible abdominal sternite with a postcoxal carina completely across its width, connected to wide intercoxal process.............................Dysidiinae

7'. First visible sternite of abdomen (or second if first visible is II, narrowly visible at lateral edges in some genera) usually without a postcoxal carina, with intercoxal process lamiform or absent........Psoinae
Dysidinae

Dysididae Lesne, 1921.
Dysidinae Lesne, 1938; Fisher, 1950.
Apoleoninae Gardner, 1933.

This group has remained in its present form since Lesne (1894) revised it under the genus name Dysides Perty. It is remarkable for its few species (3), disjunct distribution, external uniformity, and retention of pleisiomorphic character states. Even though it is not the basal clade on the bostrichid lineage, it was important in my polarization decisions due to the derived condition of the Endecatomidae.

The clearly visible head (from a dorsal view) (fig. 8, 9), lack of lateral pronotal margins, wide intercoxal process on the first visible abdominal sternite and distinct tubercles on the anteriorly narrowed pronotum distinguish this group.

As the sister-clade of the rest of the Bostrichidae, this group, together with the Endecatomidae, was used most often as the out-group for polarization in the remainder of the family. With the exception of lacking pronotal margins and a few other characters, this group exhibits rather good agreement with a conceptual primitive bostrichid.

The three currently recognized species are placed in two genera. Dysides is limited to South America and
Figure 3. *Dysides obscurus* Perty, dorsal habitus.
Figure 9. Pseudoscesus coryla, lateral habitus.
Apoleon to southeast Asia. The phylogenetic and zoogeographic history of this group will be further discussed in a revision currently in preparation.

Key to the Genera of Dysidinae

1. Antenna 9 segmented; wing with Cu2 broken; elytral setation uniform. Neotropical.................Dysidus
1'. Antenna 10 segmented; with Cu2 complete; elytral setation forming 4-5 indistinct longitudinal lines on unrubbed specimens. Oriental..................Apoleon

Polycaoninae

Polycaoninae Lesne, 1896.
Psoinae Gardener, 1933 (not of authors).

This subfamily has been placed in the Psoinae by most anglophone authors, including LeConte (1861), LeConte and Horn (1883), Horn (1878), Boving and Craighead (1931), Crowson (1961) and Gardener (1933). With the exception of the last, all these included the Polycaoninae as well, which are here considered an independent lineage. Interestingly, this group has always been considered at the same taxonomic level as the psoines by the francophone authors, Lesne and Vrydagh. A combined Psoinae-
Polycaoninae was the group I first began to revise, and the paraphyletic nature of the group resulted in this expanded examination of bostrichoid phylogeny.

The supposed special relationship of the Psoinae and Polycaonine is based on symplesiomorphies that result in a similar facies. I hypothesize the sister-group of the Polycaoninae is the Bostrichinae. These two groups share unique characteristics found nowhere else in the Bostrichidae.

The first of these characteristics is the constriction of the procoxa by the coxal cavity, resulting in an indented ring on the coxa. The other is the occurrence of a high degree of sexual dimorphism, that is characterized by a basic feminine form, with heteromorphic males that vary continuously from the feminine condition to a highly masculine condition. Usually, the variability involves degrees of expression that go toward (in masculinization) less punctuation/rugosity, more melanization, greater development of tubercles on the head and carinae on the elytra, and a widening of the frons. This latter character is not uniformly present throughout the included taxa, but is most pronounced in Melalgus and the Bostrichini. Since this is a developmental character, and not easily "characterized", its importance may be doubted; however, I find the similarity in direction of change and characters
involved too unique to be considered coincidence. The degree of difference between sexes of different species varies, with males of *Melalgus confertus* being almost without masculinization, while females of the *Melalgus battillum* species group exhibit a considerable number of masculine characteristics. This situation is deserving of much more investigation at the developmental level.

Another synapomorphy that links the Polycaoninae and Bostrichinae is the confluent gular sutures. This condition also occurs in the Dinoderinae, although I suggest that it is nonhomologous in that case. This is because of the several novelty characters that support alternatives to homology, and because the confluent condition is a widespread reduction state in the Coleoptera, thus invoking assumption #1.

The form of the procoxae described above in combination with the prognathous head, which is prominent from above, as well as the wide intercoxal process of the first visible abdominal sternite, and nontuberculate pronotum distinguish this subfamily from other Bostrichidae.

The two genera included in this subfamily will be dealt with further below.
Bostrichinae


This group has remained remarkably stable as a unit since Lacordaire (1857), due to the unique form of the prothorax (fig. 10). This easily visible monster synapomorphy is the defining feature of the subfamily. It is sometimes confused with that of the dinoderines, but it can be distinguished quite easily.

The dinoderine prothorax is gradually narrowed anteriorly from the basal one-fourth, with the frontal horns, when present, dentate and flattened. The bases of these frontal horns are contiguous, or nearly so. They are usually the obvious center pair of an arcuate row from the baso-lateral margins. Concentric semicircles of similar denticles extend to the center of the prothorax, on the apical half.

The bostrichine prothorax has the frontal horns separate at the base, usually widely so, with the frontal margin (viewed from above) flattened or emarginate between. The rasp-like tubercles on the disk, when present, are never arranged in concentric semicircles.
Figure 10. *Dinapate wrighti* Horn, lateral habitus.
Another distinguishing character of these two subfamilies is the form of the procoxae and their cavities. In the Bostrichinae the procoxae are conical, with the cavity constricting them in such a manner as to make the procoxae seem to expand on the outside, much like a balloon with a tight string around it. The lateral margins of the procoxal cavities are rounded.

In the Dinoderinae, the lateral margins of the procoxal cavity are angulate, with the procoxae transverse and less conical. Viewed from front or back they are widely triangular, and not at all constricted.

I consider a system of 5 tribes to best represent the current state of knowledge of the Bostrichinae (see below). Three of these tribes are almost certainly monophyletic, each being defined on an obvious monster synapomorphy. The Xyloperthini are also possibly monophyletic, as the form of the abdominal intercoxal process is different than that of the Apatini, and the general habitus and small size of the former is remarkably constant in the tribe. The Bostrichini are, however, almost certainly polyphyletic, and possibly paraphyletic as well. They are the more generalized genera that are left behind when the other tribes are removed. Obviously, this subfamily would benefit from a phylogenetic reconstruction, hopefully made more possible by the clarification of sister-group and
higher relationships. So far as I know, all members of this group are wood-borers. Several species are widely distributed by commerce, and the constant possibility of new introductions make the use of regional faunal works risky for identification of members of this group by those without a reference collection.

The subfamily contains 415 currently recognized species, and in the nearly 11,000 specimens I have examined, I have seen only a very few specimens that cannot be placed in a described species. Several genera badly need revision, and several of the small genera could be combined. The 3 genera *Sinoxylon*, *Micrapate*, and *Lichenophanes* together contain approximately 32% of the species, with the remaining 56 genera averaging only 5 species each. There are 20 monotypic genera.

**Key to the tribes of the Bostrichinae**

1. Intercoxal process of 1st visible sternite with a planar face, viewed from a ventral aspect; in cross section, this process is T-shaped; process always visible. Metepisternum usually broadly truncate behind, with metepimeron widely separated from metasternum posteriorly........................................2

1'. Intercoxal process of 1st visible sternite lamellate, without a planar face, viewed from a ventral aspect; in cross section, this process is |-shaped; sometimes
process is below the level of the coxae and not visible, or reduced. Metepisternum usually narrowed posteriorly, often acute, metepimeron nearly contacting metasternum posteriorly..........................4

2. Mandibles long, pointed; almost always crossing in a shearing manner; without longitudinal striae on exterior face........................................3

2'. Both mandibles short, blunt, meeting along midline, the cutting edges directly apposable; each with 2 fine longitudinal striae on external face near tip........................................Sinoxylini

3. Anterior edge of pronotum curled under, with setal fringe of margin hidden behind this rolled edge..................................................Bostrichini

3'. Anterior edge of pronotum only slightly rounded, not curled under, marginal setal fringe insertion exposed.
32 - 51 mm..................................Dinapatini

4. Intercoxal process of first visible sternite declivous, not visible except at base; females with a transverse line of setae in the middle of sternite VIII, the apical margin densely covered in long, recurved, spatulate setae; ovipositor wide and short.....Apatini

4'. Intercoxal process of first visible sternite plane, visible for entire length; female sternite VII not as above, with normal ovipositor..............Xyloperthini
Genera of bostrichine tribes (* denotes taxa examined)

Dinapatini
  *Dinapate Horn, 1 sp.

Apatini
  *Kylomedes Lesne, 7 spp.
  *Apate Fabricius, 15 spp.
  *Phonapate Lesne, 11 spp.

Sinoxylini
  *Sinocalon Lesne, 3 spp.
    Calodectes Lesne, 1 sp.
    Calodrypta Lesne, 1 sp.
  *Calopertha Lesne, 4 spp.
  *Sinoxylon Duftscheid, 52 spp.
  *Xyloperthodes Lesne, 16 spp.

Bostrichini
  *Bostrichus Muller, 1 sp.
  *Detricrates Lesne, 1 spp.
  *Lichenophanes Lesne, 40 spp.
    Calopherus Lesne, 2 spp.
  *Neoterius Lesne, 3 spp.
  *Dolichobostrychus Lesne, 5 spp.
    Parabostrychus Lesne, 2 spp.
    Megaobostrychus Chujo, 1 sp.
  *Heterobostrychus Lesne, 6 spp.
  *Bostrychopsis Lesne, 24 spp.
  *Amphicerus LeConte, 15 spp.
  *Apatides Casey, 1 sp.
  *Bostrychoplites Lesne, 15 spp.
  *Micrapate Casey, 15 spp.
    Bostrychuarus Lesne, 1 sp.
    Sinoxyloides Lesne, 1 sp.

Xyloperthini
  *Xylomeira Lesne, 1 sp.
    Amintinus Lesne, 8 spp
  *Xylopriata Lesne, 4 spp.
  *Dendrobiella Casey, 5 spp.
    Paraxylogenes Damoiseau, 1 sp.
  *Tetrapriocera Horn, 4 spp.
    Xylogenes Lesne, 6 spp.
  *Gobiccia Lesne, 11 spp.
  *Enneadesmus Mulsant, 12 spp.
    Xylophorus Lesne, 2 spp.
    Ctenobostrychus Reichardt, 1 sp.
  *Xylobiops Casey, 5 spp.
  *Xyloblaptus Lesne, 3 spp.
  *Xylodeleis Lesne, 1 sp.
    Xylocis Lesne, 1 sp.
    Xylotillus Lesne, 1 sp.
    Octodesmus Lesne 4 spp.
*Xylodectes* Lesne, 2 spp.
*Calonistes* Lesne, 1 sp.
*Xyloperthella* Fisher, 4 spp.
*Xylocripta* Lesne, 1 sp.
*Xylionculus* Lesne, 4 spp.
*Xylion* Lesne, 7 spp.
*Paraxylion* Lesne, 1 sp.
*Mesoxylion* Vrydagh, 3 spp.
*Plioxylion* Vrydagh, 1 sp.
*Xylionopsis* Lesne, 3 spp.
*Xylobosca* Lesne, 12 spp.
*Calophagus* Lesne, 1 sp.
*Xylothrips* Lesne, 4 spp.
*Xylopsocus* Lesne, 17 spp.
*Sifidius* Lesne, 2 spp.
*Xylopertha* Guerin-Meneville (not Lesne), 3 spp.

Psoinae NEW SENSE


Psoidae Böving and Craighead, 1931.

Chileniidae Lesne, 1921.


Only the most important references are listed above.

This group is the subject of a nearly completed taxonomic and phylogenetic revision, and will be treated only briefly here.

There are 6 genera and 11 species currently recognized in this group. The included genera are quite divergent in form, yet have a generally recognizable facies. All but two genera, totalling 5 of the species, are very rare in collections. This has hampered character generation, due to lack of material available for disarticulation. One
genus is known from 1 specimen, one from only 3, each held by a different institution, and 2 others with only a handful of specimens in widely scattered collections.

The group can be recognized by its synapomorphies: the first visible sternite with the intercoxal process lamiform or absent, and usually (one exception) lacking postcoxal carinae; the pronotum rounded, narrowed behind (fig. 11); procoxae very narrowly conical (fig. 12); and the head with a distinct, elongate neck. In addition, many of the species are brightly colored, with Coccographis nigrorubra easily being the most beautiful of the bostrichiforms.

The inclusion of Chilenius in this subfamily is an innovation, not, however, without its problems. It is placed here with some doubts as it is very derived, and difficult to place. Larvae of this genus would be of great help in placing it with certainty in a subfamily.

Key to the genera of Psoinae

1. Protibia with large curved apical spine; pronotum with large dorsal teeth; no closed R cell in metathoracic wing; without intercoxal process on basisternum...........

1'. Protibia with only small straight apical spines; pronotum without large dorsal teeth; metathoracic wing with closed R cell; basisternum with acute intercoxal process, free at end from the internal sternellum....2
Figure 11. *Stenomera blanchardi* Lucas, dorsal habitus.
2. Abdomen with transverse postcoxal carina.............Psoidia
2'. Abdomen lacking postcoxal carina.................................3
3. Protibia with 1 apical spine; last two visible sternites connate; elytra covered in long red setae......Coccographis
3'. Protibia with 2 apical spines; last visible sternites free; elytra not as above..............................4
4. Tarsi 4-4-4..........................................................5
4'. Tarsi 5-5-5, first segment short.........................Heteropsoa
5. Abdominal sternite II visible at sides, divided by hind coxae; abdomen lacking intercoxal process on sternite III; abdomen metallic..............................Psoa
5'. Abdominal sternite II not visible; abdomen with intercoxal process on sternite III; abdomen not metallic............................Stenomera

Genera of Psoinae

[number of species in (), all taxa have been examined]

Psoidia Herbst (4)
Psoidia Lesne (1)
Coccographis Lesne (1)
Stenomera Lucas (1)
Heteropsoa Lesne (2)
Chilenius Lesne (2)
Dinoderinae

This small, but economically important subfamily can be recognized by the cowled prothorax, which is usually evenly rounded in front; by the concentric rings of dentate tubercles on the prothorax; and by the transverse, triangularly projecting procoxae. Distinguishing this subfamily from the Bostrichinae is further discussed under that group.

The 6 genera in this subfamily are well distinguished. The subfamily is interesting biologically, various species feeding on grains (Rhyzopertha), bamboos (Dinoderus), and conifers (Stephanopachys) as larvae, adding dried foodstuffs and other plant products in the adult diet (Rhyzopertha, Dinoderus). Several species of a variety of genera (Dinoderus, Rhyzopertha, and Prostephanus) are known to attack hardwoods, and given the restriction of the Lycitiae (the hypothesized sister-group of the dinoderines) to this habit, I suspect this is the ancestral food resource.

Key to the genera of Dinoderinae

1. Elytra with apical declivity truncate or concave, declivity often with tubercles, margins, or an enlarged suture; pronotum narrowed anteriorly, the apical row of dentations V-shaped, the anteriormost pair markedly larger than the rest and adjacent at base............2
1'. Elytra evenly rounded and convex from disk to apex, not distinctly set off, never with more than simple pustulations; pronotum evenly rounded and semicircular anteriorly, the denticles arranged in a U-shape, the median pair not differentiated

2. Elytral declivity and disk smooth, occasionally with a few small pustules on face of declivity, never on sutural margin or elytral disk; one or no tubercles on margin of declivity

2'. Elytral declivity with face, suture, margins and apex all with rounded pustules; top of margin with 3 conical tubercles covered in pustules; elytral disk posteriorly with rows of pustules between punctate striae

3. Scutellum transversely rectangular, pronotal disk punctate posteriolaterally; second antennomere distinctly shorter than first

3'. Scutellum nearly square, pronotal disk punctate or tuberculate posteriolaterally; second antennomere subequal in length to first

4. Pronotal disk posteriorly with elongate punctures, approaching cribrate; elytral declivity granulate; elytra slightly obliquely truncate at suture

................................. Rhizoperthodes
4'. Pronotal disk posteriorly tuberculate, elytral declivity granulate or not; elytra conjointly rounded to suture........................................5

5. Pronotum with tubercles on apical half low, blade-like and connected at bases into semicircular ridges; posterior half with anteriorly directed, low, blunt, imbricate tubercles; elytra without tubercles, variably smooth to slightly rugose between punctures............

.........................................................Rhyzopertha

5'. Pronotum with sharp, elevated, separate tubercles on entire disk, or with obtuse tubercles on basal half; elytra usually at least pustulate on declivity.................................Stephanopachys

Genera of Dinoderinae

Rhizoperthodes Lesne, 1 sp.
*Rhyzopertha* Stephans, 1 sp.
*Stephanopachys* Waterhouse, 16 spp.
*Prostephanus* Lesne, 8 spp. (3 undescribed)
*Diocderopsis* Lesne, 3 spp.
*Diocderus* Stephens, 27 spp.

Lyctinae

Lyctidae Gerberg 1957.

This group has been treated mainly as a subfamily of the bostrichids by Old World workers, and mainly as a family by American workers. The resulting confusion has been held to a minimum, however, by uniform usage of the subdivisions of the group at the tribal level. To
recognize this group as a family, with a monophyletic taxon concept, would involve recognition of at least 6 families from within the Bostrichidae mihi, thus it seems best to follow European usage, and consider this group a subfamily of the Bostrichidae.

The 2 segmented club of the majority of species of this family (3 segmented in Cephalotoma) differs from all other Bostrichidae. The flat intercoxal process of the prothorax, made up of the sternellum; absence of a free prosternal process arising from the basisternum; and visible procoxal closures will distinguish all members of the subfamily. The dorso-ventrally flattened, parallel sided habitus, with the head visible from above and complete lateral margins of the pronotum will further distinguish this group.

The larvae of this subfamily are all wood borers, being limited to sapwood with vessel luminae, tracheae, or pores large enough to insert the ovipositor for egg laying. Conifers are immune from attack. For a review of the biology of the lycines, see Gerberg (1952).

The 12 genera of this subfamily, keyed by Gerberg (1957), are arrayed in 2 tribes. Unfortunately, little is known regarding the phylogenetic relationships of the genera, or the monophyly of the tribes. The 67 described species are placed in genera as listed below. As in the
Bostrichinae, most of the species are placed in only a few genera, with *Lyctus* and *Trogoxylon* together containing over half the species.

Tribes and genera of Lyctinae

Lyctini

*Lyctus* Fabricius, 24 spp.
*Acantholyctus* Lesne, 2 spp.
*Lyctodon* Lesne, 1 sp.
*Lyctoplites* Lesne, 1 sp.
*Minthea* Pascoe, 8 spp.
*Lyctoxylon* Reitter, 3 spp.

Trogoxylini

*Trogoxylon* LeConte, 13 spp.
*Triastaria* Reitter, 1 sp.
*Lyctopsis* Lesne, 3 spp.
*Lyctoderma* Lesne, 4 spp.
*Cephalotoma* Lesne, 3 spp.
*Phyllyctus* Lesne, 1 s.

Euderinae

Euderiiitae Lesne 1934b.
Euderinae Lesne, 1938. Crowson 1961 (adults)
Euderinae Crowson 1961 (larvae)

This subfamily contains a single genus, with 2 known species (*Euderia squamosa* Broun and one undescribed, Watt 1982: table 1). Their unique habitus is unmistakable (Watt, 1982: fig 1). Further characters that distinguish this subfamily are the elongate trochanters and first tarsomere, the conical tubercle in the center of the pronotal disc, the pronotum parallel sided and narrower than the elytral base, the hind coxae not excavate, and the 10 segmented antenna with a 3 segmented club which is
received in a groove between the conical procoxae.

These species constitute all the native bostrichids, with the exception of Anobiinae (22 native spp.), in the New Zealand fauna, and this geographic isolation is interesting, as the Euderiinae is the only subfamily so very restricted. It is interesting that these subfamilies are sister-groups but unfortunately, the phylogenetic relationships within the Anobiinae are virtually unknown, so no zoogeographic information can be drawn from this situation.

The association of *Euderia squamosa* with the southern beech (*Nothofagus*) (Crowson, 1961), may offer some predictions to solve this zoogeographic mystery. If the relationship is an ancient one, and the ancestors of *Euderia* arrived in New Zealand via continental vicariance, one would expect to find Euderiines in other parts of *Nothofagus' range*: Chile, Australia, or New Guinea. The fact that they have not turned up to date in these areas could be a result of 2 factors: collecting artifacts or misplaced taxa. *Euderia* are rarely collected, even by New Zealanders themselves (C. Watt, pers. com.), and New Zealand is the most intensively sampled area in the range of *Nothofagus*. They are not known to be taken by traps of any kind, only by beating vegetative branches in early summer (Crowson, 1961). It is not at all inconceivable
that the euderiines will yet be collected outside New Zealand.

Most coleopterists would be hard pressed to place *Euderia* in the bostrichids on sight. It is evidence of Pierre Lesne's great contribution to bostrichidology that he recognized, and placed this genus here. Broun had described it in the Anobiidae (not altogether a bad choice), and I suspect others may have done worse. I think males could be confused with Anobiinae or Euglenidae, while the females could be misplaced in a variety of families in the Cucujiformia.

If on the other hand, *Euderia* is the product of a dispersal event involving the anobiine-euderiine ancestor lineage, relictual distribution could be the result of chance. In that case, contaxons would not be predicted in specific areas.

The decision to continue to recognize this group as a subfamily is, as all such decisions are, subjective. It would be easy to treat them as Anobiinae. Three reasons argue against that action. First, nomenclatorial stability is maximized by retaining its current status, which has remained constant since the genus was first placed in the world classification system. Second, those who disagree with my hypothesis of phylogeny, or the monophyletic taxon concept would be expected to continue to use the subfamily
form, not the tribal form, resulting in differing usage by different workers. Lastly, diagnosing larvae of a subfamily that combined Euderia and the anobiines would be more difficult than either alone. Since retaining subfamily status here does not violate monophyly, I chose to do so.

**Anobiinae NEW STATUS**

Anobiidae, sensu Crowson, 1981, including Ptilinae, Gnostidae, and Ectrephidae of authors.

This group is equal to the Anobiidae of Crowson (1981). Its placement here is necessitated by the monophyletic taxon concept. It includes all taxa previously placed in the Anobiidae and Ptilinae.

The sister-group relationship of the anobiines and the euderiniines seems well established. The form of the tarsi, trochanters, wing venation, and larval vestiture are all suggestive of this relationship, and are here considered synapomorphic. The asperities of many anobiine larvae are considered homologous to the setae of Euderia, which are arranged in a similar manner. The setae of Ptilini larvae are also probably homologous. The other shared derived characters at lower levels of universality are shown on the cladogram.

I hypothesize the ancestral anobiine had a jugal lobe in the hind wing; a W cell present; 11 segmented antennae
with a 3 segmented club and segments 3–8 simple; the first tarsomere longer than the others; excavate hind coxae; complete pronotal margins; widely separated prococxae with a flat intercoxal process consisting of the sternellum; and 2 small straight tibial spines. The larva had an exerted head; 2 segmented antenna; 3 transverse folds on the abdominal tergites; spiracles with dorsal prolongations; and was clothed in long setae.

All this points to a beetle somewhat like the modern Dryophilini. A phylogenetic analysis of Anobiinae tribes and genera is badly needed, and should receive high priority in the search for a more informative classification of the bostrichids.

Demoting the anobiids to a subfamily of the bostrichids, with the ptinids placed as a tribe thereof is by far the most radical taxonomic change proposed here. This decision was not reached quickly, or easily. The reasons for doing so resulted from the problems I encountered when trying to use the anobiids for out-group comparisons in polarizing bostrichid characters. The resulting pattern of extreme homoplasy indicated a problem of out-group selection, and the next highest taxon was then used, with the anobiids included in the in-group. This problem was the initial impetus for the higher classification portions of this paper, and has ended with a
radically different position for the anobiines than in previous classifications.

My polarizations and homologies differ significantly from those of previous authors. Many of the characters have been dealt with in the section on Bostrichidae phylogeny. White (1971) discusses his concepts of the phylogeny of the anobiines, based on the hypothesis of a ptinid-anobiid sister-group relationship. Working from a broader basis, Crowson (1961) raised doubts about the relationship of the anobiids to the other bostrichids, yet in the end, left the question of relationships open. I differ from both these authors, in not considering the anobiines the sister-group of the bostrichids, which results in a different interpretation of almost all polarizations.

The Ptinini have long been placed as a separate family, but they appear to be highly derived, and divergent anobiines. Most of the morphological changes involve reduction, with the prothorax and head narrowed, bringing the antennal insertions to the dorsal part of the head; the metasternum shortening, widening the separation of the metacoxae and tipping them forward so that the excavation, if still present, would be directed toward the substrate instead of caudally; and a further reduction of the antennae from the reduced form in the higher anobiines.
The inclusion of this group in the anobiids was previously proposed by Crowson (1981), although he discussed the anobiine derivation of the ptinids in his 1955 work. Both Crowson (1955) and White (1971) agree that the ptinids are closely related to the Hedobiinae, but White considers this a basal relationship. All my polarizations suggest the opposite. One novelty character that joins these groups is the lack of a leptophragma in the cryptonephidial system, unique in all Coleoptera studied (Saini, 1964).

This is by far the largest subfamily of the Bostrichidae, with over 1300 species listed by Pic (1912a, 1912b) and an estimate of around 2000 species in 180 genera by Lawrence (1982). The taxonomy of the group is confused, with the exception of the United States and European faunas, plus a few small faunas and/or taxa. The majority of the named species in Latin America were described by Maurice Pic, and are simply impossible to identify from the descriptions (White, 1981). From the work of Richard White, it is obvious that many species remain undescribed, and the Neotropical fauna, at least, is mostly undescribed (R. White, pers. com.).

I have examined relatively few anobiines, and will leave the characters in the key to diagnose the subfamily.

The following is a list of the tribes of anobiines, with the number of described genera following. The non-
Ptilinini are from White (1974), and the Ptilinini is from Lawrence (1982). I have made no effort to check the literature on this subfamily since these publications, and the numbers should be treated as approximate.

Tribes of Anobiinae

Dryophilini, 11
Ernobiini, 14
Anobiini, 32
Ptilinini, 3
Alvarengiellini, 1
Xyletinini, 23
Dorcatominae, 42
Tricorynini, 10
Hedobiini, 4
Ptilini, 40 (estimate)
EPILOGUE

The hypotheses presented above should be seen as just that - preliminary ideas which require testing. The evolutionary scenarios should be viewed as merely suggestions of possible pathways, as they represent best-guess concepts. I hope that they make the other information more interesting and thought provoking.

It can be seen that many more questions are raised than answered about the evolution of the Bostrichiformia. Our knowledge of this group, like most major lineages of Coleoptera, is in its infancy, and this can be considered no more than an attempt to further that knowledge, not as an end to their study.
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APENDIX A

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Henry and Anne Howden, private collection, Ottawa, Ontario, Canada (HAHC).

Karl Stephan, private collection, Red Oak, Oklahoma, U.S.A (KSC).

Michael A. Ivie, private collection, Columbus, Ohio, U.S.A (MAIC).


Instytut Zoologii, Polska Akademia Nauk, Warszawa, Poland (MZFW). Dr. S. A. Slipinski.

Ohio State University Collection of Insects and Spiders, Department of Entomology, The Ohio State University, Columbus, Ohio, U.S.A. (OSUC). Dr. C. A. Triplehorn.


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Essig Museum, Division of Entomology, University of California, Berkeley, California, U.S.A. (UCBC). Dr. J. A. Chemsak.
APENDIX B

Proposed Classification of the Polyphaga, as used in this paper.

I. Lower Polyphaga (informal group)
   A. Staphyliniformia
      1. Staphylinioidea
      2. Hydrophiloidea
   B. Eucinetiformia
      1. Eucenetoidea
      2. Dascilloidea
   C. Scarabaeiformia
      1. Scarabaeoidea
   D. Elateriformia
      1. Byrrhoidea
      2. Buprestoidea
      3. Dryopoidea
      4. Elateroidea
      5. Cantharoidea

II. Higher Polyphaga (informal group)
   A. Derodontiformia
      1. Derodontoidea
         a. Derodontidae
   B. Bostrichiformia
      1. Bostrichoidea
         a. Nesodendridae
         b. Dermestidae
         c. Endecatomidae
         d. Bostrichidae
   C. Cucujiformia
      1. Jacobsonioidea
         a. Jacobsoniidae
      2. Lymexylionidae
      3. Cleroidea
      4. Cucujoidea
      5. Tenebrionoidea
      6. Chrysomeloidea
      7. Curculionoidea

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