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A Cladistic Analysis and Classification of the Subgenera and Genera of the Large Carpenter Bees, Tribe Xylocopini (Hymenoptera: Apidae)[1]

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CONTENTS

ABSTRACT   Phylogenetic analyses of the genera and subgenera of the tribe Xylocopini (Large Carpenter Bees) were made using morphological characters coded for 51 species of the ingroup. These species represented all but three of the previously recognized subgenera. Twenty species of bees constituting the outgroup also were examined to evaluate primitive and derived character states within the Xylocopini. Four different analyses were made because of uncertainty in hypotheses of character transformations and among the relationships of the outgroup taxa. Cladistic parsimony analyses showed that previous classifications were based on combinations of characters and not unique synapomorphies. Three major clades were supported in most analyses presented here; two are from the Old World, and one is from the New World. A biogeographically mixed group of subgenera are not clearly placed in this analysis; among this group are likely to be found the basal members of the tribe.

A new generic and subgeneric classification is proposed for the Xylocopini. I conclude that recognition of *Proxylocopa* Maa and *Lestis* Lepeletier and Serville as genera creates a paraphyletic genus of *Xylocopa;* these should be recognized as subgenera of an expanded *Xylocopa*. A new subgenus, *Maaiana*, is proposed here for *X. bentoni* and related species formerly recognized as members of the subgenus *Nodula*. The following subgeneric synonymies also are proposed: *Xylomelissa* Hurd & Moure is expanded to include *Epixylocopa* Hurd & Moure, *Alloxylocopa* Hurd & Moure, *Dinoxylocopa* Hurd & Moure and *Acroxylocopa* Hurd & Moure; *Ancylocopa* Maa is synonymized with *Proxylocopa* Maa; *Schonnherria* Lepeletier is expanded to include *Ioxylocopa* Hurd & Moure and *Xylocospila* Hurd & Moure; *Stenoxylocopa* Hurd & Moure is expanded to include *Xylocopina* Hurd & Moure; *Neoxylocopa* Michener is expanded to include *Megaxylocopa* Hurd & Moure; *Bomboixylocopa* Maa is expanded to include *Mimoxylocopa* Hurd & Moure; *Mesotrichia* Westwood is expanded to include *Platynopoda* Westwood, *Hoplitocopa* Lieftinck and *Hoploxylocopa* Hurd & Moure, and; *Koptortosoma* Gribodo is expanded

to include *Oxyxylocopa* Hurd & Moure, *Cyphoxylocopa* Hurd & Moure, *Cyaneoderes* Hurd & Moure and *Afroxylocopa* Hurd & Moure. A key to identify the subgenera is provided.

INTRODUCTION

The large carpenter bees, tribe Xylocopini, generally are robust, fast-flying insects, some of which are among the largest of all the bees. As their name implies, most members of this group place their nests in dead solid plant material, usually various kinds of wood, but some use the hollow culms of bamboo (subgenus *Bihma*; Maeta et al., 1985), or the pithy stems of *Aloe* (subgenus *Gnathoxylocopa*; Watmough, 1974). Females of *Proxylocopa* construct their nests in the ground. Some species of Xylocopini are important pollinators of particular plants (e.g., Corbet and Wilmer, 1980; Gottsberger et al., 1988) but none seems to restrict its pollen collecting to one or a few plant taxa. Other well-studied features of the biology of the group include its social behavior (reviewed in Gerling et al., 1988; Maeta and Sakagami, 1995; Michener, 1990), exocrine gland morphology (Minckley, 1994; Vinson, 1994) and product chemistry (Gerling et al, 1988), and male reproductive behavior (Alcock, 1992; Gerling et al., 1988; Minckley, 1994).

The Xylocopini is one of four tribes in the subfamily Xylocopinae. The other three tribes—Allodapini, Ceratinini, and Manueliini—are mostly smaller than the Xylocopini and build their nests in broken twigs or stems (Daly et al., 1987; Michener, 1974, 1990).

The purpose of this study is a cladistic analysis of the phylogenetic relationships among the genera and subgenera of the large carpenter bees, tribe Xylocopini. A worldwide revision of this group was last undertaken in 1963 by Hurd and Moure. They recognized 53 supraspecific taxa in the tribe: Three genera, *Lestis*, *Proxylocopa*, and *Xylocopa*; 48 subgenera in *Xylocopa* and two subgenera in *Proxylocopa*. Although their work is the most comprehensive study of the group to date, both with respect to the number of taxa examined and the number of characters considered, they did not provide an explicit hypothesis of phylogenetic relationships for the members of the tribe. Da Cunha (1992) did a quantitative similarity analysis of the subgenera of *Xylocopa* using the characters of Hurd and Moure (1963). This study was largely concerned with phenetic methodology and was not a taxonomic revision of the Xylocopini, so no discussion of phylogenetic relationships or classifi-

catory changes were provided. Nevertheless, it is worth noting that the relationships generated by Da Cunha's study should be used with caution, because similarity methods can result in poor estimates of phylogeny (Hillis et al., 1994; Michener, 1970), especially when the data used were intended to diagnose groups and not to infer phylogeny.

In this study, I use an exemplar approach in the cladistic analysis (see Phylogenetic Analysis). I also propose some changes in the classification based on my phylogenetic analyses. My approach for taxonomic decisions is to combine terminal taxa that are monophyletic based on the phylogenetic analyses and retain the names of the problematic taxa as they were recognized before this study. Future analyses may result in the recognition of fewer supraspecific groups than are accepted here.

MATERIALS AND METHODS

SELECTION OF TAXA

In order to examine ingroup relationships, I used exemplar taxa of all supraspecific taxa of the Xylocopini recognized by Hurd and Moure (1963) for which I could obtain both sexes. This meant the following subgenera of

Xylocopa were not included in the analyses: *Euxylocopa*, *Lieftinckella*, *Ioxylocopa*, *Monoxylocopa*, *Diaxylocopa* and *Dinoxylocopa*. *Euxylocopa* was erected by Hurd and Moure (1963) for a species *X. (Euxylocopa) fraudulenta* known only

Table 1. List of taxa examined organized by the subgenera recognized herein. An asterisk (*) indicates type species; (!) indicates the exemplars used in the phylogenetic analysis. The acronyms, as explained in Materials and Methods, show the sources of the specimens. Subgeneric assignments by previous authors, if different than those proposed here, are shown in parentheses.

Nanoxylocopa	X. ciliata Burmeister *!	(KSEM)
Cirroxylocopa	X. vestita Hurd and Moure *!	(USNM)
Xylocopoda	X. elegans Hurd and Moure *!	(KSEM)
Schonnherria	X. bambusae Schrottky ! (Xylocospila)	(KSEM)
	X. loripes Smith	(KSEM)
	X. macrops Lepeletier !	(KSEM)
	X. micans Lepeletier !	(KSEM)
	X. viridigastra Lepeletier !	(KSEM)
	X. viridis Smith	(KSEM)
	X. chrysopoda Schrottky ! (Ioxylocopa)	(USNM)
Dasyxylocopa	X. bimaculata Friese *!	(KSEM)
Xylocopsis	X. funesta Maidl *!	(KSEM)
Monoxylocopa	X. abbreviata Hurd and Moure *	(USNM)
Diaxylocopa	X. truxali Hurd and Moure *	(LACM)
Notoxylocopa	X. guatemalensis Cockerell !	(KSEM)
	X. tabaniformis androleuca Michener *	(KSEM)
	X. t. azteca Cresson	(KSEM)
	X. t. tabaniformis Smith !	(KSEM)
Xylocopoides	X. californica arizonensis Cresson !	(KSEM)
	X. cyanea Smith !	(KSEM)
	X. pallidiscopa Hurd	(KSEM)
	X. virginica Linnaeus *	(KSEM)
Calloxylocopa	X. tenuata Smith *!	(KSEM)
Neoxylocopa	X. aeneipennis (Degeer)	(KSEM)
	X. b. brasilianorum (Linnaeus) *	(KSEM)
	X. darwini Cockerell	(KSEM)
	X. fimbriata Fabricius ! (Megaxylocopa)	(KSEM)
	X. f. frontalis (Olivier) (Megaxylocopa)	(KSEM)
	X. grisescens Lepeletier	(KSEM)
	X. mexicanorum Cockerell	(KSEM)
	X. varipuncta Patton !	(KSEM)
Stenoxylocopa	X. artifex Smith *!	(KSEM)
	X. m. micheneri Hurd	(KSEM)
	X. ruficollis Hurd and Moure ! (Xylocopina)	(FMNH)
Ctenoxylocopa	X. fenestrata (Fabricius) *!	
	X. sulcatipes Maa	(KSEM)
Copoxyla	X. iris (Christ) *!	(KSEM)
Rhysoxylocopa	X. cantabrita Lepeletier *!	(KSEM)
	X. uclesiensis Pérez	(USNM)
Gnathoxylocopa	X. kobrowi Brauns	(USNM)
	X. sicheli Vachal *!	(USNM)
Xylocopa	X. valga Gerstaecker !	(KSEM)
	X. violacea (Christ) *!	(KSEM)
Biluna	X. auripennis Lepeletier !	(KSEM)
	X. tranquebarorum (Swederus)	(KSEM)
Bomboixylocopa	X. chinensis Friese !	(USNM)
	X. rufipes Smith ! (Mimoxylocopa)	(KSEM)
Nyctomellita	X. myops Ritsema	(KSEM)
	X. tranquebarica (Fabricius) *!	(KSEM)
Nodula	X. a. amethystina (Fabricius)	(KSEM)
	X. amethystina (Fabricius) *!	(KSEM)
	X. bentoni Cockerell !	(KSEM)
Zonohirsuta	X. dejeanii Lepeletier !	(KSEM)
Prosopoxylocopa	X. mirabilis Hurd and Moure *!	(AMNH)
Xylomelissa	X. absurdipes Enderlein ! (Dinoxylocopa)	(USNM)
	X. albifrons Lepeletier !	(USNM)
	X. carinata Smith *	(USNM)
	X. capitata Smith ! (Acroxylocopa)	(KSEM)
	X. erythrina Gribodo ! (Perixylocopa)	(PPI)
	X. lugubris Gerstaecker ! (Apoxylocopa)	(PPI)
	X. rufitarsis Lepeletier ! (Epixylocopa)	(KSEM)
Alloxylocopa	X. appendiculata circumvolans Smith *!	(KSEM)
Xenoxylocopa	X. chiyakensis (Cockerell) *!	(KSEM)
	X. inconstans Smith	(KSEM)
Mesotrichia	X. acutipennis Smith ! (Hoploxylocopa)	(BM)
	X. assimilis Ritsema ! (Hoplitocopa)	(RNH)
	X. flavorufa (DeGeer)	(KSEM)
	X. latipes (Drury) ! (Platynopoda)	(KSEM)
	X. tenuiscapa Westwood ! (Platynopoda)	(KSEM)
	X. torrida (Westwood) *!	(KSEM)
Koptortosoma	X. aestuans (Linnaeus)	(KSEM)

Table 1 continued

Koptortosoma (continued)		
	X. apicalis Smith	(KSEM)
	X. aruana aruana Ritsema	(KSEM)
	X. caerulea (Fabricius) ! (Cyaneoderes)	(KSEM)
	X. caffra (Linnaeus) !	(KSEM)
	X. kuhni Friese ! (Cyphoxylocopa)	(RNH)
	X. nigrita (Fabricius) *! (Afroxylocopa)	(KSEM)
	X. ocularis Pérez ! (Cyphoxylocopa)	(RNH)
	X. parva Enderlein ! (Oxyxylocopa)	(BM)
	X. pubescens Spinola!	(TAV)
	X. scioensis Gribodo	(KSEM)
	X. senior Vachal	(KSEM)
	X. sinensis Smith !	(KSEM)
	X. varipes Smith ! (Oxyxylocopa)	(BM)
Lestis	X. aeratus Smith !	(KSEM)
	X. bombylans (Fabricius)	(KSEM)
Proxylocopa	X. olivieri (Lepeletier) *	(TAV)
	X. rufa (Friese) !	(TAV)
	X. altaica (Popov) (Ancylocopa)	(ZIA)
	X. andarabana (Hedicke) (Ancylocopa)	(ZIA)
	X. nitidiventris (Smith) (Ancylocopa)	(ZIA)
	X. nix (Maa) (Ancylocopa)	(ZIA)
	X. parviceps (Morawitz) (Ancylocopa)	(ZIA)
	X. pavlovskyi (Popov) (Ancylocopa)	(ZIA)
	X. przewalskyi (Morawitz) (Ancylocopa)	(ZIA)

from females and later synonymized by Maa (1970) under X. (Perixylocopa) erythrina. I was not able to examine a male of Lieftinckella. The remaining four monotypic subgenera were examined, but are known from only one sex—Ioxylocopa and Dinoxylocopa from males and Monoxylocopa and Diaxylocopa from females. For some large or seemingly variable subgenera, additional species were included. Character analysis was restricted to these exemplars. The two subgenera of Proxylocopa differ only in one character, the size of the ocelli, so I included only Proxylocopa rufa after initial examinations. All the taxa examined and the respective repositories of specimens that I used are listed in Table 1. Because the taxonomic categories recognized by Hurd and Moure (1963) were narrowly defined, these exemplars are likely to provide a good representation of the morphological diversity and a reasonable first estimate of the phylogenetic relationships in the group.

Specimens used in this study were from the following institutions (acronyms in parentheses): Field Museum of Natural History, Chicago, A. Newton (FMNH); Los Angeles County Museum, Los Angeles, R. Snelling (LACM); National Collection of Insects, Plant Protection Research Institute, South Africa, C. Eardley (PPI); The National Museum of Natural History, Washington, R. McGinley (USNM); The Natural History Museum, London, G. Else (BM); Rijksmuseum van Natuurlijke Historie, Leiden, C. van Achterberg (RNH); Snow Entomological Museum, University of Kansas, Lawrence, C. D. Michener (KSEM); Tel-Aviv University, Tel-Aviv, D. Gerling (TAU); Zoological Institute, Academy of Sciences, Leningrad, Y. Pesenko (ZIA).

Phylogenetic relationships of the large carpenter bees with other tribes of Xylocopinae were analyzed by

TABLE 2. List of outgroup taxa examined.

Apidae: Xylocopinae
    Ceratinini
        Ceratina (Ceratina) cucurbitina (Rossi)
        C. (Euceratina) cyanea Kirby
        C. (Lioceratina) flavolateralis Cockerell
        C. (Certinidia) japonica Cockerell
        C. (Calloceratina) laeta Spinola
        C. (Crewella) rupestris
        C. (Pithitis) smaragdula (Fabricius)
        C. (Ceratinula) zeteki Cockerell
        Ctenoceratina tanganyicencis (Strand)
        Megaceratina sculpturata (Smith)
    Allodapini
        Compsomelissa zaxantha (Cockerell)
        Exonueridia hakariensis
        Exonuera bicolor Smith
        Halterapis nigrinervis (Cameron)
    Manueliini
        Manuelia gayatina (Spinola)
        M. gayi (Spinola)
        M. postica (Spinola)
Megachilidae
    Pararhophitini
        Pararhophites orobinus Morawitz
    Fideliini
        Parafidelia friesei Brauns
    Lithurgiini
        Lithurge apicalis Cresson

Sakagami and Michener (1987) and Roig-Alsina and Michener (1993). Both studies supported Ceratinini and Allodapini as sister groups and the terminal members of the subfamily. The sister group to the Ceratinini + Allodapini clade is less certain; Sakagami and Michener (1987) concluded that this group was the Xylocopini, but the analysis of Roig-Alsina and Michener (1993), which used more characters, concluded that it could be either Xylocopini or Manueliini. Roig-Alsina and Michener (1993) favored the placement of the Manueliini as the most basal taxon in the subfamily because Xylocopini, Allodapini and Ceratinini share a derived shape of sternum eight in the males. They also addressed relationships of groups outside the subfamily Xylocopinae. The next more basal taxon to the Xylocopinae was the family Megachilidae (consisting of the subfamilies Megachilinae, Fideliinae and Osmiinae).

I chose components of the outgroup for this study based largely on the analysis of Roig-Alsina and Michener (1993). For three of the analyses I polarized ground-plan states of characters based on a topology of Manueliini as the basal taxon in the subfamily Xylocopinae and a sister-group relationship among Xylocopini and Allodapini + Ceratinini. From the family Megachilidae, I used three taxa (*Lithurge apicalis*, *Parafidelia friesei* and *Pararhophites orobinus*) considered basal in the family as additional outgroups. Names of all outgroup taxa are listed in Table 2. Unless otherwise

stated, I use the term outgroup to refer to a hypothetical ancestor that represents the inferred ground-plan state of all characters. Ground-plan character states for the Xylocopini were hypothesized using the optimization technique of Maddison et al. (1984). This hypothetical ancestor has all characters coded as zero, with a few exceptions (Table 3).

SELECTION OF CHARACTERS

I used all characters that fulfilled the conditions of homology (Remane, 1956), including some characters of the males that are homoplasious in other bees. *A priori*, I could think of no reasonable criterion that would allow me to decide whether one character or character system (e.g., male genitalia vs. external sexual characteristics of the male) was phylogenetically more informative than any other. This approach relies on the congruence with other characters to determine the general "goodness of fit" of any single character (Kluge, 1989). Furthermore, in a large group, such as the Xylocopini, it seems reasonable to expect that some characters homoplasious within some clades will serve as synapomorphies of other clades.

Homology assessment was problematic for some characters in *Proxylocopa*, females of which have a well-developed basitibial plate at the base of the tibia and a large conspicuous pygidial plate. These conditions are typical for most other ground-nesting bees, but in the rest of the large carpenter bees the pygidial plate consists of only one or several spines, and the basitibial plate is reduced (sometimes only represented by its apex) and positioned on the apical two-thirds of the tibia. The placement and development of these structures in *Proxylocopa* have led some workers to consider it as the most primitive taxon in the subfamily (Xylocopinae *sensu* Hurd, 1958; Malyshev, 1913). Others have argued that these structures collectively represent an adaptive complex associated with nesting in the ground and have evolved secondarily (Daly et al., 1987). Morphological evidence supports the latter view; in *Proxylocopa* the pygidial plate and basitibial plate are swollen lobes and completely lack a line or carina around the lateral edges as is typical of other bees. Furthermore, if the Manueliini, a wood-nesting group, is the basal taxon in the subfamily Xylocopinae, the inferred ground-plan state for the Xylocopini would be that its ancestor nested in wood and *Proxylocopa* would have secondarily reverted to nesting in the ground. In this study, I treated the above conditions in *Proxylocopa* as unique derived features. However, because no comparable structures exist elsewhere in the ingroup (Xylocopini) and some characters are transformation series with multiple states, I coded all characters associated with the basitibial plate and pygidial plate as missing in *Proxylocopa*. Preliminary analyses (not shown) made with these features coded as primitive usually pro-

Table 3. Data matrix used in the phylogenetic analyses for Analysis 1, 1A, 3, and 3A. Matrices for Analyses 2, 2A, 4 and 4A are explained in the text. Numbers across the top of matrix correspond to character numbers used in the text. Taxon abbreviations used were *Xylocopoides*[1] = *X. californica arizonensis*, *Xylocopoides*[2] = *X. cyanea*, *Xylocopa*[1] = *X. violacea*, *Xylocopa*[2] = *X. valga*, *Koptortosoma*[1] = *X. sinensis*, *Koptortosoma*[2] = *X. caffra*, *Koptortosoma*[3] = *X. pubescens*, *Schonnherria*[1] = *X. viridagastra*, *Schonnherria*[2] = *X. micans*, *Schonnherria*[3] = *X. macrops*, *Nodula*[1] = *X. bentoni*, *Nodula*[2] = *X. amethystina*, *Notoxylocopa*[1] = *X. tabaniformis* and *Notoxylocopa*[2] = *X. guatemalensis*.

Character Taxon	 123456789	1 0123456789	2 0123456789	3 0123456789	4 0123456789	5 0123456
Outgroup	000?00000	0000000000	00??000000	0000000000	0000000?0	0000000
Nanoxylocopa	001000000	0100000001	0100102000	0010002000	0101000111	1020000
Cirroxylocopa	001000000	0100000001	010010!100	0010000000	0101000110	1120000
Xylocopoda[1]	001001000	0100000001	010010!100	0000000000	0101000100	1020000
Dasyxylocopa	011000000	0100000001	010010!000	0000002000	0101000112	1120100
Xylocopsis	001000000	0100000011	0100102000	0000002000	0101000111	1120100
Xylocopoides[1]	000000000	1210000101	1100004000	0100002000	0210100100	1001000
Calloxylocopa	000000000	0100000001	0100000000	0000002000	0210100100	1000000
Neoxylocopa	101001000	0110000001	0100103100	0020000011	1101000100	1120000
Megaxylocopa	101001000	0110000001	0100103100	0020000011	1101000100	1120000
Stenoxylocopa	001111000	0110000001	0100100100	0020002010	1101000100	1120000
Xylocopina	001111000	0110000001	010010!000	0000000000	1101000100	1120000
Ctenoxylocopa	000100000	1100000111	0000002000	0120002000	1100000100	0000110
Copoxyla	000100100	1100000001	0100000000	0000002000	1000000111	0000100
Rhysoxylocopa	000000000	1101000201	0100000000	0020000000	0100000110	0020000
Gnathoxylocopa	001100000	1100000111	0100100000	0010002000	1100000111	1010100
Xylocopa	000100000	1210000101	0000001000	0000002000	0110000100	0001010
Nyctomelitta	011000001	0101000111	0100102000	0000000000	0101000111	1010000
Zonohirsuta	000000000	0210002001	0111002000	0000000000	0100000000	1020000
Prosopoxylocopa	000000000	0210000000	011100!000	0000000000	0100000101	1110000
Bomboixylocopa	000000010	0210000000	0100001000	0000010001	1000000000	0021000
Mimoxylocopa	011000010	0210000001	0100115000	0000012001	1100000000	1121000
Alloxylocopa	000001000	0210000000	0111110000	0221111000	0100000000	1021000
Xenoxylocopa	100001100	0210000001	010111!010	1020011100	0000000000	1121000
Mesotrichia	000001100	0210102000	0122115011	1021211110	0110000100	1120010
Platynopoda	000000100	0210100000	0122001001	1221211010	0000010100	0011010
Hoplitocopa	011000100	1210100000	012210!001	1221211010	0000010100	1120110
Hoploxylocopa	000001100	0210112000	012211!011	1121211000	0000000000	0020010
Afroxylocopa	110001100	0210000001	0123115100	1021211100	1000000102	1121100
Oxyxylocopa	000001100	0210010000	012311!010	1221111000	0000000101	1121000
Cyancoderes	001001100	1210000000	012310!010	1221211100	0000000101	1121000
Cyphoxylocopa	001000000	0210002000	012311!010	1221111100	0000000101	1120000
Koptortosoma[1]	101000000	0210000000	010211!010	1121211100	1000000102	1021000
Koptortosoma[2]	101000000	0210100000	012311!010	1121211101	1000000101	1121000
Koptortosoma[3]	111000000	1210000000	0123115010	1101211101	1000000102	1021000
Proxylocopa	000000001	0200000!!!	!!00111000	0000000000	0!00000110	0000000
Lestis	000000000	0101000001	1100000000	0000002000	0100000111	1000011
Schonnherria[1]	001000000	0100001011	0100102000	0220000000	0101000112	1120100
Schonnherria[2]	011000100	0100000011	0100102000	0220012000	0101000112	1120000
Schonnherria[3]	001100100	0100000011	0101102000	0220002000	0101000112	1120000
Xylocospila	001000000	0100000001	010010!000	0020002000	0101000112	1120000
Epixylocopa	001000000	1000000201	0100012000	0020002001	1100000111	0020000
Perixylocopa	011001000	0000001201	0100102000	0000002001	1100000111	0020000
Acroxylocopa	000101010	0000001201	0100112000	0020000001	1100000111	0020000
Biluna	000000000	0000001000	0100112100	0020000000	1100000110	0020000
Apoxylocopa	000000000	0000001201	0100102000	0020000001	1100000111	0020000
Xylomelissa	000000000	0001000201	0100102000	0020000001	1100000111	0020000
Nodula[1]	001000000	0101000201	0100111000	0020000001	1100000110	0020000
Nodula[2]	000000000	0110000201	0111000000	0020000001	1100000110	0020000
Notoxylocopa[1]	001000000	0110000001	0100110000	0000002001	0101001112	1010100
Notoxylocopa[2]	001100000	0210000101	0100110000	0000002000	0101001112	1010100
Xylocopa[2]	001100000	1210000101	0000001000	0000012000	0100000100	0001010
Xylocopoides[2]	001000010	1210000101	1100004000	0100002000	0210100100	1001001

duced trees with *Proxylocopa* arising as the basal taxon in the tribe.

Terminology generally follows that of Michener (1944, 1965) and Hurd and Moure (1963), except that I use medial (as opposed to lateral) instead of mediolongitudinal for structures on the tibial spine, propodeum, terga and sterna. Terga and sterna are designated as T and S, respectively, and segments are numbered from anterior to posterior, e.g., S1, S2, etc. I follow Brothers (1976) in the use of metapostnotum instead of propodeal triangle, and Michener (1975) and Reyes (1991) in the use of ventroapical plate for the ventral distal projection of the male gonocoxite. Mandibular structures are described using the terminology of Michener and Fraser (1978).

Examination of the reservoirs of the mesosomal glands of the males required dissection of the posterior part of the thorax using techniques described by Minckley (1994); this was limited to specimens for which I had permission to dissect. For ready comparison, the characters are given the same number in the cladistic analysis and the group descriptions. The cladograms were produced using the computer program PAUP (Phylogenetic Analysis Using Parsimony) Version 3.1.1 (Swofford, 1993) and analyzed with MacClade version 3.05 (Maddison and Maddison, 1993).

CHARACTERS AND CODING

The characters, as numbered below, correspond to the numbers in all the subsequent tables and trees and in the group descriptions. Numbers in parentheses are the codes used in the data matrix and on the cladograms. Unless noted otherwise, 0 is considered the plesiomorphic state.

1. Color of male vestiture.—(0) dark brown, black, green, or pale; (1) tawny or ferruginous on at least dorsum of body. State 1 is not found in the outgroup.

2. Subapical tooth or convexity on upper carina of male mandible.—(0) Absent (Fig. 1B); (1) present (Fig. 1A, 1C). State 1 is widespread in bees and occurs in the genus *Ctenoceratina* (Ceratinini) of the outgroup. Because *Ctenoceratina* has a number of derived features (Daly, 1988), it is not likely to be an ancestral group in the Ceratinini and therefore not closely related to the Xylocopini; I infer State 1 to be apomorphic for the Xylocopini.

3. Subapical tooth on upper carina of female mandible.—(0) Absent; (1) present. See preceding character.

4. Number of teeth on apical margin of female mandible.—(0) Two (Fig. 1A); (1) three (Fig. 1B). Mandibles as shown in Figure 1C are coded as having three teeth because the two upper teeth are considered to be fused. In the outgroup, the Ceratinini, Allodapini and *Lithurge* (Michener and Fraser, 1978) have three teeth on the apical margin of the mandible, and *Manuelia, Pararhophites* and *Parafidelia* have two teeth. Based on outgroup analysis the
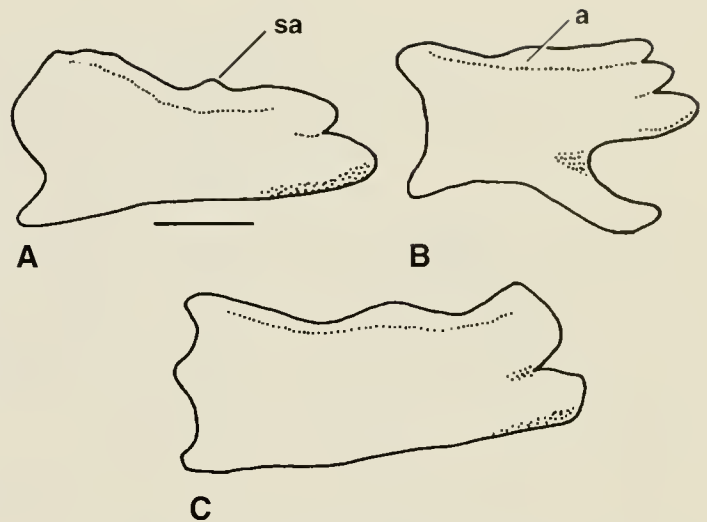

Fig. 1. External views of left mandibles of females: A. *Xylocopa (Megaxylocopa)* * *fimbriata*. B. *X. (Gnathoxylocopa) sicheli*. C. *X. (Stenoxycolopa) micheneri micheneri*. Abbreviations: a = acetabular groove, sa = subapical tooth. Scale = 1 mm. Fig. B redrawn from Hurd and Moure (1964). *Regarded as a member of the subgenus of *Neoxylocopa* herein.

polarity decision is equivocal. Furthermore, in those outgroup taxa with three mandibular teeth (Ceratinini, Allodapini and *Parafidelia*), the medial tooth is longest, but in the Xylocopini the ventral tooth (ventral tooth of the rutellum) is longest, possibly suggesting that the additional tooth of some Xylocopini has arisen *de novo*. I consider three teeth homologous in this analysis and coded the groundplan state as equivocal.

5. Upper rutellar tooth and preapical tooth (i.e. apex of pollex).—(0) Separated by an emargination (Fig. 1B); (1) fused and forming a continuous edge (Fig. 1C; Hurd 1978, Figs. 1, 2). State 1 is not found in the outgroup. This apomorphy is shared by *Stenoxylocopa* and *Xylocopina* and is the same as the "inner tooth" of Hurd (1978). Two-toothed mandibles (Fig. 1A) were coded 0.

6. Epistomal suture of female.—(0) Not raised or broadly impunctate (Hurd and Moure, 1963, Fig. 16); (1) continuously carinate and broadly impunctate (Hurd and Moure, 1963, Figs. 14, 15, 17, 18). In some ingroup taxa, a carina is present on the upper epistomal suture but it does not extend completely down the lateral edges, a condition I coded as 0. State 1 does not occur in the outgroup.

7. Supraocellar pits of female.—(0) Punctiform or not present; (1) deeply excavated and crater-like. In the outgroup, supraocellar pits, if present, are punctiform.

8. Malar space of female.—(0) Shorter than width of flagellar segment 1 (Hurd and Moure, 1963, Fig. 51); (1) much longer than width of flagellar segment 1 (Hurd and Moure, 1963, Fig. 16). State 1 is not found in the outgroup exemplars used here, but it is present among other species
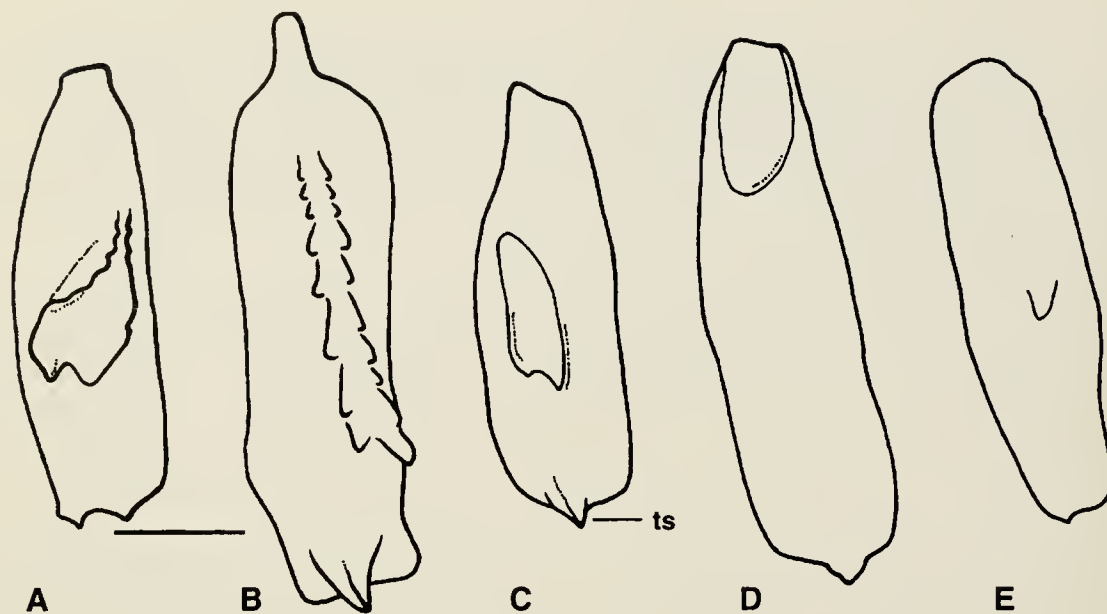
Fig. 2.   Outer view of hind tibiae of females: A. *Xylocopa* (*Xylocopoides*) *cyanea*. B. *X.* (*Ctenoxylocopa*) *fenestrata*. C. *Lestis* bombylans*. D. *Proxylocopa*rufa*. E. *X.* (*Alloxylocopa*) *circumvolans*. Abbreviation: ts = tibial spines. Scale = 1 mm. *Regarded as a subgenus of *Xylocopa* herein.

in the outgroup that I did not consider (Michener, 1975; Reyes, 1993).

9. Ocelli.—(0) Not modified; (1) enlarged. State 1 occurs in the subgenera *Nyctomelitta* and *Proxylocopa* (sensu stricto) of *Xylocopa*. All outgroup taxa have normal-sized ocelli.

10. Male facial maculations.—(0) Yellow on at least some part of face; (1) without yellow markings, i.e., entirely black. This is a highly variable character in the Apoidea but in the outgroup, males of all taxa except *Lithurge*, have yellow maculations on the clypeus.

11. Number of spines on outer apex of male hind tibia.—(0) None; (1) one; (2) two (Hurd and Moure, 1963; Fig. 37). Outgroup taxa lack these spines. The transformation series was coded as additive.

12. Number of spines on outer apex of female hind tibia.—(0) One (Fig. 2B, 2C, 2D, 2E); (1) two (Fig. 2A; Hurd and Moure, 1963, Figs. 36, 38). Females of the outgroup have one or two spines.

13. Tibial spine of female.—(0) Originating at tibial apex and lacking medial carina (Fig. 2A, 2D, 2E); (1) well-developed and originating above, but extending to, apex of tibia (Fig. 2B, 2C). State 1 is found only in taxa with one outer tibial spine. State 1 is not found in the outgroup.

14. Shape of female hind trochanter.—(0) Not modified (Fig. 3B, 3C); (1) roughly triangular in ventral view (Fig. 3A). State 1 is not found in the outgroup.

15. Mid and hind trochanter of male.—(0) Spines absent; (1) ventral surface of each with spine. State 1 does not occur in the outgroup.

16. Ventral surface of male hind femur.—(0) Not modified; (1) with basal tubercle (Fig. 3B); (2) with spine on basal half (Fig. 3C). In the outgroup, modifications such as these are known only in some *Ceratina* (Hirashima, 1969). This character was coded as nonadditive.

17. Anterior and posterior edges of female basitibial plates.—(0) Weakly developed or rising little from surface of leg; (1) with numerous tubercles on both edges (Fig. 2A, 2B); (2) with numerous tubercles only on posterior edge. The polarity proposed here may be wrong , because those ingroup taxa with the most strongly developed basitibial plates (a plesiomorphic condition?) have tubercles along both edges (e.g. *Ctenoxylocopa*, *Xylocopa* sensu stricto). Those taxa with a single row of tubercles (State 2) on the posterior edge completely lack a carina, or tubercles, on the anterior edge. State 1 is unknown in the outgroup. This transformation series was coded as additive.

18. Apex of male basitibial plate.—(0) Entire or absent; (1) bifid. As discussed in Character 17, the polarity of this character may be the reverse of that presented here. In all ingroup taxa with well-developed basitibial plates, the apex of the structure is bifid and usually strongly so. In the outgroup the basitibial plate, when present, invariably has an entire apex. The character was coded with an entire apex as the plesiomorphic condition.
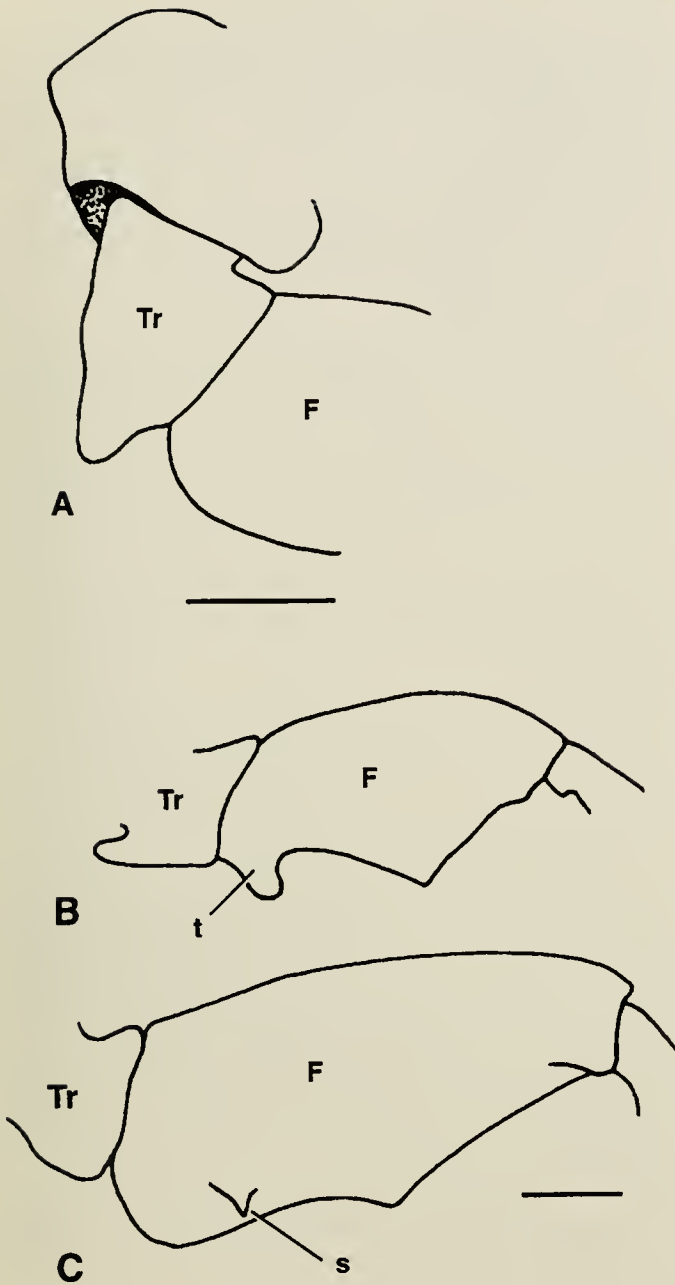
Fig. 3.   A. Ventral view of the hind trochanter of female *Xylocopa* (*Mesotrichia*) *latipes*. B. Anterior view of the femur of the male of *X.* (*Ctenoxylocopa*) *hottentota*. C. Anterior view of the femur of the male of *X.* (*Afroxylocopa*)* *nigrita*. Abbreviations: F = femur, t = tubercle, Tr = trochanter, s = spine. Modified from Eardley, 1983. Scale = 1 mm. *Regarded as a member of the subgenus *Koptortosoma* herein.

19. Apex of female basitibial plate.—(0) Entire (Fig. 2D, 2E); (1) bifid (Fig. 2A, 2B, 2C). See preceding character.

20. Female basitibial plate.—(0) Open basally or, if closed, extending onto basal fourth of tibia; (1) foveate and on apical 3/4 of tibia (Fig. 2A, 2C; Hurd, 1961, Fig. 9). State

1 is unique to *Xylocopoides* and *Lestis*. Other taxa in *Xylocopa* have lateral edges that converge basally, but do not completely close (e.g. *X.* [*Xylomelissa*] *erythrina*, *X.* [*Notoxylocopa*] *guatemalensis*), a condition that could be considered as a weak fovea, but I have not considered these to be homologous to State 1.

21. Female basitibial plate.—(0) Extending to basal fourth of tibia (Fig. 2B); (1) reduced, not extending to base of tibia (Fig 2A, 2C, 2E). See discussion of Character 17.

22. Beginning of posterior thoracic declivity of male.—(0) Smoothly rounded, beginning undefined (Hurd and Moure, 1963, Figs. 24, 27; Minckley, 1994, Figs. 1A, 1C, 3A, 3C, 4A, 4C, 4E); (1) abruptly rounded (Hurd and Moure, 1963, Figs. 39; Minckley, 1994, Fig. 3E); (2) sharply angled (Hurd and Moure, 1963, Fig. 33; Minckley, 1994, Fig. 5A). See discussion in following character.

23. Beginning of posterior thoracic declivity of female.—(0) Profile smoothly rounded, position often undefined (Hurd and Moure, 1963, Figs. 27, 28; Minckley, 1994, Figs. 1A, 1C, 3A, 3C, 4A, 4C, 4E, 5C, 5E); (1) abruptly rounded (Hurd and Moure, 1963, Fig. 39; Minckley, 1994, Fig. 3E); (2) as a transverse carina that does not overhang metanotum (Hurd and Moure, 1963, Fig. 33; Minckley, 1994, Fig. 1E); (3) marked by transverse carina that overhangs entire metanotum (Hurd and Moure, 1963, Fig. 34; Minckley, 1994, Fig. 5A). Because states 0 and 1 both occur in the outgroup, I consider the ground-plan state to be equivocal. States 2 and 3 are unknown in the outgroup and are strong apomorphies within *Xylocopa*. This transformation series was treated as additive.

24. Male metapostnotum.—(0) Present; (1) absent. The metapostnotum in bees is highly variable in size and shape and, when present, is distinguished from the propodeum by a change in the sculpturing of the cuticle and/or by a line along its edge with the propodeum. Apparently the metapostnotum can be lost in two ways: (1) absence of unique sculpturing and marginal lines; or (2) by an increase in the size of the propodeum relative to the metapostnotum until the latter is completely absent externally. In the Xylocopini the metapostnotum invariably is delimited by a line along the edge with the propodeum and a continuous size-gradation across taxa is evident. The metapostnotum in some taxa is well developed and in other taxa is vestigial or absent. Furthermore, in species the males of which have an enlarged posterior mesosoma that accommodates the mesosomal gland reservoir, the metapostnotum typically is absent (Minckley, 1994). These observations suggest that loss of the metapostnotum in the Xylocopini is by a change in the size of the propodeum. In the Ceratinini, the presence of the metapostnotum is usually made evident by a change in sculpturing, and no gradation in size of the propodeum is apparent; the
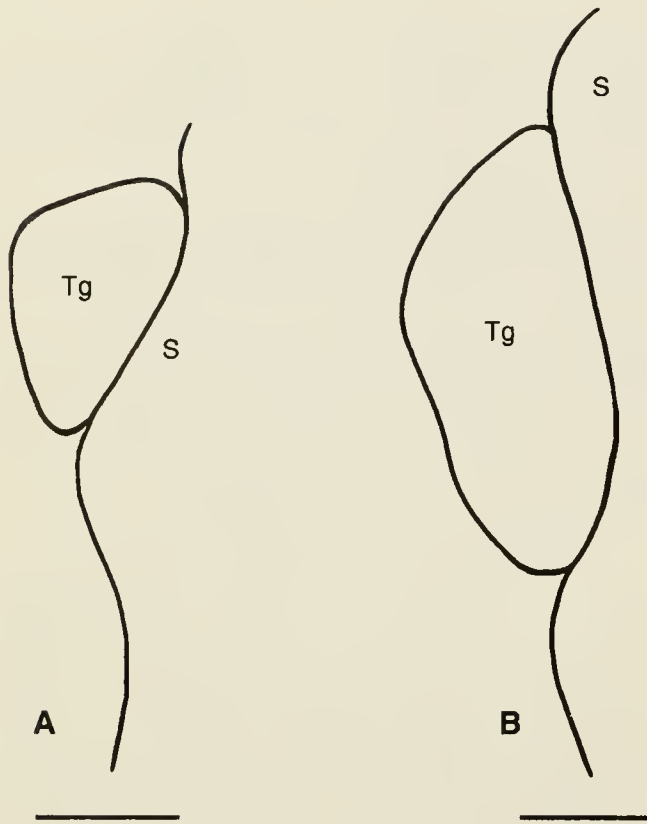
Fig. 4.   Left tegula of the male of (A) *Xylocopa varipuncta* and (B) *X. (Platynopoda)* tenuiscapa*. Abbreviations: S = scutum, Tg = tegula. Scale = 1 mm. *Regarded as a member of the subgenus *Mesotrichia* herein.

metapostnotum is either well developed or completely absent. I infer from this pattern that in the Ceratinini the metapostnotum is lost by a reduction in its surface differentiation from the propodeum and not by a change in size of the propodeum or the metapostnotum. Therefore, I consider the presence of a defined metapostnotum to be the ground-plan condition in the Xylocopini.

25. Female metapostnotum. —(0) Present, including those where it is minute; (1) absent. See discussion in preceding character.

26. Reservoir of the male mesosomal gland.—(0) Absent; (1) two widely separated pouches (Minckley, 1994, Figs. 1C, 1D, 1E, 1F, 3A, 3B); (2) single layer of tubules, usually abutting in the middle (Minckley, 1994, Figs. 3C, 3D, 4A, 4B, 4C, 4D); (3) highly convoluted tubules, as in *Neoxylocopa* (Minckley, 1994, Fig. 5E, 5F); (4) single medial pouch with one opening (Minckley, 1994, Fig. 1A, 1B); (5) numerous, highly convoluted tubules, as in *Koptortosoma* (Minckley, 1994, Fig. 5A, 5B). The presence of a reservoir is a unique character of most Xylocopini. The reservoir in at least some species is associated with a gland that produces a sex-attractant pheromone, although, in the vast majority

of large carpenter bees, the function for this structure has not been examined. There is tremendous variation in such features as the shape of the tubules that make up the gland reservoir and the size of the reservoir (Minckley, 1994), which makes homology assessment difficult for some taxa. In these difficult taxa I have opted to preserve information and have split the characters into a number of often autapomorphic states rather than simply scoring the character into states of presence or absence. This character was coded as nonadditive.

27. Beginning of the thoracic declivity of male.—(0) Anterior to the propodeum (Hurd and Moure, 1963, Figs. 29-34; Minckley, 1994, Fig. 1A, 1C); (1) on the propodeum (Hurd and Moure, 1963, Fig. 27; Minckley, 1994, Fig. 5C, 5E). State 1 is not found in the outgroup.

28. Propodeum at its connection with metasoma.—(0) Not modified; (1) dorsally elongated, forming a spine. This apomorphy is unknown in the outgroup.

29. Male tegula.—(0) Not modified (Fig. 4A); (1) elongate posteriorly (Fig. 4B). State 1 is not found in the outgroup.

30. Shape of the gradulus on T1.—(0) Gradulus of T1 continued posteriorly adjacent to lateral margin of metasoma (Hurd and Moure, 1963, Fig. 43); (1) transverse (Hurd and Moure, 1963, Fig. 44). State 1 is not found in the outgroup.

31. Distribution of graduli on male terga.—(0) present on T1, T2 and T3, or more; (1) present on T1 and T2; (2) present on T1 only. All members of the outgroup have graduli on at least T1–T3, except for the ceratinine genus *Pithitis*, which has a gradulus only on T1 (Hirashima, 1969). Based on this information and the argument that a gradulus on each tergum is generally considered to be plesiomorphic in bees (Michener, 1944), the inferred ground-plan state for the ingroup is graduli on all terga posterior to T3, as well as on more anterior terga. The character was treated as additive.

32. Distribution of graduli on female terga.—(0) T1, T2 and T3, or more; (1) T1 and T2; (2) T1 only. See discussion of preceding character.

33. Modifications of anterior surface of T1 of males.—(0) Absent; (1) a fovea (Hurd and Moure, 1963, Fig. 42). See discussion in following character.

34. Modifications of anterior surface of T1 of female.—(0) Absent; (1) a fovea (Hurd and Moure, 1963, Fig. 42); (2) with an entrance to a acarinarium (Fig. 5; Eardley, 1983, Figs. 23, 24, 27). Neither a fovea nor an invaginated mite pouch occurs in other bees. The transformation series was coded as additive.

35. Medial groove of T1 of female.—(0) Linear; (1) deeply sulcate (Hurd and Moure, 1963, Fig. 41). In the outgroup, the medial groove is linear.
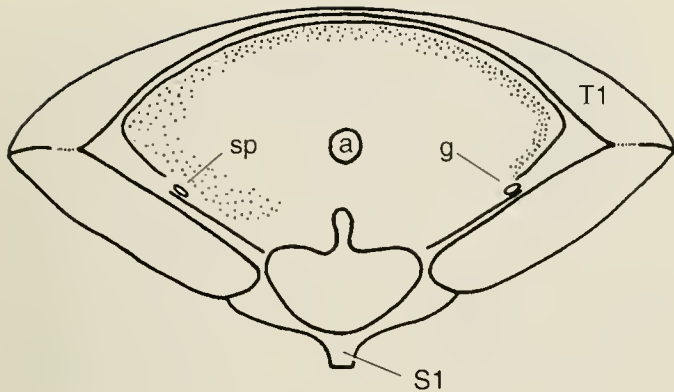
Fig. 5.   Anterior face of T1 of a female *Xylocopa (Platynopoda)** *tenuiscapa*. Abbreviations: a = entrance to the acarinarium; g = gradulus; T1 = dorsal surface of tergum 1; S1 = sternum 1; sp = spiracle. *Regarded as a member of the subgenus *Mesotrichia* herein.
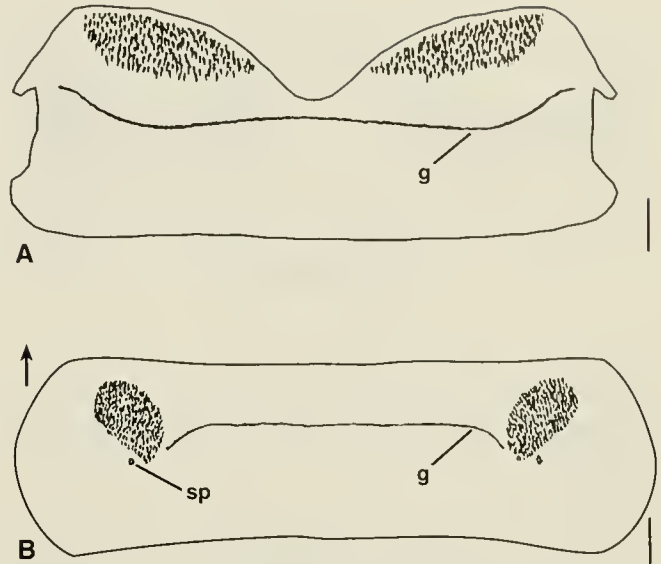
36. Apical margin of Sl.—(0) Entire, not produced; (1) produced (Hurd and Moure, 1963, Fig. 44); (2) medially emarginate (Hurd and Moure, 1964, Fig. 43). State 1 occurs in all outgroup taxa. This character was coded as nonadditive.

37. Medial carina on S6 of male.—(0) Absent or not developed into a keel; (1) strongly developed, forming a keel. In *Ceratina*, a member of the outgroup, a carina is present on S6 but is never developed into a strong keel.

38. Medial carina on metasomal sternum of female.—(0) Carina not present on all sterna or not continuous; (1) continuous and present on all sterna. A well-defined medial carina on all female sterna clearly is apomorphic for the ingroup, although in some outgroup taxa (*Ceratina laeta*, *C. rupestris* and *Megaceratina sculpturata*) a weakly developed medial carina occurs on S6 and in many members of the ingroup, a carina occurs on all sterna, although it is weakly developed or not continuous.

39. Pregradular areas on sterna of male.—(0) Paired setal patches absent; (1) paired setal patches present on at least one sternum (Fig. 6A). In the ingroup, these most often are on S2–S6, but in many taxa they occur on fewer sterna. State 1 is not found in the outgroup.

40. Distinct patch of appressed short setae anterior and dorsal to one or more metasomal spiracles of male.—(0) Absent; (1) present (Fig. 6B). In most taxa these are found on T2– T5, but in some taxa they are on fewer terga. State 1 is not found in the outgroup.

41. Pygidial spine of T6 of female.—(0) Not armed with lateral preapical spines (Fig. 7A); (1) with pair of preapical lateral spines (Fig. 7B); (2) with many preapical lateral spines (Fig. 7C). The pygidial plate of all wood-nesting *Xylocopa* (excluding *Proxylocopa*), and *Manuelia*, is represented by a raised spine that originates before, and extends beyond, the distal edge of T6. At its base, the spine may be

Fig. 6.   *Xylocopa (Neoxylocopa) varipuncta* male: A. Pregradular area of S4 showing patches of appressed setae. B. Side view of T4 with appressed setal patch; arrow indicates anterior; abbreviations: sp = spiracle, g = gradulus. Scale = 1 mm.

flanked by one or many preapical spines (prepygidial spines of Hurd and Moure, 1963). When there are many such spines they delimit a triangular area that may be a remnant of a pygidial plate. In Ceratinini and Allodapini, a developed spine is absent although the distal edge of T6 is medially elongated, forming a point. This character was coded as additive.

42. Gonostylus of male genitalia.—(0) A slender projection fused to apex of gonocoxite (Figs. 8A, 8B, 8C, 9A, 9B, 9C, 9D, 9E, 9F); (1) a rounded or conical setose area at apex of gonocoxite (Hurd and Moure, 1963, Figs. 242, 244). *Lestis* (Fig. 9B) was coded as having State 0 because its conical gonostylus is different from that coded as 1. This decision is based on the two features not found in other taxa with such gonostyli, a dense brush of medially oriented hairs on the gonostylus and a strong carina on the apex of the gonostylus. All outgroup taxa have a distinct slender gonostylus similar to state 0.

43. Lateral edge of penis valve.—(0) Smooth, without a carina (Fig. 9A, 9B, 9C, 9D, 9E, 9F); (1) protuberance or carina present (Fig. 8A, 8B, 8C). State 1 is found in the outgroup only in some members of the Allodapini (Michener, 1975). The ground-plan state for the ingroup is inferred to be State 0.

44. Apex of penis valve.—(0) Not hirsute (Fig. 8A, 8B, 8C); (1) hirsute (Hurd, 1961, Figs. 1, 3, 4). This apomorphy unites *Xylocopoides* and *Calloxylocopa* and does not occur in the outgroup.
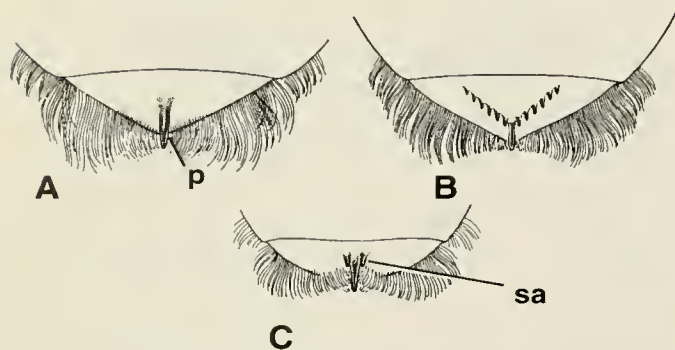
Fig. 7.   Dorsal surface of T6 of females: A. *X. (Mesotrichia) flavorufa*. B. *X. (Xylocopoides) californica*. C. *X. (Notoxylocopa) tabaniformis* (modified from Hurd and Moure, 1963). Abbreviations: p = pygidial spine; sa = preapical spine.

45. Penis.—(0) Entirely membranous; (1) sclerotized basally on venter. State 0 characterizes all outgroup taxa.

46. Spatha.—(0) Reduced or absent (Fig. 8A, 8B, 8C); (1) well developed (Hurd and Moure, 1963, Figs. 131, 134). State 1 is an autapomorphy for *Notoxylocopa*. Although a spatha is present in many groups of bees, it is not so well developed in the outgroup.

47. Gonostylus of male genitalia.—(0) Slender, elongate and erect, over 1/2 as long as gonocoxite (Fig. 9D); (1) slender and less than 1/2 as long as gonocoxite (Figs. 8A, 8B, 8C, 9A, 9B, 9C, 9E, 9F), or entirely fused with gonocoxite and represented only by the rounded or conical setose area at apex of gonocoxite (Character 42-1). An elongate, slender gonostylus with numerous setae is considered to be plesiomorphic for bees. The outgroup is variable in this respect, but in each tribe some member has this plesiomorphic condition, i.e., *Pararhophites* (Pararhophitini), *Parafidelia* (Fideliini), *Euceratina* (Ceratinini), *Manuelia* (Manueliini), and *Compsomelissa* (Allodapini) and some *Allodapula* (Allodapini).

48. Gonostylus of male genitalia.—(0) Lacking a dense patch of setae on its apex (Fig. 8C); (1) with dense apical patch of setae (Figs. 8A; 9B). State 1 is not found in the outgroup.

49. Apex of gonostylus with medially projecting lobe.—(0) Absent (Figs. 8B, 8C; 9C, 9D); (1) present, not well developed (Fig. 9B); (2) present, well developed (Fig. 8A). The apex of the gonostylus is entire in all outgroup taxa.

50. Ventromedial margins of gonocoxites.—(0) Diverging continuously from at, or near, ventral gonocoxal bridge (Fig. 9A, 9F); (1) roughly parallel from ventral gonocoxal bridge and not diverging until well above ventral gonocoxal bridge (Figs. 8A, 8B, 8C, 9B, 9C, 9D, 9E). This character is variable in the outgroup. The ground-plan state has been inferred based on State 0 being a consistent feature of the Ceratinini and Megachilidae (i.e., *Pararhophites*,
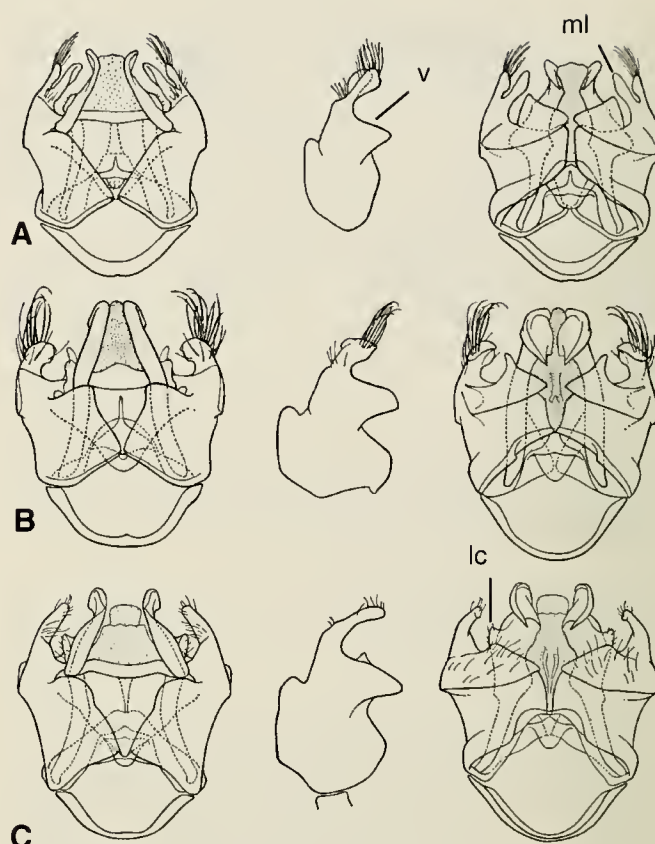

Fig. 8.   Dorsal, lateral, and ventral views of male genitalia (modified from Hurd and Moure, 1963): A. *Xylocopa (Xylocospila)* bambusae*. B. *X. (Cirroxylocopa) vestita*. C. *X. (Neoxylocopa) varipuncta*. Abbreviations: lc = lateral carina of penis valve, ml = medial lobe of gonocoxite, v = ventroapical plate. *Regarded as a member of the subgenus *Schonnherria* herein.

Parafidelia and *Lithurge*) and one member of the Manueliini (*Manuelia gayatina*).

51. Medial area of posteroventral margin of gonocoxite.—(0) Not produced (Figs. 8B, 9A, 9C); (1) with posterior projection (Figs. 8A, 8C, 9B, 9C). State 1 is not found in the outgroup.

52. Ventroapical plate of gonocoxite.—(0) Absent (Fig. 9A, 9B, 9C, 9E, 9F); (1) present, but not carinate and not well defined (Hurd and Moure, 1963, Figs. 135, 136); (2) carinate (Figs. 8A, 8B, 8C, 9D). The ventroapical plate of the Xylocopini is possibly comparable to that found in the Allodapini (Michener, 1975; Reyes, 1991). Nonetheless, the inferred ground-plan state of the outgroup is absence of such a structure.

53. Projection or spine on inner basal margin of under surface of gonocoxite.—(0) Absent; (1) present (Fig. 9D). Many ingroup taxa have a spine along the ventral margin of the base of the gonocoxite that is more lateral than the condition defined here. This condition was coded as 0. No such projection is found in the outgroup.
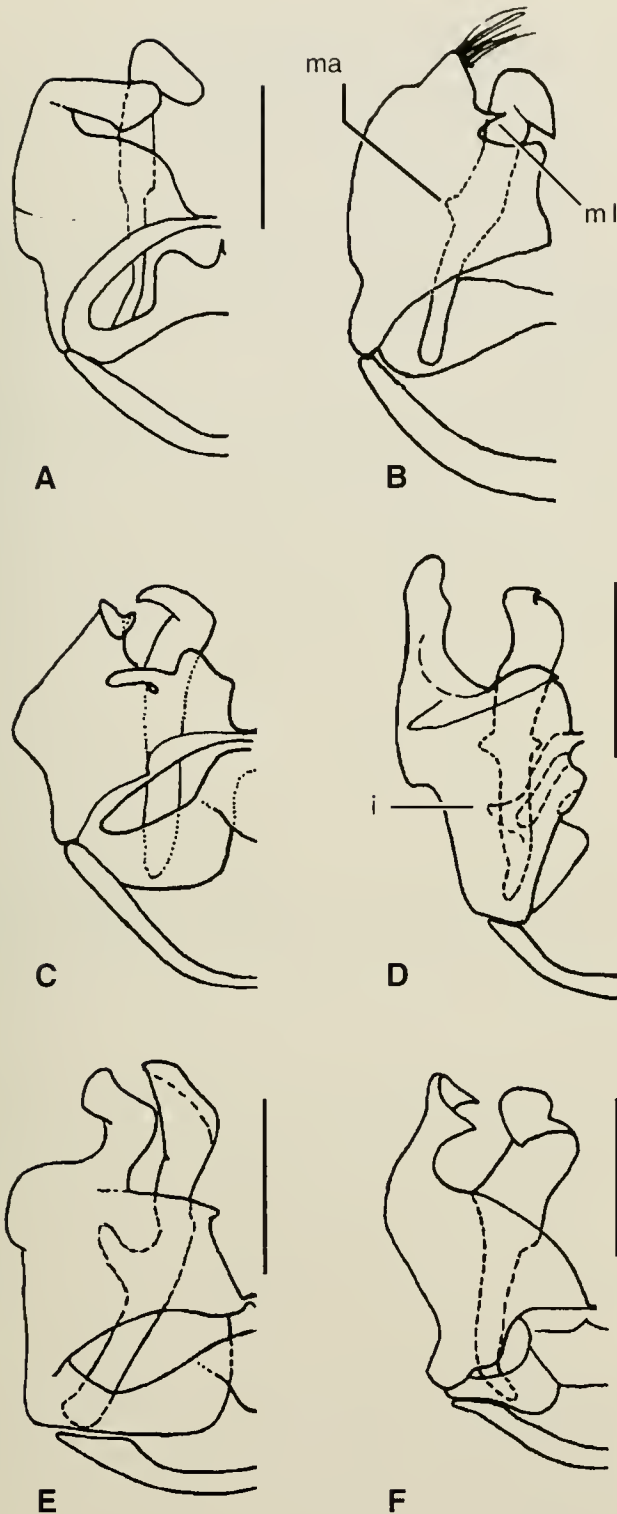
Fig. 9. Ventral views of the right sides of male genitalia: A. *X. (Xylocopa) valga*. B. *Lestis* aeratus*. C. *X. (Prosopoxylocopa) mirabilis*. D. *X. (Bomboixylocopa) rufipes*. E. *X. (Ctenoxylocopa) fenestrata*. F. *Proxylocopa* (Proxylocopa) rufa*. Abbreviations: i = internal medial projection, ma = medial apodeme, ml= medial lobe. Scale = 1 mm. *Regarded as a subgenus of *Xylocopa* herein.

54. Posterior margin of male T7.—(0) Entire; (1) with pair of dentiform projections. State 1 is not found in the outgroup.

55. Penis valves.—(0) Apically expanded (Figs. 8A, 8B, 8C, 9D); (1) slender and parallel (Fig. 9A, 9C). Though some outgroup taxa have relatively slender penis valves they are not as slender and parallel-sided as in State 1, so I have tentatively inferred this condition to be apomorphic in the Xylocopini.

PHYLOGENETIC ANALYSES

Four separate sets of analyses (described below) were made. For each analysis the matrix was first analyzed with all characters weighted equally and a second time using successive approximation weighting (Farris, 1988). Successive approximation is an *a posteriori* character weighting procedure that weights each character based on its best performance (= fewest steps) in the previous analysis. The weighting scheme is applied repeatedly until weights of all characters stabilize. Before each successive approximation analysis the characters are coded in additive binary form to insure that the weights assigned to states of multistate characters are correct. The alternative coding method for such characters is with all states in one column. Coding multistate characters in the latter way can result in assignment of an average weight of all states; if coded in additive binary form, both characters that perform poorly (show high homoplasy) receive more weight and characters that perform well (show low homoplasy) receive a lower weight than they would otherwise. Carpenter (1988) provided an example of how these different coding schemes can affect tree topologies. PAUP provides many options for calculating weights for successive approximations. For ease of comparison, I followed the weighting scheme used by the Hennig86 parsimony program (Farris, 1988; explained by Fitzhugh, 1989), which assigns weights to characters from 0 to 10. Nevertheless, my results may differ from those obtained from Hennig86, because some characters coded as polymorphic in the PAUP data matrix would have to be considered missing in a Hennig86 format (Hennig86 does not accept polymorphic characters) and might be optimized differently or assigned different weights.

The large size of the matrix restricted the search for the shortest trees to heuristic searches in the PAUP program version 3.01 (Swofford, 1990). Because these types of searches cannot guarantee finding the most parsimonious tree for the data, I searched by two methods in each analysis. In the first search the following settings were used: Starting trees by stepwise addition, addition sequence simple, hold 75 trees at each step and swap on all starting trees including trees that were nonminimal. The second search used the random addition sequence option, which

begins searches from trees produced at random by the program. Five hundred replications were run and set to swap on no more than 30 trees at each step up to and including the fewest steps obtained by the first search.

The four analyses were undertaken to investigate uncertainties in assumptions about the evolutionary changes or homology assessment of characters, and of the relationships of the outgroups discussed above in the section on Selection of Taxa. For brevity, the four analyses are referred to hereafter as Analysis 1, 2, 3 and 4. Results from these four analyses after successive approximations weighting are followed by the letter A (e.g., Analysis 1A, 2A etc.).

Analysis 1, equal weighting.—This analysis was based on the full matrix (Table 3). Assumptions about character ordering were as described in the Character Analysis section (i.e., some characters were coded as additive and others as nonadditive), and ground-plan states for all characters were inferred by assuming Manueliini to be the sister group to Xylocopini + (Ceratinini + Allodapini) in the subfamily Xylocopinae.

Analysis 1A, successive approximations.—This analysis used the same matrix as in Analysis 1 with successive approximations character weighting applied.

Analysis 2, equal weighting.—This analysis was done with *Proxylocopa* excluded because I had coded some characters as missing for this taxon in Analysis 1. Other than the lack of *Proxylocopa*, this was the same matrix and character assumptions as used in Analysis 1.

Analysis 2A, successive approximations.—This analy-sis was done by applying successive approximations to the reduced matrix used in Analysis 2.

Analysis 3, equal weighting.—This analysis was done using the same matrix as in Analysis 1 but with all characters coded as unordered.

Analysis 3A, successive approximations.—This analysis was done using successive approximation weighting on the matrix used in Analysis 3. Because islands of equally parsimonious trees were found in Analysis 3, six analyses were run starting with each of the six islands produced in Analysis 3.

Analysis 4, equal weighting.—This analysis was done to investigate the role that the uncertain relationships among the tribes of the Xylocopinae might have on the polarity assessment of the character states used in this study. Ground-plan states of all characters were determined with the Xylocopini as the sister group to Manueliini + (Ceratinini + Allodapini). This reanalysis resulted in a change of the hypothesized groundplan state for characters 25 and 36 from 0 to polymorphic (0, 1).

Analysis 4A, successive weights.—This analysis was done using successive approximation weighting on the matrix used in Analysis 4.

The following abbreviations are used in describing the trees from each analysis: C.I. = consistency index, R.I. = retention index and T.L. = treelength. For those trees resulting from successive approximations weighting, statistics are given for equally weighted characters to facilitate comparisons with the other analyses, and for weighted characters.

RESULTS

The eight different analyses were attempts to explore the effect that various assumptions have on tree topology. The influence on tree topologies of coding characters as missing (Analyses 1, 1A, 3, 3A, 4, 4A), or of deleting taxa altogether (Analyses 2 and 2A) remains insufficiently understood (Gauthier et al., 1988; Maddison, 1993; Platnick et al., 1991; Weins and Reeder, 1995). Additive coding of character states (Analyses 1, 1A, 2, 2A, 4, 4A) assumes that an *a priori* knowledge of the evolutionary direction of character change is correct, an approach that has been questioned unless ontological data are available (Nelson, 1985). Successive approximation weighting has been investigated only by Farris (1969) who used a hypothetical data set with complete character independence and a known phylogeny. These considerations emphasize that the results of this study are only hypotheses, and should be treated as such. Because of reservations concerning the transformation order for several multistate characters (discussed in the Character List and Coding section), I consider Analysis 3 that had all taxa included, characters weighted equally and

characters coded as nonadditive (unordered) to have the least assumptions. However, it seems reasonable that the strongest hypotheses for relationships are those that were repeatedly supported under different assumptions.

I discuss each analysis and show one fully resolved cladogram and strict consensus trees for unique topologies. Topologies largely redundant with those from other analyses are not presented. Consensus trees are not accompanied with character changes because of problems with character optimization when polytomies are present (Maddison and Maddison, 1992). Successive approximation weighting produced more trees than corresponding analyses with all characters weighted equally in all analyses, except Analysis 2. This result was because the weighting algorithm assigns weights of zero to many characters, effectively removing them from the analysis. Hence, some nodes were left with no character support. Successive approximation weighting was also highly sensitive to the topologies of the initial trees. For example, in Analysis 3, three sets of relationships were generated even though the

weighting iteration began with a set of equally parsimonious trees from the same data set. If this weighting approach could reliably distinguish characters that were truly homologous from those that were homoplasious, a greater level of congruence should be obtained in the weighted trees than was found here. A thorough study on how multiple islands of trees influence results using successive weighting is beyond the scope of the present paper.

In the following text and cladograms, I refer to those subgenera represented by more than one exemplar by their subgeneric name if the exemplars were shown to be monophyletic in all analyses. Thus, in the text *Schonnherria*, *Xylocopoides*, and *Notoxylocopa* are used, but each refers to multiple exemplar species (Table 3). Monophyly was not consistently supported for the exemplars of *Nodula*, *Xylocopa*, and *Koptortosoma*. For the first two groups, I use species names of all exemplars in the discussion and on the cladograms. I restrict use of *Koptortosoma* to *X. caffra* and *X. pubescens*, and designate *X. sinensis* separately; the first two exemplars were grouped together consistently, whereas the relationship of the latter species to the other species of *Koptortosoma* varied among analyses.

The following section is a summary of the relationships among the major groups in the tribe. This is followed by a section discussing the relationships of the component taxa within these larger clades.

RELATIONSHIPS AMONG LARGER CLADES OF THE *XYLOCOPINI*

In most analyses, three groups were shown to be monophyletic; for ease of discussion, I have given each an informal name. These are: (1) the Ethiopian group consisting of *Afroxylocopa*, *Alloxylocopa*, *Bomboixylocopa*, *Cyaneoderes*, *Cyphoxylocopa*, *Hoplitocopa*, *Hoploxylocopa*, *Koptortosoma*, *Mesotrichia*, *Mimoxylocopa*, *Oxyxylocopa*, *Platynopoda*, *Prosopoxylocopa*, *Xenoxylocopa*, and *Zonohirsuta*; (2) the New World group consisting of *Cirroxylocopa*, *Dasyxylocopa*, *Megaxylocopa*, *Nanoxylocopa*, *Neoxylocopa*, *Schonnherria*, *Stenoxylocopa*, *Xylocopoda*, *Xylocopsis*, and *Xylocospila*; and (3) the *Rhysoxylocopa* group consisting of *Acroxylocopa*, *Apoxylocopa*, *Biluna*, *Epixylocopa*, *Nodula* (both exemplar species), *Perixylocopa*, *Rhysoxylocopa* (sensu stricto), and *Xylomelissa*.

The Ethiopian and New World groups are large and are further divided into subgroups. For the Ethiopian group these are; (1) the *Mesotrichia* subgroup consisting of *Hoplitocopa*, *Hoploxylocopa*, *Mesotrichia*, and *Platynopoda*; and (2) the *Koptortosoma* subgroup consisting of *Afroxylocopa*, *Cyaneoderes*, *Cyphoxylocopa*, *Koptortosoma*, and *Oxyxylocopa*. In the New World group, I refer to a *Neoxylocopa* subgroup which includes *Megaxylocopa*, *Neoxylocopa*, *Stenoxylocopa*, and *Xylocopina*.

Analysis 1, equal weighting.—Manueliini is basal in the subfamily; some characters were coded as additive and others as nonadditive. *Proxylocopa* is included. (Fig. 10A). This analysis yielded eight minimum length trees (C.I. = 0.27, R.I. = 0.67, T.L. = 288.) Differences in the topology of the eight trees produced by this analysis were among *Cyaneoderes* and *Cyphoxylocopa* and their relationship to *Koptortosoma*, *X.* (*Koptortosoma*) *sinensis* and *Afroxylocopa*. For all other subgenera and genera of the tribe this analysis produced a single hypothesis of relationships. Four major clades are shown to be monophyletic. The most basal group consists of a biogeographically diverse set of taxa that includes the Australian *Lestis* as the sister group to the North American subgenera *Calloxylocopa* and *Xylocopoides*. Together, these taxa comprise a sister taxon to the Old World subgenera *Copoxyla* + (*Ctenoxylocopa* + *X.* (*Xylocopa*) *violacea* and *X.* (*Xylocopa*) *valga*). The monophyly of all members of this clade is supported by Character 36, the emarginate shape of Sl. This character is highly homoplasious and appears independently six times in the tribe, thereby suggesting little confidence should be placed in this grouping.

This clade and the next more-derived branch with the genus *Proxylocopa* are separated by the absence of the male metapostnotum (Character 24-1) and presence of a male mesosomal gland (Character 26-1). Both characters are lost and gained repeatedly in the tribe and furthermore are functionally correlated; presence of the mesosomal gland is often associated with absence of the metapostnotum (Minckley, 1994). As such, the relationship of *Proxylocopa* and the taxa shown to be more basal to it is best considered as unresolved.

Those taxa that are derived relative to *Proxylocopa* are defined in this analysis by possession of a carina on the venter of the gonocoxite (Character 52-2), and elaboration of the reservoir of the male mesosomal gland from two small pouches to a series of tubules (Character 26-2). Development of this carina is a strong feature that arises once in this topology, although it becomes rounded (Character 52-1) in the *Rhysoxylocopa* group. Three major clades are included herein; the *Rhysoxylocopa* group is basal and the sister group to a clade that includes the Ethiopian group and a clade of taxa that occur primarily in the New World (the *Neoxylocopa* group, *Xylocopoda*, *Cirroxylocopa*, *Notoxylocopa*, *Xylocopsis*, *Dasyxylocopa*, *Nanoxylocopa*, *Schonnherria*, and *Xylocospila*) but with two Old World members (*Gnathoxylocopa* and *Nyctomelitta*).

Few characters separate these main groups; yet several of these features probably are unique within the Xylocopini and show little homoplasy in my analyses. The sister group relationship of the Ethiopian group plus the large group of New World taxa (including *Gnathoxylocopa* and *Nyctomelitta* in this topology) is supported by the parallel ventromedial margin of the gonocoxites (Character 50, Fig. 9B; lost in *Platynopoda*, *Hoploxylocopa*, and *Bomboixylocopa*)
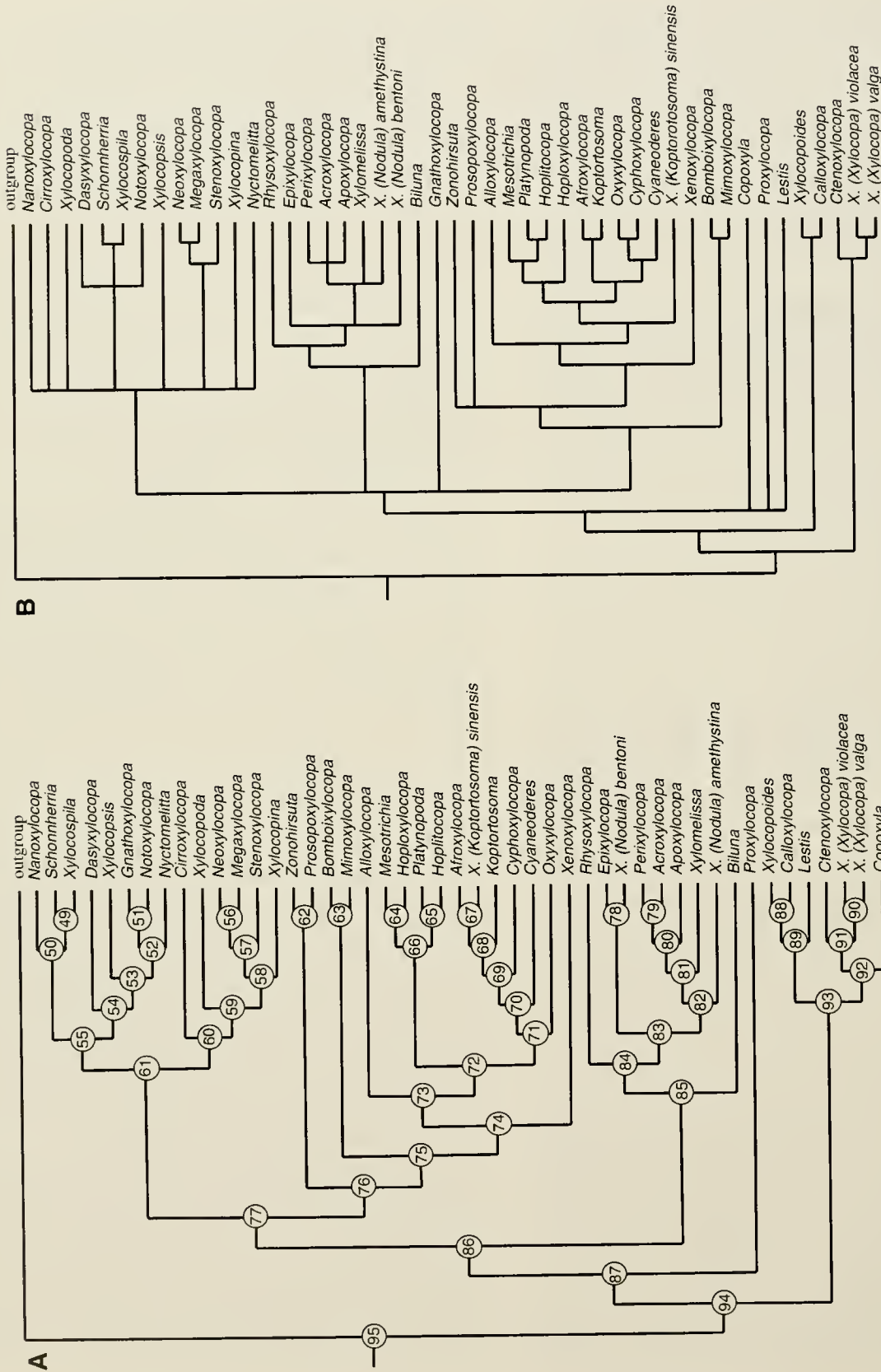
Fig. 10.   Analysis 1. A. One randomly chosen, fully-resolved tree of the eight most parsimonious trees found. Analysis was done with both additive and nonadditive multistate characters (as described in the text) and weights of all characters held equal. Character distribution is described in Appendix 1. B. Strict consensus cladogram of 89 trees generated by the successive approximations analysis.

and possession of a process or spine on the venter of the gonocoxite (Character 51, Fig. 9C; lost repeatedly). Monophyly of the Ethiopian group is supported by the possession of two spines on the male hind tibia (Character 11-2) and female (Character 12-1, lost in *Afroxylocopa*), beginning of the thoracic declivity abruptly rounded in the female (Character 23-1; lost in *Bomboixylocopa* and *Mimoxylocopa*), derived loss of a slender elongate gonostylus (Character 47-0; regained in the *Mesotrichia* and *Koptortosoma* groups), and sparse setae on the gonostylus (Character 48). These characters are found in other groups, but the congruence of characters is support for the monophyly of this clade.

The clade composed of the New World group and (*Notoxylocopa* + *Gnathoxylocopa*) + *Nyctomelitta* is defined by the presence of a subapical tooth on the mandible of the female (Character 3-1) and a lateral projection on the penis valve (Character 43-1). The subapical mandibular tooth is a derived loss in *Gnathoxylocopa* and is present in groups outside this clade. This placement of *Gnathoxylocopa* is unlikely (discussed below).

Analysis 1A, successive approximations.—Successive approximations were applied to the matrix used in Analysis 1A (Fig. 10B). This analysis yielded 89 minimum length trees (unweighted statistics, T.L. = 331, C.I. = 0.23, R.I. = 0.65; weighted statistics, T.L. = 362, C.I. = 0.64, R.I. = 0.92). Except for the most basal clade, this analysis recovered the same major groups as in Analysis 1. The monophyletic group positioned at the base of the tribe in Analysis 1 is represented as a grade of five sequential clades along the base of the cladogram in this analysis. Hypotheses of relationships among members within these larger clades were more numerous than in the equally weighted analysis, and more polytomies exist in the consensus trees resulting from these analyses.

Analysis 2, equal weighting.—Manueliini is basal in the subfamily; some characters were coded as additive and others as nonadditive. *Proxylocopa* is excluded. This analysis produced 48 trees divided among three groups, or "islands," of 16 trees each (T.L. = 282, C.I. = 0.28, R.I. = 0.70). Strict consensus trees of each of the three islands differ from those of Analysis 1 most notably in the relationship of *Biluna* to the other members of the *Xylomelissa* group. Island 3 places *Rhysoxylocopa* (sensu stricto) as a sister group to the remainder of the *Rhysoxylocopa* group, and in Island 2 *Biluna* is a more derived member of the clade. Recognition of the major clades was the same as those produced in Analysis 1. Because of the similarity of results to those in Analysis 1, the results of this analysis are not shown as a cladogram.

Analysis 2A, successive approximations.— Manueliini is basal in the subfamily, some characters were

coded as additive and others as nonadditive. *Proxylocopa* is excluded; successive approximations were applied. After five weighting iterations, character weights stabilized and produced 25 minimum length trees (unweighted statistics T.L. = 298, C.I. = 0.25; R.I. = 0.67, weighted statistics T.L. = 511, C.I. = 0.49; R.I. = 0.86). All islands of trees converged on the same consensus tree, wherein the large clades were much the same as those in Analyses 1 and 1A. Taxa supported as a monophyletic group in Analysis 1 form a basal grade of taxa in this analysis. In the resolved tree and in the consensus tree, the Ethiopian group plus the *Rhysoxylocopa* group and the New World assemblage are a single clade. The relationships among members within these three major groups are unresolved in the consensus tree.

Analysis 3, equal weighting.—Manueliini is basal in the subfamily; all characters were unordered. *Proxylocopa* is included (Figs. 11A, 11B, 13A, 13B, 15). Coding all characters unordered resulted in 408 trees distributed across 6 islands (T.L. = 297, C.I. = 0.27, R.I. = 0.65). The numbers of trees for each island are: Island 1 = 24; Island 2 = 72; Island 3 = 144; Island 4 = 72; Island 5 = 72; Island 6 = 24. Consensus trees of all trees in each of these islands generally are not well resolved but some unique relationships were found. The Ethiopian group was shown as monophyletic in three of six islands (Islands 2, 4, 5; Fig. 13A, 13B). In the three islands in which monophyly for this group was not supported, the two basal taxa, *Zonohirsuta* and *Prosopoxylocopa*, were not included with the remainder of the Ethiopian group. Island 1 (Fig. 11A, 11B) placed *Zonohirsuta* + *Prosopoxylocopa* as the sister group to the clade of *Xylocopa* + (*Calloxylocopa* + *Xylocopoides*) based on the derived loss of the metapostnotum in the male (Character 24-0) and female (Character 25-0). Together, this clade is the sister group to the remainder of the Ethiopian clade, minus *Zonohirsuta* and *Prosopoxylocopa*. In Island 3 (not shown), *Zonohirsuta* + *Prosopoxylocopa* are part of a polytomy that includes the remainder of the Ethiopian group and other taxa. In Island 6 (Fig. 15), *Zonohirsuta* + *Prosopoxylocopa* are a sister group to *Notoxylocopa* + *Proxylocopa* and the remainder of the Ethiopian group.

These analyses raise the possibility that *Zonohirsuta* and *Prosopoxylocopa* are not sister taxa to the rest the Ethiopian clade; perhaps they are parts of a more inclusive group that taken together are basal to the rest of the Ethiopian group. *Proxylocopa* is associated with the basal lineage of the Ethiopian group in all islands. *Xylocopa*, *Notoxylocopa*, *Xylocopoides*, and *Calloxylocopa* are basal to the Ethiopian groups in Islands 1, 3, 5, 6. All of these taxa and the Ethiopian group have two spines on the hind tibia of the male (Character 11-2) and female (Character 12-1; lost in *Calloxylocopa* and *X*. (*Xylocopoides*) *cyanea*). The topologies of Islands 1 (Fig. 11A), 5, (Fig. 13A) and 6 (Fig. 15) require
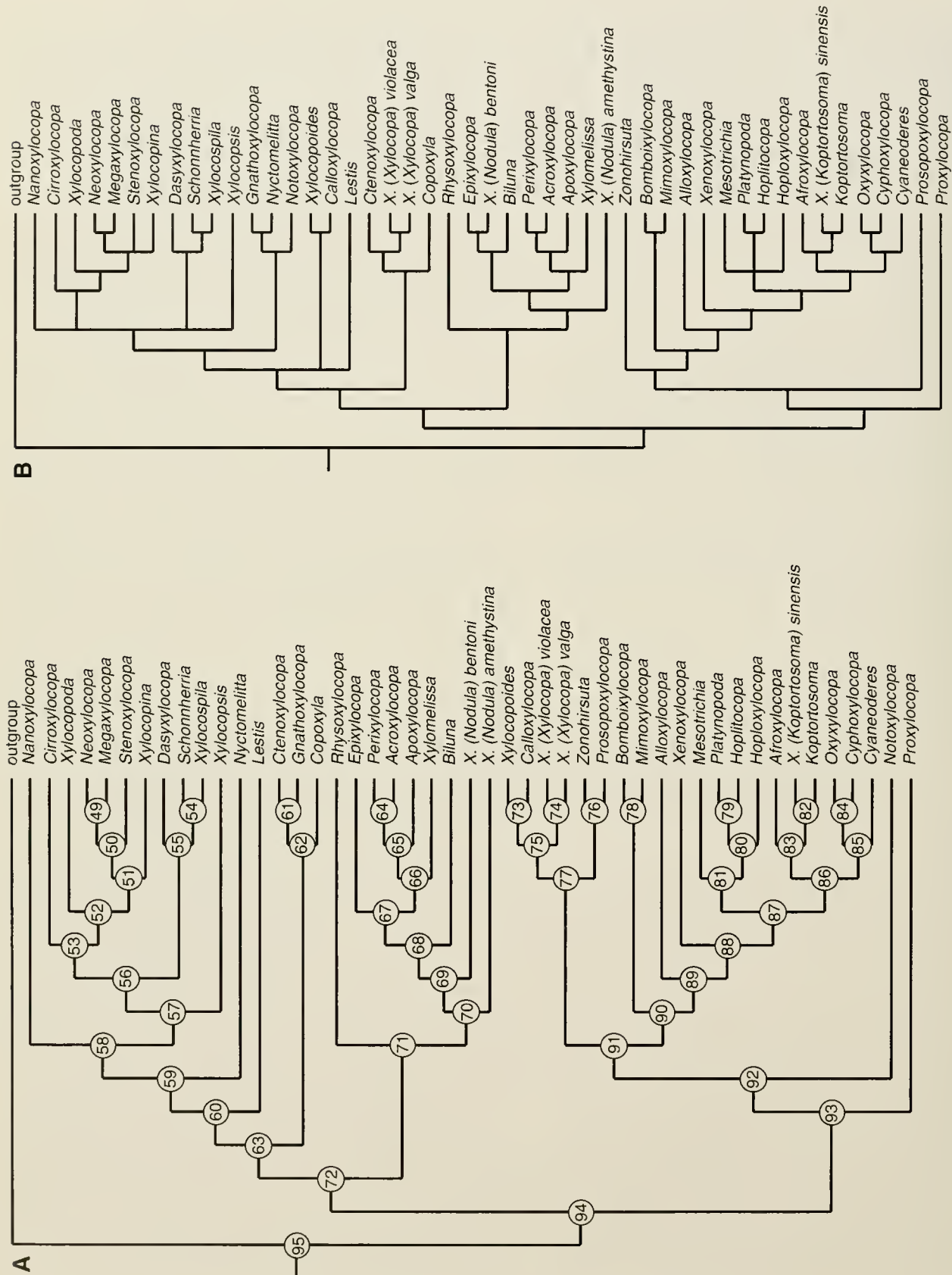
Fig. 11.   Analysis 3. Island 1. Phylogenetic relationships based on one island of trees. Analysis was done with all taxa and all characters included. Multistate characters were coded as nonadditive. A. One fully resolved tree randomly chosen from the 24 trees found; character distribution shown in Appendix 2. B. Strict consensus tree of equally weighted analysis.

that Character 11-2 be gained and lost once, whereas in other topologies, multiple gains and losses of this feature must be postulated. Character 12-1 also occurs in the *Neoxylocopa* group and *Nanoxylocopa* and as such is weakened. In all analyses with characters coded as additive (Analysis 1, 1A, 2, 2A, 4, 4A), there was support for a monophyletic Ethiopian group, as I have informally defined it. However, if the order of character evolution assumed in the other analyses proves to be incorrect, the relationships of the other taxa to the Ethiopian group shown in the analysis with all characters coded as non-additive may be robust.

Island 5 (Fig. 13A, B) places the *Rhysoxylocopa* group basal in the tribe. This analysis is the only one in which the *Rhysoxylocopa* group is placed in this position. *Proxylocopa* + *Notoxylocopa* , *Xylocopoides* + *Calloxylocopa*, *Xylocopa* (both species) are a grade along the stem of the Ethiopian group. *Lestis*, *Copoxyla* + (*Ctenoxylocopa* + *Gnathoxylocopa*) and *Nyctomelitta* are placed along the stem leading to the New World group.

All islands recovered monophyletic *Rhysoxylocopa* and *Neoxylocopa* groups; however, I consider the relationship of these subgenera to each other to be unresolved. Each island of trees associated the Old World taxon, *Nyctomelitta*, as the sister group to the large New World group referred to above. Basal to this New World clade plus *Nyctomelitta* was a group of Old World taxa that, depending on the analysis, included *Lestis*, *Copoxyla* and *Ctenoxylocopa* + *Gnathoxylocopa*.

Analysis 3A, successive approximations.— Manueliini is basal in the subfamily, all characters were coded as unordered. *Proxylocopa* is included (Figs. 12, 14.) Six analyses were run starting with each of the six islands produced in Analysis 3. After the characters stabilized, three of the six analyses generated unique consensus trees. The starting islands (from Analysis 3) and the statistics are: Topology 1 (Fig. 12) was found by starting at the trees in Islands 1, 3, and 6 (n = 110 trees; unweighted statistics: T.L. = 344, C.I. = 0.22, R.I. = 0.64; weighted statistics: T.L. = 347, C.I. = 0.52, R.I. = 0.88). Topology 2 was found by starting at Island 2 and 4, (n = 700+ trees [stopped before all trees were recovered]; unweighted statistics: T.L. = 343, C.I. = 0.22, R.I. = 0.64; weighted statistics: T.L. = 359, C.I. = 0.50, R.I. = 0.88). Topology 3 (Fig. 14) was found by starting at Island 5 (n =700+ trees [stopped before all trees were recovered]); unweighted statistics: T.L. = 353, C.I. = 0.22, R.I. = 0.63; weighted statistics: T.L. = 347, C.I. = 0.57, R.I. = 0.89).

Successive approximations applied to each of the islands produced three very different topologies. Topology 1 (Fig. 12) divides the tribe into two large clades. In one of these clades *Proxylocopa*, *Notoxylocopa*, *Zonohirsuta* + *Prosopoxylocopa*, X. (*Xylocopa*) *violacea* + (*Calloxylocopa* + *Xylocopoides*) and X. (*Xylocopa*) *valga* are progressively more
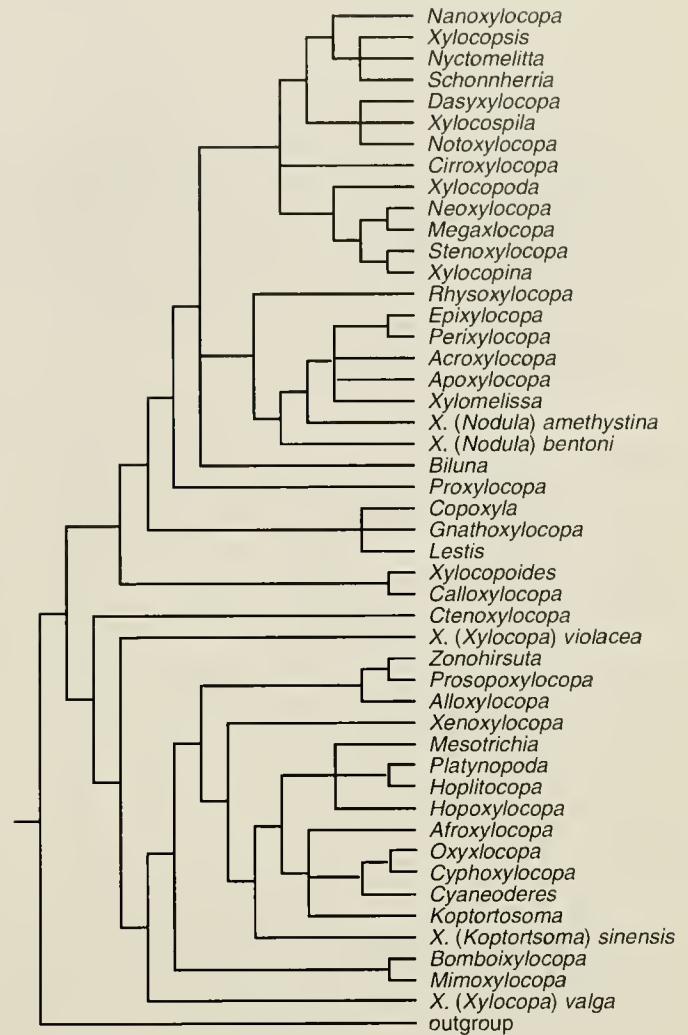

Fig. 12.   Analysis 3. Island 1. Strict consensus cladogram of six trees found after successive approximations weighting.

derived taxa, respectively, along the stem to the Ethiopian group (less *Zonohirsuta* and *Prosopoxylocopa*). The second clade is not well resolved. *Lestis*, the *Rhysoxylocopa* group, *Copoxyla* + (*Ctenoxylocopa* + *Gnathoxylocopa*), form a polytomy that collectively is the sister to the New World group.

Topology 2 divided the members of the more basal clades found in Topology 1 into a number of separate branches. The most basal branch in the tribe consists of *Ctenoxylocopa* as the sister group to both species of *Xylocopa* (sensu stricto) and *Xylocopoides* + *Calloxylocopa* are associated with the base of the Ethiopian group. *Proxylocopa* is a basal taxon and the sister group to the *Rhysoxylocopa* group, *Copoxyla*, *Lestis*, *Notoxylocopa* + (*Gnathoxylocopa* + *Nyctomelitta*) and the New World group.

Topology 3 (Fig. 14) was poorly resolved with *Proxylocopa*, both species of *Xylocopa*, and *Ctenoxylocopa*
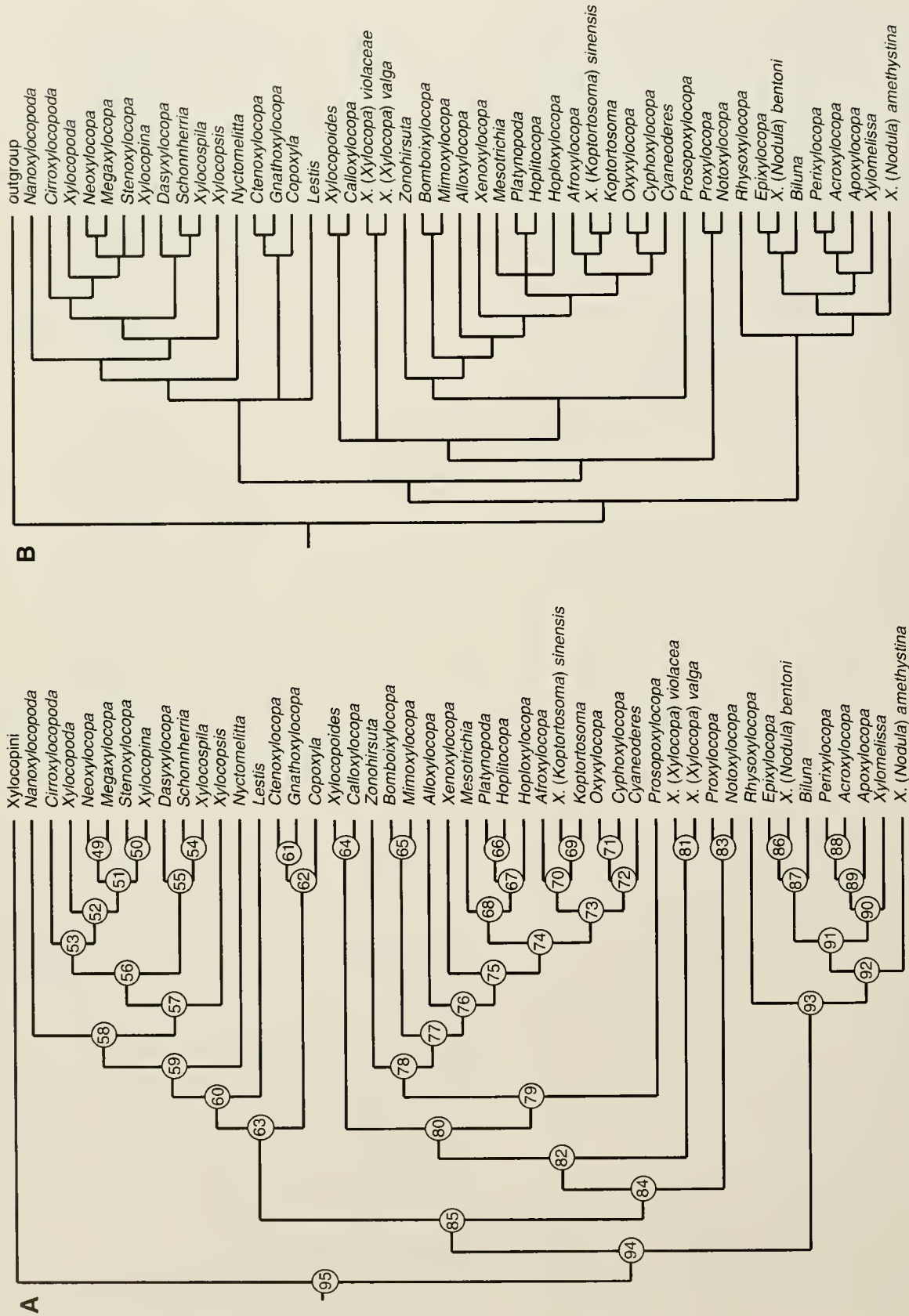
Fig. 13.   Analysis 3. Island 5. Phylogenetic hypothesis based on another island of trees from matrix shown in Figure 11. A. One fully resolved tree randomly chosen from the 72 trees found; character distribution shown in Appendix 3. B. Consensus tree of equally weighted analysis.

basal in the tribe. The *Rhysoxylocopa* is not monophyletic and is placed near the base of the Ethiopian group.

Analysis 4, equal weighting.—Xylocopini is basal in the subfamily; some characters were coded as additive and others as nonadditive. *Proxylocopa* is included. Eight minimum-length trees were found in this analysis (T.L. = 302, C.I. = 0.26, R.I. = 0.69). The changes in character coding resulted in few changes among the relationships of the ingroup. This result suggests that the problems in resolution found in the other analyses are not a result of polarity assessment based on the use of different outgroups. Because this analysis provides little new information on relationships, I do not present the cladograms or consider the results in the following discussion.

Analysis 4A, successive weighting.—Xylocopini is basal in the subfamily; some characters were coded as nonadditive. *Proxylocopa* is included. This analysis produced 123 most parsimonious trees (unweighted statistics: T.L. = 324, C.I. = 0.24, R.I. = 0.66; weighted statistics: T.L. = 364, C.I. = 0.62, R.I. = 0.92). Results of this search are not shown for the same reasons discussed for Analysis 4 above.

In summary, these data provide strong support for the monophyly of some groups among the Xylocopini, but the relationships among groups are often not strongly established. The monophyly of the *Neoxylocopa* group and the *Rhysoxylocopa* groups were supported in all analyses. Monophyly of the Ethiopian clade was supported in all but three islands of Analysis 3, where there were differences they were among the position of the basal members of this clade. The derived members of the Ethiopian group were associated in all analyses. A number of other subgenera not placed in the above mentioned informal groupings were placed in most analyses near the base of the tribe, either as monophyletic groups with poor character support or as members of a grade of taxa.

Relationships among Members of the Major Clades and Taxonomic Recommendations

Rhysoxylocopa group .—In the *Rhysoxylocopa* group, I include the following subgenera recognized by Hurd and Moure (1964): *Perixylocopa, Acroxylocopa, Apoxylocopa, Xylomelissa, Nodula, Epixylocopa, Rhysoxylocopa,* and *Biluna.* A gradulus on T1 of the female (Character 32-2; lost in *Perixylocopa*) was the only synapomorphy for the group in all analyses. In the other analyses, various other characters also supported the monophyly of this group including a row of tubercles on the edge of the basitibial plate (Character 17; Analysis 3, all islands), the continuous divergence of the inner ventral margins of the gonocoxites (Character 50; Analysis 1A, 2, 2A, 3 [Island 3]), and the carinate ventroapical plate of the male gonocoxite (Character 52-2). Although these are unusual features for bees, each occurs independently in other *Xylocopa.*
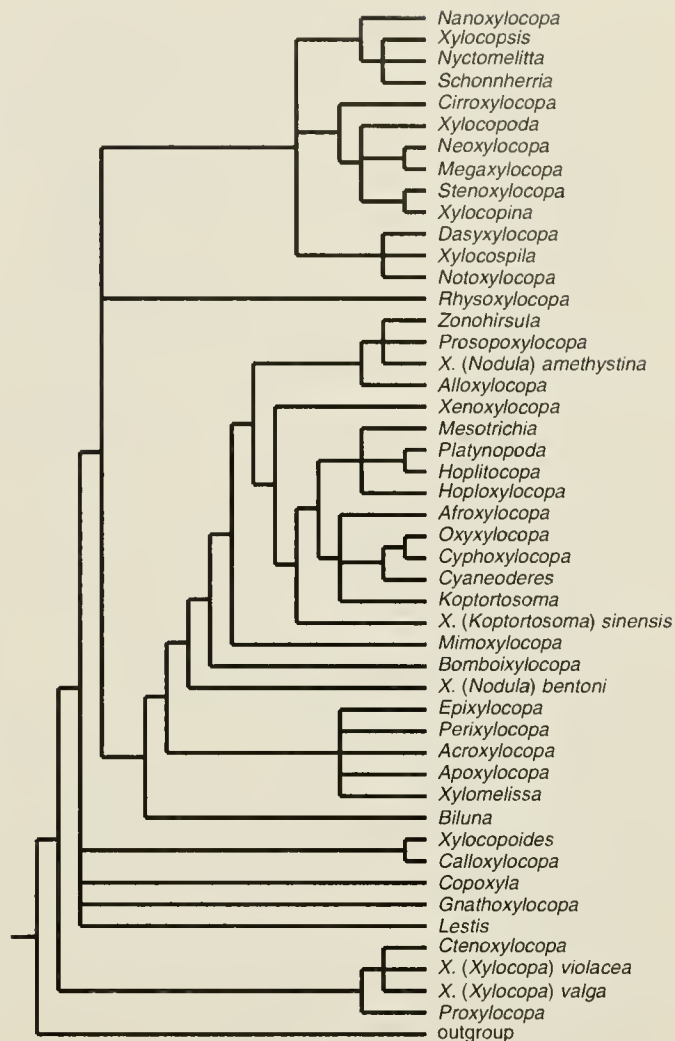

Fig. 14.   Analysis 3. Island 5. Strict consensus tree of 700 trees after successive approximations weighting. Lengths of horizontal lines are proportional to number of characters on each internode.

In the analyses with both nonadditive and additive characters (Analyses 1, 1A, 2, 2A), *Biluna* was placed at the base of the *Rhysoxylocopa* clade. In Analysis 3 (all characters coded as nonadditive), the basal branch of this clade was *Rhysoxylocopa* (sensu stricto). Depending on the topology accepted, a derived loss must be hypothesized for one of two characters shared by most members of this group. With *Biluna* as the basal branch, the mesosomal gland reservoir of males (Character 24) is secondarily lost in *Rhysoxylocopa* and *Xylocopa* (*Nodula*) *amethystina.* With *Rhysoxylocopa* as the basal branch, the reservoir of the mesosomal gland originates once in this clade but the row of tubercles on the posterior edge of the female basitibial plate (Character 17) is lost in *Biluna.* A case can be made in favor of this second scenario. For example, other reductions in the basitibial plate occur in *Biluna,* including com-
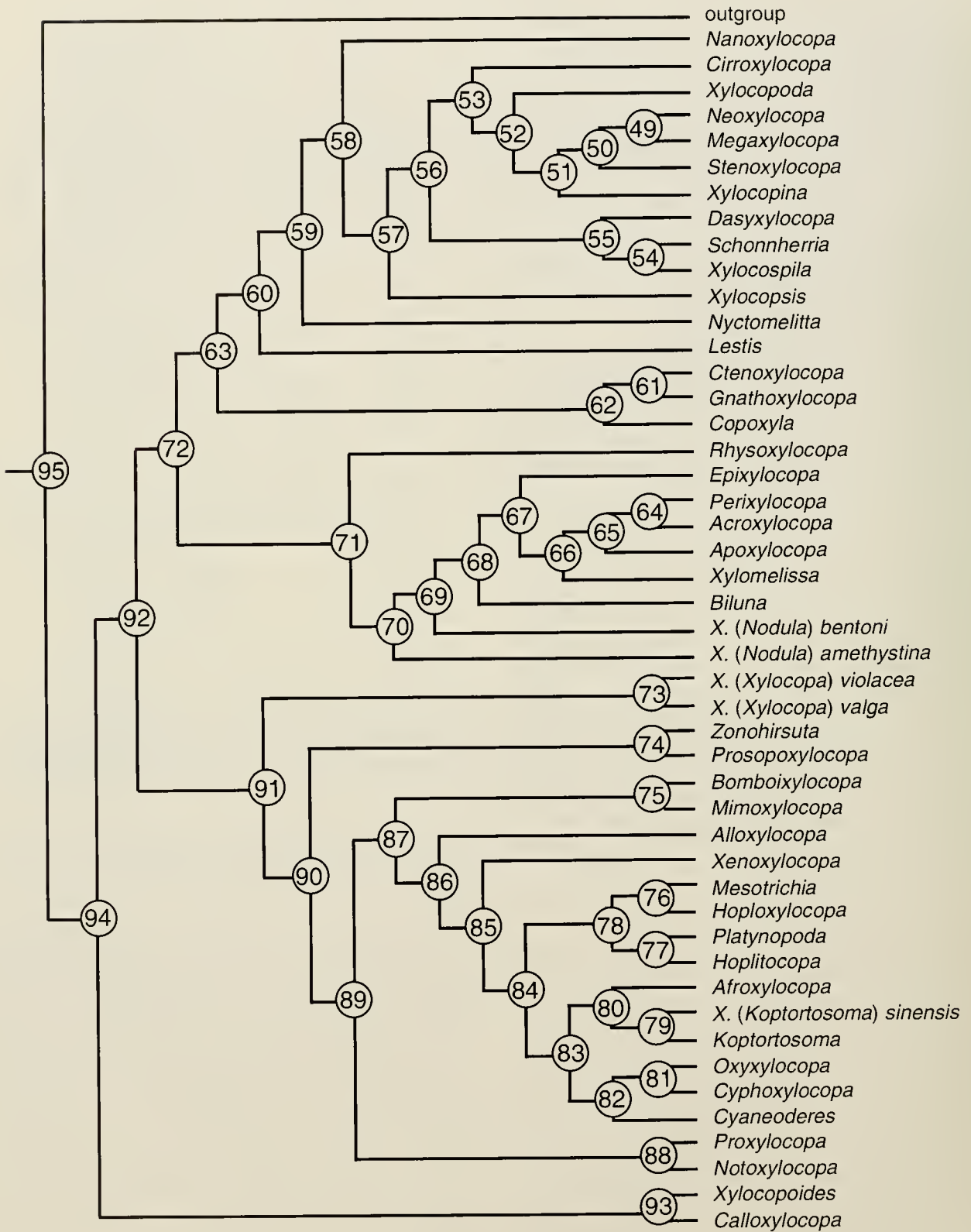
Fig. 15.   Analysis 3. Island 6. Phylogenetic hypothesis based on another island of trees from matrix shown in Figure 11. One fully resolved tree randomly chosen from the 24 trees; character distribution shown in Appendix 4.

plete absence of a basitibial plate in the males and reduction or absence of a midtibial spine in both sexes. These probably are associated with movement along the smooth inner surface of the bamboo culms used for nesting (Malyshev, 1931; Maeta et al., 1985). In females, the midtibial spines are functionally replaced by an apical mat of highly modified, thickened setae on the outer midtibia. Thus, the loss of tubercles of the female basitibial plate may be associated with loss of other structures on the leg.

Two characters are found only among members of the *Rhysoxylocopa* group: the absence or reduction of an apex or spine on the outer apex of the hind tibia of the male (Character 11-0), and the presence of a row of tubercles on the posterior edge of the basitibial plate of the female (Character 17-2). Character 11-0 is found in four African taxa *Perixylocopa, Acroxylocopa, Apoxylocopa* and *Xylomelissa* and one Asian taxon, *Xylocopa (Nodula) amethystina*. Character 17-2 is shared by these same taxa plus *X. (Nodula) bentoni* and *Rhysoxylocopa*. Reduction of the hind tibial spine of the male is approached in *Epixylocopa* and *Biluna*. For some specimens of *Epixylocopa* and *Biluna*, it was difficult to code unambiguously a spine as present or absent. The hind tibia flares at its apex and, depending on the angle in which it is viewed, the spine can appear absent, as a rounded projection, or present. Hurd and Moore (1963) listed *X. (Nodula) amethystina* as having this structure and *Epixylocopa* and *Biluna* as lacking it. In the specimens available to me, the conditions were reversed in these groups. I have not examined the specimens that Hurd and Moore used in their study, so this character may vary intraspecifically, or it was mistakenly assessed.

Despite the number of topologies found for members of the *Rhysoxylocopa* group, I have proposed some synonymies. Hurd and Moore (1963) recognized nine subgenera of which four were monotypic, even though they were aware that the *Rhysoxylocopa* group was poorly understood. Eardley (1983), in his study of South African species of *Xylocopa*, pointed out that subgeneric rank for some of these taxa is questionable.

The monophyly of *Rhysoxylocopa* and *Biluna* is well supported. *Rhysoxylocopa* all have extremely small propodeal spiracles in the males. The males of *Biluna* lack spines on the hind tibia, and females possess a dense mat of hairs on the mid-tibia. *Xylomelissa* and its near relatives are more problematic. In all analyses, *Xylomelissa* and *Apoxylocopa* + (*Perixylocopa* + *Acroxylocopa*) are either a monophyletic group or closely allied. Support for their monophyly is based on the absence of an angle or spine on the hind tibia of the male (Character 11-0). This derived loss also occurs in *Xylocopa (Nodula) amethystina*, and in some analyses (Analyses 1A, 2, 2A), this species was grouped with the other taxa that lack this structure. Inclusion of *X. (Nodula) amethystina* within *Xylomelissa* would entail a greatly ex-

panded definition of *Xylomelissa*. Males of *X. (Nodula) amethystina* completely lack a reservoir for the mesosomal gland (Character 26), as do males of *Rhysoxylocopa*, whereas in *Xylomelissa, Perixylocopa, Acroxylocopa, Apoxylocopa,* and *Epixylocopa*, the male mesosomal gland reservoirs consist of a single layer of tubules approximately as deep as they are wide in cross section. Therefore, I define *Xylomelissa* on the basis of structure of the gland reservoir, and include one species, *X. (Xylomelissa) ruficollis*, with a well-defined spine on the apex of the male hind tibia; all other species lack or have reduced forms of this structure. Recognition of this species as the subgenus *Epixylocopa* was based on the absence of yellow maculation on the face of the males (Character 10-1) by Hurd and Moore (1963). They clearly stated that other than this character *Epixylocopa* was close to *Xylomelissa*. Because yellow maculation varies within other subgenera and intraspecifically in *X. (Xylocopoides) californica arizonensis* (Minckley, pers. obs.), this feature does not warrant recognition as a subgeneric character.

None of my analyses grouped the two species of *Nodula* as a monophyletic group. As the above discussion indicates, the two exemplars I used, *Xylocopa (Nodula) amethystina* and *X. (Nodula) bentoni*, differ notably. The outer apex of the hind tibia of the female (Character 12) has one spine in *X. amethystina* and two spines in *X. bentoni*; the reservoir for the male mesosomal gland (Character 26) is not present in *X. amethystina* but is present in *X. bentoni*; and the beginning of the posterior thoracic declivity is abrupt in *X. amethystina* and smoothly rounded in *X. bentoni*. The male genitalia are similar, but I have found no discrete characters that serve as synapomorphies to unite these species. Maa (1938) recognized two groups in his original description of *Nodula*, which are represented by the two exemplars I used here. Thus, I have retained this subgenus to include the group typified by *X. (Nodula) amethystina* and propose that the group represented by *X. (Nodula) bentoni* be recognized as a new subgenus.

Ethiopian group.—As discussed above, support for the monophyly of the Ethiopian group varied. All females of the Ethiopian group, except *Bomboixylocopa* and *Mimoxylocopa*, have the beginning of the thoracic declivity abruptly rounded in the female (Character 23-1) and few setae on the male gonostylus (Character 48-1).

Prosopoxylocopa appears as a basal member of the Ethiopian clade in most analyses, either as the sister group to *Zonohirsuta* (Analyses 1, 1A, 3 [Islands 1, 6]) or as the sister group to *Zonohirsuta* plus the rest of the Ethiopian clade (Analyses 2, 2A, 3 [Islands 2, 3, 4, 5]). *Prosopoxylocopa* is distinct from *Zonohirsuta* based on interpretation of the development of the ventroapical plate of the male gonocoxite. In *Prosopoxylocopa*, the ventroapical plate is present, but lacks a carina, whereas in *Zonohirsuta* and the rest of the Ethiopian clade (except *Platynopoda*) the

ventroapical plate has a distinct carina (Characters 52-1, 52-2). Because the carina of the ventroapical plate seems to be a strong character in the Xylocopini, I favor the recognition of *Prosopoxylocopa* and *Zonohirsuta* as separate subgenera. If further studies find *Prosopoxylocopa* is a member of *Zonohirsuta*, separate subgeneric status for both taxa will not be warranted.

The next most derived lineages within the Ethiopian group, in all of the analyses except Analysis 2A, includes *Bomboixylocopa* + *Mimoxylocopa*, *Xenoxylocopa*, *Alloxylocopa*, the *Mesotrichia* group and the *Koptortosoma* group. As stated above, all have a distinct carina on the ventroapical plate of the male genitalia (Char. 52-2), a medial sulcus on T1 (Char. 35) and a projection on the inner basal margin of the venter of the gonocoxite (Char. 53-1).

Although superficially dissimilar, many features unite *Bomboixylocopa* and *Mimoxylocopa*. These include the long malar space in the female (Char. 8-1), a rounded thorax in the female (a derived loss, Char. 23-0), paired setal patches on the pregradular areas of the male (Char. 39), and patches of appressed setae near the metasomal spiracles (Char. 40). *X. rufipes* is the sole species of the subgenus *Mimoxylocopa*. Maa (1940) originally placed it in the subgenus *Zonohirsuta*. Hurd and Moure (1963) considered *Bomboixylocopa* most closely related to *Nyctomelitta*. All my analyses, however, support a sister group relationship to *Mimoxylocopa*.

The monophyly of *Xenoxylocopa*, *Alloxylocopa*, the *Mesotrichia* group, and the *Koptortosoma* group is supported by 4–6 characters in all analyses, including one feature that is uniquely derived—the produced apical edge of S1 (Character 36-1). The placement of the two basal taxa of this clade differed between analyses. In Analysis 1 (Fig. 10A, B), 1A, 2 (all islands) and 2A, *Alloxylocopa* is the sister group to the *Mesotrichia* and *Koptortosoma* groups, whereas in all islands of Analysis 3 (Figs. 11A, B; 13 A, B; 15) and 3A (Fig. 12) *Xenoxylocopa* is their sister group. The best supported topology depends on judgment of the strength of three characters, all of which are unique to the Xylocopini. Character 30, the shape of the gradulus on T1, is unreversed if *Xenoxylocopa* is considered to be the sister group to the *Mesotrichia* and *Koptortosoma* groups. In contrast, if *Alloxylocopa* is placed as the sister group to the *Mesotrichia* and *Koptortosoma* groups, two characters are unreversed— presence of a fovea on the anterior surface of T1 in the male (Character 33) and either a fovea or the entrance to an acarinarium on the anterior surface of T1 in the female (Character 34). Because characters 33 and 34 could be correlated (similar character states in both sexes), neither topology may be favored numerically.

Most analyses showed a sister group relationship between the *Mesotrichia* and *Koptortosoma* groups. The exception was in Islands 1 (Fig. 12), 2, 3, and 6 of Analysis 3A

(successive weighting analysis applied to data matrix with all characters coded as nonadditive), which places *Xylocopa sinensis* as the sister group to the remainder of the *Koptortosoma* group and the *Mesotrichia* group. This probably is a spurious result because of the high weight assigned to the carinate beginning of thoracic declivity (Character 23-2, see below). Females of *X. sinensis* have a rounded thoracic shape, but other characters place them with certainty into *Koptortosoma*. I consider this character to be a derived loss in *X. (Koptortosoma) sinensis*. The perpendicular angle of the beginning of the posterior thoracic declivity in both sexes (Characters 22-2, 23-2) provides the strongest support for the monophyly of the clade consisting of the *Mesotrichia* and *Koptortosoma* groups. The *Mesotrichia* group (*Hoploxylocopa*, *Mesotrichia*, *Hoplitocopa*, and *Platynopoda*) is supported by seven inferred synapomorphies; three of these are strong. An elongate tegula in the male (Character 29) is unique and unreversed; the triangular shape of the hind trochanter in the female (Character 14-1) is strong, but found in some species of *Koptortosoma* (sensu Hurd and Moure, 1963); and the slender penis valves of the male genitalia (Character 55) are found elsewhere in the ingroup only in *Xylocopa* (sensu stricto) and *Xylocopoides*.

Mesotrichia and *Platynopoda* + *Hoplitocopa* are supported as a monophyletic group by the reduced length of the male gonostylus (Character 47). *Hoploxylocopa* retains the elongate gonostylus and is thus inferred to be the basal member of this clade, although this condition is approached by some species of *Mesotrichia* (sensu Hurd and Moure, 1964 [see LeVeque, 1928]). *Platynopoda* and *Hoplitocopa* are shown to have a sister relationship based on six synapomorphies; the strongest one is the possession of a sclerotized base of the penis (Character 45). Despite this evidence, there are similarities of the male genitalia of *Hoplitocopa* and *Mesotrichia* (e. g., the broadly fused gonostylus and large projection from the posteroventral margin of the gonocoxite) that suggest an examination of the other species of *Mesotrichia* and *Platynopoda* might support a different topology than that shown here.

The monophyly of the *Koptortosoma* group is supported by the presence of a transverse carina on the scutellum that in most females overhangs the metanotum (Character 23-3). Relationships among the taxa of this group (*Oxyxylocopa*, *Cyphoxylocopa*, *Cyaneoderes*, *Afroxylocopa*, and *Xylocopa* [*Koptortosoma*] *sinensis*, and *Koptortosoma*) were resolved by characters that display considerable homoplasy or are continuously distributed. The most constant of these characters, the possession of a medial keel on S6 of the male (Character 37), supports a clade of *Cyphoxylocopa*, *Cyaneoderes*, *Afroxylocopa*, and *Koptortosoma* (sensu Hurd and Moure, 1963), but leaves *Oxyxylocopa*

defined by plesiomorphies. Furthermore, the median keel on S6 is lost in males of some members of *Koptortosoma*, and occurs in *Mesotrichia* (sensu Hurd and Moure, 1963) and *Xenoxylocopa*. I found no derived features that unite *Oxyxylocopa*, *Cyphoxylocopa*, and *Cyaneoderes* into a single clade. The apomorphies that Hurd and Moure (1963) used to differentiate these taxa, such as the shape of the male face and eyes, differences in the color of the vestiture, and the presence or absence of a mite pouch in T1 of the females, are highly variable. I conclude that these subgenera should be united with the subgenus *Koptortosoma*.

The four taxa in the *Koptortosoma* group with the greatest number of derived characters (*Afroxylocopa*, *Xylocopa caffra*, *X. pubescens*, and *X. sinensis*) are defined by four inferred synapomorphies, three of which display considerable homoplasy. A relatively strong character is the well-developed medial lobe at the apex of the gonostylus (Character 49-2). This character is similar to the condition found in *Schonnherria* and *Dasyxylocopa*. However, the gonostylus at its attachment to the gonocoxite is thick in *Schonnherria* (sensu lato) and *Dasyxylocopa*, and slender in *Koptortosoma* (sensu Hurd and Moure, 1963), thereby suggesting independent origins in these taxa. In my analysis, the vestiture on the dorsum of the male entirely yellow (Character 1), is a strong synapomorphy, but because it is not found in all species of *Koptortosoma* (sensu Hurd and Moure, 1963) (pers. obs.; also see Eardley, 1983), it provides weak support for the monophyly of the group. *Koptortosoma* (and its allied taxa as discussed herein) is the most species-rich taxon in the Xylocopini, and relationships among the constituent taxa would require more detailed study than I have undertaken. The shape of the medial lobe of the gonostylus (Character 49-2; Hurd and Moure, 1963, Fig. 241) of *Afroxylocopa*, *X. pubescens* and *X. sinensis* may prove phylogenetically useful and should be considered in any future revision.

Neoxylocopa **and** *Schonnherria* **clades.**—Analysis 3, with all characters coded as nonadditive and weighted equally, indicated a monophyletic New World group. In other analyses (Analyses 1, 1A, 2[Island 3]), *Notoxylocopa*, *Nyctomelitta*, and *Gnathoxylocopa* were variously placed between the clades that include *Schonnherria* and *Neoxylocopa*. These taxa, *Notoxylocopa*, and the Old World subgenus *Nyctomelitta*, share three characters: a carina or protuberance on the outer lateral edges of the penis valves (Character 43), the presence of a tooth on the upper carina of the female mandible (Character 3), and the absence of a metapostnotum in the males (Character 24). Character 43 is unique to this group. Characters 3 and 24 are highly homoplasious.

The relationships among the taxa associated with the *Neoxylocopa* group and *Schonnherria* (i.e., *Nanoxylocopa*, *Dasyxylocopa*, *Xylocopsis*, *Notoxylocopa*, and *Nyctomelitta*) differ greatly among the analyses that included additive characters (Analyses 1, 2, 4). Many characters serving as synapomorphies in this group are highly homoplasious, and few characters support these branches of the cladogram. One strong feature in *Schonnherria* (including *Xylocospila*), *Dasyxylocopa*, *Xylocopsis*, *Nanoxylocopa* and the *Neoxylocopa* group is a sharply-angled ventroapical plate of the male genitalia. I did not include this as a character in the data matrix, because the ventroapical plate varies continuously across taxa from a rounded condition with no evidence of a carina, to a rounded condition with a weak carina (Hurd and Moure, 1963, Fig. 135), to a flattened plate with a sharply-angled carina (Fig. 8A, B, C). Character 52, which concerns the ventroapical plate, was coded according to the presence or absence of this carina. *Notoxylocopa* and *Nyctomelitta* do not possess these features, and they have other features in common with taxa that do not have the sharply-angled ventroapical plate. In *Notoxylocopa*, such features are the absence of a reservoir of the male mesosomal gland (Char. 26-0), tubercles on both sides of the basitibial plate of the female (Character 17-1, in *Xylocopa guatemalensis*), and the thickly hirsute and broadly attached gonostylus (Character 48). In *Nyctomelitta*, these features are tubercles on both lateral edges of the basitibial plate of the female (Character 17-1) and the thickly hirsute and broadly attached gonostylus (Character 48). *Notoxylocopa* and *Nyctomelitta* may be sister groups to the New World group of taxa, but many characters cited above occur in the Old World clades. In the case of *Nyctomelitta*, its biogeography, like that of the South African endemic *Gnathoxylocopa*, strongly suggests their relationship with other Old World taxa.

Some characters suggest groupings within the clade that includes all of the New World taxa except *Xylocopoides*, *Calloxylocopa* and *Notoxylocopa*. These are: (1) Character 27-1, the beginning of the thoracic declivity on the scutellum of the male (*Cirroxylocopa*, *Stenoxylocopa*, *Xylocopoda*, and *Xylocopina*), or on the propodeum (*Neoxylocopa* and *Megaxylocopa*); (2) Character 48-0 (a loss), a slender, elongate gonostylus with few setae (*Megaxylocopa*, *Neoxylocopa*, *Stenoxylocopa*, *Xylocopina*, and *Xylocopoda*); and (3) Character 6-1, the presence of a carina or smooth zone along the epistomal suture (*Megaxylocopa*, *Neoxylocopa*, *Stenoxylocopa*, *Xylocopina*, and *Xylocopoda*).

Stenoxylocopa (sensu lato, see below) and *Neoxylocopa* (sensu lato, see below) were closely grouped in all analyses. They share three synapomorphies; the strongest is the presence of two spines on the outer apex of the female hind tibia (Character 12). *Stenoxylocopa* is defined here to include *Xylocopa ruficollis*, because it shares with *Stenoxylocopa* (sensu Hurd and Moure, 1963) fusion of the upper rutellar

tooth with the preapical tooth (Fig. 1C). *Xylocopa ruficollis* was previously placed in the monotypic subgenus *Xylocopina* by Hurd and Moure (1963); this assignment was based on four characters: Two are plesiomorphies—the shape of the apex of S1 and the yellow markings restricted to the lower part of the face—and two are autapomorphies—the short clypeus and the shape of the tegula. Neither of these types of characters is useful in establishing relationships (Wiley, 1978); without including *Xylocopina*, *Stenoxylocopa* is paraphyletic, or *Xylocopina* is defined entirely by plesiomorphies.

The subgenera *Neoxylocopa* and *Megaxylocopa* are united by features of the males—yellow vestiture (Character 1-1), patches of appressed setae on the pregradular area (Character 39), and the distinctive shape of the tubules and large size of the male mesosomal gland (Character 26-3). Character 26-3 and a modification of the scutellum foramen that accommodates the tubules of the mesosomal gland (Minckley, 1994, Fig. 5E, F) are unique synapomorphies of *Neoxylocopa* and *Megaxylocopa*. Hurd and Moure (1963) limited the subgenus *Megaxylocopa* to those species having a conspicuous carina over each of the lateral ocelli in the female. Although I agree that the subgenus *Megaxylocopa* is distinct, its recognition clearly renders *Neoxylocopa* paraphyletic and ignores the strong similarity between *Neoxylocopa* and *Megaxylocopa*.

The clade consisting of *Dasyxylocopa*, *Nanoxylocopa*, *Schonnherria*, *Xylocopsis*, and *Xylocospila* can be defined by the presence of a well defined ventroapical plate of the male genitalia (Character 52-2) and the morphology of the male mesosomal gland (Character 26-2; Minckley, 1994, Fig. 4 B). The monotypic subgenus *Nanoxylocopa* was placed as a basal taxon of this group (Analysis 3A [Islands 1, 5), as the basal taxon to the entire New World group (Analysis 3 [Islands 1, 2, 3, 5, 6]), or the sister group to *Schonnherria* (sensu lato) (Analyses 1, 2 [Islands 1, 3).

Schonnherria, *Xylocopsis*, *Dasyxylocopa*, and *Xylocospila* share a well-developed medial lobe on the apex of the gonostylus (Character 49-2). This character occurs elsewhere only in *Koptortosoma*. The male genitalia of *Xylocospila* share all features found in *Schonnherria* and warrant inclusion of this monotypic subgenus as a member of that group. Like *Nanoxylocopa* and *Xylocopsis*, *Dasyxylocopa* is monotypic, and was defined by Hurd and Moure (1963) largely by the lack of features found in *Schonnherria* (sensu Hurd and Moure, 1963). These four taxa share no strong features with other groups in the Xylocopini, and may be plesiomorphic members of the *Schonnherria* lineage. Features of the mesosomal gland are coded as missing for some of these taxa and might provide insight into the relationships of these subgenera to the lineages associated with *Schonnherria*, *Neoxylocopa*, and their allies. Until the relationships among these taxa are

further clarified (see further discussion below), I leave these taxa as separate subgenera.

Miscellaneous other clades.—The remaining taxa (*Xylocopa* [sensu stricto], *Ctenoxylocopa*, *Copoxyla*, *Gnathoxylocopa*, *Xylocopoides* + *Calloxylocopa*, *Proxylocopa*, and *Lestis*) have distinct characters, some of which may be synapomorphies, but they also share a number of plesiomorphic features. Most relationships among these taxa were not well resolved by my analyses.

The relationship of *Calloxylocopa* and *Xylocopoides* is strongly supported; a row of preapical spines from the pygidial spine (Char. 41-2) and the hirsute outer apex of the penis valves (Char. 44) are features known in no other bees.

Other relationships reveal disturbing character conflicts among these groups such as, among *Xylocopoides*, *Calloxylocopa* and *Xylocopa* s. str. Three strong apomorphies found elsewhere only in the Ethiopian clade are found in *Xylocopoides* and *Xylocopa* s. str.: two spines on the outer apex of the hind tibia in both sexes (Char. 11-2 and 12), and an angle or projection on the base of the ventral side of the gonocoxite (Char. 53). As previously discussed, these characters may indicate relationship of this group to the Ethiopian group. In addition to character 53, *Xylocopoides* and *X. (Xylocopa) violacea* completely lack gonostyli and have a foveate basitibial plate (known elsewhere only in *Lestis* and *X. (Xylocopa) convexior* Hedicke, according to the description of Maa, 1954). *Xylocopa* s. str. and *Xylocopoides* are also the two most northerly distributed groups in the tribe (Popov and Ponomareva, 1961; Hurd, 1954); most other Xylocopini are tropical. However, if these are sister taxa this relationship forces two characters, not found in other bees, to evolve convergently in *Calloxylocopa* and *Xylocopoides*; a series of spines along the lateral edges of the pygidial plate (Char. 41-2) and setae on the outer apex of the penis valves (Char. 44). The relationship proposed thus seems unlikely. I consider it more probable that *Calloxylocopa* is a derived member of the subgenus *Xylocopoides*, and that *X. (Xylocopa) violacea* represents the sister group to *Xylocopoides*.

This hypothesized relationship is complicated by the inclusion of *X. valga* in the subgenus *Xylocopa*, as it requires the gain of a well-developed gonostylus in *X. valga* from the fully fused condition (Char. 42) found in *X. (Xylocopa) violacea*. Gonostyli are commonly lost in bees, but it seems unlikely that once lost they would be subsequently regained. This might be evidence that *Xylocopa* s. str., as defined by Hurd and Moure (1963), is polyphyletic or paraphyletic. If so, *X. valga* is probably more closely related to *Ctenoxylocopa* because both share many features and have gonostyli that are slender and largely without setae (the latter feature was not coded in this analysis).

The ground-nesting group, *Proxylocopa*, is thought by some to be the most ancestral taxon in the tribe (see Introduction). Its relationship to the other Xylocopini is largely unresolved in this analysis, in part, because of my inability to homologize features of the basitibial plate and pygidial plate. Nonetheless, those structures I could homologize suggest that it is a plesiomorphic taxon. The male genitalia of *Proxylocopa* are most similar to those of the *Rhysoxylocopa* clade and/or *Copoxyla*. The gonostylus of these taxa is thickly hirsute apically and broadly attached to the gonocoxite (Char. 48) and the gonocoxites diverge continuously from the ventral gonocoxal bridge (Char. 52). The absence of a defined metapostnotum in the female (Char. 25) and one tibial spine in the male (Char. 11) are features that also occur among some of members of the *Xylomelissa* group and not in *Copoxyla*, and may be further evidence of close relationship. *Copoxyla* and *Proxylocopa* lack the ventroapical plate of the gonocoxite.

I conclude that among these taxa (*Xylocopa* s. str., *Ctenoxylocopa*, *Copoxyla*, *Gnathoxylocopa*, *Xylocopoides* + *Calloxylocopa*, *Proxylocopa* and *Lestis*) the most plesiomorphic members of the tribe are likely to be found. The relationships require further analysis before any substantiated statements of relationships can be made. Pref-

erably future analyses should include more of the species in these groups, which should reveal new characters or redefine some of those used in this study. I have retained all these groups as subgenera of *Xylocopa*.

These analyses show that many of the characters historically used to define the subgenera and genera of the Xylocopini arise repeatedly in the tribe and many groups are defined by unique combinations of characters rather than by characters that do not occur in any other group. A possible problem with these analyses is the use of outgroup comparison for structures that might be drastically influenced by a tremendous increase in size. In general, the members of the Xylocopini are many times larger than most members of the outgroup. Structures that are readily influenced by the large size may make determination of the groundplan states for these characters difficult or impossible. An example might be the basitibial plate as it is known to readily respond to changes in body size in other bees (Reyes, 1993).

Except for Table 1, up to this point the taxa recognized by Hurd and Moure (1963) have been used. From here on in the paper, the relationships indicated in the preceding sections are accepted, as are the nomenclatural results. For example, *Lestis* and *Proxylocopa* are hereafter treated as subgenera of *Xylocopa*.

KEYS TO THE SUBGENERA OF *XYLOCOPA*

New World Females

1. Pygidial plate with lateral margins marked by numerous spines and strongly divergent anteriorly on disc of T6 (Fig. 7C) 2

   Pygidial plate with lateral margins not marked by numerous spines and not strongly divergent anteriorly, sometimes represented by a spine that often has a shorter preapical spine on each side of its base and thus not or scarcely represented on disc of T6 (Fig. 7B) 3

2 (1). Basitibial plate foveate, closed basally (Fig. 2A); outer apex of hind tibia with two spines; median tubercle of labrum broad, rather globose, sometimes cleft apically [southeastern Canada and northwestern United States to southern Mexico] .... *Xylocopoides*

   Basitibial plate open at the base, not foveate; outer apex of hind tibia with long curved spine; median tubercle of labrum narrow (body elongate, subcylindrical) [Costa Rica to southern Mexico] .... *Calloxylocopa*

3 (1). Medial longitudinal carina on all metasomal sterna; clypeus usually bounded by continuous impunctate ridge 4

   Medial longitudinal carina is not on all metasomal sterna or entirely absent; clypeus bounded by discontinuous impunctate ridge, or ridge is entirely absent .. 5

4 (3). Upper tooth of mandible much wider than lower tooth (Fig. 1C) [southern Arizona in the United States to southern Argentina] .... *Stenoxylocopa*

   Upper tooth of mandible as wide as or narrower than lower tooth (Fig. 1 A) [southern South America to southwestern United States, introduced on Hawaii and Guam] .... *Neoxylocopa*

5 (3). Propodeal triangle present 6

   Propodeal triangle absent [western United States to Colombia] .... *Notoxylocopa*

6 (5). Labrum with 4 or fewer tubercles 7

   Labrum with 5 tubercles (abundant long setae) [central Argentina to southern Brazil] .... *Xylocopsis*

7 (6). Frontal carina elongate 8

   Frontal carina short, transverse, tuberculiform and not extending between antennal sockets [central Argentina to southern Brazil] .... *Nanoxylocopa*

8 (7). Clypeus at least half as long as broad; median clypeal length longer than the distance between clypeus and anterior ocellus 9

   Clypeus less than half as long as broad; median clypeal length shorter than the distance between clypeus and anterior ocellus 10

9 (8). Apex of S1 entire, not produced [south-central Brazil to Paraguay] .... *Cirroxylocopa*

Apex of S1 distinctly produced [extreme southern Brazil] .... *Dasyxylocopa*

10 (8). Eyes more convergent above than below; body integument often brilliantly metallic [southern United States to Argentina] .... *Schonnherria*

Eyes at least equally convergent above and below; body integument at most feebly metallic in bright light .. 11

11 (10). Mandible with three teeth on apical margin; parocular area with a large elongate depression adjacent to lateral sides of antennal sockets [south-central Brazil] .... *Diaxylocopa*

Mandible with two teeth on apical margin; parocular area not modified as above 12

12 (11). Thickly plumose hairs on the disc of the first metasomal tergum; eyes equally convergent above and below [central Argentina to southern Brazil] .... *Xylocopoda*

Sparsely plumose hairs on the disc of first metasomal tergum; eyes more convergent below than above [south-central Brazil] .... *Monoxylocopa*

New World Males

1. Graduli on T1, T2 or more terga; integument usually non-metallic, sometimes very weakly metallic 2

Graduli absent on T2–T5, integument usually brilliant metallic (often with apex of basitibial plate symmetrically or asymmetrically bifid) [southern United States to Argentina] .... *Schonnherria* (in part)

2 (1). Apex of basitibial plate asymmetrically or symmetrically bifid (Fig. 3A, B, C) 3

Apex of basitibial plate entire (Fig. 3D, E) 4

3 (2). Vestiture chiefly black, integument on discs of T1–T5 black and covered with dark setae [central Argentina to southern Brazil] .... *Xylocopsis*

Vestiture chiefly brownish, integument bare on discs of T1–T5 and largely eburneus [Argentina] .... *Schonnherria* (in part)

4 (3). T7 without dentiform projections on apex 5

T7 with dentiform projections on apex [western United States to Colombia] .... *Notoxylocopa*

5 (4). Anterior half of T3 broadly depressed on each side of basally carinate median line anterior margin of each depression bearing transverse row of very long, posteriorly directed plumose hairs which overlie the depression [Costa Rica to southern Mexico] ...... *Calloxylocopa*

T3 not modified as above 6

6 (5). Hind tibia with spines or high, thin lamella on ventral surface 7

Hind tibia not modified 8

7 (6). Hind tibia with high, thin lamella beginning near base of hind tibial spur and extending obliquely forward across ventral surface of tibia [central Argentina to southern Brazil] .... *Xylocopoda*

Hind tibia without lamella; inner hind tibial spur absent; apex of tibia beneath with large, flattened, highly polished tubercle [south central Brazil to Paraguay] ... . *Cirroxylocopa*

8 (6). One spine on outer apex of hind tibia 9

Two spines on the outer apex of the hind tibia [southeastern Canada and northwestern United States to southern Mexico] .... *Xylocopoides*

9 (8). Disc of scutellum entirely subhorizontal; posterior declivity of thorax beginning on the metanotum or propodeum 10

Disc of scutellum not entirely subhorizontal, posterior declivity of thorax undefined (antennal scape yellow, tegula punctate throughout or thickly pubescent circummarginally) [central Argentina to southern Brazil] .... *Nanoxylocopa*

10 (9). Integument mostly ferruginous or yellowish with ferruginous or fulvous pubescence; tegula ferruginous; scape entirely ferruginous or with longitudinal yellow frontal stripe [southern South America to southwestern United States, introduced on Hawaii and Guam].. .... *Neoxylocopa*

Integument mostly black at least on dorsum with blackish, whitish, or griseous pubescence; tegula black; scape largely or entirely black, without a longitudinal yellow frontal stripe 11

11 (10). Face with yellow maculations extending to vertex of head [southern Arizona in the United States to southern Argentina] .... *Stenoxylocopa*

Face with yellow maculations extending to just above antennal sockets [extreme southern Brazil] .... *Dasyxylocopa*

Old World Females (Excluding *Lieftinckella*)

1. Beginning of thoracic declivity represented by a transverse carina that divides the scutellum into a dorsal and vertical surfaces 2

Beginning of thoracic declivity represented by a gently or abruptly rounded angle 3

2 (1). Body length generally greater than 25 mm [Africa, Indian subcontinent to Indonesia and north to China] .... *Mesotrichia*

Body length generally less than 25 mm [Africa, east to the Pacific, southern Australia to northern China] .... *Koptortosoma*

3 (1). Midtibia with a spine on outer apex 4

Midtibia lacking spine on outer apex (anterior ocellus bounded on either side by an impunctate, crescent-shaped swelling) [Taiwan and southern China, to Indonesia and west to Indian subcontinent] .... *Biluna*

4 (3). Pygidial plate with lateral margins not strongly divergent anteriorly, represented by a spine that often has a shorter preapical spine on each side of its base and thus not or scarcely represented on disc of T6 (Fig. 7B, C) .. 5

Pygidial plate with lateral margins strongly divergent anteriorly on disc of T6, more than seven times wider anteriorly than posteriorly [Asia Minor to Turkestan region] .... *Proxylocopa*

5 (4). Outer apex of the hind tibia with one spine or convexity (Fig. 2B, C, D, E) 6

Outer apex of the hind tibia with two spines or convexities (Fig. 2A) 12

6 (5). Ocelli normal, diameter much less than twice the width of the scape 7

Ocelli enlarged, diameter greater than twice the width of the scape (basitibial plate bifid; integument reddish-brown to black with ferruginous pubescence) [Indian subcontinent to Java] .... *Nyctomelitta*

7 (6). Pygidial spine with a preapical spine on each side at base (Fig. 7C) 8

Pygidial spine without a preapical spine on each side at base (Fig. 7B) [Europe to central Asia] .... *Copoxyla*

8 (7). Mandible with two teeth on apical margin (Fig. 1B) .. 9

Mandible with three teeth on the apical margin (Fig. 1A) 11

9 (8). Scutellum modified, forming a conspicuous posteriorly-directed lobe that overhangs entire metanotum [Sri Lanka and peninsular India] .... *Nodula*

Scutellum not forming a conspicuous posteriorly-directed lobe 10

10 (9). Parocular area without tubercle; maxillary palpus six-segmented [northwestern India to southern Turkestan] .... *Maaiana*

Parocular area with tubercle below antennal socket; maxillary palpus four-segmented [northern and eastern Australia] .... *Lestis*

11 (8). Mandible with hook-like process on the lower edge (Fig. 1B) [Africa south of the Sahara] .. *Gnathoxylocopa*

Mandible without hook-like process (basitibial plate with tubercles along both lateral edges (Fig. 2B)) [Africa south of the Sahara, Turkestan region to the Indian subcontinent] .... *Ctenoxylocopa*

12 (5). Minimum length of malar space less than length of second flagellar segment; one or both lateral edges of the basitibial plate crenulate (Fig. 2B) 13

Minimum length of malar space more than length of second flagellar segment; lateral edges of the basitibial plate entire (Fig. 2C, E) [northeastern China and Korea] .... *Bomboixylocopa*

13 (12). Beginning of thoracic declivity represented as an abrupt rounded angle in scutellar profile 14

Beginning of thoracic declivity broadly rounded, i.e. not defined, thoracic shape being evenly rounded in profile 17

14 (13). Pygidial spine with a preapical spine on each side at base (Fig. 7C) 15

Pygidial spine without a preapical spine on each side at base (Fig. 7B) (lateral line of T1 transverse; vertical fold of anterior face of T1 broad and deep) [Middle East to southern China] .... *Alloxylocopa*

15 (14). Anterior face of T1 with medial, vertical sulcus that is broad and deep; lateral line of T1 transverse [Africa south of the Sahara] .... *Xenoxylocopa*

Anterior face of T1 lacking a vertical sulcus altogether or, if present, sulcus not as well developed as above; posterior part of the lateral line of T1 curved posteriorly, more or less parallel to lateral margin of metasoma .. 16

16 (15). Apex of basitibial plate bifid, sometimes feebly so (Fig. 2A, B, C) [Tibet through the tropical Orient to Sulawesi Is.] .... *Zonohirsuta*

Apex of basitibial plate simple (Fig. 2D, E) (supraclypeal area strongly swollen, bigibbose) [Madagascar] .... *Prosopoxylocopa*

17 (13). Length of metanotum greatest medially 19

Length of metanotum subequal from side to side [Mediterranean Basin to central Asia] .... *Xylocopa*

18 (17). Discal hairs of T1 simple or sparsely plumose; first flagellar segment shorter than combined lengths of succeeding three segments; medial groove of propodeum distinct [Africa] .... *Xylomelissa*

Discal hairs of T1 thickly plumose; first flagellar segment equal to or longer than the succeeding three segments; medial groove of propodeum indistinct [northern Africa, southern Europe into Asia Minor] .... *Rhysoxylocopa*

OLD WORLD MALES (EXCLUDING *LIEFINCKELLA*)

1 Basitibial plate absent, or its apex entire (Fig. 2E) 2

Basitibial plate present, apex asymmetrically or symmetrically bifid (Fig. 2A, B, C) 3

2 (1). Dorsal surface of T1 angulately (or subangulately rounded in *Alloxylocopa*) onto anterior surface; lateral line of T1 transverse 5

Dorsal surface of T1 sloping or rounding onto declivous anterior surface; lateral line of T1 curved posteriorly,

more or less parallel to lateral margin of metasoma . 8

3 (2). Ocellus normal, diameter less than twice the width of the scape 4
Ocellus enlarged, diameter greater than twice the width of the scape [Indian subcontinent to Java] .. *Nyctomelitta*

4 (3). Beginning of posterior thoracic declivity on scutellum (posterolateral lobe of pronotum prolonged posteriorly so as to extend well onto mesepisternum and nearly attaining preepisternal groove) [Africa south of the Sahara, Turkestan region to the Indian subcontinent] .... *Ctenoxylocopa*
Beginning of posterior thoracic declivity on metanotum [Africa south of the Sahara] .... *Gnathoxylocopa*

5 (2). Tegula normal, outer margin convex, rounded behind (Fig. 4A), posterolateral third may or may not be impunctate, glabrous and shining 6
Tegula elongate, outer margin at least slightly concave (Fig. 4B), posterolateral third impunctate, glabrous, and shining [Africa, Indian subcontinent to Indonesia and north to China] .... *Mesotrichia*

6 (5). Dorsal surface of T1 nearly horizontal, abruptly and angulately divided from anterior surface 7
Dorsal surface of T1 sloping forward, subangulately rounding onto anterior surface (tegula punctate throughout) [Middle East to southern China] .... *Alloxylocopa*

7 (6). Anterior surface of T1 without a fovea [Africa south of the Sahara] .... *Xenoxylocopa*
Anterior surface of T1 with a fovea [Africa, east to the Pacific, Australia to northern China] .... *Koptortosoma*

8 (2). Outer apex of mid tibia with a spine 9
Outer apex of mid tibia without a spine (anterior ocellus bounded on either side by impunctate, crescent-shaped swelling) [Taiwan and southern China, to Indonesia and west to Indian subcontinent] .... *Biluna*

9 (8). Outer apex of the hind tibia with one spine (Fig. 2B, C, D, E) 10
Outer apex of the hind tibia with two spines (Fig. 2A) ... 20

10 (9). Minimum malar length shorter than second flagellar segment; face entirely black or with yellow maculations only on areas below the lateral ocelli 11
Minimum malar length as long as length of second flagellar segment; face with two parallel stripes running along the inner margins of the eyes from the vertex to the bases of the mandibles (entire metanotum exposed dorsally and base of propodeum horizontal, at least laterally) [China] ....
.... *Bomboixylocopa*, in part (*X. rufipes*)

11 (10). Flagellum cylindrical; maxillary palpus five or six segmented; second submarginal cell of forewing much

longer posteriorly than anteriorly 12
Flagellum crenulate on inferior surface; maxillary palpus four-segmented; second submarginal cell of forewing nearly in form of parallelogram (integument brightly metallic) [Australia] .... *Lestis*

12 (11). Labrum apically entire 13
Labrum apically emarginate 14

13 (12). Eyes closest medially, inner orbits convex, bowed towards antennal sockets; frontal carina sulciform, not elevated at distal apex; beginning of thoracic declivity represented as abruptly rounded angle in scutellar profile [Madagascar] .... *Prosopoxylocopa*
Inner orbits of eyes concave, curved inward towards central eye axis; frontal carina cariniform; scutellum rounded in profile [northeastern China and Korea] .... *Bomboixylocopa* (in part)

14 (12). Clypeus black 15
Clypeus with yellow maculations 17

15 (14). Apex of T7 entire 16
Apex of T7 with pair of dentiform spines [Europe to central Asia] .... *Copoxyla*

16 (15). Propodeal spiracles small and asymmetrical; minimum interorbital distance equal to or greater than length of antennal scape [northern Africa, southern Europe into Asia Minor] .... *Rhysoxylocopa*
Propodeal spiracles normal, not modified; minimum interorbital distance shorter than length of antennal scape [Africa] .... *Xylomelissa* (in part)

17 (14). Beginning of thoracic declivity indicated by an abruptly rounded angle in scutellar profile 18
Beginning of thoracic declivity not defined, thorax evenly rounded in profile 19

18 (17). Posterolateral third of tegula impunctate, glabrous and shining (northwestern India to southern Turkestan) .... *Maaiana*
Tegula punctate throughout [Tibet through the tropical Orient to Sulawesi] .... *Zonohirsuta*

19 (17). Hind femur with tubercle on ventral surface; lateral ocellus not bounded laterally by conspicuous transverse ridge (Africa) .... *Xylomelissa* (in part)
Hind femur without tubercle; lateral ocellus often bounded laterally by conspicuous transverse ridge (Sri Lanka and peninsular India) .... *Nodula*

20 (9). Propodeal triangle defined [Mediterranean Basin and central Europe to central Asia] .... *Xylocopa* (sensu stricto)
Propodeal triangle absent [Asia Minor to Turkestan region] .... *Proxylocopa*

DIAGNOSES AND DESCRIPTIONS OF SUBGENERA OF *XYLOCOPA*

The following descriptions are presented in the order used for characters in the Character List and Coding section; numbers are the same as those used there. Unique apomorphies are in bold face type.

Subgenus *Xylomelissa* Hurd and Moure

Xylomelissa Hurd and Moure, 1963: 219. Type species: *Xylocopa carinata* Smith, 1874, by original designation.

Epixylocopa Hurd and Moure, 1963: 223. Type species: *Xylocopa rufitarsis* Lepeletier, 1841, by original designation. New synonymy.

Apoxylocopa Hurd and Moure, 1963: 226. Type species: *Xylocopa lugubris* Gerstaecker, 1857, by original designation. New synonymy.

Dinoxylocopa Hurd and Moure, 1963: 230. Type species: *Xylocopa absurdipes* Enderlein, 1903, by original designation. New synonymy.

Euxylocopa Hurd and Moure, 1963: 232. Type species: *Xylocopa fraudulenta* Gribodo, 1894 by original designation. Synonymy with *Xylomelissa* by Maa, 1968: 106.

Perixylocopa Hurd and Moure, 1963: 232. Type species: *Xylocopa erythrina* Gribodo, 1894: 232, by original designation. Synonymy with *Xylomelissa* in part, by Maa, 1968:106.

Acroxylocopa Hurd and Moure, 1963: 236. Type species: *Xylocopa capitata* Smith, 1854, by original designation. New synonymy.

This subgenus is closely related to *Nodula*, *Maaiana*, and *Rhysoxylocopa*. Males can be distinguished from all other members of the tribe by the combination of the complete lack of spines on the outer apex of the hind tibia, (although this is flared in some taxa) and the presence of a basitibial plate. Females are similar to those of *Rhysoxylocopa* but can be distinguished by the presence of a distinct medial groove on the propodeum. All species are African. In some analyses presented here the Oriental subgenus *Biluna* was placed in this group, although, as discussed below, *Biluna* is probably not a member of the clade. *Xylocopa absurdipes*, the only species placed in *Dinoxylocopa* and known only from males, shares all of the apomorphies of this group and so should be included in *Xylomelissa*. Maa (1968: 106) effectively synonymized *Perixylocopa* with *Xylomelissa* in his species citation, even though in the discussion he stated that he left the subgenus *Perixylocopa* intact.

Description.—(1) Color of vestiture on male dorsum predominately dark brown or black. (2) Upper carina of male mandible without a tooth, except in *Xylocopa erythrina*. (3) Upper carina of female mandible without a tooth, except in *X. erythrina* and *X. rufitarsis*. (4) Two teeth on apical margin of female mandible except for *X. capitata* which has three teeth. (5) Upper rutellar tooth and preapical tooth of female mandible separated by emargination. (6) Female epistomal suture smooth, without a ridge, except in *X. capitata* and *X. erythrina*. (7) Supraocellar pits of female punctiform. (8) Female malar space shorter than width of first flagellar segment, except in *X. capitata*. (9) Ocelli not enlarged. (10) Male with yellow facial maculations, except in *X. rufitarsis*. (11) **Outer apex of male hind tibia without spines.** (12) Outer apex of female hind tibia with one spine. (13) Tibial spine of female originating at tibial apex and

without a medial carina, except in *X. albifrons*. (14) Hind trochanter of male subcylindrical, not triangular. (15) Male mid- and hind trochanter not modified. (16) Male hind femur with basal tubercle, except for *X. rufitarsis* and *X. albifrons*. (17) Posterior edge of female basitibial plate with a row of tubercles. (18) Apex of male basitibial plate entire. (19) Apex of female basitibial plate bifid. (20) Female basitibial plate open basally. (21) Female basitibial plate reduced, not extending to near base of tibia. (22) Thoracic profile of male smoothly rounded, beginning of thoracic declivity undefined. (23) Thoracic profile of female smoothly rounded, beginning of thoracic declivity undefined. (24) Male metapostnotum absent, except in *X. rufitarsis*. (25) Female metapostnotum present except in *X. capitata* and *X. rufitarsis*. (26) Mesosomal gland reservoir a single layer of parallel running tubules. (27) Beginning of thoracic declivity of male on scutellum. (28) Propodeum at its connection with metasoma not modified. (29) Male tegula not elongated posteriorly. (30) Gradulus on T1 continued posteriorly adjacent to lateral margin of the metasoma. (31) Graduli present on T1 to T5 of male. (32) Gradulus only on T1 of female except in *X. erythrina* which has graduli on T1–T5. (33) Anterior surface of T1 of male without a fovea. (34) Anterior surface of T1 of female without a foveal pit or entrance to acarinarium. (35) Medial groove of T1 of female linear. (36) Apical margin of S1 entire, not produced except in *X. rufitarsis* and *X. erythrina*, in which it is medially emarginate. (37) Medial carina restricted to posterior half or absent on S6 of male. (38) Medial carina on sternum of females weakly developed. (39) Pregradular areas on S3–S5 of males with paired patches of long setae. (40) Patches of appressed setae present near spiracles on T2–T6 of males. (41) Pygidial spine of female with pair of preapical lateral spines. (42) Gonostylus of male genitalia distinct although fused to gonocoxite. (43) Outer edge of penis valve not modified, without lateral projection. (44) Penis valve apex not hirsute. (45) Penis entirely membranous. (46) Spatha absent. (47) Gonostylus broadly attached to gonocoxite. (48) Gonostylus broadly attached to gonocoxite and apically with dense patch of setae. (49) Gonostylus apex with weakly developed, medially projecting lobe. (50) Medial ventral margin of gonocoxites diverging continuously from dorsal gonocoxal bridge or nearby. (51) Gonocoxite lacking a projection or spine from posterior ventral margin. (52) Ventroapical plate of gonocoxite rounded, with a carina. (53) Medial projection or spine at base of ventral gonocoxite absent. (54) Apex of T7 of male entire. (55) Penis valves apically expanded.

Subgenus *Nodula* Maa

Nodula Maa, 1938: 290. Type species: *Apis amethystina* Fabricius, 1793, by original designation.

Maa (1938) noted that this subgenus is represented by two "natural groups;" exemplars of both were included in my analysis. I found no characters that define members of this subgenus as a monophyletic group, although the male genitalia are phenetically similar. The evidence suggests that *Nodula*, as presently recognized, is either a paraphyletic or polyphyletic assemblage and I have recognized the group typified by *X. bentoni* as a separate subgenus *Maaiana*. This leaves *Nodula* consisting of the following species: *X. amethystina*, *X. madurensis*, *X. meyeri*, *X. nigrotarsata*, *X. phanerocephala*, *X. prashadi*, *X. ramakrishnai* and *X. remota*. A key to them and those in the subgenus *Maaiana*, modified from Maa (1938 and 1954), was given in Hurd and Moure (1963). *Nodula* is closely related to *Maaiana*, *Xylomelissa* (s. lat.) and *Rhysoxylocopa*. The males of *Nodula* can be distinguished from those of *Xylomelissa* by the presence of a spine on the outer apex of the hind tibia of the male and from those of *Rhysoxylocopa* by the unmodified propodeal spiracles. The females of *Nodula* can be distinguished from those of the subgenus *Rhysoxylocopa* by carinae dorsal to the lateral ocelli and a sharply rounded scutellum.

Description.— As in *Xylomelissa*, except as follows: (11) Outer apex of male hind tibia with one spine. (12) Outer apex of female hind tibia with two spines. (16) Male hind femur without basal tubercle or spine. (22) Beginning of posterior thoracic declivity of male abruptly rounded. (23) Beginning of posterior thoracic declivity of female abruptly rounded. (24) Male metapostnotum evident. (26) Mesosomal gland reservoir absent. (49) Gonostylus apex entire, without medially projecting lobe.

Subgenus **Maaiana** new subgenus

Type species.—*Xylocopa bentoni* Cockerell 1919: 172.

The relationship of this group to *Nodula* and allied subgenera is discussed above under *Nodula*. As defined herein, *Maaiana* consists of the following species; *X. angulosa*, *X. bentoni*, *X. bicristata*, *X. punctigena* and *X. punctilabris*. A key to the species, as the *punctigena* group of *Nodula*, was presented by Maa (1954) and in modified form by Hurd and Moure (1963). Males of *Maaiana* can be distinguished from those of *Nodula* by the abrupt beginning of the posterior thoracic declivity on the scutellum, from *Xylomelissa* by the presence of a spine on the outer apex of the hind tibia, and from *Rhysoxylocopa* by the unmodified propodeal spiracles. Females of *Maaiana* can be distinguished from those of the subgenus *Rhysoxylocopa* by the presence of a carina dorsal to each lateral ocellus and a sharply rounded scutellum.

Etymology.—The name *Maaiana* is in recognition of T. C. Maa for his important work on Old World Xylocopini.

Description.—As in *Xylomelissa*, except as follows: (11) Outer apex of male hind tibia with one spine. (13) Hind tibial spine of female strongly developed. (16) Male hind femur without basal tubercle or spine. (26) Mesosomal gland reservoir present. (49) Gonostylus apex entire, without medially projecting lobe.

Subgenus *Biluna* Maa

Biluna Maa, 1938: 270, 276. Type species: *Xylocopa nasalis* Westwood, 1842, by original designation.

This subgenus is a group of large, elongate bees that, as far as known, nest solely in bamboo. Associated with the very smooth inner surface of this nesting substrate are morphological modifications of the legs and mandibles. Males can be distinguished from those of all other taxa by the combination of lacking a basitibial plate and of spines on the outer apex of the tibia. Females can be distinguished by two features of the mid-tibia: a dense mat of short, stout setae and absence of spines on the outer apex. Hurd and Moure (1963) considered *Biluna* to be closely related to the subgenus *Xylocopa*. In my analyses, this subgenus is clearly allied with a clade consisting of *Xylomelissa*, *Rhysoxylocopa*, and *Nodula*. In most analyses, *Biluna* is shown as the most basal taxon of this clade.

Description.—As in *Xylomelissa*, except as follows: (17) Basitibial plate of female with edges slightly raised from surface of tibia. (18) Basitibial plate of male absent. (19) Apex of female basitibial plate entire. (25) Metapostnotum of female absent. (27) Beginning of thoracic declivity of male on propodeum in *X. tranquebarorum*, metanotum in *X. nasalis* and *X. auripennis*. (39) Pregradular areas of male sterna without lateral setal patches. (49) Gonostylus entire, without a medial lobe.

Subgenus *Rhysoxylocopa* Hurd and Moure

Rhysoxylocopa Hurd and Moure, 1963: 178. Type species: *Xylocopa cantabrita* Lepeletier, 1841, by original designation.

This group is closely related to *Xylomelissa*, *Nodula*, *Maaiana* and *Biluna*. Females of *Rhysoxylocopa* can be distinguished from those taxa by the absence of a medial groove on the propodeal triangle. Males are easily distinguished from all other taxa by the unusual propodeal spiracles which Hurd and Moure (1963) described as "small, asymmetrical, lower extremity broadened, anterior margin, as determined by deeply impressed line, forming an elongate triangular flap whose lower anterior margin projects strongly forward."

Description.—As in *Xylomelissa*, except as follows: (10) Male face entirely black. (11) Outer apex of male hind tibia with one spine. (13) Female hind tibia with tibial spine strongly developed, originating well before tibial apex and with medial carina. (26) Male without a mesosomal gland

reservoir. (39) Pregradular area of male without lateral setal patches. (40) Male without patches of short setae near metasomal spiracles. (49) Gonostylus apex entire, without medially projecting lobe.

Subgenus *Proxylocopa* Hedicke, New status

Xylocopa (Proxylocopa) Hedicke, 1938: 192. Type species: "X. olivieri Brll." (=*Xylocopa olivieri* Lepeletier, 1841), by original designation.
Proxylocopa (Proxylocopa) Maa, 1954: 116: 190, 193.
Ancylocopa Maa, 1954: 190, 198. Type species: *Xylocopa nitidiventris* Smith, 1878, by original designation. New synonymy.

This subgenus is notable in having a distinctively long face in females as compared to other members of the tribe; this feature probably is associated with loss of the strong mandibular musculature for gnawing in wood. Females are easily distinguished by the well-developed basitibial plate located at the base of the hind tibia and by the well-developed pygidial plate. Males can be recognized by the set of characters including short, ovate, parapsidal lines, no more that three times as long as wide, and two spines on the outer apex of the hind tibia. The recognition of *Proxylocopa* as a genus requires that it be the sister group to the rest of the genus *Xylocopa*. If *Proxylocopa* is more closely related to any of the derived subgenera of *Xylocopa*, the recognition of *Proxylocopa* as a genus makes *Xylocopa* paraphyletic. As discussed above, the distinctiveness of *Proxylocopa* lies primarily with the structures associated with soil nesting, and there is morphological and phylogenetic evidence that these structures have evolved secondarily. Those characters of *Proxylocopa* that I can homologize with structures of other Xylocopini are not generically distinct from the other taxa in the tribe. The male genitalia suggest that this group is most closely related to *Copoxyla* and/or the clade of *Rhysoxylocopa, Biluna, Nodula, Maaiana,* and *Xylomelissa*. I favor emphasizing the homogeneity of the tribe, and create an unequivocally monophyletic genus *Xylocopa* by assigning subgeneric rank to *Proxylocopa*. Furthermore, it is obvious that there is no clear distinction between the two presently recognized subgenera, *Proxylocopa* (sensu stricto) and *Ancylocopa*. Ocellar diameter and length of the malar space were the primary characters used by Maa (1954) to distinguish these groups. Based on my examination of *P. rufa* and *P. olivieri* of *Proxylocopa* (sensu stricto) and all species of *Ancylocopa*, the ocellar diameters and the malar space grade continuously together. Therefore, l synonymize *Ancylocopa* with the subgenus *Proxylocopa*.

Description.—As in *Xylomelissa*, except as follows: (9) Ocelli enlarged in some species, diameter greater than that of antennal socket. (11) Outer apex of male hind tibia with two spines. (16) Male hind femur without basal tubercle or spine. (25) Female metapostnotum absent. (26) Mesosomal gland reservoir consisting of two small, widely

separated pouches. (32) Graduli on T1–T5 of female. (39) Pregradular areas of male sterna without setal patches. (40) Male without patches of short appressed setae near metasomal spiracles. (49) Gonostylar apex entire, without medially projecting lobe. (52) Ventroapical plate of gonocoxite absent.

Subgenus *Nyctomelitta* Cockerell

Nyctomelitta Cockerell, 1929: 303. Type species: *Bombus tranquebarica* Fabricius, 1804, by original designation.

Both sexes of the species of *Nyctomelitta* can be distinguished from all other members of the genus *Xylocopa* by their large size and greatly enlarged ocelli. The phylogenetic relationship of this group is not well established by this study. Although seemingly allied to a clade consisting of the majority of New World species, some structural features and its biogeography suggest that this group is closely related to *Rhysoxylocopa* and its allies. Examination of other species in the subgenus should help to clarify these matters.

Description.—As in *Xylomelissa*, except as follows: (2) Upper carina on male mandible with subapical tooth. (3) Upper carina of female mandible with subapical tooth. **(9) Ocelli enlarged, diameter greater than that of antennal socket.** (11) Outer apex of male hind tibia with one spine. (16) Male hind femur without basal spine or tubercle. (18) Apex of male basitibial plate bifid. (26) Mesosomal reservoir of male present. (32) Female with graduli on T1–T5. (39) Pregradular areas of male sterna without setal patches. (40) Male without patches of short appressed setae near metasomal spiracles. (43) Penis valve with lateral projection. (50) Medial ventral margins of gonocoxites roughly parallel distad from ventral gonocoxal bridge. (52) Ventroapical plate of gonocoxite weakly developed.

Subgenus *Ctenoxylocopa* Michener

Ctenopoda Maa, 1938: 270, 285 (preoccupied by *Ctenopoda* McAtee and Malloch, 1933). Type species: *Apis fenestrata* Fabricius, 1798, by original designation.
Ctenoxylocopa Michener, 1942: 282, new name for *Ctenopoda* Maa, 1938.
Baana Sandhouse 1943: 530, new name for *Ctenopoda* Maa, 1938.

Males of this subgenus are distinctive; the posterolateral lobes of the pronotum are prolonged posteriorly so that they are nearly in line with the preepisternal groove on the mesepisternum, and the spiracles on T3 bear an elevated, posteriorly directed, scalelike process. Females can be distinguished from all other groups by the combination of: (1) the well-developed basitibial plate with a row of tubercles along each lateral edge, (2) mandible with two teeth on its apical edge, and (3) hind tibia with one spine on its outer apex. *Ctenoxylocopa* is apparently most closely related to some members of the subgenus *Xylocopa* (sensu stricto).

Description.—As in *Xylomelissa*, except as follows: (4) Apical edge of female mandible tridentate. (10) Male face

entirely black. (11) Male hind tibia with one outer apical spine. (16) Male hind femur without basal tubercle or spine. (17) Anterior and posterior edges of female basitibial plate each with row of tubercles. (18) Apex of male basitibial plate bifid. (21) Female basitibial plate extending to near base of tibia. (24) Male metapostnotum present. (31) T1 and T2 of male with graduli. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas of male sterna without paired setal patches. (48) Gonostylus slender and digitiform, with very few apical setae. (49) Gonostylar apex without medially projecting lobe. (52) Ventroapical plate of male gonocoxite absent. (54) Male T7 with pair of apical dentiform processes. (55) Penis valves slender.

Subgenus *Xylocopa* Latreille (sensu stricto)

Xilocopa Latreille, 1802:431. Rejected by Internatl. Comm. Zool. Nomencl., Opinion 743, 1965.
Xylocopa Latreille, 1802:379. Emended name placed on Official List of Generic Names in Zoology by Internatl. Comm. Zool. Nomencl., Opinion 743, 1965. Type species: *Apis violaceae* Linnaeus, 1758, by subsequent designation of Westwood, 1840:86.

The subgenus *Xylocopa* is in need of further study before its phylogenetic affinities can be clarified. The two species used in this study suggest that this subgenus is paraphyletic or polyphyletic; *X. violacea* shows clear affinities with the New World subgenus *Xylocopoides*, whereas *X. valga* probably is most closely related to the Old World subgenus *Ctenoxylocopa*. Females of both species can be distinguished from all other members of the tribe by the combination of the two spines on the outer apex of the hind tibia and the tridentate apical edge of the mandible. Males can be distinguished from all other Old World groups by the combination of face without yellow maculations, the rounded profile of the posterior part of the thorax, and the two spines on the outer apex of the hind tibia.

Description.—As in *Xylomelissa*, except as follows: (3) Upper carina of female mandible without a tooth, except in *X. valga*. (4) Apical edge of mandible of female tridentate. (10) Male face entirely black. (11) Outer apex of male hind tibia with two spines. (12) Outer apex of female hind tibia with two spines. (16) Male hind femur without basal tubercle or spine. (17) Lateral edges of female basitibial plate each with a row of tubercles. (18) Apex of male basitibial plate bifid. (21) Female basitibial plate extending to near base of tibia. (24) Male metapostnotum present. (26) Mesosomal gland present. (32) Graduli present on T1–T5 of female. (35) Medial groove linear on T1 of female except in *X. valga*. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas on male sterna without paired setal patches. (40) Metasomal spiracle without associated setal patch. (42) Gonostylus of male genitalia completely fused to gonocoxite in *X. violacea*; fused but recognizable, long, slender, and with few setae in *X. valga*. (48) Gonostylus slender and digitiform, with very few se-

tae at apex. (49) Gonostylar apex without medially projecting lobe. (52) Ventroapical plate of gonocoxite absent. (53) Mesal margin of venter of gonocoxite with tooth or projection. (55) Penis valves slender.

Subgenus *Xylocopoides* Michener

Xylocopoides Michener, 1954: 105. Type species: *Apis virginica* Linnaeus, 1771, by original designation.

Females of the subgenus *Xylocopoides* uniquely possess two rows of numerous preapical spines delineating the pygidial plate on the surface of T6 and a foveate basitibial plate. Males can be distinguished from those of all other Xylocopini, except *X. violacea*, by the two spines on the outer apex of the tibia, the dark blue metallic coloration, and the lack of a distinct gonostylus. Although I have left *Xylocopoides* and *Xylocopa* (sensu stricto) as separate groups, both share several highly derived synapomorphies and *Xylocopa* (sensu stricto) probably is paraphyletic with respect to *Xylocopoides*.

Description.—As in *Xylomelissa*, except as follows: (3) Upper carina of female mandible without tooth except in *X. cyanea*. (8) Malar space of female shorter than width of flagellar segment 1 except in *X. cyanea*. (10) Male with yellow facial maculations except most specimens of *X. californica arizonensis*. (11) Outer apex of male hind tibia with two spines. (12) Outer apex of female hind tibia with two spines. (16) Male hind femur without basal tubercle or spine. (17) Lateral edges of female basitibial plate without tubercles. (18) Apex of male basitibial plate bifid. (20) Female basitibial plate closed basally. (21) Female basitibial plate reduced, not extending to base of tibia. (24) Male metapostnotum present. (26) Male mesosomal gland present. (31) Graduli on T1 and T2 of male. (32) Gradulus present on T1–T5 of female. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas on sterna of males without paired setal patches. (40) Setal patches absent near metasomal spiracles of male. (41) Pygidial plate margined by two rows of many preapical lateral spines converging at base of pygidial spine. (42) Gonostylus completely fused to, and indistinct from, gonocoxite. (44) Penis valve apex hirsute. (48) Gonostylus slender and digitiform, with very few apical setae. (49) Gonostylar apex without medially projecting lobe. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (53) Ventral surface of gonocoxite with basal angle or spine. (52) Ventroapical plate of male gonocoxite absent. (55) Penis valves slender.

Subgenus *Calloxylocopa* Hurd and Moure

Calloxylocopa Hurd and Moure, 1963: 142. Type species: *Xylocopa tenuata* Smith 1874, by original designation.

This is a monotypic subgenus and probably derived from *Xylocopoides*. Females share with the subgenus

Xylocopoides the numerous preapical spines margining the pygidial plate, but can be distinguished from that group by the basitibial plate, which is open basally and barely rises above the leg surface. Males are easily distinguished by the third sternum, which is depressed on the anterior half, forming two deep depressions, and covered by long hairs that originate on its anterior margin.

Description.—As in *Xylomelissa*, except as follows: (10) Face of male entirely black. (11) Outer apex of male hind tibia with one apical spine. (16) Male hind femur without basal tubercle or spine. (17) Both lateral edges of basitibial plate barely rising above tibial surface, without tubercles. (18) Apex of male basitibial plate bifid. (21) Female basitibial plate extending nearly to base of tibia. (24) Male metapostnotum present. (26) Reservoir of mesosomal gland of male absent. (31) Graduli on T1–T3 of male. (32) Graduli on T1–T5 of female. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas on sterna of males without paired setal patches. (40) Male metasomal spiracles without nearby setal patches. (41) Pygidial plate margined by two rows of numerous preapical lateral spines converging at base of pygidial spine. (42) Gonostylus of male genitalia fused completely to, and indistinct from, gonocoxite. (44) Penis valve apex hirsute. (48) Gonostylus slender and digitiform, with very few apical setae. (49) Gonostylar apex without medially projecting lobe. (50) Medial ventral margins of gonocoxite roughly parallel beyond ventral gonocoxal bridge. (52) Ventroapical plate of male gonocoxite absent. (55) Penis valves slender.

Subgenus *Copoxyla* Maa

Copoxyla Maa, 1954: 191, 211. Type species: *Apis iris* Christ, 1791, by original designation.

The species of the subgenus *Copoxyla* are among the smallest of the Xylocopini and are closely related to *Ctenoxylocopa*. Females can be distinguished by the combination of a smoothly rounded thorax, the absence of preapical spines beside the pygidial spine, and the presence of three teeth on the apical margin of the mandible. Males of *Copoxyla* can be distinguished from *Ctenoxylocopa* by their small size, and by the presence of a defined metapostnotum. These features and two others—the entirely black face of the male, and the single spine on the outer apex of the hind tibia—will differentiate males of this group from all others.

Description.—As in *Xylomelissa*, except as follows: (4) Apical edge of female mandible tridentate. (7) Supraocellar pits deep. (10) Male face entirely black. (11) Outer apex of male hind tibia with one apical spine. (16) Male hind femur without basal tubercle or spine. (17) Anterior and posterior edge of basitibial plate of female each with row of tubercles. (18) Apex of male basitibial plate bifid. (21) Female basitibial plate extending nearly to base of tibia.

(24) Male metapostnotum present. (31) Graduli on T1 and T2 of male. (32) Graduli present on T1–T5 of female. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas on male sterna without paired setal patches. (41) Preapical spines of female pygidial spine absent. (49) Gonostylus of male with a weakly developed medially projecting lobe. (52) Ventroapical plate of male gonocoxite absent. (54) Male T7 with pair of apical dentiform processes.

Subgenus *Gnathoxylocopa* Hurd and Moure

Gnathoxylocopa Hurd and Moure 1963: 182. Type species: *Xylocopa sicheli* Vachal, 1898, by original designation.

Females of *Gnathoxylocopa* are easily distinguished by the long, curved hook that arises from the ventral margin of the mandible. Males can be distinguished by the lengthened thoracic dorsum (i.e., the posterior thoracic declivity begins on the posterior half of the metanotum), and by the bifid apex of the basitibial plate. This group seems to be relatively plesiomorphic and most closely related to *Ctenoxylocopa* and *Copoxyla*. Nevertheless, until more species of *Ctenoxylocopa*, *Xylocopa*, and other allied groups are examined, relationships among these taxa should be considered as tentative.

Description.—As in *Xylomelissa*, except as follows: (3) Female mandible with tooth on upper carina. (4) Apical edge of female mandible tridentate. (10) Male face entirely black. (11) Outer apex of male hind tibia with one apical spine. (16) Male hind femur without basal tubercle or spine. (17) Anterior and posterior edges of female basitibial plate each with row of tubercles. (18) Apex of male basitibial plate bifid. (26) Reservoir of mesosomal gland present, well-developed with numerous convoluted tubules. (31) Graduli present on T1–T3 of male. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas on male sterna without paired setal patches. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (52) Ventroapical plate of gonocoxite absent. (54) Male T7 with pair of apical dentiform processes. (55) Penis valves slender.

Subgenus *Lestis* Lepeletier and Serville, New status

Lestis Lepeletier and Serville, 1828: 795, 799, 800. Type species: *Apis bombylans* Fabricius, 1779 (Opinion 657, Bull. Zool. Nomencl., 20:181–182,1963).

This group of two Australian species is distinguished by the four-segmented maxillary palpi, the second submarginal cell of the wing which is very nearly a parallelogram and not attenuate on the posterior edge as in all other *Xylocopa*, and strong metallic integument of both sexes. Females are unique in having a large, swollen tubercle on the parocular area below the antennal socket. The gonostylus of the male genitalia is almost completely fused to the gonocoxite and has a spinelike medial lobe at the

apex, a unique feature in the tribe. This group, recognized previously as a genus, seems to be most closely related to the other groups allied to *Xylocopa* (sensu stricto), although its affinities within this group are uncertain. It is clearly a relict group, but, if recognized as a genus, would make the genus *Xylocopa* paraphyletic. Therefore, I consider *Lestis* to be a subgenus of *Xylocopa*.

Description.—As in *Xylomelissa*, except as follows: (11) Outer apex of male hind tibia with one spine. (13) Tibial spine of female strong, originating before tibial apex and with a longitudinal medial carina. (17) Basitibial plate not margined with tubercles. (20) Female basitibial plate foveate, closed basally. (24) Male metapostnotum present. (26) Mesosomal gland reservoir present. (32) Gradulus present on T1–T5 of female. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas on male sterna without paired setal patches. (40) Setal patches near male metasomal spiracles not present. (48) Gonostylar apex of male genitalia with dense setal patch. (49) Gonostylar apex with medially projecting lobe, but not bifid. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (52) Ventroapical plate of gonocoxite absent. (55) Penis valves apically slender.

Subgenus *Notoxylocopa* Hurd

Notoxylocopa Hurd, 1956: 2. Type species: *Xylocopa tabaniformis* Smith, 1854, by original designation.

This New World subgenus is defined by the possession in males of an elongation of the dorsal bridge of the penis valve, or spatha, a feature shared with no other member of the tribe. Females can be distinguished from all other New World *Xylocopa* by the absence of a defined metapostnotum. Hurd and Moure (1963) considered *Notoxylocopa* to be most closely related to the Old World subgenus *Rhysoxylocopa*. My analysis does not place this group firmly with any other subgenus, although, based on three male genital characters (strongly developed medial lobe of the gonostylus, thickly hirsute apex of the gonostylus, and especially the outward projection on the penis valves), it could be most closely related to the New World group that includes *Schonnherria*. However, the weakly developed ventroapical plate of the gonocoxite suggests this relationship is not close; hence I consider it likely that *Notoxylocopa* is the sister group to a group that includes the rest of the New World *Xylocopa*, except *Xylocopoides* and *Calloxylocopa*.

Description.—As in *Xylomelissa*, except as follows: (3) Tooth on upper carina of female mandible. (11) Outer apex of male hind tibia with one spine in *X. tabaniformis*, two spines in *X. guatemalensis*. (12) Outer apex of female hind tibia with two spines. (17) Anterior and posterior edges of female basitibial plate weakly developed or rising little from surface of tibia in *X. tabaniformis*, with tubercles along both lateral edges in *X. guatemalensis*. (26) Mesosomal gland reservoir absent. (31) Graduli present on T1–T4 of male. (32) Graduli present on T1–T4 of female. (36) Apical margin of S1 medially emarginate. (39) Pregradular areas on male sterna without paired setal patches, although setal patches occur in some subspecies of *X. tabaniformis*. (40) Patches of setae near male metasomal spiracles absent. (43) Conspicuous carina on outer edge of penis valve. (46) Spatha present. (49) Medially projecting lobe of gonostylar apex well developed. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (52) Ventroapical plate of male gonocoxite weakly developed. (54) Apex of T7 of male with pair of dentiform projections.

Subgenus *Schonnherria* Lepeletier

Schonnherria Lepeletier, 1841: 207. Type species: *Xylocopa micans* Lepeletier, 1841 by designation of Sandhouse, 1943: 598.
Schönherria Lepeletier, 1841: 207.
Schornherria Ashmead, 1899: 71. Misspelling of *Schonherria* Lepeletier, 1841.
Xylocospila Hurd and Moure, 1963:109. Type species: *Xylocopa bambusae* Schrottky, 1902, by original designation. New synonymy.
Ioxylocopa Hurd and Moure, 1963: 116. Type species: *Xylocopa chrysopoda* Schrottky, 1902, by original designation. New synonymy.

This is a speciose New World subgenus. Most species are brightly metallic and fast-flying, but some species are decidedly drab and hairy. They can be distinguished from all other New World groups by the presence of graduli only on T1 in females and by the bifid apex of the gonostylus and a large spine on the ventroposterior margin of the gonocoxite in males. As defined here, this group is expanded to include *Xylocospila* and *Ioxylocopa*. Both of these taxa possess the two strongest synapomorphies that define *Schonnherria* (sensu Hurd and Moure, 1963), i.e., a strongly bifid apex of the gonostylus and the spine on the ventral apex of the gonocoxites. Three other monotypic subgenera (*Nanoxylocopa*, *Dasyxylocopa*, and *Xylocopsis*) erected by Hurd and Moure (1963), differ from *Schonnherria* primarily in the number of graduli on the terga of the female and may eventually be shown to be plesiomorphic members of the *Schonnherria* clade. However, until the relationships between *Notoxylocopa*, the *Neoxylocopa* group and the *Schonnherria* group are more firmly established, I have retained *Nanoxylocopa*, *Dasyxylocopa*, and *Xylocopsis* as subgenera.

Description.—As in *Xylomelissa*, except as follows: (2) Subapical tooth on upper carina of male mandible absent except in *X. micans*. (3) Tooth on upper carina of female mandible. (4) Two teeth on apical margin of female mandible except in *X. viridigastra* which has three. (7) Supraocellar pits of female punctiform or deeply excavated in *X. macrops* and *X. micans*. (11) Outer apex of male hind tibia with one spine. (16) Male hind femur without basal tubercle except in *X. viridigastra*. (17) Anterior and poste-

rior edges of female basitibial plate weakly developed, or rising little from surface of tibia. (18) Male basitibial plate bifid at apex. (23) Beginning of female posterior thoracic declivity smoothly rounded, or abruptly rounded in *X. macrops*. (26) Mesosomal gland reservoir present as a single layer of parallel-running tubules. (31) Gradulus on T1 of male; T1 and T2 in *X. bambusae*. (32) Gradulus on T1 of female. (35) Medial groove of female T1 linear; deeply impressed in *X. micans*. (36) Apical margin of S1 medially emarginate; entire in *X. viridigastra*. (39) Setal patches absent on pregradular areas of male sterna. (40) Patches of appressed setae near spiracles of male metasoma absent. (43) Strong carina present on lateral edge of penis valve. (49) Medially projecting lobe on gonostylar apex elongate, forming a bifid apex. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with a conspicuous spine on posterior ventral margin. (54) Apex of male T7 without pair of dentiform projections, except in *X. viridigastra*.

Subgenus *Dasyxylocopa* Hurd and Moure

Dasyxylocopa Hurd and Moure 1963: 113. Type species: *Xylocopa bimaculata* Friese, 1903, by original designation.

As noted by Hurd and Moure (1963), the sexes of this species are distinctive because of the thick pubescence. This subgenus is similar to *Schonnherria* but can be distinguished from males of that group by the greater number of graduli in *Dasyxylocopa* (T1–T5) than on *Schonnherria* (T1 only). The phylogenetic position of this group is discussed under *Schonnherria*.

Description.—As in *Xylomelissa*, except as follows: (2) Upper carina of male mandible with tooth. (3) Upper carina of female mandible with tooth. (11) Outer apex of male hind tibia with one spine. (16) Male hind femur without basal tubercle or spine. (17) Anterior and posterior edges of female basitibial plates weakly developed, rising little from surface of tibia. (26) Mesosomal gland reservoir not examined. (32) Graduli present on T1–T4 of female. (36) Apical margin of S1 medially emarginate. (39) Setal patches of pregradular areas of male sterna absent. (40) Patches of appressed setae near spiracles of male metasoma absent. (43) Lateral edge of penis valve with strong carina. (49) Medially projecting lobe on gonostylus apex weakly developed. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with conspicuous spine on posterior ventral margin. (54) Apex of male T7 with pair of dentiform projections.

Subgenus *Xylocopsis* Hurd and Moure

Xylocopsis Hurd and Moure 1963: 124. Type species: *Xylocopsis funesta* Maidl, 1912, by original designation.

Females of *Xylocopsis* can be distinguished from all other New World taxa by the possession of five tubercles on the

labrum. Males can be distinguished by the combination of a distinctive yellow stripe on the scape, an abruptly rounded beginning of the thoracic declivity and two spines on the apex of T7. The phylogenetic position of this group is discussed under *Schonnherria*.

Description.—As in *Xylomelissa*, except as follows: (3) Tooth on upper carina of female mandible. (4) Two teeth on apical margin of female mandible. (7) Supraocellar pits of female punctiform. (11) Outer apex of male hind tibia with one spine. (16) Male hind femur without basal tubercle. (17) Anterior and posterior edges of female basitibial plates weakly developed, rising little from surface of tibia. (18) Apex of male basitibial plate bifid. (26) Mesosomal gland reservoir present. (31) T1 of male with gradulus. (32) T1 and T2 of female with graduli. (36) Apical margin of S1 medially emarginate. (39) Setal patches of pregradular areas of male sterna absent. (40) Patches of appressed setae near spiracles of male metasoma absent. (43) Lateral edge of penis valve with strong carina. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with a conspicuous spine at posterior ventral margin. (54) Apex of male T7 with pair of dentiform processes.

Subgenus *Nanoxylocopa* Hurd and Moure

Nanoxylocopa Hurd and Moure, 1963: 99. Type species: *Xylocopa ciliata* Burmeister, 1976, by original designation.

This monotypic subgenus can be distinguished from the other New World groups by the evenly punctate tegula in males and by the "transversely tuberculiform" (Hurd and Moure, 1963) shape of the frontal carina in females. The phylogenetic position of this group is discussed under *Schonnherria*.

Description.—As in *Xylomelissa*, except as follows: (3) Upper carina of female mandible with tooth. (11) Outer apex of male hind tibia with one spine. (16) Male hind femur without basal tubercle. (17) Anterior and posterior edges of female basitibial plates weakly developed, rising little from surface of tibia. (26) Mesosomal gland reservoir present. (36) Apical margin of S1 medially emarginate. (39) Setal patches of pregradular areas of male sterna absent. (40) Patches of appressed setae near spiracles of male metasoma absent. (43) Lateral edge of penis valve with strong carina. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with conspicuous spine on posterior ventral margin.

Subgenus *Cirroxylocopa* Hurd and Moure

Cirroxylocopa Hurd and Moure, 1963: 102. Type species: *Xylocopa vestita* Hurd and Moure, 1963, by original designation.

Hurd and Moure (1963) suggested that *Cirroxylocopa* was a basal taxon, near *Nanoxylocopa*, of the lineage that

gave rise to the *Schonnherria* and *Neoxylocopa* clades. My analysis suggests that it is the basal member of the clade leading to the *Neoxylocopa* lineage.

Description.—As in *Xylomelissa* except as follows: (3) Upper carina of female mandible with tooth. (11) Outer apex of male hind tibia with one spine. (16) Male hind femur without basal tubercle. (17) Anterior and posterior margins of female basitibial plate weakly developed, rising little from surface of tibia. (26) Mesosomal gland reservoir not examined. (27) Beginning of thoracic declivity on male propodeum. (32) T1 and T2 of female with graduli. (40) Patches of appressed setae near spiracles of male metasoma absent. (43) Lateral edge of penis valve with strong carina. (49) Apex of gonostylus without medial lobe. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with a conspicuous spine on posterior ventral margin.

Subgenus *Xylocopoda* Hurd and Moure

Xylocopoda Hurd and Moure, 1963: 105. Type species: *Xylocopa elegans* Hurd and Moure, 1963, by original designation.

This is a monotypic subgenus. Males can be distinguished uniquely by the presence of a high, thin lamella that begins near the base of the hind tibial spur and extends obliquely forward and across the ventral surface of the tibia. Females also are easily identified by the parocular areas, which are abruptly raised near the lower margins of the eye. In my analysis, *Xylocopoda* is the sister group to *Stenoxylocopa* and *Neoxylocopa*.

Description.—As in *Xylomelissa*, except as follows: (3) Tooth on upper carina of female mandible. (6) Female epistomal suture continuously carinate and broadly impunctate. (11) Outer apex of male hind tibia with one spine. (16) Male hind femur without basal tubercle or spine. (17) Anterior and posterior edges of female basitibial plate weakly developed, rising little from surface of tibia. (26) Mesosomal gland reservoir not examined. (27) Beginning of thoracic declivity of male on propodeum. (32) T1–T5 of female with graduli. (36) Apical margin of S1 medially emarginate. (39) Setal patches of pregradular areas on male sterna absent. (40) Patches of appressed setae near spiracles of male metasoma absent. (43) Lateral edge of penis valve with strong carina. (48) Gonostylus with few setae, not with a dense brush at its apex. (49) Medial lobe of gonostylar apex absent. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with a conspicuous spine on posterior ventral margin.

Subgenus *Stenoxylocopa* Hurd and Moure

Stenoxylocopa Hurd and Moure, 1960: 809. Type species: *Xylocopa artifex* Smith, 1874a, by original designation.
Xylocopina Hurd and Moure, 1963: 160. Type species: *Xylocopa ruficollis* Hurd and Moure, by original designation. New synonymy.

This group is exclusively New World, and most species are Neotropical. An enlarged upper mandibular tooth, as wide or wider than the lower tooth, distinguishes females of this group from all others in the tribe. Males can be distinguished by the combination of two spines on the outer apex of the hind tibia and the tegula being impunctate on its posterolateral third. Except for *Xylocopina ruficollis*, males of all species have two parallel yellow stripes running from the vertex of the head to the base of the mandibles. *Xylocopina ruficollis* was considered to be subgenerically distinct from *Stenoxylocopa* by Hurd and Moure (1963) based on two plesiomorphies—the entire, but not produced, apex of S1 and yellow markings restricted to the lower part of the face—and two autapomorphies, the short clypeus and the shape of the tegula.

Description.—As in *Xylomelissa*, except as follows: (3) Upper carina of female mandible with tooth. (4) Female mandible with three teeth on apical margin. **(5) Upper rutellar tooth and preapical tooth (i.e., apex of pollex) fused and forming a continuous edge.** (6) Female epistomal suture continuously carinate and broadly impunctate. (11) Outer apex of male hind tibia with one spine. (12) Outer apex of female hind tibia with two spines. (16) Male hind femur without basal tubercle. (17) Anterior and posterior edges of female basitibial plate weakly developed, rising little from surface of tibia. (26) Mesosomal gland reservoir present, consisting of several layers of disc-shaped tubules. (27) Beginning of thoracic declivity of male on propodeum, except in *Xylocopina ruficollis*. (35) Medial groove of T1 of female linear. (36) Apical margin of S1 medially emarginate; entire and not produced in *X. ruficollis*. (38) Medial carina on female sternum continuous across all segments; present but not continuous in *X. ruficollis*. (39) Pregradular areas on male sterna with setal patches, except in *X. ruficollis*. (40) Setal patches present near spiracles of male metasoma. (43) Lateral edge of penis valve with strong carina. (48) Gonostylus with few setae, without dense brush of setae at its apex. (49) Medial lobe on apex of gonostylus absent. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with conspicuous spine on posterior ventral margin.

Subgenus *Neoxylocopa* Michener

Neoxylocopa Michener, 1954:155, 157–158. Type species: *Apis brasilianorum* Linnaeus, 1767, by original designation.
Megaxylocopa Hurd and Moure, 1963: 151. Type species: *Apis frontalis* Olivier, 1789, by original designation. New synonymy.

This subgenus is the most speciose and widely distributed of the New World subgenera. Females can be distinguished from all other members of the tribe by the combination of two teeth on the apical margin of the mandible, a continuous impunctate ridge along the epistomal suture,

and a strong medial carina along the entire sternum of the metasoma. Males are distinguished by their yellow vestiture (most species) and the beginning of the posterior thoracic declivity on the propodeum. Hurd and Moure (1963) based the subgenus *Megaxylocopa* on their extremely large size and conspicuous carinae over the lateral ocelli. Recognition of *Megaxylocopa* makes the subgenus *Neoxylocopa* paraphyletic.

Description.—As in *Xylomelissa*, except as follows: (1) Male vestiture on dorsum of body entirely tawny or ferruginous (most species). (3) Tooth on upper carina of female mandible. (6) Female epistomal suture a continuous ridge and broadly impunctate. (11) Outer apex of male hind tibia with one spine. (12) Outer apex of female hind tibia with two spines. (16) Male hind femur without basal tubercle. (17) Anterior and posterior edges of female basitibial plates weakly developed, rising little from surface of tibia. **(26) Reservoir of male mesosomal gland extremely large and consisting of many layers of highly convoluted tubules, sometimes visible through cuticle of metanotum.** (27) Beginning of thoracic declivity of male on propodeum. (36) Apical margin of S1 medially emarginate. (38) Medial carina on sternum of female continuous across all segments. (39) Pregradular areas of male sterna without paired setal patches. (40) Setal patches present near spiracles of male metasoma. (43) Lateral edge of penis valve with strong carina. (48) Gonostylus with few setae, without dense brush of setae at its apex. (49) Medial lobe on gonostylar apex absent. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with a conspicuous spine on posterior ventral margin.

Subgenus *Prosopoxylocopa* Hurd and Moure

Prosopoxylocopa Hurd and Moure, 1963: 215. Type species: *Xylocopa mirabilis* Hurd and Moure, by original designation.

This subgenus is likely the sister group to the remainder of the Ethiopian clade. The strongly produced projection of the posteriormost ventral part of the gonocoxite (Fig. 9C) and the continuous yellow maculations from the labrum to the supraclypeal area of the face of the male distinguish it from all other large carpenter bees. Females can be distinguished by the abruptly rounded beginning of the thoracic declivity and by the basitibial plate, which is represented by a single, very strongly projecting carina.

Description.—As in the *Xylomelissa*, except as follows: (11) Outer apex of male hind tibia with two spines. (12) Outer apex of female hind tibia with two spines. (16) Male hind femur without tubercle or spine. (17) Posterior edge of female basitibial plate with carina arising perpendicularly from leg, without row of tubercles. (19) Female basitibial plate apex entire. (22) Beginning of posterior thoracic declivity of male abruptly rounded. (23) Beginning

of posterior thoracic declivity of female abruptly rounded. (24) Male metapostnotum present. (26) Mesosomal gland reservoir not examined. (32) Graduli present on T1–T5 of female. (39) Pregradular areas of male sterna without paired setal patches. (40) Setal patches near male metasomal spiracles absent. (50) Medial ventral margins of gonocoxites roughly parallel from ventral gonocoxal bridge. **(51) Gonocoxite with a bifid spine originating at the ventroposterior margin (Fig. 9C).** (52) Ventroapical plate of gonocoxite weakly developed.

Subgenus *Zonohirsuta* Maa

Zonohirsuta Maa, 1938: 270, 300. Type species: *Xylocopa collaris* Lepeletier, 1841, not Olivier, 1789 (= *X. dejeanii* Lepeletier, 1841), by original designation.

The subgenus *Zonohirsuta* is similar to *Prosopoxylocopa*. They differ by the basally open basitibial plate in females of *Zonohirsuta* and by the single spine on the outer apex of the hind tibia of males. An additional apomorphy of *Zonohirsuta* is that both of the lateral edges of the female basitibial plate are strongly carinate and project perpendicularly from the tibial surface.

Description.—As in *Xylomelissa*, except as follows: (11) Outer apex of male hind tibia with one spine. (12) Outer apex of female hind tibia with two spines. (16) Male hind femur armed with basal spine. (17) Posterior edge of female basitibial plate with carina arising perpendicularly from leg, without row of tubercles. (22) Beginning of posterior thoracic declivity of male abruptly rounded. (23) Beginning of posterior thoracic declivity of female abruptly rounded. (24) Male metapostnotum present. (26) Mesosomal gland reservoir present. (32) Graduli present on T1–T5 of female. (39) Pregradular areas on male sterna without paired setal patches. (40) Setal patches near male metasomal spiracles absent. (47) Gonostylar apex without dense setal patch. (48) Gonostylus slender. (49) Gonostylar apex without medially projecting lobe. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (52) Ventroapical plate of gonocoxite present, with a carina.

Subgenus *Bomboixylocopa* Maa

Bomboixylocopa Maa, 1939: 155. Type species: *Xylocopa bomboides* Smith, 1879, by original designation.
Mimoxylocopa Hurd and Moure, 1963: 203. Type species: *Xylocopa rufipes* Smith, 1852, by original designation. New synonymy.

Females of this subgenus can be distinguished from all other members of the Xylocopini by the combination of long malar space (longer than the width of first flagellar segment) and two spines on the outer apex of the tibia. Males can be distinguished by the presence of appressed setae, both on the pregradular areas of the metasomal sterna and near the metasomal spiracles, and by two spines on the outer apex of the tibia.

Description.—As in *Xylomelissa*, except as follows: (2) Upper carina of male mandible without tooth, except in *Xylocopa rufipes*. (3) Upper carina of female mandible without tooth, except in *X. rufipes*. (8) Malar space of female longer than width of first flagellar segment. (11) Two spines on outer apex of male hind tibia. (12) Two spines on outer apex of female hind tibia. (16) Male hind femur without basal spine or tubercle. (17) Anterior and posterior edges of female basitibial plates rising little from surface of tibia. (19) Female basitibial plate apex entire, or asymmetrically bifid in *X. rufipes*. (24) Male metapostnotum present in *X. chinensis*, absent in *X. rufipes*. (25) Female metapostnotum present, extending to propodeal pit. (26) Mesosomal gland reservoir present. (32) Graduli present on T1–T5 of female. (35) Medial groove of female T1 deeply sulcate. (36) Apical margin of S1 medially emarginate in *X. rufipes*, rounded in *X. chinensis*. (41) Pygidial spine lacking lateral spine at base in *X. chinensis*; these spines present in *X. rufipes*. (47) Gonostylus slender and elongate, over half as long as gonocoxite (Fig. 9D). (48) Gonostylus lacking dense setal patch on apex. (49) Gonostylar apex without medially projecting lobe. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge, divergent in *X. chinensis*. (51) Gonocoxite with spine on posterior ventral margin. (53) Gonocoxite with projection along inner mesal margin of base.

Subgenus *Xenoxylocopa* Hurd and Moure

Xenoxylocopa Hurd and Moure, 1963: 243. Type species: *Mesotrichia chiyakensis* Cockerell, 1908, by original designation.

Females can be distinguished from all other members of the tribe by the abruptly rounded beginning of the posterior thoracic declivity and by the presence of a pair of preapical spines at the base of the pygidial spine. Males can be distinguished by the combination of sharp beginning of the declivity of T1 (as occurs in *Koptortosoma* and *Mesotrichia*), lack of a fovea on the anterior surface of T1, and the nearly entirely punctate tegula. *Xenoxylocopa* and/or *Alloxylocopa* are/is the sister group to *Mesotrichia* and *Koptortosoma*. (See section on Relationships among Members of the Major Clades and Taxonomic Recommendations.)

Description.—As in *Xylomelissa*, except as follows: (1) Male vestiture tawny or ferruginous over entire dorsum of body. (6) Female epistomal suture with a continuous smooth ridge. (7) Supraocellar pits of female deeply excavated and craterlike. (11) Two spines on outer apex of male hind tibia. (12) Two spines on outer apex of female hind tibia. (16) Male hind femur without basal spine or tubercle. (17) Anterior and posterior edges of female basitibial plates rising little from surface of tibia. (23) Beginning of posterior thoracic declivity of female abruptly rounded. (25) Female metapostnotum absent. (26) Mesosomal gland reservoir not examined. (28) Propodeum at its connection with

metasoma dorsally elongated, forming a spine. (30) Gradulus of T1 nearly coincident with lateral ventral margin of metasoma. (35) Medial groove of T1 of females deeply sulcate. (36) Apical margin of S1 entire and produced. (37) Medial carina on S6 of male strongly developed, forming a keel. (39) Pregradular areas of male sterna without setal patches. (40) Setal patches near male metasomal spiracles absent. (41) Pygidial spine absent. (47) Gonostylus of male slender and elongate; over half as long as gonocoxite (Fig. 9D). (48) Gonostylar apex lacking dense setal patch. (49) Gonostylar apex without medially projecting lobe. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge. (51) Gonocoxite with a spine on posterior ventral margin. (53) Gonocoxite with projection along inner mesal margin of base.

Subgenus *Alloxylocopa* Maa

Alloxylocopa Maa, 1939: 155. Type species: *Xylocopa appendiculata* Smith, 1852, by original designation.

The subgenus *Alloxylocopa* is similar to *Xenoxylocopa* but differs in females by the lack of preapical spines beside the pygidial spine and in males by the dark coloration and presence of a fovea on the anterior face of T1. In the phylogenetic analysis, this group is often placed as the sister group to *Mesotrichia* and *Koptortosoma*.

Description.—As in *Xenoxylocopa*, except as follows: (1) Male vestiture black or dark brown on sides and pale on dorsum. (7) Supraocellar pits of female normal. (19) Apex of female basitibial plate entire. (22) Beginning of posterior thoracic declivity of male abruptly rounded. (28) Propodeum at its connection with metasoma not elongated. (30) Gradulus of T1 obliquely curved on anterior ventral margin of metasoma. (31) Gradulus only on T1 of male. (33) Anterior surface of T1 of male with fovea. (34) Anterior surface of T1 of females with fovea. (41) Basal pair of pygidial spines present. (51) Gonocoxite without a spine on posterior ventral margin.

Subgenus *Mesotrichia* Westwood

Mesotrichia Westwood, 1838: 112. Type species: *Mesotrichia torrida* Westwood, 1838, original description.
Platynopoda Westwood, in Jardine, 1840: 271. Type species: *Apis latipes* Drury, 1773, by designation of Ashmead, 1899: 71. New synonymy.
Audinetia Lepeletier, 1841: 203. Type species: *Apis latipes* Drury, 1773, synonym of *Platynopoda* by designation of Sandhouse, 1943: 529.
Platinopoda Dalla Torre, 1896: 202. Emendation of *Platynopoda* Westwood
Hoplitocopa Lieftinck, 1955: 9, 27. Type species: *Xylocopa assimilis* Ritsema, 1880, by original designation. New synonymy.
Hoploxylocopa Hurd and Moure, 1963: 260. Type species: *Xylocopa acutipennis* Smith, 1854, by original designation. New synonymy.

This subgenus is the sister group to the subgenus *Koptortosoma*. Females can be distinguished from all other large carpenter bees by the perpendicular angle of the beginning of the thoracic declivity, the deeply excavated (craterlike) supraocellar pits and triangular hind tro-

chanter. Males can be distinguished by the posteriorly elongate tegulae (Fig. 4B). This is a structurally diverse group as the description indicates; yet a number of characters provide evidence for its monophyly. *Mesotrichia*, as recognized herein, is an equivalent taxon to *Koptortosoma*; by combining the four subgenera recognized by Hurd and Moure (1963), the evolutionary relationships of the species are emphasized.

Description.—As in *Alloxylocopa*, except as follows: (3) Upper carina of male mandible without a tooth, except in *Xylocopa assimilis*. (3) Upper carina of female mandible without a tooth, except in *X. assimilis*. (6) Epistomal suture of female continuously carinate and smooth in *X. torrida* and *X. acutipennis*, but not so in *X. latipes* and *X. assimilis*. (7) Supraocellar pits of female deeply excavated and craterlike. (10) Male with yellow facial maculations except in *X. assimilis*. **(14) Female hind trochanter roughly triangular in ventral view.** (15) Mid- and hind trochanter of male without spine or tubercle except in *X. acutipennis*, which has a spine. (16) Male hind femur with basal spine in *X. torrida* and *X. acutipennis*, without this projection in *X. latipes* and *X. assimilis*. (22) Beginning of posterior thoracic declivity of male sharply angled. (23) Beginning of posterior thoracic declivity of female a transverse carina not extending posteriorly beyond metanotum. (24) Male metapostnotum absent, except in *X. latipes*, in which it is vestigial. (Among specimens of *X. tenuiscapa* I have examined, the metapostnotum is exposed in some individuals and absent in others.) (25) Female metapostnotum present in *X. latipes* and *X. assimilis*, but absent in *X. torrida* and *X. acutipennis*. (26) Reservoir of male mesosomal gland present and variable; two, widely separated pouches that are not developed into tubules in *X. latipes*, and highly convoluted mass of tubules in *X. torrida*. (28) Propodeum at its connection with metasoma not modified in *X. latipes* and *X. assimilis* but dorsally elongated, forming a spine in *X. torrida* and *X. acutipennis*. **(29) Male tegula elongated posteriorly.** (30) Gradulus of S1 virtually coincident with anterior ventral margin of metasoma. (31) Distribution of graduli on male terga variable: T1–T5 in *X. torrida*, T1–T3 in *X. acutipennis* and only T1 in *X. latipes* and *X. assimilis*. (34) Anterior surface of T1 of female with entrance to a mite pouch. (37) Medial carina on S6 of male present but not strongly developed, except in *X. torrida*. (38) Medial carina on sterna of female continuous and present on all segments; present but not continuous in *X. acutipennis*. (41) Pygidial spine lacking preapical lateral spines at base, except in *X. torrida*. (42) Gonostylus of male genitalia slender in *X. tenuiscapa* and *X. acutipennis*, completely undifferentiated from gonocoxite in *X. torrida*, and broadly fused but still recognizable in *X. assimilis*. (45) Penis entirely membranous in *X. torrida* and *X. acutipennis*, and sclerotized basally beneath in *X. latipes* and *X. assimilis*. (47)

Gonostylus of male slender and less than half as long as gonocoxite (also see Character 42 above). (48) Apex of gonostylus setose, with few setae in *X. latipes*. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge; divergent in *X. latipes*. (51) Gonocoxite with strong spine from posterior ventral margin in *X. torrida* and *X. assimilis* but produced only slightly as a rounded lobe in *X. latipes* and *X. acutipennis*. (52) Ventroapical plate of gonocoxite present or absent in *X. latipes*. (53) Gonocoxite without projection on inner mesal margin except in *X. torrida*. (54) Apex of T7 of male entire, with dentiform projections in *X. assimilis*. (55) Penis valves slender and parallel.

Subgenus *Koptortosoma* Gribodo

Koptortosoma Gribodo, 1894: 271. Type species: *Koptortosoma gabonica* Gribodo, 1894, by designation of Sandhouse, 1943: 561.

Koptorthosoma Dalla Torre, 1896: 202. Unjustified emendation of *Koptortosoma* Gribodo.

Coptorthosoma Pérez, 1901:3. Unjustified emendation of *Koptortosoma* Gribodo and *Koptorthosoma* Dalla Torre.

Orbitella Maa, 1938: 270, 305 (not *Orbitella* Douville, 1915).

Maiella Michener, 1942: 50:282 . Replacement name for *Orbitella* Maa, 1938.

Euryapis Sandhouse, 1943: 551 Replacement name for *Orbitella* Maa, 1938.

Oxyxylocopa Hurd and Moure, 1963: 275. Type species *Xylocopa varipes* Smith, 1854, by original designation. New synonymy.

Cyaneoderes Ashmead, 1899: 70. Type species: C[*yaneoderes*] *fairchildi* Ashm[ead, 1899] [= *Bombus caeruleus* Fabricius, 1841, by original designation. New synonymy.

Cyphoxylocopa Hurd and Moure, 1963: 283. Type species: *Xylocopa ocularis* Pérez, 1901, by original designation. New synonymy.

Afroxylocopa Hurd and Moure, 1963: 264. Type species: *Apis nigrita* Fabricius, 1775, by original designation. New synonymy.

This subgenus is the sister group to *Mesotrichia* (sensu lato). The pronounced transverse carina on the scutellum that completely overhangs the metanotum of females of most species distinguishes these taxa from females of all other large carpenter bees. Males share many features with those of *Mesotrichia* and can be separated most easily by the tegula, which is not modified in *Koptortosoma* and is elongated posteriorly in *Mesotrichia*. The apomorphies identified herein and by Hurd and Moure (1963) that define the monophyly of *Oxyxylocopa*, *Cyphoxylocopa*, *Cyaneoderes*, and *Afroxylocopa* are all highly homoplasious and do not justify recognizing these taxa as separate subgenera. (See section on Relationships among Members of the Major Clades and Taxonomic Recommendations.)

Description.—As in *Alloxylocopa*, except as follows: (1) Male vesture blue in *Xylocopa caerulea* to tawny or ferruginous over entire dorsum of body in *X. nigrita*, *X. pubescens*, *X. caffra* and *X. sinensis*. (2) Male mandible without tooth on upper carina, except in *X. nigrita* and *X. pubescens*. (3) Upper carina of female mandible with tooth except in *X. nigrita*, *X. caerulea* and *X. ocularis*. (6) Female epistomal suture without continuous ridge and devoid of setae, except in *X. nigrita*, *X. caerulea* and *X. ocularis*. (7)

Supraocellar pits of female punctiform; deeply excavated in *X. nigrita* and *X. varipes*. (10) Male with yellow facial maculations, except in *X. pubescens* and *X. caerulea*. (12) Outer apex of female hind tibia with one spine, except in *X. nigrita*. (14) Female hind trochanter roughly cylindrical, not triangular in ventral view, except in *X. caffra*. (15) Mid- and hind trochanter of male without spines, except in *X. varipes*. (16) Male hind femur without spine or tubercle in most species, with basal spine in *X. nigrita* and *X. ocularis*. (19) Apex of female basitibial plate entire, except in *X. nigrita*. (22) Beginning of posterior thoracic declivity of male sharply angled, except in *X. sinensis*. (23) Beginning of posterior thoracic declivity of female a transverse carina that overhangs entire metanotum but rounded in *X. sinensis*. (25) Female metapostnotum absent or present in *X. caerulea*. (26) Reservoir of male mesosomal gland a highly convoluted, many-layered mass of tubules. (27) Beginning of thoracic declivity of male on metanotum, except in *X. nigrita*, in which it is on the propodeum. (28) Propodeum at its connection with metasoma dorsally elongated forming a spine except in *X. nigrita*. (29) Graduli present on male T1 and T2 or only on T1 in *X. nigrita*. (30) Gradulus on S1 virtually coincident with anterior ventral margin of metasoma. (32) Graduli present only on T1 of female or T1 and T2 in *X. pubescens*. (34) Anterior surface of T1 of female with entrance to mite pouch or with fovea in *X. varipes* and *X. ocularis*. (35) Medial groove of T1 of females deeply sulcate. (37) Medial carina of S6 of male strongly developed, forming a keel, except in *X. varipes*. (39) Pregradular areas of male sterna with paired setal patches; absent in *X. pubescens*. (40) Setal patches present near metasomal spiracles of males, except in *X. varipes*, *X. caerulea* and *X. ocularis*. (41) Pygidial spine lacking pair of preapical lateral spines at base. (47) Gonostylus of male genitalia less than half as long as gonocoxite, with setae at apex. (48) Gonostylus lacking dense setal patch on apex. (49) Gonostylar apex with medially projecting lobe in *X. varipes*, *X. caerulea*, *X. ocularis* and *X. caffra*, and lobe producing a bifid point in *X. sinensis*, *X. pubescens* and *X. nigrita*. (50) Medial ventral margins of gonocoxites roughly parallel beyond ventral gonocoxal bridge or divergent in *X. chinensis*. (51) Gonocoxite with spine on posterior ventral margin, except in *X. pubescens* and *X. nigrita*. (53) Gonocoxite with projection along inner mesal margin of base, except in *X. ocularis*. (54) T7 of male with apex entire or with pair of dentiform spines on *X. nigrita*.

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APPENDIX 1

CHARACTER CHANGES AND NODE SUPPORT FOR THE TREE SHOWN IN FIGURE 10 A (ANALYSIS 1, CHARACTER WEIGHTS EQUAL)

Accelerated transformation (ACCTRAN) of characters has been assumed. Node numbers are those shown in Figure 10; numbers in parentheses indicate character states as they are numbered in the text, and the direction of character state change. Arrows in parentheses with single lines (→) indicate losses and gains in the character do not occur along subsequent nodes. Arrow in parentheses with double lines (⇒) indicate that reversals or gains occur among subsequent nodes, M=male, F=female, B=both sexes.

NODES 95→94: 11. One spine on outer apex of hind tibia M (0→1); 19. Basitibial plate apex bifid F (0→1); 21. Basitibial plate reduced F (0→1); 41. Paired marginal spines of pygidial plate F (0→1); 47. Gonostylus slender, short M (0→1).

NODES 94→87: 24. Metapostnotum not evident M (0⇒1); 26. Mesosomal gland reservoir M (0→1).

NODES 87→86: 26. Mesosomal gland reservoir M (1→2); 52. Ventroapical plate of gonocoxite M (0⇒2).

NODES 86→77: 50. Ventromedial margin of gonocoxites diverge M (0⇒1); 51. Spine on posteroventral margin of gonocoxite M (0⇒1).

NODES 77→61: 3. Subapical tooth on mandible F (0→1); 43. Lateral edge of penis valve modified M (0→1).

NODES 61→55: 36. Apical margin of S1 B (0⇒2); 49. Medially projecting lobe on apex of gonostylus M (0⇒1).

NODES 55→50: 32. Number of tergal graduli F (0→1).

NODES 50→49: 32. Graduli on T1-3 F (0⇒2); 49. Medially projecting lobe on apex of gonostylus M (1⇒2).

NODES 55→54: 54. Spines on posterior margin T7 M (0→1).

NODES 54→53: 18. Basitibial plate apex bifid M (0→1).

NODES 53→52: 17. Modified margins of basitibial plate F (0→1); 51. Spine on posteroventral margin of gonocoxite M (1⇒0); 52. Ventroapical plate of gonocoxite M (2⇒1).

NODES 52→51: 26. Mesosomal gland reservoir lost M (2→0).

NODES 61→60: 26. Mesosomal gland reservoir M (2→3); 27. Beginning of thoracic declivity M (0→1).

NODES 60→59: 6. Epistomal suture F (0⇒1); 48. Setae on apex of gonostylus M (1⇒0).

NODES 59→58: 4. Apex of mandible tridentate F (0→1); 5. Upper rutellar tooth and preapical tooth F (0→1); 12. Number of spines on outer apex of hind tibia F (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 58→57: 32. Graduli on T1-3 F (0⇒2); 38. Medial carina of metasomal sterna F (0⇒1).

NODES 57→56: 1. Vestiture M (0⇒1); 4. Apex of mandible bidentate F (1→0); 5. Upper rutellar tooth and preapical tooth F (1→0); 39. Pregradular areas of sterna M (0→1).

NODES 77→76: 11. Two spines on outer apex of hind tibia M (1⇒2); 12. Number of spines on outer apex of hind tibia F (0→1); 23. Beginning of thoracic declivity F (0→1); 47. Length of gonostylus M (1→0); 48. Setae on apex of gonostylus M (1→0).

NODES 76→62: 22. Beginning of thoracic declivity M (0⇒1); 24. Metapostnotum M (1→0).

NODES 76→75: 25. Metapostnotum F (0→1); 26. Mesosomal gland reservoir M (2⇒5); 35. Medial groove of T1 F (0→1); 41. Marginal spines of pygidial plate F (1→0); 53. Inner basal margin of venter of gonocoxite M (0→1).

NODES 75→63: 8. Malar space F (0→1); 23. Beginning of thoracic declivity F (1→0); 39. Pregradular areas of sterna M (0→1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 75→74: 6. Epistomal suture F (0⇒1); 7. Supraocellar pit F (0→1); 28. Propodeal tooth B (0→1); 30. Shape of gradulus on T1 F (0→1); 32. Graduli on T1-3 F (0⇒2); 36. Apical margin of S1 B (0⇒1).

NODES 74→73: 19. Basitibial plate apex F (1→0); 22. Beginning of thoracic declivity M (0⇒1); 31. Distribution of tergal graduli M (0⇒2); 33. Anterior face of T1 M (0⇒1); 34. Anterior face of T1 F (0⇒1).

NODES 73→72: 22. Beginning of thoracic declivity M (1⇒2); 23. Beginning of thoracic declivity F (1⇒2); 34. Anterior face of T1 F (1→2); 47. Length of gonostylus M (0⇒1).

NODES 72→66: 14. Triangular hind trochanter F (0⇒1); 29. Tegula shape M (0⇒1); 38. Medial carina of metasomal sterna F (0→1); 53. Inner basal margin of venter of gonocoxite M (1→0); 55. Penis valves M (0⇒1).

NODES 66→64: 16. Spine on ventral surface of hind femur M (0⇒2); 31. Distribution of tergal graduli M (2⇒1).

NODES 66→65: 6. Epistomal suture not raised F (1⇒0); 25. Metapostnotum distinct F (1⇒0); 26. Mesosomal gland reservoir M (5→1); 28. Propodeal tooth lost B (1→0); 45. Penis M (0→1).

NODES 72→71: 23. Beginning of thoracic declivity F (2⇒3); 49. Medially projecting lobe on apex of gonostylus M (0→1).

NODES 71→70: 3. Subapical tooth on upper carina of mandible F (0→1); 37. Medial carina of S6 M (0→1).

NODES 70→69: 6. Epistomal suture F (1→0); 7. Supraocellar pit not deeply excavated F (1→0).

NODES 69→68: 1. Vestiture M (0⇒1); 2. Subapical tooth on mandible M (0→1); 31. Distribution of tergal graduli M (2⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1); 49. Medially projecting lobe on apex of gonostylus M (1⇒2).

NODES 68→67: 51. Spine lost on posteroventral margin of gonocoxite M (1→0).

NODES 86→85: 32. Graduli on T1-3 F (0⇒2); 40. Appressed setae near metasomal spiracles M (0→1).

NODES 85→84: 17. Tubercles on posterior margin of basitibial plate F (0⇒2); 24. Metapostnotum distinct M (1→0).

NODES 84→83: 39. Pregradular areas of sterna with setal areas M (0→1).

NODES 83→78: 3. Subapical tooth on upper carina of mandible F (0⇒1); 25. Metapostnotum not defined F (0→1).

NODES 83→82: 11. No spines on outer apex of hind tibia M (1→0).

NODES 82→81: 24. Metapostnotum not defined M (0→1); 49. Medially projecting lobe on apex of gonostylus M (0⇒1).

NODES 81→80: 16. Tubercle on ventral surface of hind femur M (0→1).

NODES 80→79: 6. Epistomal suture raised F (0⇒1).

NODES 94→93: 36. Apical margin of S1 B (0→2).

NODES 93→89: 20. Basitibial plate foveate F (0→1); 50. Ventromedial margins of gonocoxites diverge M (0⇒1).

NODES 89→88: 41. Many spines along pygidial plate margin F (1⇒2); 42. Gonostylus M (0⇒1); 44. Bifid apex of penis valves M (0⇒1); 48. Setae on apex of gonostylus M (1→0).

NODES 93→92: 4. Apex of mandible tridentate F (0⇒1); 10. Facial maculations absent M (0→1); 40. Appressed setae near metasomal spiracles M (0→1); 54. Spines on posterior margin T7 M (0→1).

NODES 92→91: 17. Tubercles along margins of basitibial plate F (0⇒1); 21. Extent of basitibial plate F (1⇒0); 26. Mesosomal gland reservoir M (0→1); 48. Setae on apex of gonostylus M (1⇒0); 55. Penis valves M (0→1).

NODES 91→90: 11. Two spines on outer apex of hind tibia M (1⇒2); 12. Two spines on outer apex of hind tibia F (0⇒1); 40. Appressed setae near metasomal spiracles M (1→0); 53. Inner basal margin of venter of gonocoxite M (0⇒1); 54. Posterior margin T7 M (1→0).

APPENDIX 2

CHARACTER CHANGES AND NODE SUPPORT FOR TREE SHOWN IN FIG. 11 A (ANALYSIS 3. ISLAND 1, CHARACTER WEIGHTS EQUAL)

Abbreviations and conventions as in Appendix 1.

NODES 95→94: 11. One spine on outer apex of hind tibia M (0→1); 19. Basitibial plate apex bifid F (0→1); 21. Extent of basitibial plate F (0→1); 41. Paired marginal spines of pygidial plate F (0→1); 47. Gonostylus slender, short M (0→1).

NODES 72→63: 26. Mesosomal gland reservoir M (0→2); 36. Apical margin Sl emarginate B (0⇒2); 49. Medially projecting lobe on apex of gonostylus M (0→1).

NODES 63→60: 13. Tibial spine F (0→1); 50. Ventromedial margin of gonocoxites diverge M (0→1).

NODES 60→59: 3. Subapical tooth on upper carina of mandible F (0⇒1); 24. Metapostnotum riot evident M (0⇒1); 43. Lateral edge of penis valve modified M (0⇒1); 52. Ventroapical plate of gonocoxite M (0→1).

NODES 59→58: 13. Tibial spine F (1→0); 52. Ventroapical plate of gonocoxite M (1→2).

NODES 58→57: 51. Spine on posteroventral margin of gonocoxite M (0=>1).

NODES 57→56: 49. Medially projecting lobe on apex of gonostylus M (1→0).

NODES 56→53: 26. Mesosomal gland reservoir M (2→3); 27. Beginning of thoracic declivity M (0⇒1); 36. Apical margin of Sl entire B (2⇒0).

NODES 53→52: 6. Epistomal suture F (0⇒1); 48. Setae on apex of gonostylus M (1→0).

NODES 52→51: 4. Apex of mandible tridentate F (0→1); 5. Upper rutellar tooth and preapical tooth fused F (0→1); 12. Two spines on outer apex of hind tibia F (0⇒1); 40. Appressed setae near metasomal spiracles M (0→1).

NODES 51→50: 32. Graduli on Tl-3 F (0⇒2); 38. Medial carina of metasomal sterna F (0⇒1).

NODES 50→49: 1. Vestiture M (0→1); 4. Apex of mandible bidentate F (1→0); 5. Upper rutellar tooth and preapical tooth (1→0); 39. Pregradular areas of sterna without setal areas M (0⇒1).

NODES 56→55: 2. Subapical tooth on mandible M (0→1); 49. Medially projecting lobe on apex of gonostylus M (0→2).

NODES 55→54: 32. Graduli on T1-3 F (0⇒2).

NODES 63→62: 4. Apex of mandible tridentate F (0⇒1); 10. Facial maculations absent M (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1); 54. Spines on posterior margin T7 M (0⇒1).

NODES 62→61: 17. Margins of basitibial plate F (0⇒1); 18. Basitibial plate apex bifid M (0⇒1); 32. Number of tergal graduli F (0→1).

NODES 72→71: 17. Margins of basitibial plate F (0⇒2); 32. Graduli on Tl-3 F (0⇒2); 52. Ventroapical plate of gonocoxite M (0=>2).

NODES 71→70: 39. Pregradular areas of sterna M (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 70→69: 24. Metapostnotum not defined M (0⇒1); 25. Metapostnotum not defined F (0⇒1); 26. Mesosomal gland reservoir M (0→1).

NODES 69→68: 26. Mesosomal gland reservoir M (1→2).

NODES 68→67: 49. Medially projecting lobe on apex of gonostylus M (0⇒1).

NODES 67→66: 11. No spines on outer apex of hind tibia M (1→0); 25. Metapostnotum F (1→0).

NODES 66→65: 16. Tubercle on ventral surface of male hind femur (0→1).

NODES 65→64: 6. Epistomal suture raised F (0→1).

NODES 94→93: 11. Two spines on outer apex of hind tibia M (1→2); 24. Metapostnotum not defined M (0⇒1); 25. Metapostnotum not defined F (0⇒1).

NODES 93→92: 12. Two spines on outer apex of hind tibia F (0⇒1); 36. Apical margin of Sl B (0⇒2); 50. Ventromedial margin of gonocoxites diverge M (0⇒1); 52. Ventroapical plate of gonocoxite M (0→1).

NODES 92→91: 48. Setae on apex of gonostylus M (1→0); 52. Ventroapical plate of gonocoxite M (1→2); 53. Inner basal margin of venter of gonocoxite M (0→1).

NODES 91→77: 24. Metapostnotum defined M (1⇒0); 25. Metapostnotum defined F (1⇒0).

NODES 77→75: 10. Facial maculations absent M (0→1); 17. Margins of basitibial plate F (0→1); 42. Gonostylus M (0→1); 52. Ventroapical plate of gonocoxite M (2→0).

NODES 75→73: 12. Two spines on outer apex of hind tibia F (1⇒0); 41. Marginal spines of pygidial plate F (1⇒2); 44. Apex of penis valves M (0⇒1).

NODES 75→74: 21. Extent of basitibial plate F (1⇒0); 26. Mesosomal gland reservoir M (0⇒1); 50. Divergence of ventromedial margin of gonocoxites M (1⇒0); 55. Penis valves M (0⇒1).

NODES 77→76: 22. Beginning of thoracic declivity M (0⇒1); 23. Beginning of thoracic declivity F (0⇒1); 26. Mesosomal gland reservoir M (0→2); 36. Apical margin of Sl B (2→0); 53. Inner basal margin of venter of gonocoxite M (1→0).

NODES 91→90: 19. Basitibial plate apex F (1→0); 26. Mesosomal gland reservoir M (0⇒5); 35. Medial groove of Tl F (0⇒1); 47. Length of gonostylus M (1→0).

NODES 90→78: 8. Malar space F (0⇒1); 39. Pregradular areas of sterna M (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 90→89: 6. Epistomal suture F (0=>1); 23. Beginning of thoracic declivity F (0⇒1); 32. Graduli on Tl-3 F (0⇒2); 33. Anterior face of Tl M (0→1); 36. Apical margin of Sl B(2⇒1).

NODES 89→88: 7. Supraocellar pit F (0⇒1); 28. Propodeal tooth B (0⇒1); 30. Shape of gradulus on Tl (0⇒1); 37. Medial carina of S6 M (0⇒1); 41. Marginal spines of pygidial plate F (1⇒0); 51. Spine on posteroventral margin of gonocoxite M (0⇒1).

NODES 88→87: 22. Beginning of thoracic declivity M (0⇒2); 23. Beginning of thoracic declivity F (1⇒2); 34. Anterior face of Tl F (0⇒2); 47. Length of gonostylus M (0⇒1).

NODES 87→81: 14. Triangular hind trochanter F (0⇒1); 16. Spine on ventral surface of hind femur M (0⇒2); 29. Shape of tegula M (0⇒1); 38. Medial carina of metasomal sterna F (0→1); 53. Inner basal margin of venter of gonocoxite (1→0); 55. Penis valves M (0⇒1).

NODES 81→80: 26. Mesosomal gland reservoir M (5→1); 31. Distribution of tergal graduli M (0→1); 37. Medial carina of S6 M (1⇒0); 50. Divergence of ventromedial margin of gonocoxites M (1→0); 51. Spine on posteroventral margin of gonocoxite M (1→0).

NODES 80→79: 6. Epistomal suture not raised F (1⇒0); 16. Unmodified ventral surface of hind femur M (2→0); 25. Metapostnotum defined F (1⇒0); 28. Propodeal tooth absent B (1⇒0); 31. Distribution of tergal graduli M (1→2); 45. Penis M (0→1).

NODES 87→86: 3. Subapical tooth on upper carina of mandible F (0→1); 23. Beginning of thoracic declivity F (2⇒3); 49. Medially projecting lobe on apex of gonostylus M (0→1).

NODES 86→83: 1. Vestiture M (0⇒1); 2. Subapical tooth on mandible M (0→1); 40. Appressed setae near metasomal spiracles M (0⇒1); 49. Medially projecting lobe on apex of gonostylus M (1→2).

NODES 83→82: 6. Epistomal suture F (1⇒0); 7. Supraocellar pit F (1⇒0); 31. Distribution of tergal graduli M (0⇒1); 51. Spine on posteroventral margin of gonocoxite M (1⇒0).

NODES 86→85: 31. Distribution of tergal graduli M (0⇒2).

NODES 85→84: 34. Anterior face of Tl F (2⇒1).

APPENDIX 3

CHARACTER CHANGES AND NODE SUPPORT FOR TREE SHOWN IN FIGURE 13 A (ANALYSIS 3, ISLAND 5, CHARACTER WEIGHTS EQUAL).

Abbreviations and conventions as in Appendix 1.

NODES 95→94: 11. One spine on outer apex of hind tibia M (0→1); 19. Basitibial plate apex bifid F (0→1); 21. Extent of basitibial plate F (0→1); 41. Paired marginal spines of pygidial plate F (0→1); 47. Gonostylus slender, short M (0→1).

NODES 94→85: 36. Apical margin of S1 (0⇒2).

NODES 85→63: 26. Mesosomal gland reservoir M (0⇒2); 49. Medially projecting lobe on apex of gonostylus M (0⇒1).

NODES 63→60: 13. Two outer tibial spines F (0→1); 50. Ventromedial margin of gonocoxites diverge M (0⇒1).

NODES 60→59: 3. Subapical tooth on upper carina of mandible F (0⇒1); 24. Metapostnotum not defined M (0⇒1); 43. Lateral edge of penis valve modified M (0⇒1); 52. Ventroapical plate of gonocoxite M (0→1).

NODES 59→58: 13. One outer tibial spine F (1→0); 52. Ventroapical plate of gonocoxite M (1→2).

NODES 58→57: 51. Spine on ventroposterior margin of gonocoxite M (0⇒1).

NODES 57→56: 49. Medially projecting lobe on apex of gonostylus M (1→0).

NODES 56→53: 26. Mesosomal gland reservoir M (2→3); 27. Beginning of thoracic declivity M (0⇒1); 36. Apical margin of Sl B (2⇒0).

NODES 53→52: 6. Epistomal suture F (0⇒1); 48. Setae on apex of gonostylus M (1→0). NODES 52→51: 12. One spine on outer apex of hind tibia F (0⇒1); 32. Number of tergal graduli F (0⇒2); 38. Medial carina of metasomal sterna F (0→1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 51→49: 1. Vestiture M (0⇒1); 39. Pregradular areas of sterna M (0⇒1).

NODES 51→50: 4. Number of apical teeth of mandible F (0⇒1); 5. Upper rutellar and preapical tooth fused F (0⇒1); 26. Mesosomal gland reservoir M (3→8).

NODES 56→55: 2. Subapical tooth on mandible M (0→1); 49. Medially projecting lobe on apex of gonostylus M (0→2).

NODES 55→54: 32. Graduli on Tl–3 F (0⇒2).

NODES 63→62: 4. Apex of mandible tridentate F (0⇒1); 10. Facial maculations absent M (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1); 54. Spines on posterior margin T7 M (0→1).

NODES 62→61: 17. Margins of basitibial plate F (0⇒1); 18. Basitibial plate apex bifid M (0⇒1); 32. Number of tergal graduli F (0→1).

NODES 85→84: 11. Two spines on outer apex of hind tibia M (1→2); 12. Two spines on outer apex of hind tibia F (0→1).

NODES 84→82: 48. Setae on apex of gonostylus M (1⇒0).

NODES 82→80: 50. Ventromedial margin of gonocoxites diverge M (0⇒1).

NODES 80→64: 12. One spine on outer apex of hind tibia F (1→0); 41. Marginal spines of pygidial plate F (1→2); 42. gonostylus M (0⇒1); 44. Apex of penis valves M (0⇒1).

NODES 80→79: 19. Basitibial plate apex entire F (1→0); 22. Beginning of thoracic declivity M (0→1); 23. Beginning of thoracic declivity F (0→1); 26. Mesosomal gland reservoir M (0→2); 36. Apical margin of S1 B (2→0); 52. Ventroapical plate of gonocoxite M (0→1).

NODES 79→78: 47. Length of gonostylus M (1⇒0); 52. Ventroapical plate of gonocoxite M (1→2).

NODES 78→77: Beginning of thoracic declivity M (1→0); 24. Metapostnotum defined M (0→1); 25. Metapostnotum defined F (0→1); 26. Mesosomal gland reservoir M (2→5); 35. Medial groove of Tl F (0⇒1); 53. Inner basal margin of venter of gonocoxite M (0⇒1).

NODES 77→65: 8. Long malar space F (0⇒1); 23. Beginning of thoracic declivity F (1⇒0); 39. Pregradular areas of sterna M (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 77→76: 6. Epistomal suture F (0⇒1); 32. Graduli on Tl–3 F (0⇒2); 33. Anterior face of Tl M (0→1); 36. Apical margin of Sl B (0⇒1).

NODES 76→75: 7. Supraocellar pit F (0⇒1); 28. Propodeal tooth B (0⇒1); 30. Shape of gradulus on Tl F (0⇒1); 37. Medial carina of S6 M (0⇒1); 41. Marginal spines of pygidial plate F (1→0); 51. Spine on ventroposterior margin of gonocoxite M (0⇒1).

NODES 75→74: 22. Beginning of thoracic declivity M (0⇒2); 23. Beginning of thoracic declivity F (1⇒2); 34. Anterior face of Tl F (0⇒2); 47. Length of gonostylus M (0⇒1).

NODES 74→68: 14. Triangular hind trochanter F (0⇒1); 16. Spine on ventral surface of hind femur M (0⇒2); 29. Shape of tegula M (0⇒1); 38. Medial carina of metasomal sterna F (0→1); 53. Inner basal margin of venter of gonocoxite M (1→0); 55. Penis valves M (0⇒1).

NODES 68→67: 26. Mesosomal gland reservoir M (5→1); 31. Distribution of tergal graduli M (0→1); 37. Medial carina of S6 M (1→0); 50. Divergence of ventromedial margin of gonocoxites M (1→0); 51. Spine on ventroposterior margin of gonocoxite M (1→0).

NODES 67→66: 6. Epistomal suture F (1→0); 16. Unmodified ventral surface of hind femur M (2→0); 25. Metapostnotum defined F (1→0); 28. Propodeal tooth B (1→0); 31. Distribution of tergal graduli M (1⇒2); 45. Penis M (0⇒1).

NODES 74→73: 3. Subapical tooth on upper carina of mandible F (0→1); 23. Beginning of thoracic declivity F (2⇒3); 49. Medially projecting lobe on apex of gonostylus M (0→1).

NODES 73→70: 1. Vestiture M (0⇒1); 2. Subapical tooth on mandible M (0→1); 40. Appressed setae near metasomal spiracles M (0⇒1); 49. Medially projecting lobe on apex of gonostylus M (1→2).

NODES 70→69: 6. Epistomal suture F (1→0); 7. Supraocellar pit F (1→0); 31. Distribution of tergal graduli M (0⇒1); 51. Spine on posteroventral margin of gonocoxite M (1→0).

NODES 73→72: 31. Distribution of tergal graduli M (0→2).

NODES 72→71: 34. Anterior face of Tl F (2⇒1).

NODES 82→81: 10. Facial maculations M (0⇒1); 17. Margins of basitibial plate F (0⇒1); 21. Extent of basitibial plate F (1→0); 26. Mesosomal gland reservoir M (0⇒1); 53. Inner basal margin of venter of gonocoxite M (0⇒1); 55. Penis valves M (0⇒1).

NODES 84→83: 24. Metapostnotum not defined M (0⇒1); 25. Metapostnotum not defined F (0⇒1).

NODES 94→93: 17. Margins of basitibial plate F (0⇒2); 32. Graduli on Tl–3 F (0⇒2); 52. Ventroapical plate of gonocoxite M (0⇒1).

NODES 93→92: 11. One spine on outer apex of hind tibia M (1→0); 39. Pregradular areas of sterna with setal patches M (0→1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 92→91: 24. Metapostnotum not defined M (0⇒1); 26. Mesosomal gland reservoir M (0⇒2).

NODES 91→87: 11. One spine on outer apex of hind tibia M (0⇒1); 25. Metapostnotum not defined F (0⇒1).

NODES 87→86: 3. Subapical tooth on upper carina of mandible F (0⇒1).

NODES 91→90: 49. Medially projecting lobe on apex of gonostylus M (0⇒1).

NODES 90→89: 16. Tubercle on ventral surface of hind femur M (0⇒1).

NODES 89→88: 6. Epistomal suture F (0⇒1).

APPENDIX 4

CHARACTER CHANGES AND NODE SUPPORT FOR TREE SHOWN IN FIGURE 15 (ANALYSIS 3. ISLAND 6, CHARACTER WEIGHTS EQUAL).

Abbreviations and conventions as in Appendix 1.

NODES 95→94: 11. One spine on outer apex of hind tibia M (0→1); 19. Basitibial plate apex bifid F (0→1); 21. Extent of basitibial plate F (0→1); 36. Apical margin of S1 (0→2); 41. Paired marginal spines of pygidial plate F (0→1); 47. Gonostylus slender, short M (0→1).

NODES 92→72: 48. Setae on apex of gonostylus M (0→1).

NODES 72→63: 26. Mesosomal gland reservoir M (0→2); 49. Medially projecting lobe on apex of gonostylus M (0→1).

NODES 63→60: 13. Two spines on outer apex of hind tibia F (0→1); 50. Ventromedial margin of gonocoxites diverge M (0→1).

NODES 60→59: 3. Subapical tooth on upper carina of mandible F (0→1); 24. Metapostnotum not defined M (0→1); 43. Lateral edge of penis valve modified M (0→1); 52. Ventroapical plate of gonocoxite M (0→1).

NODES 59→58: 13. One spine on outer apex of hind tibia F (1→0); 52. Ventroapical plate of gonocoxite M (1→2).

NODES 58→57: 51. Spine on ventroposterior margin of gonocoxite M (0⇒1).

NODES 57→56: 49. Medially projecting lobe on apex of gonostylus M (1→0).

NODES 56→53: 26. Mesosomal gland reservoir M (2→3); 27. Beginning of thoracic declivity M (0⇒1); 36. Apical margin of S1 M (2⇒0).

NODES 53→52: 6. Epistomal suture F (0⇒1); 48. Setae on apex of gonostylus M (1⇒0).

NODES 52→51: 4. Apex of mandible tridentate F (0→1); 5. Upper rutellar tooth and preapical tooth fused F (0→1); 12. Two spines on outer apex of hind tibia F (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 51→50: 32. Graduli on T1–3 F (0⇒2); 38. Medial carina of metasomal sterna F (0⇒1).

NODES 50→49: 1. Vestiture M (0⇒1); 4. Apex of mandible bidentate F (1→0); 5. Upper rutellar tooth and preapical tooth separate F (1→0); 39. Pregradular areas of sterna M (0⇒1).

NODES 56→55: 2. Subapical tooth on mandible M (0→1); 49. Medially projecting lobe on apex of gonostylus M (0→2).

NODES 55→54: 32. Graduli on T1–3 F (0⇒2).

NODES 63→62: 4. Apex of mandible tridentate F (0⇒1); 1 0. Facial maculations absent M (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1); 54. Spines on posterior margin T7 M (0⇒1).

NODES 62→61: 17. Margins of basitibial plate F (0⇒1); 18. Basitibial plate apex bifid M (0⇒1); 32. Number of tergal graduli F (0→1).

NODES 72→71: 17. Margins of basitibial plate F (0⇒2); 32. Graduli on T1–3 F (0⇒2); 36. Apical margin of S1 B (2→0); 52. Ventroapical plate of gonocoxite M (0→2).

NODES 71→70: 39. Pregradular areas of sterna M (0⇒1); 40. Appressed setae near metasomal spiracles M (0→1).

NODES 70→69: 24. Metapostnotum not defined M (0⇒1); 25. Metapostnotum not defined F (0⇒1); 26. Mesosomal gland reservoir M (0→1).

NODES 69→68: 26. Mesosomal gland reservoir M (1→2).

NODES 68→67: 49. Medially projecting lobe on apex of gonostylus M (0⇒1).

NODES 67→66: 11. Two spines on outer apex of hind tibia M (1⇒0); 25. Metapostnotum defined F (1⇒0).

NODES 66→65: 16. Tubercle on ventral surface of hind femur M (0⇒1).

NODES 65→64: 6. Epistomal suture F (0⇒1).

NODES 92→91: 11. Two spines on outer apex of hind tibia M (1→2); 12. One spine on outer apex of hind tibia F (0→1); 26. Mesosomal gland reservoir M (0→1).

NODES 91→73: 10. Facial maculations absent M (0⇒1); 17. Margins of basitibial plate F (0⇒1); 21. Extent of basitibial plate F (1⇒0); 53. Inner basal margin of venter of gonocoxite M (0⇒1); 55. Penis valves M (0⇒1).

NODES 91→90: 36. Apical margin of S1 B (2→0); 50. Ventromedial margin of gonocoxites diverge M (0⇒1); 52. Ventroapical plate of gonocoxite M (0→1).

NODES 90→74: 22. Beginning of thoracic declivity M (0⇒1); 23. Beginning of thoracic declivity F (0⇒1); 26. Mesosomal gland reservoir M (1→2).

NODES 90→89: 24. Metapostnotum not defined M (0⇒1); 25. Metapostnotum not defined F (0⇒1).

NODES 89→87: 19. Basitibial plate apex F (1→0); 26. Mesosomal gland reservoir M (1⇒5); 35. Medial groove of T1 F (0⇒>1); 47. Length of gonostylus M (1⇒0); 52. Ventroapical plate of gonocoxite M (1⇒2); 53. Inner basal margin of venter of gonocoxite M (0⇒1).

NODES 87→75: 8. Long malar space F (0⇒1); 39. Pregradular areas of sterna M (0⇒1); 40. Appressed setae near metasomal spiracles M (0⇒1).

NODES 87→86: 6. Epistomal suture F (0⇒1); 23. Beginning of thoracic declivity F (0⇒1); 32. Graduli on T1–3 F (0⇒2); 33. Anterior face of T1 M (0⇒1); 36. Apical margin of S1 B (0⇒1).

NODES 86→85: 7. Supraocellar pit F (0⇒1); 28. Propodeal tooth B (0⇒1); 30. Shape of gradulus on T1 F (0⇒1); 37. Medial carina of S6 M (0⇒1); 41. Marginal spines of pygidial plate F (1⇒0); 51. Spine on ventroposterior margin of gonocoxite M (0⇒1).

NODES 85→84: 22. Beginning of thoracic declivity M (0⇒2); 23. Beginning of thoracic declivity F (1⇒2); 34. Anterior face of T1 F (0⇒2); 47. Length of gonostylus M (0⇒1).

NODES 84→78: 14. Triangular hind trochanter F (0⇒1); 29. Shape of tegula M (0⇒1); 37. Medial carina of S6 M (1→0); 38. Medial carina of metasomal sterna F (0→1); 53. Inner basal margin of venter of gonocoxite M (1→0); 55. Penis valves M (0⇒1).

NODES 78→76: 16. Spine on ventral surface of hind femur M (0⇒2).

NODES 78→77: 6. Epistomal suture F (1→0); 25. Metapostnotum defined F (1→0); 26. Mesosomal gland reservoir M (5→1); 28. Propodeal tooth M (1⇒0); 31. Distribution of tergal graduli M (0⇒2); 45. Penis M (0→1).

NODES 84→83: 3. Subapical tooth on upper carina of mandible F (0→1); 23. Beginning of thoracic declivity F (2→3); 49. Medially projecting lobe on apex of gonostylus M (0→1).

NODES 83→80: 1. Vestiture M (0⇒1); 2. Subapical tooth on mandible M (0→1); 40. Appressed setae near metasomal spiracles M (0⇒1); 49. Medially projecting lobe on apex of gonostylus M (1⇒2).

NODES 80→79: 6. Epistomal suture F (1⇒0); 7. Supraocellar pit F (1⇒0); 31. Distribution of tergal graduli M (0⇒1); 51. Spine on ventroposterior margin of gonocoxite M (1⇒0).

NODES 83→82: 31. Distribution of tergal graduli M (0⇒2).

NODES 82→81: 34. Anterior face of T1 F (2→1).

NODES 89→88: 48. Setae on apex of gonostylus M (0⇒1).

NODES 94→93: 41. Marginal spines of pygidial plate F (1→2); 42. Gonostylus M (0⇒1); 44. Apex of penis valves M (0→1); 50. Ventromedial margin of gonocoxites diverge M (0⇒1).

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