REVIEW OF THE GENUS *POPILIUS* AND PRELIMINARY PHYLOGENY OF PASSALIDAE (COLEOPTERA)

A Dissertation

by

ALAN ROY GILLOGLY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2005

Major Subject: Entomology

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Approved as to style and content by:

James B. Woolley
(Chair of Committee)

Horace R. Burke
(Member)

Merrill H. Sweet, II
(Member)

Jane M. Packard
(Member)

Kevin M. Heinz
(Head of Department)

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ABSTRACT

Review of the Genus *Popilius* and Preliminary Phylogeny of Passalidae (Coleoptera).
(May 2005)
Alan Roy Gillogly, B.S., University of California, Riverside;
M.S., University of California, Riverside
Chair of Advisory Committee: Dr. James B. Woolley

Preliminary phylogenetic analyses of Passalidae and the genus *Popilius* are presented based on 207 characters for the family level part of this study and 232 characters for the generic portion. The strict consensus and successive approximation trees show that the New World passalid fauna is monophyletic, and that *Popilius* is paraphyletic and intertwined with several closely related, also paraphyletic, genera (at least *Heliscus*, *Odontotaenius* and *Petrejoides*).

An unrooted analysis of *Popilius* identified four species groups, two that are monophyletic, one that is probably paraphyletic (more closely related to *Petrejoides* than to other members of *Popilius*) and one for a distinct species, the single specimen of which was not available for examination.

New character systems were investigated and the metendosternite, eversible internal sac of the male genitalia, prostheca of the right mandible, epipharynx, and hypopharynx provided useful characters to supplement those traditionally used.

A new autapomorphy for the family is reported, an organ on the inner surface of both elytral humeri. The structure has a membranous covering and appears to contact an apophysis on the base of the wing. Its position and structure suggest that it may be a sound receptor.

A rigorous investigation of the relationships among the genera closely related is required to define generic boundaries and identify the out-group taxa most appropriate for the analysis of the component taxa.

Dedicated to Patricia O. Gillogly, Thomas E. T. Gillogly, Lorin R. Gillogly and Gwendolyn M. Gillogly, without whose inspiration and loving support this work would not have been possible.

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CHAPTER I
INTRODUCTION

BACKGROUND

Passalidae is a distinct and monophyletic family of scarabaeoid beetles with remarkably uniform external appearance. Various authors have proposed morphology-based phylogenies of Scarabaeoidea, including Iablokoff-Khnzorian (1977), Howden (1982), Browne & Scholtz (1994), and Scholtz & Chown (1995). The consensus is that Passalidae is near the base of Scarabaeoidea, closest (and perhaps sister taxon) to Diphyllostomatidae+Lucanidae. A study of basal scarabaeoid families proposes that Passalidae originated about 140 million years before present (MYBP), after the Triassic mass extinction event, in the Jurassic radiation of the primitive families of the Scarabaeoidea (Scholtz & Chown, 1995).

The family Passalidae is characterized by the following adult characters: 10-segmented, non-geniculate antenna with 3- to 6-segmented, sublamellate club; eye with a distinct canthus; exocone ommatidial structure; a movable inner tooth near the base of each mandible in all but a few species; absence of a membranous prostheca on the mandible; pointed galea and lacinia; three-segmented labial palp; bilobed mentum and distinct prementum; male genitalia trilobed, with a genital capsule and extrusible internal sac (Reyes-Castillo, 1970b; Nel & Scholtz, 1990; Scholtz, 1990). Passalid larvae are distinguished from those of other scarabaeoids by having a two-segmented antenna, three-segmented maxillary palp, transverse anal slit, metathoracic legs reduced to unsegmented stubs which function as stridulatory organs, distinctive positioning of the spiracles, and by the lack of a ventral process on the mandible (Carlson, 1991).

The limits of Passalidae have remained essentially unchanged since it was recognized as distinct from Lucanidae, and given the name Passalida by Leach in 1815; in 1819, Macleay accepted this division, and first used the name Passalidae (Reyes-Castillo, 1970b). The family consists of almost 700 species and is essentially pantropical. The species are not notably vagile and most species have restricted ranges. Few species have reached non-continental islands and about fifteen percent are flightless. No genera are common to both the New and Old Worlds, and the few genera found on more than one continent are shared between Asia and Australia, and between North and South America.

This dissertation follows the style of *Systematic Entomology*.

BIOLOGY

Passalids are subsocial beetles that maintain gallery systems in dead, rotting wood, with adult pairs tending their offspring through all stages of development. The unusual biology and complex acoustic communication among adults and larvae are unique within insects (Reyes-Castillo, 1970b; Schuster, 1983; Reyes-Castillo & Halffter, 1983, 1984); Schuster & Schuster, 1985, 1997).

All species of passalids for which the reproductive biology is known are monogamous, with adult pairs constructing, maintaining and defending tunnel systems in which they deposit eggs and rear their offspring. This dependence by the offspring on adult care results in a considerable overlap in generations within the gallery system of the family group, presumably because of the eight to ten weeks needed for teneral adults to reach the fully sclerotized, though still juvenile (not reproductive) state (Schuster & Schuster, 1997). The age of reproductive maturity probably varies among species. Courtship activity is known to occur four months after ecdysis in *Heliscus tropicus* (Valenzuela-Gonzalez & Castillo, 1984); however, *Odontotaenius disjunctus* (Illiger), a Nearctic species, appears to have a single generation per year, and reproduces about ten to eleven months after ecdysis (Schuster & Schuster, 1985). The adults of some species are known to live two years in nature, and some have survived four to five years in captivity (Schuster & Schuster, 1985, 1997).

Two to four (rarely six) eggs a day are placed in especially provisioned nest areas, though they may be laid in other parts of the gallery system and carried by adults in their mandibles to the nest (Reyes-Castillo & Halffter, 1984; Castillo & Reyes-Castillo, 1997; Schuster & Schuster, 1997). The total number of eggs in a nest may reach 20-35 (up to 250-500 in at least two subcortical species discussed below), but the number of larvae, pupae and teneral adults present in a tunnel system is usually far lower, presumably due to the cannibalistic tendencies of the larvae (Schuster & Schuster, 1997). Oviposition may extend over eight to ten weeks.

The larvae develop rapidly, progressing from egg to teneral adult in two and one-half to three months, and some tropical species can produce at least three egg clutches a year (Schuster, 1975a; Schuster & Schuster, 1997). All developmental stages, egg, larva, pupa, and teneral, juvenile and parental adults, may occasionally be present together in the gallery, and both the parental pair and their juvenile adult offspring assist pre-pupal third-instar larvae in preparing their protective pupal chambers and cooperate in repairing damaged chambers (Miller, 1932; Reyes-Castillo & Halffter, 1984; Schuster & Schuster, 1997; Valenzuela-Gonzalez, 1993).

The three larval instars feed on wood that is bitten from the gallery walls by adults, then shredded and chewed, and on feces of the mature adults which are richer in protein than the wood (Schuster & Schuster, 1997). Digestion is assisted by microorganisms present in the adult gut and in the mixed fecal material and wood chips that line the tunnels. Although other microorganisms may also be involved, saccharomycete yeast strains capable of fermenting xylose have been isolated from the gut of two passalid species, suggestive of a commensal or symbiotic relationship (Suh, et al., 2003). The fecal/chip mixture is reingested by both larvae and adults, presumably after additional digestion of the cellulose and hemicellulose to glucose and xylose, respectively. This extracorporeal microbial digestive activity is termed an "external rumen" (Odum, 1971).

There is considerable overlap between generations, presumably because of the eight to ten weeks needed for teneral adults to reach the fully sclerotized though still juvenile (not reproductive) state. Adult passalids and their juvenile adult offspring cooperate in assisting late third instar larvae construct their pupal chambers, and in repairing ruptured chambers (Schuster & Schuster, 1985). Migration of sclerotized adults occurs throughout the year, but it is most common at the beginning of the rainy season. Some species may be colonial, as individual nests of two species in southern Mexico contained from 264 to 532 eggs, far more than could be produced by a single female (Schuster & Schuster, 1997). No study has yet been done to determine the parentage or relatedness of such an egg clutch.

The constraints of their tunneling and subsocial behavior have molded the characteristic shape of passalids. The environmental pressures forcing the most efficient form for long life, maintaining open galleries and an external rumen within wood, and care of immature stages presumably prevent extreme expression of variation, especially in the development of long mandibles and horns, as occur in the related families, Lucanidae and Scarabaeidae, the species of which are found in a much wider range of habitats (Arrow, 1907). There is a strikingly uniform appearance among Passalidae, as well as great similarity among the species whose life histories are known. The few differences reported have been in the microhabitat occupied. The majority of species appear to be heartwood specialists, colonizing dead trees in later stages of decomposition and mining the rotten, inner parts, their galleries often following the pattern of fungus invasion of the wood (personal observations). These passalids tend to be subcylindrical. and include most of the species in temperate regions and at higher elevations within the tropics. The flightless species are, to my knowledge, exclusively in this habitat range.

Several groups have evolved, presumably independently, the ability to take advantage of the subcortical microhabitat offered by decay of the cambium layer beneath the bark of recently dead trees. These taxa share a similar body form, being distinctly more flattened that the heartwood specialists (Reyes-Castillo & Halffter, 1983; Johki & Kon, 1987; Lobo & Castillo, 1997). Most of these species are tropical, partitioning the dead tree resources with the heartwood specialists**.** One exception to this is the presence of a species of *Leptaulax* in the temperate, northwest corner of South Korea, where no heartwood species have been recorded (Nomura et al., 1993).

The other specialist species reported are from microhabitats that might also be expected to have fungus-infested plant material. *Ptichopus angulatus* Percheron, from Mesoamerica and Mexico, often colonizes the garbage dumps of leaf-cutting ants of the genus *Atta* that culture and subsist on fungi; these repositories are often in underground chambers and are packed with the fungus-degraded plant material discarded by the ants, although it has also been collected in rotting wood (Hendrichs & Reyes, 1963; Reyes-Castillo, 1970b; Holldobler & Wilson, 1990). *Ceracupes fronticornis* Arrow is reported to be the most common beetle in the root masses of epiphytic ferns (*Asplenium* spp.), often found in galleries in large numbers ("tens of adults and hundreds of larvae"), and is only occasionally found in rotten wood (Kabakov, 1967). *Taeniocerus bicanthatus* (Percheron) reportedly forms a gallery in the interface between a downed log and the substrate, with the adults and larvae aggregated, but not in a distinct gallery (Kon & Johki, 1987). This may be very similar to the habitat of the ancestral passalid. The ancestral scarabaeoid diet has been suggested as being soil or humus for larvae, and fungus for adults (Scholtz & Chown, 1995). Although these authors suggested wood as the food of both larvae and adults of passalids in their analysis of the evolution of food references, it appears that passalids are dependent on wood-degrading fungi (Suh, et al., 2003). If this is verified for all passalid species, it would strengthen the intermediate placement of passalids in the phylogeny and dietary framework of Scholtz & Chown (1995) by indicating that the passalid diet is also transitional, between humus feeding and wood feeding. The atypical habits of *Ptichopus angulatus* and *Ceracupes fronticornis* would then appear due to be secondary movement into these habitats, and that of *Taeniocerus bicanthatus* may indeed be plesiomorphic.

Little is known of the host preferences of most passalid species. The noteworthy exception is a study of the passalid fauna in the area of Los Tuxtlas, Veracruz, Mexico in which identified logs of 62 tree species were examined for passalids, with detailed data collected on the type of forest, stage of decomposition of the log, microhabitat occupied by the beetles, co-occurrence of species, and other details (Castillo, 1987).

Passalids are found primarily in dicotyledonous angiosperms, though both monocotyledonous angiosperms (palms) and, less commonly, gymnosperms (conifers) may serve as hosts (Reyes-Castillo & Halffter, 1984; Castillo & Lobo, 2004). Some species have a wide range of hosts, including introduced trees (Reyes-Castillo & Halffter, 1984), but there is evidence that specialization in the family may occur as two species of *Passalus* in Panama have been encountered only beneath the thick, fibrous, pitchy bark of *Calophylum longifolium* (Guttiferae) (personal observations). The smaller, flattened, subcortical specialists in the New World [e.g. *Passalus (Pertinax) alfari* (Pangella), *Passalus (Pertinax) maillei* Percheron, *Paxillus camerani* (Rosmini), *Paxillus leachi* Macleay)] tend to colonize dead trees or lianas with thin bark (personal observations). This partitioning of resources often results in a succession of passalid taxa invading a dead tree.

Most passalids appear to be generalist feeders as dead trees certainly represent a patchy and temporary environment (Schuster, 1975; Castillo, 1987). It is also presumed that flightless taxa are likely to be generalist feeders due to their limited dispersal and search abilities, and that the flattened, subcortical specialists are most likely to be active fliers because of the especially transient availability of their patchy habitat.

The life spent almost entirely in the dark, frequently reduced eyes, and almost complete lack of external secondary sexual differences in passalids suggest that acoustic, tactile and chemical mechanisms may be of far more importance in distinguishing potential mates than are visual stimuli.

Of these, only acoustic differences have been investigated (Schuster, 1975b, 1983). Other potential precopulation barriers possibly resulting from sexual selection or diverging evolution in isolation may prevent interspecific matings, e.g. differences in genitalia, relative body size, etc. Of these, only acoustic differences have been investigated (Schuster, 1983).

Both adults and larvae are capable of stridulation, although they use different structures for this purpose. Sound phonotones (chirps) are produced by the adult by rubbing spinose patches on the surface of the sixth abdominal tergite against the underside of fully developed or atrophied wings, with differences in sounds manifested between species (Reyes-Castillo & Jarman, 1980; Palestrini et al., 2003). Even in flightless species with the most strongly atrophied wings, there remains a rigid rod that serves for sound production (Arrow, 1904; Reyes-Castillo, 1970b). Fourteen signals (five different sounds in 11 contexts were reportedly made by adults of *Odontotaenius disjunctus* (Schuster, 1975b). The contexts in which stridulation was observed were courtship initiation, courtship, post-copulation, aggression, disturbance, and solos. This is the largest repertoire of acoustical signals known for any species of arthropod (Schuster, 1975b). Despite intense study of sound production in adult passalids, the mechanism of sound reception has not been detected (Reyes-Castillo & Jarman, 1980).

The larvae produce sound by scraping the highly reduced metathoracic leg against a patch of parallel ridges on the coxa of the mesothoracic leg, and three signals (one sound in three contexts) have been attributed to the larvae of *O. disjunctus* (Schuster, 1975b; Reyes-Castillo & Jarman, 1980). The sound is usually more faint and of a higher frequency than that of the adults, and it varies in pitch with the level of stimulation (Ohaus, 1900, 1909; Reyes-Castillo & Jarman, 1980). Some geotrupid larvae have a very similar method of stridulating, but the metathoracic leg is segmented, rather than fused, as in passalids (Pavan et al., 1990).

Courtship and mating in passalids presumably take place in expanded portions of the gallery system. Copulation has been infrequently described for non-captive passalids, but the full mating sequence can be observed in the laboratory (Schuster, 1975a; Castillo & Reyes-Castillo, 1989; MacGown & MacGown, 1996). Copulation is preceded by courtship behavior that usually includes stridulation and stereotyped movements of the body and antennae. Interspecific differences in sound frequency and rhythm occur during courtship (Schuster, 1975b), and either the male or both sexes may stridulate. After preliminary courtship behavior, the male typically turns over, positioning himself venter to venter with the female, and both individuals brace against the container or substrate before mating. Species have been reported mating with the pair oriented end to end, facing opposite directions (Schuster, 1975a), and pairs of *O. disjunctus* flying *en copulo* have been reported (MacGown & MacGown, 1996), although these positions may have been preceded by venter to venter contact and intromission.

Chemical communication has not been investigated in passalids. A distinct odor has been reported during aggressive behavior of *O. disjunctus* (Mullen & Hunter, 1973), and freshly opened galleries and captive individuals of the genus *Verres* Kaup have a strong and characteristic odor (personal observations), possibly used for species recognition or defense. Schuster (1975b) noted that interspecific aggression among passalids can occur without acoustical signaling, and that an individual of *Odontotaenius disjunctus* appears to be able to distinguish the sex of the occupant before entering an active gallery in the field.

In summary, Passalidae offer many intriguing lines of research, including phylogenetic relationships, character displacement in sympatric species, the coevolution of behavioral and structural characters. These will best be approached by integration of behavioral, chemical and molecular data to that derived from traditional morphological systems.

TAXONOMIC HISTORY

The primary emphasis of specialists in this group has been the description of the adults of new taxa. Few phylogenetic studies have been done, and only two of these have been formally published (Fonseca, 1987, unpublished dissertation; Hunzicker et al., 1993, abstract only; Marshall, 2000, unpublished dissertation; Schuster et al., 2003). The description of immature stages, primarily larvae, has burgeoned in the last 25 years (Schuster & Reyes-Castillo, 1981, 1990; Schuster, 1992), but little attempt has been made to use this information for systematic or phylogenetic purposes. The few detailed reports of behavior have been mainly descriptive (Reyes-Castillo & Halffter, 1984; Valenzuela-Gonzalez, 1986; Schuster & Schuster, 1997), and behavior is still known from too few species to permit meaningful comparisons, although ultimately it may prove to be of great importance.

The name Passalida was proposed by Leach to include this distinct group of beetles, which had previously been placed in the genus *Passalus* Fabricius of the family Lucanidae. Macleay accepted this division, and first used the name Passalidae. Description of new species of *Passalus* continued until more than a hundred species were included. Macleay described a second genus, *Paxillus*, but the name was disregarded for the next 50 years (Reyes-Castillo. 1970b).

For the most part, these species were inadequately described. The monographs by Percheron (1835, 1841, 1844) and Burmeister (1847) substantially improved the quality of descriptions, and Burmeister’s coverage of the family summarized the knowledge to that date, including detailed observations on external morphology (adults, pupae and larvae), and the nervous and digestive systems (adults and larvae).

In 1871, Kaup completed publication of a monograph of the family, including the original descriptions of 67 new species and 58 new genera (Kaup, 1868a, 1868b, 1869, 1871). Although his intent was to clarify the taxonomy of the family and demonstrate relationships among the described species, his decisions were influenced by his novel world view (Kaup, 1871). This was an expansion of ideas of Macleay (Arrow, 1950) and especially Oken (1840), two of the "Naturphilosophen" who sought to discover an underlying metaphysical morphological and mathematical orderliness among living organisms (Kaup, 1871; Panchen, 1992). At about the same time as Darwin was publishing his theories on evolution and sexual selection, Kaup accepted the concept that the natural world was based on a complex and mystical quinary system, in which each taxonomic group was composed of five subgroups, which might also be subdivided into five more. His five passalid subfamilies included two which were further subdivided into genus groups (equivalent to tribes), making a total of 65 genera and 325 species of passalids postulated by this system. According to Kaup (1871), 60 genera and 171 species of these had been discovered, and he even predicted and diagrammed where in his system the undiscovered taxa would fall. However, it should be said that Kaup noted that it would be an insignificant problem to condemn the quinary system, and that he wanted to be the first to do so, should anyone discover a sixth species in any of his genera (Kaup, 1871, p.12). He asked only (quote translated) "…that no local variety or chance dwarf form be passed off as an actual, legitimate species." Kaup apparently did not survive long enough to discredit his system.

By 1890, Kuwert had begun the next and most recent monographic work of the family, and published a scathing critique of Kaup's philosophy and systematic ability in a three-part editorial (Kuwert, 1890). Kaup's paucity of material, manipulation of generic limits in order to fit his system, inconsistency in descriptions, and disregard of wear (particularly of mandibles and projections of the head) were especially criticized, and allegedly caused subsequent authors (e.g. Schaufuss, Kirsch) to describe new species in incorrect genera (Kuwert, 1890).

Kuwert first published an overview of the species and genera in key form (Kuwert, 1891). However, the descriptions were so inadequate that the editor of Novitates Entomologicae (W. von Rothschild) promised publication of a monographic treatment of the family because (quote translated) "…further work on passalids without publication of the detailed manuscript would be much more difficult.", according to the preface added by Dr. K. Jordan to the first section of the monograph (Kuwert, 1896).

This was not the only accusation of substandard taxonomic work by Kuwert, as Kraatz (1891) roundly criticized Kuwert's work on the heterocerids of Europe, calling attention to errors in illustrations, scientific name priority, and type localities, and the concealment of the locations of the type specimens and series described in this publication.

Kuwert's monograph of Passalidae (1896, 1897, 1898), published in key format, suffered considerably from being published posthumously. It was such a "voluminous manuscript" that the editors of the journal resorted to drastic editing. The text is in the form of an extended key (with species descriptions thus spread throughout various pages), and incorporated into the narrative a catalogue that was originally in appendix form (note by Jordan in preface to Kuwert, 1896). This has created some confusion, as numerous "Kuwert, *l.c.*" entries in the text of the species sections (Kuwert, 1897, 1898) were presumably in the appendix, but were then inserted by the editors into the text, verbatim. Since the species are treated and described here for the first time, the "*l.c.*" entries actually refer to species treatments in this work, rather than in some earlier publication.

In his meticulous search for differentiating characters, Kuwert seems to have ignored his own criticism of Kaup's monograph, as he also split species using criteria for which he criticized Kaup, such as differences due to wear, and he accepted erroneous locality data without question (Arrow, 1907; Gravely, 1913). The numbers of described species tripled, genera doubled, and subfamilies increased from 5 to 38 under Kuwert's hand.

Great credit must be given to F. H. Gravely, of the Indian Museum, Calcutta, for unifying the monographic works of earlier authors with the excellent, but piecemeal, clarifying publications by Arrow and Zang. This far more orderly classification was based, in large part, on the concordance that he noted between distribution and classification. Gravely began with a study of the Oriental passalids (1914), and then took advantage of the purchase by the Indian Museum of a large, representative. worldwide collection, to expand his synthesis to include the entire family (1918). Although he referred to this work as "A Contribution towards a Revision…", he reorganized Passalidae into the currently accepted classification, although relatively minor alterations have been made since.

Gravely (1918) relegated many of the genera created by Kaup and Kuwert to synonymy and proposed seven subfamilies: Aulacocyclinae (for a small, highly distinctive group of Australasian genera); Pseudacanthinae (for the New World genera possessing an exposed clypeus and a "clypeofrontal" suture, now recognized as the transfrontal sulcus); Proculinae (for genera with an exposed clypeus, without a transfrontal sulcus, and without outer tubercles); Passalinae (for the New World genera with outer tubercles and rarely with the clypeus exposed); Solenocyclinae (for the African genera, including those from Madagascar, all of which have a pair of secondary tubercles on the anterior margin of the head, between the outer tubercles and outer angles of the head); Macrolininae (for the Ausralasian genera with rarely more than one pair of tubercles on the anterior margin of the head, and often with more than three antennal lamellae); and Leptaulacinae (for the genera always possessing more than one pair of of tubercles on the anterior margin of the head, and only three antennal lamellae). This masterful work is still useful as it contains the rationale for his system, cogent comments on the problems within the higher taxa, and keys to the subfamilies, genera, and to the species with which he was familiar.

The last 85 years have seen many taxonomic publications on passalids, the majority matching the rigorous standard set by Gravely (1918). The higher classification, though, remained unchanged until Arrow (1950) reduced the number of subfamilies to two, Aulacocyclinae and Passalinae, based on his observation that Aulacocylinae was far more distant from the rest of Gravely's subfamilies than they were from each other. He thought that this reduction worked quite well for the limited Indian passalid fauna, and saw no need for tribal subdivisions.

Arrow's lead was followed in a study of New World genera by Reyes-Castillo (1970b), in which he recognized the distinctiveness of Aulacocyclinae and a group of Mesoamerican genera. Within Passalinae, Reyes-Castillo proposed two tribes: Proculini, which included Gravely's Proculinae, Pseudacanthinae and three genera of Passalinae; and Passalini, which contained the remaining three genera of Gravely's Passalinae, and all of Gravely's Solenocyclinae, Macrolininae and Leptaulacinae. Both Arrow and Reyes-Castillo based their systematic conclusions on geographically and taxonomically limited faunas, rather than doing a rigorous study of the entire family.

This classification was not questioned until Fonseca (1987), based on a laborious and thorough examination of most of the genera of Passalidae, proposed a phylogeny of the family. The most controversial suggestion was that the two subfamilies should be raised to family status, although this appears to have been due as much to the author's desire to provide names for each of the categorical levels in his cladogram as to the degree of the differences between these clades. In his phylogenetic methodology Fonseca applied a different name to each of the five major node levels of his phylogeny; (generic) groups, subtribes, tribes, subfamilies, and to accommodate the fifth level, families.

Specimens of almost all of the known genera were examined, described and figured by Fonseca; two genera were not seen, and three others were not dissected, due to the rarity of specimens. However, the matrix contains no missing data; the cells for wing, intestine, male genitalia, larva and karyotype data for these taxa are filled. All of the characters used were binary; polymorphic coding of character states was not done. Although exemplar species were examined, some genera were represented by several species, and polymorphic coding of character states would have been necessary to accurately characterize some of the states. In addition, there were inconsistencies in character states between the text and matrix, possibly due to transcription errors. Analysis of the matrix was apparently done without the aid of a computer.

Based on his analysis of Passalidae (in his sense), Fonseca concluded that the African clade, Solenocyclinae (identical to that of Gravely, 1918), was sister to Passalinae, containing all of the remaining genera. Passalinae, in turn, was divided into Leptaulacini (identical to Gravely's Leptaulacinae) and Passalini. The latter contained two subtribes, Macrolinina (Gravely's Macrolininae), and the New World Passalina, which was further subdivided into the Proculus and Passalus groups. The Passalus Group contained the New World genera included by Reyes-Castillo (1970b) in Passalinae, and the Proculus Group was composed of the same genera as

Reyes-Castillo’s Proculini. Thus, he proposed that Proculini (sensu Reyes-Castillo) is a monophyletic, highly derived group within Passalinae, rather than the sister taxon to that clade. This major modification to the classification of Passalidae has not been published, and has not been adopted by other coleopterists. Nevertheless, Fonseca’s work was an admirable first effort at developing a phylogeny of the family, and is of considerable interest and utility.

Reyes-Castillo’s proposed arrangement of two subfamilies, one with two tribes (1970b), continues to be generally accepted, although some authors use Gravely’s (1918) subfamily classification (Johki & Kon, 1987; Lobo & Castillo, 1997). The subfamilies are Aulacocyclinae, which is distributed in Asia, Australia and New Caledonia, and Passalinae in both the New World and Old World tropics.

Within Passalinae, Passalini is well represented in both the Old and New Worlds, and includes the majority of the species in the family. The nineteen genera of Proculini occur only in the New World, with the center of diversity in the highlands of Guatemala and southern Mexico (Reyes-Castillo, 1970b). The tribe has received considerable attention from systematists over the last 35 years; the higher classification of Proculini was revised by Reyes-Castillo (1970b), and most of the genera have received systematic attention, including generic revisions (e.g. Reyes-Castillo, 1978; Reyes-Castillo & Schuster, 1983, Quintero & Reyes-Castillo, 1983, Reyes-Castillo et al, 1987, Schuster & Reyes-Castillo, 1990, Schuster et al., 2003). Three of the remaining genera, *Publius*, *Verres* and *Veturius* are currently being revised (S. Boucher, C. Marshall, personal. communcations). Preliminary studies suggest that at least two of the small genera should be synonymized (Hunzicker et al., 1993; Gillogly, unpublished data).

Various authors have synonymized large numbers of both Kaup's and Kuwert's species and genera, as well as most of the subfamilies, and about 60 genera are currently recognized. Between the new species described since 1900 and the many earlier names being placed in synonymy, the size of the family has increased only slightly to almost 700 species.

CHARACTER SYSTEMS

The systematic treatment of taxa above the species level is currently based on differences in external morphology of adults, primarily topological characters of the adult head, mouthparts and sternum. Species-level characters are generally lesser differences in topological characters, punctation, setation, and sculpturing of the pronotum, elytra and sternum, and in antennal structure. The characters used in this study are discussed and defined in the respective chapters.

There is usually no consistent external sexual dimorphism in passalids, although the females of some species tend to be larger (personal observations). The known exceptions are some *Leptaulax* spp., in which the female terminal sternite(s) is setose and that of the male is glabrous (Doesburg Sr., 1942; Doesburg Jr., 1992), and some *Paxillus* spp., in which the setae of the elytral humeri of females are longer than those of males (Doesburg Jr., 1974; Reyes-Castillo & Fonseca, 1997).

DIVERSITY

Passalids are a major factor in breaking down the structural integrity of dead wood, providing access to other organisms and leading to the degradation and recycling of tree components. Recognizing passalids as important, constant and easily measurable components of tropical forest ecosystems, biologists and politicians in Guatemala are currently using formal reports of surveys of passalid diversity and endemism to evaluate the importance of areas proposed for special protection (Schuster, 1985b; Schuster et al., 1997, 2000). To accurately measure diversity, surveys of this type should be based not only on a count of species (or morphospecies), but also on the higher categories (genera, tribes, etc.) represented and their relative position in the phylogeny of the family. The use of the passalid fauna as a gauge of forest diversity and health has proven to be practical, however, the data already gathered will be even more valuable and meaningful when a rigorous phylogenetic study of the family is done, and the full measure of that diversity can be determined.

ZOOGEOGRAPHY

The low vagility of passalids suggests that they could also be useful in zoogeographic investigations, when a well-supported phylogeny of the family or of significantly large clades becomes available. Such a phylogeny would provide a systematic framework for: testing zoogeographic hypotheses; evaluating morphological or behavioral character displacement and resource partitioning; investigating coevolution of passalids with the parasitic and saprophagous mites and other fauna that inhabit their tunnel systems; and studying the evolution of subsocial behavior and complex communication systems in passalids, both of which are unique in Coleoptera, and surpassed in Insecta only by the eusocial taxa in Isoptera (termites) and Hymenoptera (ants, bees and wasps).

The current, and as yet undisputed, zoogeographic hypothesis in the published literature is that Passalidae shows a typical gondwanan distribution. Dispersal and radiation of the two subfamilies followed breakup of Gondwana and the New World Passalini diversified in South America and Proculini in Mesoamerica (Reyes-Castillo, 1970b; Reyes-Castillo & Halffter, 1978). The ancestral lineage that gave rise to the two tribes is suggested to have been in what is now northern South America, with an ancestral form related to the genus *Passalus* “island hopping” to Mesoamerica in the Oligocene or Miocene (6-37 MYBP), in the typical Mesoamerian dispersal Pattern proposed by Halffter (Reyes-Castillo & Quintero, 1977; Reyes-Castillo & Halffter, 1978).

Reyes-Castillo (1970b) noted that cephalic characteristics suggests that Proculini is a primitive group, and that Passalini appears to be more distant from the Ethiopian Region Passalinae than from the southeast Asian Passalinae. Aside from this, the basal relationships of the two tribes were not explicitly addressed until Fonseca’s (1987) phylogenetic study of the family, which included comments on the zoogeography of Passalidae. He concluded that all five of his clades above the generic group grade originated prior to the breakup of Gondwana (about 150 MYBP), and that their present distribution is due to vicariance, followed by extinction of most of these clades on most of the major landmasses. He also proposed that the basal position of his Solenocyclinae was due to the separation of the African landmass (including Madagascar) from Gondwana prior to that of the other continents. The Mesoamerican center of diversity of his Proculus Group was also attributed to vicariance, with the ancestral lineage being separated from that of the Passalus Group of South America as the continents moved apart.

Fonseca proposed that Aulacocyclinae is basal and sufficiently distinct to warrant family status, and that Proculini is a monophyletic, highly derived genus group of Passalinae. His interpretation of the resulting phylogeny and the current distribution of passalids is that the two subfamilies arose prior to the separation of Pangaea, and that the major lineages within Passalinae appeared before the breakup of Gondwana (Fonseca, 1987). This interpretation requires that all major extant lineages were present by the Late Jurassic (about 150 MYBP), and that each continent experienced the extinction of most of these lineages.

Passalini mirrors the worldwide distribution of the Passalinae, but Proculini occurs only in the New World. The center of diversity and endemicity of New World Passalini is in northern South America, and species are found on most of the major islands in the Caribbean; that of Proculini is in the highlands of Mesoamerica (Reyes-Castillo, 1970b; Reyes-Castillo & Halffter, 1978). Relatively recent dispersal to South America appears to have been the origin of that much smaller proculine fauna, with the possible exception of the genus *Veturius*. Only three species of Proculini are reported from offshore islands: *Verres furcilabris* (Eschscholtz), from Trinidad and

Tobago; *Verres hageni* (Kaup*)*, from Cocos Island, Costa Rica (about 300 miles into the Pacific); and *Popilius lenzi* (Kuwert), also from Cocos Island, and the only endemic island proculine known.

The current zoogeographic view is that the dispersal and radiation of the two subfamilies followed breakup of Gondwana, and that the New World fauna evolved from ancestral Passalini isolated in South America (Reyes-Castillo, 1977). It is suggested that elements of this fauna moved into Mesoamerica over an early land bridge, and that the Isthmus of Tehuantepec was a barrier to northward movement (Reyes-Castillo, 1970b). This is supported by a study of basal scarabaeoid families, which proposes that the Passalidae originated about 140 MYBP, after the Triassic mass extinction event, in the Jurassic radiation of primitive scarabaeoid families (Scholtz & Chown, 1995).

Fossils that appear to belong to extant primitive families in the Scarabaeoidea are known from the Early and Middle Jurassic (about 175-200 MYBP) (Ponamarenko, 1995; Scholtz & Chown, 1995), but the only known true passalid fossils are from the Oligocene (24-37 MYBP) of Oregon and Miocene (6-24 MYBP) of eastern China. The North American fossil has been placed in the extant genus *Passalus*, and appears to fit within a recognized species group (Reyes-Castillo, 1977). This distribution is attributed to a penetration of North America by South American passalids across a Late Cretaceous to Eocene (45-70 MYBP) land bridge (Reyes-Castillo, 1977). The Asian fossil has been placed in *Macrolinus*, also an extant genus, with current distribution in southeast Asia (Zhang, 1989). However, the habitus figure (ventral), size and three long and one short antennal lamellae of this specimen suggest that it may actually belong to the genus *Leptaulax*, and that it may be a form transitional between *Leptaulax* (normally three lamellae) and the other southeast Asian Passalinae (usually 5-6 lamellae).

CHAPTER II

PHYLOGENETIC RELATIONSHIPS OF PASSALIDAE

MORPHOLOGY

Overviews of passalid morphology have been published as part of revisionary works by Percheron (1835), Burmeister (1847), Kuwert (1896), Gravely (1914, 1918), and Reyes-Castillo (1970b). However, the most detailed discussion is that included in the doctoral thesis of Chris Marshall (2000), who unifies the terminology from the various terms and languages used historically, supplemented by extensive and detailed original observations and interpretations. For consistency, I have adopted Marshall's terminology in this study, supplemented by a few comments and observations noted below.

Head

In interpreting the complex topology of the anterior and dorsal portions of the head capsule, the following assumptions were employed:

- The anterior marginal sulcus of the clypeus may be dorsal or anterior, and may co-occur with the transfrontal sulcus, but is never absent in Passalidae.
- The paired inner tubercles, when present, are usually at the ends of the frontal ridges.
- The paired outer tubercles are at the lateral ends of the transfrontal sulcus (when present), and are never completely absent in Passalinae.
- One or more, usually paired, secondary tubercles may occur on the anterodorsal margin of the clypeus, either between or lateral to the outer tubercles. Similar projections may occur on the anteroventral margin of the anterior clypeal marginal sulcus, as in *Odontotaenius disjunctus* (Illiger), but they are not homologous with the secondary tubercles.
- One or more supplementary tubercles may occur on the frontal ridge, between the central tubercle and each inner tubercle.

Transfrontal Sulcus. I agree with Marshall (2000) that this is not the frontoclypeal suture, but a secondary structure that has presumably evolved to strengthen the frontoclypeus in response to stress associated with adduction of the mandibles. This dorsally visible sulcus is fused to the reflexed, ventral surface of the clypeus, at least in *Odontotaenius disjunctus* (personal observation).

Secondary Tubercles. Marshall (2000) applies this term to tubercles on the frontal ridge between the inner tubercles. The term has been used by Luederwaldt (1931, as "tuberculos secundarios"), and Reyes-Castillo (1970b), as "tuberculos secundarios" in his discussion of the subgenera of *Passalus*), to refer to tubercles on the anterior border of the clypeus. I have chosen to use the term in the sense of the earlier authors.

Posterolateral Ridge. This ridge appears to be the laterodorsal margin of the anterior marginal sulcus. When present, it extends posterolaterally from the outer tubercle, and may be parallel to, but does not cross, the frontogenal suture.

Mouthparts

Mandibles. The mandibles of the outgroup exemplars and some passalids are reduced and features on them are somewhat difficult to homologize. The mandibles of *Diphyllostoma* (non-feeding males) are rigid and non-functional.

Lower Anterior Tooth of the Mandibles. Burmeister (1847) noted that the form of the lower anterior tooth varied between specimens of the Old and New Worlds; those of Old World taxa are approximately horizontal, while those of New World taxa are close to vertical, and approximately in line with the upper two apical teeth. The only exceptions to this rule that I have noted are the Old World Aulacocyclinae, which have the vertical tooth form, and *Ptichopus*, a New World genus, which has a horizontal lower anterior tooth.

Epipharynx. The epipharynx is difficult to homologize between the in-group and out-group. That of the Lucanidae and Diphyllostomatidae is an elongated lobe, or intermandibular projection, while that of the Bolboceratidae and Passalidae is fused to the underside of the labrum (Nel & Scholz, 1990). The statement by these authors, attributed to Reyes-Castillo (1970b), that "…the shape of the anterior edge of the epipharynx and its setal distribution are valuable systematic characters at generic and species level in adult Passalidae" is in error; Reyes-Castillo was referring to the labrum, and specifically states that the distribution of the setae has minimal taxonomic value, and that the epipharynx had not been studied from a taxonomic viewpoint. He also notes that the epipharynx is similar to those of *Geotrupes* and *Ceratotrupe*s (Geotrupidae).

Prostheca. When present, the prostheca in Coleoptera is normally a membranous, setose lobe located medially on the inner surface of both mandibles, between the molar area and apex (Matsuda, 1965). In most passalids (except *Aulacocyclus*, *Comacupes* and *Taeniocerus*), a strong, articulating, movable tooth is found in this position. Neither Nel & Scholtz (1990) nor Marshall (2000) homologize this tooth with the prostheca, perhaps because no intermediate forms have been reported. Therefore, polarity of the presence or absence of this tooth is not yet apparent.

Marshall (2000) uses the term prostheca to refer to an articulated, lightly sclerotized, finger-shaped, one-segmented structure located proximal to the molar area at the medial base of only the right mandible. This structure was first noted, figured and discussed by Percheron (1835), but was apparently not mentioned again until Reyes-Castillo (1970b) applied the term "dientecillo movil" to it. It is present in all passaline taxa examined, as well as in *Cylindrocaulus patalis* (Lewis), but not in the other aulacocycline genera (*Aulacocyclus*, *Ceracupes*, *Comacupes*, *Taeniocerus*) (personal observations). Fonseca (1987) illustrated the mandibles of almost all of the genera of Passalidae, but used only the left mandible and probably did not notice the prostheca. Nel & Scholtz (1990) failed to note this structure, although they figured the right mandible of two species of Passalinae. No function has yet been proposed for it; I suggest that it may serve as a proprioceptor to monitor the fullness of the pharynx.

In this study, the term prostheca refers to the medial membranous lobe found in the bolboceratid exemplar, as well as to the articulated structure in most passalids, although these are probably not homologous. They are differentiated in the character list by their location – mesal versus basal.

Prementum. The labial palp is three-segmented, as noted by Marshall (2000), and not two-segmented, as reported by Nel & Scholtz (1990).

Prosternum

Prosternal Process. In the characters describing the shape, texture or setation of this structure, this term refers only to the expanded, posterior portion of the prosternal process, and not to the narrowed portion just anterior.

Elytra

Elytral Locking Mechanism. The elytral locking mechanism of passalids is similar to that of other Coleoptera that exhibit a "handedness" (Crowson, 1981), with the projecting shelf being either on the left or right elytron. Examination of a short series of *Odontotaenius disjunctus,* in addition to the exemplars, suggests that right- and left-handed types occur at an approximately equal frequency among both the out-groups and passalids in this study. The "handedness" state of the elytra was not investigated as a taxonomic character for this study, since it would require examination (including relaxing and opening the elytra) of numerous specimens of each taxon, and because Crowson (1981) notes that both types of dovetailing occur in various groups of beetles, although he notes that it is always right-handed in Curculionidae.

Possible Vibration Detector. Specialized organs for receiving vibrational signals (ears) have evolved in the Orthoptera, Lepidoptera, Homoptera, Heteroptera, Neuroptera and Coleoptera, (Bailey, 1991; Gerhardt & Huber, 2002), including at least two genera of Scarabaeidae (Forrest et al., 1997). Some of these appear to have evolved relatively recently, as a counter to the use of ultrasound by bats to locate insect prey. Bailey (1991) notes that few studies of sound reception in Coleoptera have been done, despite widespread sound production within the order.

As far as is known, all passalids can stridulate, wedging the wings within the elytra, forming a sound box, and scraping the underside of the wings with the sixth abdominal tergite (Babb, 1901; Reyes-Castillo, 1970b; Reyes-Castillo & Jarman, 1983). Schuster & Schuster (1971) reported distinctive mating songs in passalids, quite different from their aggression/defense sounds, and suggested that the mating songs serve primarily as a signal between passalid pairs of the level of sexual interest, as well as distinguishing conspecifics. They note that the males always produce a courtship song, and that the females of some species have a response song. I have verified these observations in additional species of passalids, and noted that the song of the female of *Passalus cuneatus* Hincks is distinctly different from that of the male.

Schuster & Schuster (1971) note, and I verify, that a singing male contacts a female and continues to sing, while tapping the female rapidly with his antennae. The pair moves laterally in a narrow circle, in constant contact, side by side, or most often with the head of the male nudging the pronotum or anterolateral portion of the elytra of the female. If passalids have a specific organ for receiving vibrational signals, a likely site might be near where the beetles come in contact during their mating dance, perhaps employing the same apparatus used in sound production, the elytra and/or wings.

In all passalid taxa examined, in the anterolateral inner surface of each elytron (beneath the humeral angle), there is a tympanum-like membrane, covering a patch of tissue. None of the out-group exemplars has this structure.

I have not tested this structure for sensitivity to vibrations, nor conducted a histological examination of the tissue, but I propose that it may serve as an organ of sound/vibration reception in Passalidae.

Wings

Setae. Short, strong setae are often present on the dorsal or ventral surfaces of the anterior margin of the wing, or on both. Most of the characters tested did not prove useful at this level, however, these setae may prove to be useful in differentiating species.

Flightlessness. The co-occurrence of a large suite of characters accompanies reduction in flight ability (Gravely, 1918; Reyes-Castillo, 1970b; Crowson, 1981). Inclusion of these characters would add considerable homoplasy to a morphological dataset of passalids, since some Aulacocyclinae, many species of various genera of Proculini, and some Passalini from both the New World and Old World are flightless. Only two of the exemplar taxa (*Cylindrocaulus patalis* and *Ogyges marilucasae* Reyes-Castillo & Castillo) used in this study have highly reduced wings, and another species (*Pleurarius brachyphyllus* Stoliczka) is reported not to fly, although it has normal-appearing wings (Gravely, 1918). These species are not closely related, and do not appear to have added an undo amount of homoplasy.

Mesepimeron

The posterior margin of this sclerite is inflexed in passalids, and appears to border the opening of a secretory pore or channel. If this proves to be true, an external, ventral groove (the sternacosta) may assist in directing and spreading the secretion medially. This groove may be laterally hidden beneath the metasternum or visible on the posterior mesosternum, sometimes connecting medially. Mites are often found clustered around the opening.

Metanotum

The structure of this area is complex and three-dimensional in the outgroup exemplars, in which the metascutellar ridge (scutoscutellar suture of Matsuda, 1970) lies internally, beneath the alacrista (Matsuda, 1970; allocrista of Konstantinov, 2002), with a phragma connecting the two. The metascutellar ridges converge anteriorly, while the alacristae usually converge posteriorly and border the metascutellar groove. In passalids, the metascutellar ridge and alacrista appear to have coalesced, and there is no interior phragma. This may be related to differential dependence on flight, as passalids are not known to fly strongly or frequently.

Prothoracic Leg

Protibial Spur. This structure is the same as the protibial spine of Marshall (2000). I choose to refer to the structure as a spur, since it articulates with the tibia.

Protibial Comb. This term refers to the fence-like row of erect, blade-like setae that is present surrounding the base of the protibial spur. Reyes-Castillo (1970b) figured and noted the comb, using the term “peine”. Although figured by Marshall (2000), no name was applied.

Antennal Brush. Marshall (2000) applies the term “antennal brush” to a dense patch of setae on the anteriodorsal face of the profemur, the “cepillo” of Reyes-Castillo (1970b).

Mesendosternite

The mesendosternite, an internal structure within the mesothorax, of passalids is distinctive, and varies both within the family and in the Scarabaeoidea in the number of bridges joining the internal medial margins of the mesocoxae, and whether or not the two sides are fused anteromedially.

Metendosternite

The passalid metendosternite is also distinctive, but certainly readily homologizable with that of other Coleoptera, despite the conclusion and extensive discussion of Pretorius & Scholtz (2001), in their interesting study of geometric morphometrics in the analysis of the metendosternites in the Scarabaeoidea. Unfortunately, the structure figured in their paper as the passalid metendosternite is actually the mesendosternite (verified by dissection of a specimen of the same species, *Ogyges marilucasae*). Typical passalid metendosternites were figured by Crowson (1938) and Iablokoff-Khnzorian (1977), both of whom were cited by Pretorius & Scholtz (2001).

Crowson (1938) reported on the systematic importance of the metendosternite (or furca), and later used this structure extensively in his classification of the families of Coleoptera (Crowson, 1955). His exemplar taxon for Passalidae was an undetermined species of *Passalus* (Crowson, 1938). Although the metendosternite has proven to be useful in distinguishing and suggesting relationships among families, it has not been examined comparatively within the Passalidae. The excellent study of passalid adult morphology introducing Reyes-Castillo's (1970b) revision of the higher classification of New World passalids, makes no mention of internal sclerotized structures such as the tentorium and metendosternite. The only other mention of a passalid metendosternite is by Iablokoff-Khnzorian (1977), who selected an Old World species of *Macrolinus* Kaup (Passalini) to represent the family in his study of scarabaeoid phylogeny, characterized the metendosternite, and provided a figure. There are distinct differences between the figures of this species of *Macrolinus* and Crowson's (1938) *Passalus* sp., and a number of metendosternal characters were used in this study.

Male Genitalia

The male genitalia of insects are often distinctive and have proven to be useful or indispensable in distinguishing taxa. Differences between closely-related taxa are postulated to result from divergence driven by ever-changing sexual selection by female choice (Eberhard, 1985). The male genitalia of many Coleoptera, including most Scarabaeoidea, have an eversible internal sac that may be completely membranous, or may bear a variety of sclerotized structures.

Some attention has been given to genitalic structures in the Passalidae, beginning with the extensive overview of beetle genitalia by Sharp & Muir (1912). The latter authors examined the genitalia of ten species of passalids, briefly described the genitalic capsules and extrusible internal sacs of three species, and included the struts of the median lobe in one diagram. Unfortunately, they did not provide figures of the distinctly different internal sacs. This potential source of taxonomic information was overlooked for the next 60 years.

Description of the genitalic capsule became a standard part of new species descriptions, beginning with the work of Reyes-Castillo (1970a), but the internal sac was ignored until Baker (1973) noted that the three species of *Pentalobus* Kaup, an African genus, could be differentiated by the setal patterns on the sac. Buehrnheim (1978) evaluated the use of male genitalia in passalid systematics, but did not mention the differences noted by Sharp & Muir (1912) or Baker (1973). Although descriptions and figures of the male genitalia are now routinely included in the descriptions of passalid species, only the shape of the genitalic capsule is addressed, and the informative potential of the internal sac has remained untapped. The only exception to this appears to be the unpublished revision of *Verres* (Marshall, 2000).

There has also been little attention given to using differences, such as development of the parameres and degree of sclerotization and pigmentation of sclerites, as diagnostic characters for either species or higher taxa. This lack of interest may be due to the difficulties in relaxing dry specimens, extracting the genitalia, and teasing out or inflating the internal sac, as well as to ignorance of the work of Baker (1973), and the suggestions of the importance of these structures by other authors (Sharp & Muir, 1912; D'Hotman & Scholtz, 1990). Only recently have the median struts been described as taxonomic characters and the genitalia well-discussed in passalids, though in only two, distantly related species (D'Hotman & Scholtz, 1990). The latter authors noted that, although the aedeagi differed considerably between the two species, there were unique similarities which suggest that passalid genitalia are highly derived within the Scarabaeoidea, and that the family branched off early in the evolution of the superfamily.

The preliminary observations of the male genitalia of passalids presented in this study suggest that there are striking and significant differences in the surface structure of the internal sac. All passalids examined in this study have an eversible internal sac, with the degree of ornamentation varying among taxa, ranging from completely membranous to almost completely covered with long setae, and sometimes armed with sclerotized tubercles, plates, or a terminal scoop-like structure. The most distinctive arrays of setae and tubercles appear to occur in the Passalini. The internal sac of the male genitalia of most genera within this tribe is highly ornamented, in contrast to the primarily membranous condition in the Proculini. However, some species of several proculine genera, including some *Popilius*, do have prominent sclerotized structures and patches at the base of the internal sac. I know of no description that has been published of the internal sac of any species of Aulacocyclinae.

A number of informative characters were obtained from examining the internal sac of this limited range of exemplars, and it may provide additional characters useful in separating the subgroups and species of such complex, so far almost intractable, genera as *Passalus* and *Leptaulax*.

The scoop-like structure, differing among the exemplars, is present at the tip of the internal sac of the exemplar taxon of *Paxillus* (New World) and two of the exemplar taxa of *Leptaulax* (Australasia). These are two of the passalid genera that are subcortical specialists. The flattened form associated with this habit appears to have evolved independently in several groups of passalids as a specialization to more efficiently exploit the decaying cambium layer beneath the bark of recently dead trees. This is a very temporary, essentially two-dimensional environment, in contrast to the three-dimensional habitat of those taxa that live in the longer-lasting heartwood.

The presence of this type of structure at the tip of the internal sac of the male genitalia in presumably distantly related clades suggests that sperm competition and mechanical sperm removal may be more important for subcortical species than for those inhabiting in heartwood habitats. This may also imply that the social structure may differ between subcortical and heartwood specialists. Passalid family groups are typically composed of one pair of adults and their offspring in a gallery system maintained separate from those of all other family groups. The eggs are all deposited in a single niche and covered with wood chips.

During field observations of *Paxillus leachi* Macleay in Panama, I have noted that the gallery systems of this species may not be discrete. However, this is difficult to determine in the field, as the gallery walls are disrupted by removal of the bark, and the disturbed beetles do not remain their galleries, but move rapidly over the surface in their attempt to escape. I have also noted that a single egg niche may contain 40 or more eggs, far more than would be expected from a single female. Far higher numbers have been reported (Schuster & Schuster, 1997), introducing the probability that more than one female is using the same niche, and that there may be more than the usual level of intraspecific interaction and perhaps cooperation in this species. If males come in contact with females more often than do the monogamous heartwood species, this could lead to more reproductive competition among males, and an advantage to those able to replace the sperm of other males.

This opens an interesting avenue of research, not only into the varied social structures of passalids, but also of the possible evolutionary steps from subsociality to full eusociality.

Length

The length of specimens was measured from the middle of the labrum to the tip of the elytra. However, these measurements should be interpreted with care, because of the telescoping structure of these beetles. The labrum can be extended or retracted (Reyes-Castillo, 1970b), and both the head and mesothorax are free to move into and out of the pronotum (Gravely, 1914). The total length of a single specimen can vary by over 10%, depending on the method of mounting and the degree of separation of these parts (personal observation).

Larval Characters

Considerable effort has been spent in the description of passalid larvae, and a key to the larvae of New World genera has been published (Schuster & Reyes-Castillo, 1981). Larvae of passalids are readily identified by association with adults collected from the same tunnel system (Reyes-Castillo & Halffter, 1984), as well as by their stridulatory structure, the fused metathoracic and reduced metathoracic leg that scrapes on an array of ridges on the mesocoxa (Reyes-Castillo 1970b). The larvae of about 15% of the known species of passalids have been described in the last 20 years (Schuster & Reyes-Castillo, 1981, 1990; Costa & Fonseca, 1986;

Schuster, 1992). However, passalid larval taxonomy is still in the descriptive stage, and larval characters have not yet been used in rigorous systematic studies. These authors have found relatively few, primarily chaetotactic, characters useful for differentiating species, and there has been disagreement in the literature over the value of these characters, especially for distinguishing categories above the species level (Costa & Fonseca, 1986; Schuster, 1992). This may be due, in part, to the lack of standardization in the characters described, even within a single paper (e.g. Costa & Fonseca, 1986).

The larva of Diphyllostomatidae is still unknown (Grebennikov & Scholtz, 2004), and the larvae of relatively few (15 of 43) of the in-group exemplar taxa used in this study have been described. To avoid adding large sections of missing data, larval characters were not included in this study.

DISSECTIONS

Dissection of specimens was essential for examination of many characters, including most of the new ones used in this study.

Intact, dry (usually pinned) specimens were softened until limp by soaking in hot (not boiling) water.

The head was removed by cutting the cervical membrane. Both sides of the gular area were cut from the cervix to the base of each mandible, and the esophagus was cut, allowing the gula, mentum, labial palps and maxillae to be removed in one piece. The labrum, epipharynx and antennae were left attached to the head capsule.

The prothorax was removed by cutting the membrane between the prothorax and mesothorax. Both elytra were removed at the basal joint. The notum (mesonotum, metanotum, and abdominal tergites) were removed, usually in one piece, by cutting around the pleural area and posterior to the scutellum, thereby also separating the scutellum. One wing was removed from the metanotum at the basal axillary sclerites.

The genitalia of male specimens were removed from the abdominal cavity. The aedeagus was pushed through the genitalic capsule (9th abdominal segment, including the spiculum), to expose the sclerotized portions of the aedeagus.

All of the dissected parts were placed in a hot (not boiling) solution of potassium hydroxide (KOH) until free of unwanted tissue, with the wings and elytra being removed first. The internal sac of the male genitalia of passalid specimens was teased out until everted, using microforceps and insect pins with hooked tips.

Some of the exemplars were collected as dead, disarticulated specimens. The dissection procedure above was followed as closely as practical, although the loss of membranous connections often resulted in many more pieces, as well as the loss of the alimentary canal and internal sac of the aedeagus.

The parts were rinsed in water and placed in a vial of 70-80% ethanol, with all accompanying labels.

CHARACTER SELECTION

In a preliminary, morphological phylogenetic analysis of the genus *Popilius*, species of various proculine genera were used as out-groups to test for the monophyly of *Popilius*. Results indicated that *Popilius* was paraphyletic, regardless of the out-group(s) employed. However, the lack of resolution and support in the resulting trees suggested that the number of characters, which was approximately equal to the number of taxa in the dataset, was insufficient. The number of characters necessary to have a chance of obtaining strong support values is about three times the number of taxa, if binary characters are used, there is no homoplasy, and there is an even distribution of characters (Felsenstein, 1985; Bremer et al., 1999). The relatively low number of characters traditionally used to differentiate passalid taxa meant that a large number of new characters would be needed to provide any chance of obtaining robust results. This proved to be challenging, as it is much more difficult to add new morphological characters than, for instance, molecular characters.

Since the vast majority of characters historically employed in distinguishing passalid taxa are external and readily visible on dried specimens, I determined to search for new characters and character systems internally, as well as externally. This required extensive dissection of the specimens, rendering them no longer usable as dry, pinned, mounted representatives – the typical museum specimens.

PHYLOGENETIC ANALYSIS

Selection of In-group Taxa

Various proculine genera were included, to examine the monophyly or degree of separation of the clades included within the tribe and within the genus *Popilius*. Representatives of Passalini and Aulacocyclinae were added to generate a tentative phylogeny, trace evolutionary tendencies, test zoogeographical hypotheses, and allow comparison with current taxonomy and that proposed by Fonseca (1987). Several groups of congeneric taxa were included, to test for consistency of the data at different levels within the current taxonomy of the family.

The availability of specimens that I was willing to sacrifice limited the selection of the taxa, so this study is not intended to be complete. However, I hope that this work, in conjunction with that of Fonseca (1987), may provide the basis and impetus for a future, morphologically-based phylogenetic analysis of the entire family that may be compared and combined with molecular studies, hopefully resulting in a robust phylogeny of the family and its place within the Scarabaeoidea.

Selection of Out-group Taxa

Based on the results of phylogenetic studies of Scarabaeoidea (Iablokoff-Khnzorian,1977; Howden, 1982, Browne & Scholtz (1995); Scholtz & Chown, 1995), representatives of these Diphyllostomatidae and Lucanidae are included as out-groups. Preliminary results of an extensive molecular phylogeny of the superfamily suggest that Bolboceratidae appears be closer to Passalidae than do Diphyllostomatidae and Lucanidae (Hawks, personal communication, 2003), so an exemplar bolboceratid is also included.

Exemplar Taxa Examined (46)

Diphyllostomatidae

Diphyllostoma fimbriata Fall: USA, CA, Tulare Co., Ash Mountain, Kaweah Power Station #3 (male)

Bolboceratidae

Bolboceras thoracicornis (Wallis): USA, TX, Grimes Co., 3 miles east of Navasota (male)

Lucanidae

Sinodendron rugosum Mannerheim: USA.CA,San Bernardino Co., L. Hook Creek (male)

Passalidae (29 of 60 genera)

Aulacocyclinae (5 of 5 genera - Australasia)

Aulacocyclus edentulus (Macleay): no data, undoubtedly Australia (female)

Aulacocyclus papuanus (Heller): Papua New Guinea, Morobe Prov., Aseki (female)

Ceracupes fronticornis (Westwood): Thailand, Chiang Mai Prov., Mae Chaem (male)

Comacupes stoliczkae Gravely: Malaysia, Sabah, Mt. Trus-Madi (male)

Cylindrocaulus patalis (Lewis): no data, undoubtedly southern Japan (1 male, 1 female)

Taeniocerus bicanthatus (Percheron): Malaysia, Sabah, Mt. Trus-Madi (male)

Passalinae (24 of 55 genera – New World and Old World)

Passalini (13 of 36 genera – New World and Old World)

Southeast Asia (6 of 22 genera)

Aceraius grandis (Burmeister): Thailand, Chiang Mai Prov., Chiang Dao W.R. Res. Stn., 500m (1 male, 1 female)

Aceraius helferi Kuwert: Thailand, Chiang Mai Prov., Chiang Dao W.R. Res. Stn., 500m (2 males, 1 female)

Aceraius indicus (Stoliczka): India,"South India" (male)

Aceraius sp.: Malaysia, Sabah, Mt. Trus-Madi (male)

Cacoius jacquesi Boucher: Malaysia, Sabah, Mt. Trus-Madi (male)

Leptaulax dentatus (Fabricius) complex: Malaysia, Sabah, Mt. Trus-Madi (male)

Leptaulax bicolor (Fabricius) complex: Malaysia, Sabah, Mt. Trus-Madi (4 ex., including at least 1 male)

Leptaulax planus (Illiger): Malaysia, Sabah, Mt. Trus-Madi (male)

Macrolinus sikkimensis (Stoliczka): Thailand, Chiang Mai Prov., Chiang Dao W.R. Res. Stn., 500m (male)

Mastochilus australasicus (Percheron): Australia

Pleurarius brachyphyllus Stoliczka): India,"South India" (male)

Africa (2 of 3 genera)

Erionomus planiceps (Eschscholtz): Cameroon, Abang Mindi (female)

Pentalobus barbatus (Fabricius)

Madagascar (1 of 6 genera)

Semicyclus grayi Kaup: Madagascar, La Mandraka (1 male, 1 female)

New World (4 of 5 genera)

Paxillus leachi Macleay – Honduras, Yoro Pr., Macora (male)

Passalus (Passalus) interruptus Linnaeus: Panama, Panama Prov., Pacora (female); Colon Prov., Rio Piedras, 2 km. SE Maria Chiquita, el. ~10m. (genitalia from pinned male)

Passalus (Passalus) cuneatus (Hincks): Panama, San Blas Prov., Nusagandi, 400m. (male)

Passalus (Pertinax) nr. *caelatus* Erichson: Panama, Darien Prov., Cana, 1370m. (male)

Ptichopus angulatus (Percheron): Mexico, Tamaulipas, 4 km. West Altamira (sex indeterminable); Sinaloa, 2 km. South Vado Hondo, 300m. (male)

Spasalus crenatus (Macleay): Puerto Rico, no data (female – only one male known from Puerto Rico, out of hundreds of specimens collected)

Proculini (11 of 19 genera - New World)

Chondrocephalus sp. – Mexico (Chiapas; Cerro.Huitepec)

Heliscus rotundicornis (Luederwaldt): Panama, Chiriqui Prov., Reserva la Fortuna, RioHondo 1200-1300m. (male); Chiriqui Prov., Pass 4 km. N. Hornito, 1200 m. (genitalia from pinned male)

Heliscus tropicus (Percheron): Mexico, Tamaulipas, El Cielo (male)

Odontotaenius disjunctus (Illiger): USA, TX, Brazos Co., Edge (male), and College Station (8 ex., including at least 2 males)

Odontotaenius striatopunctatus (Percheron): Guatemala, “Peten” (probably not accurate locality), (2 males, 1 head/pronotum)

Ogyges marilucasae Reyes-Castillo & Castillo: Mexico, Chiapas, Sierra Madre de Chiapas, El Triunfo, 1960m. (male)

Petrejoides n.sp.: Panama, Bocas del Toro Prov., 2km.NW of Fortuna Hwy at Bocas del Toro border, 950m. (1 male, 1 female)

Petrejoides tenuis Kuwert: Panama, Chiriqui Prov., east side Volcan Baru, 2100m. (1 male, 1 female, both dead and disarticulated); 2 km. West Alto Quiel, 2000 m. (genitalia from pinned male)

Popilius eclipticus (Truqui): Guatemala, “Peten” (probably not accurate locality), (1 female, pterothorax and abdomen of 1 male, and 1 head/pronotum)

Popilius erotylus Reyes-Castillo & Castillo: “Panama”

Popilius punctatissimus Luederwaldt: Panama, Chiriqui Prov., Las Lagunas del Volcan, 1340m. (male)

Popilius sp.5 Panama : Panama, Bocas del Toro Prov., 2km.NW of Fortuna Hwy at Bocas del Toro border, 1050m. (1 male, 1 female, both damaged during collection)

Pseudacanthus violetae Reyes-Castillo & Castillo: Mexico, Chiapas, Lagunas de Montebello, 1500m. (female, dead disarticulated); same locality, 1550m. (genitalia of pinned male)

Spurius bicornis (Truqui): Panama, Panama Prov., km. 7.5, El-Llano-Carti Rd. (male); Verqaguas Prov,.Cerro Tute (male)

Verres corticicola (Truqui): Guatemala, “Peten” (probably not accurate locality), (1 male, 2 females, 1 head/pronotum)

Veturius sp. nr. *platyrhinus* (Westwood) – Panama, inaccurate label (Panama Prov., “Pacora”), probably from western Panama, ~1000m., Chiriqui Prov. or Bocas del Toro Prov.) (male)

Vindex sp.: Mexico, Chiapas, Sierra Madre de Chiapas, El Triunfo, Sendero Palo Grande (male)

CHARACTER ANALYSIS

For consistency, only I examined and coded the specimen. Any errors due to misinterpretation of characters, mistaken entry of character states while coding, and possibly some mistakes in the transfer of hard copy data to the MacClade matrices (Maddison & Maddison, 2000) are mine. The list of the 207 characters used to code the 46 exemplar specimens is included as Appendix C-1.

ANALYTICAL PROCEDURE

Cladistic analysis based on maximum parsimony was performed using heuristic searches (100-1000 randomized addition sequences followed by TBR branch swapping) on PAUP 4.0b10 (Swofford, 2002). The characters were weighted equally, and all were unordered, implying that change is equally likely between any two states. The character state data was analyzed using PAUP {Swofford, 2002) and MacClade (Maddison & Maddison, 2000). References to “distance” between taxa refer to the number of unambiguous character state changes.

The influence of the choice of out-group(s) on in-group topology was analyzed by comparison of equally parsimonious topologies of the full dataset (43 in-group and 3 out-group taxa) with those resulting from parsimony analysis of the in-group using all two-taxon combinations of the three out-groups. The three out-group taxa were then tested individually, first with the entire in-group, and then with subsets of the in-group taxa that which had been partitioned into the two currently accepted subfamilies, Aulacocyclinae and Passalinae (Reyes-Castillo, 1970b).

The internal topology of selected monophyletic clades in the in-group was evaluated, using a phylogenetically adjacent taxon as out-group, in order to evaluate the effects of homoplasy at higher taxonomic levels.

Clade stability was estimated using bootstrap values and branch support. Bootstrap analyses (100 bootstrap replicates, 100 random replicates per bootstrap replicate, 10 trees held at each step) were performed. Decay indices (Bremer, 1988) were calculated by searching for the shortest trees not compatible with the constraint of monophyly of the taxa on selected branches; the constraint trees for these analyses were generated using either the software program TreeRot (Sorenson, 1999) or constraint statements in PAUP.

Equally parsimonious topologies in reduced-taxa partitions of the dataset were investigated by deleting, one by one, the terminal taxa with the longest branches, and those that moved location between one topology and another (“jumping taxa”). Each of these taxa was removed, individually, from the tree, and then individually added back to the pruned tree, in a manner similar to the trunk phylogeny method of Anderson (2001). A parsimony analysis was done after each pruning or addition step.

The use of data partitions in systematics is widespread in the analysis of molecular datasets composed of multiple gene sequences, and has been used in morphological analyses containing data from more than one life stage (Judd, 1996).

Although containing only characters from the adult stage of passalids, the size of this morphological dataset and ratio of characters to taxa, are large enough to allow internal partitioning, as done in molecular studies using multiple gene sequences. To test the utility of character partitioning in assessing the morphological evolution of passalids, the data were divided into eight partitions based on different parts of the: mouthparts (characters 1-10, 56-61, 81-102), mandibles (characters 63-80), frontoclypeus (characters 11-55), antennae and legs (characters 103-105, 151-165), wings and elytra (characters 114-125), external (characters 106-113, 126-150), internal (characters 62, 166-181), and male genitalia (characters 182-207). Partitioned Bremer support values were calculated for each data partition (Baker & DeSalle, 1997, Baker et al., 1998, Sota & Vogler, 2001, Cognato & Vogler, 2001). Constraint trees for these analyses were prepared using TreeRot.

Congruence between each pair of partitions was measured with Spearman’s rank correlation of partitioned branch support values. A positive correlation indicates congruence between partitions, a negative correlation indicates incongruence, and no correlation indicates that two partitions are no significantly congruent or incongruent. Partitioned Bremer support and the correlation among the partitions were calculated using two datasets; Bolboceras as out-group to Passalidae, and Passalinae with *Erionomus planiceps* as a functional out-group

For simplicity, the names of most of the exemplar species mentioned throughout the rest of this chapter will be abbreviated to just the generic name. This does not suggest that all congeneric species are expected to occupy the same monophyletic branch as the exemplar taxa, under current generic definitions. On the contrary, when a thorough phylogeny of Passalidae is finished, it is expected that a number of the genera, as currently delimited, will turn out to be paraphyletic.

RESULTS

Parsimony Analysis

Preliminary analyses indicated that Diphyllostoma is the most distant from Passalidae of the three out-groups, based on comparison of the lengths of the most parsimonious trees obtained with the three out-group exemplars, individually; *Diphyllostoma* – 1382 steps, *Bolbocera*s – 1374 steps, and *Sinodendron* – 1370 steps. Parsimony analysis of the full dataset, with *Diphyllostoma* as the root, resulted in four equally parsimonious trees of 1457 steps, with consistency index (CI) of 0.298, and retention index (RI) of 0.543. The strict consensus tree suggests that *Sinodendron* is the closest of the three out-groups, *Cylindrocaulus* is the most basal passalid, *Ceracupe*s is the sister to Passalinae, and that Aulacocyclinae is not monophyletic. The lack of resolution in the subfamily Passalinae is due to two equally parsimonious topologies; three trees support *Erionomus* as the basal taxon in Passalini, while one tree suggests that the root of Passalinae is within the current Proculini.

These topologies are structurally very similar, with the primary difference being the placement of the root of the Passalinae. Monophyly of Passalidae is very strongly supported by 50 unambiguous character state changes, and a Bremer Support (BS) index of 45; Passalinae is also strongly supported by 37 changes and a BS index of 24. Aulacocyclinae is paraphyletic, with *Cylindrocaulus* basal to a monophyletic clade containing the remaining taxa.

Within these trees, the weak support and relatively long branch lengths among the out-group taxa, and the amount of change between the out-group and in-group, suggest that none of the out-group taxa is closely related to Passalidae, and that homoplasy within the Passalidae might be reduced by using only the single, closest out-group taxon.

Analysis of each of the three possible pairs of the out-group taxa with all of Passalidae indicates that the combination of *Bolboceras* and *Sinodendron* (B+S) produces a single most parsimonious tree (MPT) at 1412 steps (Appendix A-1). The other combinations produced longer trees; *Diphyllostoma* and *Sinodendron* (D+S) - 3 MPTs at 1414 steps, and *Bolboceras* and *Diphyllostoma* (B+D) - 6 MPTs at 1422 steps. *Erionomus* is indicated as the basal taxon in

Passalinae in the D+S and B+D analyses, while the B+S analysis has the same basal separation within Proculini noted in one of the four trees resulting from the analysis including all three out-group taxa.

Further analyses using each of the out-group taxa singly indicate that *Diphyllostoma* is the least related taxon to Passalidae in this dataset, based on the total number of steps in resulting trees was greater (1382 steps) than for the other two out-group exemplars.

By the same reasoning, *Sinodendron* is the closest out-group to Passalidae, as it has the shortest tree length (1 tree of 1370 steps); *Bolboceras* is intermediate (6 MPTs of 1374 steps). The tree resulting from *Sinodendron* as the out-group is similar to that of B+S , with the root of Passalinae within Proculini; Aulacocyclinae is paraphyletic, with *Cylindrocaulus* just basal to, and *Ceracupes* just apical to, a monophyletic clade containing the remaining exemplar taxa.

The six MPTs obtained when using *Bolboceras* as the sole out-group all show Aulacocyclinae, Passalinae and Proculini as monophyletic, along with two additional monophyletic clades within Passalinae: *Semicyclu*s+*Pentalobu*s+*Leptaulax* spp., and all of the Southeast Asian Passalinae, except for the three *Leptaulax* species (Appendix A-2). Proculini is largely unresolved in these consensus trees, because the placement of *Pseudacanthus* is equally parsimonious as either basal near *Ogyges* (Appendix A-3), or apical as sister to *Odontotaenius disjunctus* (Appendix A-4).

These analyses consistently placed *Cylindrocaulus* as the basal passalid. To reduce the homoplasy introduced by including the distant out-groups, Passalidae was analyzed treating *Cylindrocaulus* as a functional out-group (Watrous & Wheeler, 1981). Parsimony analysis produced seven MPTs, all of which place the remaining Aulacocyclinae (all except the out-group, *Cylindrocaulus*) in a monophyletic clade, two representatives of the Ethiopian region in a monophyletic clade with *Leptaulax* spp., and all of the remaining Asian species (all except the exemplars of Aulacocyclinae and *Leptaulax*) in a monophyletic clade. Six of the trees place *Erionomus* as the basal passaline, with a consensus topology essentially the same as that obtained with Bolboceras as the out-group for Passalidae. The seventh tree has *Ogyges* as the basal in-group taxon, Proculini split between two basal branches, and a monophyletic Ethiopian Region+*Leptaulax* clade sister to a monophyletic clade containing the southeast Asian exemplars except for *Leptaulax*.

Analysis of a further pruned dataset, excluding Aulacocyclinae and employing *Erionomus* as the functional out-group for Passalinae, resulted in 3 MPTs, with the topology of this subfamily similar to that produced by analysis of *Bolboceras* as the out-group to Passalidae (Appendices A-3, A-4).

Proculini is largely unresolved in most of the previous analyses, due primarily to the alternative placement, either basal (Appendix A-3) or apical (Appendix A-4) of *Pseudacanthus*. Investigation of the proper position of *Pseudacanthus*, employing the trunk phylogeny procedure (Sorenson, 2001), indicates that this genus belongs basally in Proculini, but is attracted to the apical *Odontotaenius disjunctus* by shared, homoplasious loss of frontoclypeal characters. Parsimony analysis of Passalidae with *Bolbocera*s as the out-group, following exclusion of the six frontoclypeal characters (16-21) describing the lateral and frontal ridges, resulted in the unambiguous basal placement of *Pseudacanthus* near *Ogyges*. The basal position is, therefore, selected as the preferred placement. Additionally, exclusion of *Pseudacanthus* from the *Bolboceras*+Passalidae dataset results in four most parsimonious trees, all of which place *Erionomus* as the most basal passalid.

Sensitivity to choice of out-group of alternative topologies within each subfamily was investigated by using the three out-group taxa singly with separate partitions corresponding to Aulacocyclinae and Passalinae. When each of the out-groups is analyzed with Aulacocyclinae, Sinodendron produces much shorter MPTs (two trees at 252 steps, CI of 0.861, RI of 0.568) than either *Diphyllostoma* (one tree at 261 steps) or *Bolbocera*s (one tree at 262 steps). Alternatively, when each of the out-groups is analyzed with Passalinae, *Bolboceras* is found to produce considerably shorter trees (9 trees at 1179 steps, CI of 0.320, RI of 0.473) than *Sinodendron* (three trees at 1190 steps) or *Diphyllostoma* (three trees at 1195 steps).

The topology of Aulacocyclinae is similar in all three analyses, and one tree is common to all three analyses, with *Cylindrocaulus* basal, then *Ceracupes*, *Taeniocerus*, and terminally with *Comacupe*s as sister to *Aulacocyclus* spp. Because of this consistency, this topology is selected as the preferred topology for Aulacocyclinae (Appendix A-5). The topology of Passalinae is almost identical with either *Bolboceras* or *Diphyllostoma* as the out-group, and very similar to that of the preferred tree, even though use of these out-groups results in different tree lengths. However, although with *Sinodendron* as out-group, the tree length is intermediate between those of the other out-groups, and the topology of the Ethiopian Region and New World clades is also similar to that of the preferred tree, Passalinae is rooted within the southeast Asian clade, in sharp contrast to every other analysis done.

Although there is no doubt of the monophyly of Passalidae, the out-groups appear to be so far removed from Passalidae that there is considerable character conflict among them. This conflict makes it appear that *Sinodendron* is more closely related to Aulacocyclinae than are the other two out-group taxa, and that *Bolboceras* is more closely related to Passalinae than the other out-groups.

All of the preceding analyses support *Passalus caelatus* Erichson as the nearest taxon to the Proculini. Analysis of the dataset pruned to include only the Proculini, with *Passalus caelatus* added as the out-group, resulted in eight MPTs. Two of these place *Pseudacanthus* as sister to *Odontotaenius disjunctus*, and are eliminated from consideration because this relationship was shown above to be due to homoplasious loss of frontoclypeal characters.

Two of the six MPTs obtained by analyzing *Bolboceras* as the out-group to Passalidae have a topology consistent with the preferred topology of Aulacocyclinae, one of the three MPTs resulting from the analysis of Passalinae rooted at *Erionomus*, and the basal placement of *Pseudacanthus* within Proculini. In one of these two trees, the arrangement of the taxa within Proculini is exactly the same as in one of the four MPTs resulting from analysis of the entire dataset, one of the three MPTs in the analysis of Passalidae rooted at *Erionomus*, and one of the eight MPTs in the analysis of *Passalus caelatus* as sister to Proculini. Because of the consistency of this topology at various levels of analysis, it is selected as the preferred topology (Appendix A-3). The preferred tree has 1360 steps, CI of 0.296 and RI of 0.514. Exclusion of *Diphyllostoma* and *Sinodendron* eliminates considerable homoplasy between these out-groups and both *Bolboceras* and the in-group.

In the preferred tree (Appendix A-3), the monophyly of Aulacocyclinae is supported by 10 unambiguous character changes (Bremer Support index of 6), Passalinae by 26 characters (BS of 21), southeast Asian Passalinae (less *Leptaulax*) by 11 characters (BS of 5), New World taxa by 4 characters (BS of 2), and Proculini by 9 characters (BS of 6). *Semicyclu*s, *Pentalobus* and *Leptaulax* also form a monophyletic clade supported by 5 characters (BS of 3). The remaining Australasian passaline taxa form a monophyletic clade that is sister to all of the New World taxa, with *Pleurarius* at the base of the former and Ptichopus basal in the latter. Although the monophyly of Proculini is well supported (9 unambiguous character changes, BS of 6), the internal relationships are unstable. Four of the genera within this clade, *Heliscus*, *Odontotaenius*, *Petrejoides* and *Popilius*, appear to be paraphyletic. All four belong to the complex of genera included by Gravely (1918), Dibb (1938, 1940) and Luederwaldt (1941) in *Popilius*, but which were then resurrected by Reyes-Castillo (1970b). Bremer Support analyses, in which results were constrained to produce monophyly of each of the focal genera, determined that the congeneric exemplars would occur together only in considerably longer trees: *Heliscus* – 13 additional steps, *Odontotaenius* – 6 additional steps, *Petrejoides* – 5 additional steps, and *Popilus* – 4 additional steps. In none of the parsimony analyses were all four of the exemplars of *Popilius* monophyletic.

During analysis of the dataset, it was noted that deletion of just *Pentalobus* results in *Leptaulax* spp. jumping from within the present clade to a position within the southeast Asian clade, despite a Bremer support index of 3 for that node in the most preferred tree.

Clade Support

Bootstrap analysis of the reduced dataset (*Bolboceras*+Passalidae), which includes the preferred tree, supports the monophyly of Aulacocyclinae (81%), Passalinae (100%), and Proculini (75%), with the latter nested within Passalinae. The preferred tree (Appendix A-3) is consistent with the 50% majority rule consensus tree from this bootstrap analysis (Appendix A-6).

Passalini, as currently defined (Reyes-Castillo, 1970b), not supported (16%), nor is a monophyletic clade containing all of the New World Passalini (less than 5%).

Partitioned Bremer Support and the correlations among data partitions were calculated using two datasets: the passalid dataset containing the preferred tree and *Bolboceras* as the out-group, and a reduced dataset including only Passalinae, with *Erionomus* as the functional out-group.

Morphological Partitions

Spearman's rank correlations of the Partitioned Bremer Support indices show that several of the data partitions are significantly correlated (Appendices B-1 and B-2). Closer examination reveals that the character partitions mouthparts, mandibles, antennae and legs, wings and elytra and external tend to be positively correlated with each other. The partitions internal and male genitalia are also positively correlated to each other, but negatively correlated with the previous five partitions. The partition frontoclypeus is negatively correlated with the first five, positively correlated (though not significantly) with internal, and about neutral in regards to male genitalia.

The trees resulting from separate parsimony analysis (heuristic analyses with 1000 randomized addition sequences followed by TBR branch swapping) of each of the morphological partitions of the larger dataset were generally poorly resolved, due to the small number of parsimony-informative characters (12-43) in relation to the number of taxa (43 and 37). A similar analysis of the smaller dataset was not done, because it has fewer parsimony-informative characters and preliminary analyses indicated that even less resolution would result. The following comments address the results of analysis of the larger dataset. Although six of the partition analyses were aborted within the first 1-2 iterations, because the number of saved trees (31,000-33,000) exceeded the memory capacity of the computer, some results were obtained. No useful resolution was provided by the partitions external (25 informative characters), wings and elytra (12 characters), internal (14 characters) or male genitalia (21 characters). The mandibles partition (16 characters) supports the aulacocycline exemplars as being adjacent, but not monophyletic, Passalinae as monophyletic, and *Pentalobus*+*Leptaulax* within the southeast Asian passaline clade. The antennae and legs partition (12 characters) supports monophyly of Aulacocyclinae.

Parsimony analyses were completed only for partitions mouthparts (35 characters) and frontoclypeus (43 characters). The mouthparts partition supports monophyly of Aulacocyclinae and Passalinae, and places *Leptaulax* with the other southeast Asian passaline exemplars; frontoclypeus supports the monophyly of Aulacocyclinae, Passalinae, and Proculini, places *Passalus caelatus* as the sister to Proculini, and does not include *Leptaulax* with the other southeast Asian passalines.

Since groupings of similarly correlated partitions were evident in the Spearman's rank correlation analyses, two groups of partitions were combined: mouthparts, mandibles, antennae and legs, wings and elytra, and external (MMAWE – 94 informative characters); frontoclypeus plus internal (FI – 57 characters); and internal plus male genitalia (IM – 35 characters). Heuristic analyses were done on these groupings. MMAWE (94 characters) supports monophyletic Aulacocyclinae, Passalinae and a southeast Asian passaline clade that includes *Leptaulax*. FI recognizes Passalinae and the southeast Asian passalinae (less *Leptaulax*) as monophyletic clades, places Aulacocylinae together, but not monophyletic, and Proculini basal in the Passalinae and not monophyletic. Analysis of IM resulted in an unresolved tree.

DISCUSSION

Out-group Relations

The choice of out-group is shown to greatly affect the topology of the passalid phylogeny. The three out-group taxa examined in this study are very distant from Passalidae, with 50 unambiguous character changes, and a Bremer Support (BS) index of 45 supporting monophyly of the in-group. This distance results in character conflict among the out-groups and between the out-groups and elements of Passalidae. Analyses using *Bolboceras* as the sole out-group resulted in the shortest most parsimonious trees in analyses of Passalidae and Passalinae, while use of *Sinodendron* as the sole out-group produced the shortest MPTs in the analysis of Aulacocyclinae.

Although these out-group taxa may be the closest living relatives of Passalidae, it will be worthwhile to search for taxa that may be more closely related, in the hope of reducing homoplasy. As a result of an extensive, on-going molecular phylogenetic study of the Scarabaeoidea, representatives of the bolboceratid genera *Bolbelasmus* and *Bolbocerosoma* have recently been suggested as possibly more closely related out-groups (David Hawks, personal communication, 2004). Exemplars of these taxa will be examined and added to this database in the future.

In-group Relations

Although this dataset includes fewer than half of the described passalid genera, and perhaps a quarter of the distinct species groups, it is noteworthy that parsimony analyses result in relatively few, reasonably well-resolved, most parsimonious trees.

The relationships among the monophyletic clades in these analyses are intriguing, and suggest that the taxonomy of Passalidae at the subfamily and tribe level requires additional investigation. Although the currently recognized division between subfamilies (by Reyes-Castillo, 1970b) is supported, the basal division of Passalinae into two tribes, a Mesoamerican clade (Proculini) versus all of the remaining (tropicopolitan) taxa (Passalini), is not recovered in these analyses.

Instead, the taxa from the Ethiopian Region (plus the southeast Asian *Leptaulax* spp.) are shown to be basal and a monophyletic clade containing the remaining southeast Asian taxa is supported as the sister to all of the New World taxa. Passalini is shown to be paraphyletic, in regard to Proculini, with Proculini nested terminally (Appendices 3 and 4).

Aulacocyclinae is monophyletic and well-supported in the preferred tree, with *Cylindrocaulus* placed basally in the clade, and closest to the Passalinae (Appendix 3). However, the tribe Passalini (sensu Reyes-Castillo, 1970b) includes some or all of the taxa in all of the monophyletic clades within Passalinae, while Proculini, although monophyletic and well-supported (Bremer support of 7), appears to be a derivative clade of New World taxa. Instead of all of Passalini being the sister group to Proculini, *Passalus caelatus* is supported as the sister group. Passalini (sensu Reyes-Castillo, 1970b) is paraphyletic with regards to Proculini.

This dataset supports division of Passalinae into four clades, roughly parallel to the subfamilial interpretation of Gravely (1918), the arrangement accepted until 1970; a basal clade, including only *Erionomus*, a clade that includes the two remaining exemplars from the Ethiopian Region plus the *Leptaulax* spp., a clade comprised of the remaining southeast Asian exemplars, and a strictly New World clade.

Gravely placed all nine of the passalid genera from the Ethiopian Region (Africa and Madagascar) in the subfamily Solenocyclinae. Only three of these genera are represented in this study, and only one of the six genera from Madagascar is included. The latter are all endemic to that island; at least one unusual form, *Stephanocephalus*, may prove be very informative in elucidating the basal relationships. Unfortunately, very few specimens of this genus are known; it does not appear to have been encountered alive in the last 50 years or more, and may be extinct. Since this group is basal within Passalinae, it would be highly desirable to include exemplars of all of the genera. The addition of the remaining Ethiopian Region genera may reduce the long branch of *Erionomus* and draw it into a monophyletic clade exactly equivalent to Gravely's Solenocyclinae.

The inclusion of *Leptaulax* within the Ethiopian group may be a result of the taxon sampling method, character interpretation, or morphological homoplasy related to similarities in their specialized subcortical habits. Gravely (1919) considered *Leptaulax* to be near his subfamily Macrolininae, which is exactly equivalent to the clade of southeast Asian passaline genera in this study. He specifically noted his difficulty in homologizing tubercles on the head of *Leptaulax* with those of other groups (Gravely, 1918), and it is quite possible that I have misinterpreted the homology of these structures.

Although the placement of *Leptaulax* is well supported, this may not be its true position. If *Pentalobus* is excluded from the dataset, *Leptaulax* moves to the southeast Asian clade, suggesting that conflict in the data, due to misinterpreted character homology, may be present. If that much change can occur with deletion of a single taxon, it could also presumably be reversed with the inclusion of a different taxon. The addition of exemplars of the six remaining Ethiopian Region genera and *Trichostigmus*, tradionally viewed as the sister group to *Leptaulax*, may clarify the relationships. Problems with the interpretation of frontoclypeal characters in this study have already been uncovered by examination of the alternative topologies of Proculini, additional evidence that there may be a problem with frontoclypeal character interpretation. A conflict in the preliminary analysis was resolved by recognizing the reversal of some binary (absence versus gain) characters in apical clades, and adding a third character state – "secondarily lost".

In future work, it will be advisable not only to include exemplars of all of the distinct species groups in the family, but also critically review the assumptions on which the frontoclypeal topology was interpreted for this study.

Despite, or perhaps due to, the small representation of southeast Asian Passalinae in this study, the six exemplars, not including *Leptaulax* spp., are consistently placed in a monophyletic clade, consistent with Gravely's (1919) Macrolininae. Addition of the 14 missing genera and additional distinct species groups, as well as the missing African and Madagascan genera, may help clarify the relationship between this clade and *Leptaulax*.

The clade containing all of the New World exemplars is not strongly supported, but one genus and three distinct subgenera of Passalini and eight genera of Proculini are not represented in the dataset, nor are a number of the basal genera from the Ethiopian Region and southeast Asia. The addition of more taxa may clarify the relationships within this section of the family.

The New World genera of Passalini form a comb-like, polyphyletic grade basal to the Proculini. Monophyly of this group is not supported in the preferred tree (Appendix 3); instead, *Passalus* is paraphyletic with regard to species of *Paxillus* and *Spasalus*. The very large and varied genus *Passalus* is currently in great need of revision. It consists of several disparate subgenera and species groups that may eventually receive higher taxonomic status, and is here represented by only three exemplars belonging to two of the subgenera. None of the three *Passalus* exemplars are supported as sister taxa in any of the parsimony analyses. Even the two exemplars of the subgenus *Passalus* (*Pertinax*), *Passalus* (*Pertinax*) *cuneatus* Hincks and *Passalus* (*Pertinax*) nr. *caelatu*s, do not appear to be closely related.

Although monophyly of Proculini is well-supported (BS of 9), a number of the included genera require re-definition. *Heliscus*, *Odontotaenius*, *Petrejoides* and *Popilius* are all strongly indicated (BS of 4-13) as paraphyletic in this study. In addition, the alternative topologies within this tribe indicate that there is still character conflict within the dataset. Based on the results of excluding frontoclypeal characters or *Pseudacanthus* from the dataset, this conflict appears to be due to coding of some characters of *Pseudacanthus*, including at least some of those describing the frontoclypeus, in a manner that does not recognize the homoplasy. This may be due to an inability to recognize alternative, convergent pathways to the loss of some characters, or to misinterpretation of the homology of structures. Inclusion of *Pseudacanthus* in this dataset thus erroneously draws Proculini basally, and trees having the root of Passalinae within the Proculini are considered erroneous due to this unresolved homoplasy.

The short internal branch lengths within this entire clade may be the result of rapid evolution within the group and may presage difficulties in defining genera, at least with the character systems employed in this study. To increase the number of informative characters, investigation of additional character systems may be necessary, e.g. the digestive system, high-power microscopic examination of the sensory organs (setae, spines, etc.) on the antennal lamellae, larval morphology, and molecular structure.

This revised arrangement is not revolutionary. Although Gravely (1919), did not propose a phylogeny of Passalidae, he consolidated the 38 subfamilies recognized by Kuwert (1896) into seven. These bear a remarkable similarity to the four monophyletic clades present in the preferred tree of this study. Aulacocyclinae is comprised of the same taxa in both Gravely's classification and this study, the Ethiopian plus *Leptaulax* clade is identical to the subfamilies Solenocyclinae plus Leptaulacinae, the clade containing the remaining southeast Asian taxa is exactly equivalent to Macrolininae, and the New World clade in this study is composed of Gravely's subfamilies Passalinae, Proculinae and Pseudacanthinae.

Fonseca in his morphologically based phylogenetic analysis of Passalidae (1987), arrived at similar conclusions: that Aulacocyclinae (Aulacocyclidae, per Fonseca) is basal, followed by the monophyletic clades Solenocyclinae, Leptaulacini, and the terminal sister subtribes, Macrolinina and Passalina, the latter including all of the New World genera. He separated Passalina into two generic groups, his Passalus Group including the New World genera of Passalinae (sensu Reyes-Castillo, 1970b), and the Proculus Group identical to Reyes-Castillo's Proculini. The primary differences between his conclusions and the preferred tree are in the placement of *Leptaulax* between an Ethiopian Region clade and a clade containing the remaining southeast Asian Passalini, and in the arrangement of the New World passaline genera, which form the monophyletic sister taxon to Proculini (rather than a polyphyletic grade basal to Proculini, as in this study).

Preliminary results of an extensive molecular phylogenetic analysis of Scarabaeoidea, overlapping this study in only 8 of the 20 included passalid taxa, generally supports the phylogeny resulting from this study (David Hawks, personal communication, 2004). Hawks' analyses suggest that Aulacocyclinae is basal, although forming a comb with *Cylindrocaulus* the most basal exemplar, rather than being monophyletic. The basal passaline clade is monophyletic and consists of taxa from Africa and Madagascar. The two terminal clades are monophyletic, one including the non-aulacocycline southeast Asian taxa (with *Leptaulax* basal), and the other comprised of the New World taxa. The small number of New World taxa sequenced permits no more than the general observation that the New World Passalini (two exemplars) is sister to the Proculini (four exemplars).

A caveat may be appropriate here. The major topological change resulting from the exclusion of one of the exemplars (*Pentalobus*) in this study suggests that the taxon sampling may not be complete enough to accurately characterize the phylogeny of Passalidae. It would not be surprising to encounter fundamental changes resulting from the incorporation of one or more of the many missing genera and species groups, especially those that might fall near the base of Passalinae in the preferred tree, or from re-interpretation of characters, especially those describing the topology of the frons and clypeus.

Due to the potential for change still present in the phylogeny of passalids, no modification to the higher classification of Passalidae is proposed here, although it appears that the currently accepted arrangement of tribes within Passalinae (Reyes-Castillo, 1970b) requires reassessment.

Morphological Partitions

There is only weak support for different evolutionary vectors among the morphological partitions used in this study. The results of Partitioned Bremer Support analysis and Spearman's rank correlation of the eight morphological character partitions suggest that most of the partitions are congruent or neutral in their support of the preferred tree. The one exception is the frontoclypeus partition, which supports *Leptaulax* as the sister to *Pentalobus* in a monophyletic clade with *Semicyclus*, contrary to all of the other partitions. The concensus of the five highly correlated partitions partitions is that *Leptaulax* belongs in the southeast Asian passaline clade; both the internal and male genitalia partitions, when combined with those supporting *Leptaulax* in the southeast Asian passaline clade, also place *Pentalobus* within that clade.

Rather than representing diverging evolutionary vectors, the lack of correlation of the frontoclypeal partition with most of the otheres appears to be due to the conflicting frontoclypeal characters that contribute to the alternative placement of *Pseudacanthus* within Proculini and the close association of *Leptaulax* with *Pentalobus* and *Semicyclus* in the combined dataset (*Bolboceras* as out-group to Passalidae).

When additional taxa, especially from the Ethiopian Region, are added to this database, the correct placement of *Leptaulax* may become evident. As this is done, though, the homologies of the various structures on the frontoclypeus must also be reviewed in order to verify the assumptions and interpretations used in this study.

The almost complete lack of significant positive correlation of the male genitalia partition with any of the other seven partitions (except wings/elytra), suggests that evolution of the male genitalia of passalids may not mirror the evolutionary trajectory of the rest of the beetle. This could be the result of differences in evolutionary rates, the strong environmental constraints that dictate the optimal shape of the body may tend to slow or minimize the evolution of novel forms and structures (Hamilton, 1978). The genitalia, being completely internal, may not be subject to these same pressures, and may be free to evolve more quickly, especially if driven by female choice. The evolution of the genitalia may be too rapid to detect trends by examining generic exemplars, and might be more easily tracked using congeneric or very closely related species.

The use of morphological partitions has facilitated the identification of problem areas in character interpretation within this database, and suggests that the male genitalia may be evolving at a different rate from the other character partitions used.

Another use of the partitions to be explored in future work is examination of the relationship between morphological partitions and the level within the phylogeny, testing whether individual partitions offer significantly different levels of support at basal, intermediate or terminal nodes (Damgaard & Cognato, 2003).

Zoogeographic Implications

The family Passalidae has been suggested to have originated in Pangaea during the Jurassic, about 180-160 MYBP (Scholtz & Chown, 1995), but no passalid fossils are known until the Oligocene. Since no aulacocyclines have been recorded from the Ethiopian Region or New World, and the basal passalines appear to be from the Ethiopian Region, the origins of these two clades may have coincided with the separation of Gondwana from Laurasia, about 150-100 MYBP.

Aulacocyclinae is distributed from western China and eastern India to southern Japan, Borneo, northern and eastern Australia, New Guinea and New Caledonia. The isolation of *Cylindrocaulus* in temperate mountains of western China (two species) and southern Japan (one species) may indicate relictual distributions due to environmental pressures and/or competition from later vicariant passalid taxa, forcing the basal aulacocyclines to the perimeter of their habitable range. *Ceracupes* appears to be less limited, with species in Taiwan and neighboring Southeast Asia. The specialized habitat reported for *Ceracupes fronticornis* Arrow, the most common beetle in the root-masses of arboreal ferns in northern Vietnam (Kabakov, 1967) suggests a long relationship with these plants. The use of ferns as hosts may be conserved from a time prior to the appearance of angiosperms, or competition from other passalids or wood-inhabiting organisms may have driven this group into a peripheral ecological refuge, in contrast to the geographic refuges of *Cylindrocaulus*.

The presence on New Caledonia of a cluster of species of *Aulacocyclus* is attributed to vicariance, as this continental fragment separated from Australia in the Cretaceous (Boucher, 1991b). The close relationship between these species and the fauna of Australia, absence of other *Aulacocyclus* spp. from islands south of the Solomon Islands (e.g. Vanuatu, Fiji, New Zealand), and lack of evidence of significant dispersal over water by *Aulacocyclus* suggested to the author that these species separated from the Australian *Aulacocyclus* stock about 144-65 MYBP.

The Ethiopian Region clade (Gravely's Solenocyclinae) is restricted to the low-latitude tropical forests of Africa and to Madagascar. Although the passalid faunas are related, no genera are shared between these two areas. Inclusion of *Leptaulax* (in Gravely's Leptaulacinae) within this clade is a surprise, and is viewed with suspicion. As noted above, this placement may be due to inadequate taxon sampling, erroneous character interpretation of the frontoclypeus, or homoplasy between *Leptaulax* and *Pentalobus*. This relationship is not expected to hold up to the scrutiny of expanded passalid datasets.

Leptaulax, with its much less speciose sister taxon *Trichostigmus*, currently has a similar distribution to the southeast Asian passaline clade, although it reaches only extreme northeast Australia (no species endemic to Australia) and does not extend as far into the Pacific islands. It may have a somewhat different biogeographic history. The specialized subcortical habit (mining the cambium layer of relatively recently dead trees) may be paralleled within the southeast Asian passaline clade by other genera of flattened form occurring on the islands of the southwest Pacific (e.g. *Analaches*, *Gonatas*).

The southeast Asian passaline clade (Macrolininae of Gravely) includes well over one hundred described species in a morphologically diverse group of genera, ranging from Sri Lanka to Korea, Taiwan, southeast Asia and Australasia. The basal taxa in this dataset, *Pleurarius* and *Mastochilus*, are from southern India and eastern Australia. However, too few exemplars are included to permit more than speculation about the route taken from a putative gondwanan origin, perhaps via dispersal from eastern Gondwana to Laurasia, or vicariance to southern Asia via India. Vicariance by way of Antactica and Australia appears to be less likely. The only passalid fossil known from the Old World is of mid-Miocene age, about 15 million years before present (MYBP), and has been placed in an extant genus, *Macrolinus* (Zhang, 1989), although the description and figures suggest that the fossil might better be placed in *Leptaulax*.

The New World clade, although not strongly supported by this dataset (Bremer Support index of 2), is suggestive that the New World fauna diverged from an African source after separation of South America from Africa, the isolation completed by about 80 MYBP (Cooper et al., 1990; Coetzee, 1993). The much larger diversity of animal groups in South America, compared with Africa, is attributed to the relatively uniform forests across central Africa compared to the greater area of humid forests and habitat heterogeneity of South America

(Duellman, 1993). This contrast in diversity is true for passalids, as well. The relatively short internal branch lengths in this clade, compared to the terminal branches may reflect rapid evolution as the beetles dispersed into newly varied or isolated habitats. These new habitats may have been in the Caribbean island arcs and rising Andes in the late Cretaceous to Miocene (about 80-5 MYBP), especially within about the last 27 million years (Marshall & Sempere, 1993).

South America is the only region inhabited by all of the genera (most of the species) of the non-proculine New World taxa, as well as all of the subgenera and defined species groups within *Passalus*. The exemplars representing these groups are placed at the base of the New World clade in the preferred tree (Appendix 3) suggesting that South America is the center of diversity for this group.

The only New World passalid fossil is from the Oligocene of Oregon (near Post, in central Oregon), and is placed in or near the Neleus section of the extant subgenus *Passalus* (*Passalus*) (Reyes-Castillo, 1977). This site is about 1300 miles north of the current range of the nearest species of that section of *Passalus*, and indicates early dispersal into North America. The limited vagility of passalids and the presence of endemic species of *Passalus* on the Caribbean islands of Cuba, Hispaniola and Grenada (Hincks & Dibb, 1935; Hincks, 1958), and of *Paxillus* on Jamaica and Hispaniola (Reyes-Castillo & Fonseca, 1992), are additional evidence of the presence of a land bridge between the two continents at least once, long before the Pliocene closure of the Isthmus of Panama. Geological support for such a land bridge in the late Oligocene/early Miocene (35-32 MYBP) has been presented by Iturralde-Vinent & MacPhee (1999).

The derivative monophyletic clade, Proculini, has been shown to have a Mesoamerican center of diversity; all 18 of the 19 genera are known from the highlands of southern Mexico and Guatemala (Reyes-Castillo, 1970b; Reyes-Castillo, et al., 1987). The other genus, *Pseudoarrox*, occurs in Costa Rica (Reyes-Castillo, 1970b) and western Panama (personal observation). Only about half of these genera have been recorded from South America (Schuster, 1993b), and all except two (*Veturius* and *Popilius*) are represented there by very few species.

This, along with the preferred tree, suggests that Proculini is a monophyletic clade derived from a South American ancestor, perhaps near *Passalus* (*Pertinax*), but that it is not sister to the other genera of New World passalids. This ancestor presumably reached the Chortis Block of northern Central America, diversified and then dispersed into south-central Mexico and Central America as these became emergent and inter-connected. Elements of the clade apparently then entered South America in the Pliocene, over the Isthmus of Panama.

CONCLUSIONS

Several of the character systems newly investigated in this study show promise of utility: tentorium, hypopharynx, anterior mesosternum, mesendosternite, metendosternite, and the internal sac of the male genitalia. The anterior mesosternum and the armament and setal patches of the internal sac may prove to be especially useful in rigorously defining species groups within *Leptaulax*, a widespread, incipient, speciose genus. The setal patch patterns of the internal sac should also provide good characters for differentiating groups of New World Passalini, and some African and Australian Passalini.

The discovery of a putative, specialized hearing organ exclusive to Passalidae opens up entirely new lines of research into the mechanism and sensitivities of the organ, whether it is used to distinguish between low-frequency vibrations and the higher frequency stridulation of the beetles and their larvae, to discriminate between agonistic calls of adults or larvae and the specialized mating songs, and if varies among taxa in ways that might be phylogenetically informative.

Although the morphological partitioning produced results of limited utility and did not suggest different evolutionary vectors for different parts of the adult body, it did provide a cross check for potential errors in character interpretation. Yet to be done is a comparison of these partitions with the node level of the preferred tree, to test the influence of the partitions at different stages of the evolution of Passalidae.

Preliminary evidence is presented that the social structure of subcortical passalids may differ from that of the heartwood specialists. The flattened body form appears to have evolved in parallel in several groups of passalids as a specialization to more efficiently mine the decaying cambium layer beneath the bark of recently dead trees. The presence of scoop-like structures at the tip of the internal sac of the male genitalia of some taxa suggests that sperm competition and replacement may be more important for the species that live in a very temporary, essentially two-dimensional environment than for those that live in the longer-lasting heartwood. Comparison of the social behavior of subcortical and heartwood passalid taxa may add to the theories on the development of eusociality.

The preferred tree is well-supported by independent molecular evidence, but suggests areas of study that still need attention: selection of the best possible out-group for Passalidae, addition of more basal exemplar taxa to clarify the placement of *Leptaulax* and the relationships among the major clades, and re-definition of the generic limits within Proculini.

CHAPTER III

REVIEW OF *POPILIUS* KAUP (PASSALIDAE)

INTRODUCTION

The classification of Passalidae is rapidly shifting from the descriptive stage to revisionary systematic work, with this movement being led by detailed studies of the New World tribe Proculini. The prime motivations for this increasingly analytical activity appear to have been the review of the higher classification of the New World passalid fauna by Reyes-Castillo (1970b) and the availability of new and efficient analytical tools for phylogenetic analysis.

Reyes-Castillo restricted his study to New World taxa for practical and zoogeographic convenience, treating Proculini as restricted to the New World and Passalini as a pan-tropical taxon including all of the remaining species in the subfamily Passalinae (Reyes-Castillo, 1970b). The evidence from the phylogenetic analyses presented by Fonseca (1987) and in Chapter II of this dissertation suggest that the systematic independence of the New World and Old World faunas may well be an evolutionary reality.

Six of the nineteen genera of Proculini have already been revised, including *Ogyges* and *Petrejoides*, two of the genera with more than ten described species (Reyes-Castillo, 1978; Quintero & Reyes-Castillo, 1983; Castillo & Reyes-Castillo, 1984; Schuster & Reyes-Castillo, 1990; Schuster, 1991, 1993a; Schuster et al., 2003). Of the three remaining proculine genera with more than ten described species, *Verres* has been revised, (Marshall, 2000; not yet published,), *Veturius* (along with *Publius*) is currently being revised (S. Boucher, personal communication), and this is the report on the status of the revision of *Popilius*.

The intent of this ongoing research project is to evaluate new character systems, define *Popilius* and any distinct species groups within the genus using apomorphic characters, evaluate the status of the valid species names, identify undetermined material in major collections, create tools (dichotomous key and taxon/character matrix) for the identification of the species, place the valid species and higher taxa within the phylogenetic framework of Passalidae, and summarize the known information on these species, all in preparation for a full revision of *Popilius*. The introduction and employment of new character systems and use of rigorous phylogenetic methodology should clarify relationships within both the genus and the tribe, and lead to a better understanding of the higher classification of the entire family.

TAXONOMIC HISTORY

The taxonomic limits of *Popilius* have undergone considerable expansion and contraction since it was first described. Originally comprised of four species, the number increased to 16 in the most recent monograph of the family (Kuwert, 1891, 1896, 1897), and then to 20 species (Bates, 1886). Gravely raised the number of species to 36 by describing two new species and synonymizing three genera (*Heliscus* Zang, *Odontotaenius* Kuwert and *Passalotaenius* Kuwert) under *Popilius,* while creating a new genus, *Oileoides* for two species (Gravely, 1918). The transfer of one species from *Passalus* (Luederwaldt, 1927b), descriptions of new species (Dibb, 1938, 1940; Luederwaldt, 1927a, 1931, 1941; and Pereira, 1941), transfer of three species of *Popilius* to *Oileoides* by Pereira (1941) and synonymy of *Petrejoides* under *Popilius* (Hincks, 1953) resulted in a total of 42 species.

Reyes-Castillo (1970b), in his revision of New World genera noted that *Popilius,* after the synonymies by Gravely (1918) and Hincks (1953), was an artificial construct based on what are now considered plesiomorphic characters: normal wings, normal mandibular dentition, metasternum not pubescent medial to the lateral groove and mediofrontal structure present (Reyes-Castillo, 1970b). He suggested that *Popilius* consists of definable groups that correspond fairly well to the descriptions of some of the previously synonymized genera, and used apomorphic characters to define the resurrected genera *Heliscus*, *Odontotaenius* and *Petrejoides,* while synonymizing *Oileoides* under *Popilius*. *Popilius*, as newly defined by Reyes, contained 25 species, uniting all of the species currently considered in *Popilius* in the same genus for the first time.

However, after the distinctive groups with obvious apomorphies were removed, the heterogeneous remnants of *Popilius* were again defined by only plesiomorphies: transfrontal sulcus evident, outer tubercles present, anterior border of the clypeus narrow, anterior angles of the clypeus generally not evident or rounded, central tubercle distinctly ridged, the parietal ridges angular and located at each side of the central tubercle, protibial spur apically acute and directed downwards, clypeus more or less horizontal and internal tubercles not near the transfrontal sulcus (Reyes-Castillo, 1970b).

Since 1970, two new species have been described and two cases of synonymy has been published (Boucher, 1986; Castillo & Reyes-Castillo, 1984; Reyes-Castillo & Castillo, 1992), and one species has been transferred to *Petrejoides* (Castillo & Reyes-Castillo, 1980), for the currently recognized total of 24 species.

GROUPS WITHIN *POPILIUS*

Dibb (1938, 1940) and Luederwaldt (1931, 1941) attempted to find structure within *Popilius* (sensu Gravely, 1918), erecting a number of species groups. Dibb (1940) proposed seven species groups and provided a key to the 20 included species; four of his species groups are now contained in genera resurrected by Reyes-Castillo (1970b) and the remaining three include 11 species. Dibb's *eclipticus* Group IV included four species, now all synonymized within *P. eclipticus* (Hincks, 1953; Reyes-Castillo & Castillo, 1992; Chp. IV of this study); his *tetraphyllus* Group VI contained the four species *P. tetraphyllus*, *P. marginatus*, *P. klingelhoefferi*, and *P. mysticus*; and *intergeneus* Group VII contained three species, *P. intergeneus*, *P. sieberi* and *P. amazonicus*.

Luederwaldt (1941) in a posthumously published paper included 39 species in eight Popilius sections (and two species not placed), four of which are now in other genera. The remaining sections were III. *Eclipticus* (four species, all now united under *P. eclipticus*), IV. Abnormalis (for a single aberrant species described in the same paper), VI. Tetraphyllus (with 17 species; three now in Heliscus, two since synonymized), and VII. Recticornis (with three species, two of which are now in *Petrejoides).* Luederwaldt,
included a key to the sections and a list of species in each section, but he did not comment on or discuss them, nor did he provide diagnoses.

Species groups in *Popilius*, since Reyes-Castillo's (1970b) elevation of half of those proposed by Dibb and Luederwaldt, have not been used in the few publications that refer to species included in the genus (Buehrnheim, 1962; Boucher, 1986; Castillo, 1987; Reyes-Castillo & Amat, 1991; Reyes-Castillo & Castillo, 1992).

AFFINITIES

Gravely regarded *Popilius* as the most primitive passalid genus, based on the exposed, transverse clypeus that is separated from the frons by a distinct suture, and hypothesized that the most primitive members of the other lineages have an exposed clypeus, but without the frontoclypeal suture, and the more highly specialized members have a hidden clypeus (Gravely, 1918).

Reyes-Castillo (1978) suggests that *Popilius* is closest to *Spurius* and forms a natural group with the genera *Spurius* and *Chondrocephalus*, with *Petrejoides* and *Coniger* also considered to be closely related.

Fonseca (1987), without comment other than the diagnostic characters, placed *Popilius* with *Spurius* and *Odontotaenius* in an unresolved monophyletic clade at the base of Proculini, with the most closely placed clades including *Chondrocephalus*, *Coniger*, *Heliscus*, *Petrejoides*, *Pseudacanthus*, *Pseudoarrox* and *Vindex*.

The preliminary higher-level phylogeny in Chapter II of this study places *Popilius* in a paraphyletic array with the genera *Heliscus*, O*dontotaenius*, *Petrejoides* and *Spurius* (see Appendices A-2 and A-4).

NATURAL HISTORY

The species of *Popilius* are known from central Mexico to Argentina, although not recorded from the western side of the Andes south of Colombia, and from sea level to 3000 m elevation. However, almost all of the species have a very limited range, either in distance or elevation. The only exception is *P. eclipticus*, which is known from Mexico to Colombia (Reyes-Castillo, 1970b). Of the remaining 23 species, 9 occur in Mexico or Central America, and 14 in South America. The only species besides *P. eclipticus* that has a restricted range that includes the adjacent extremes of both continents is *P. erotylus*. The genus appears almost restricted to the continental mainland, with no island records in the Caribbean or Pacific, with the exceptions of *P. tetraphyllus* recorded from Trinidad and *P. lenzi* known only from Cocos Island.

Ecological records are scarce and incomplete. Again, with the exception of *P. eclipticus*, the species generally have an elevational range usually limited to less than 1000 meters. *P. eclipticus* has the largest published altitudinal range in the genus, from rain forest at sea level to cloud forest at 1200 meters, but has been collected up to 1700 meters (personal observations). Although there is no published record of *Popilius* from elevations above 1400 meters, label data on specimens from the highlands of Guatemala and Mexico indicate that four additional species can be found at elevations of over 1500 meters, one of which (*P. klingelhoefferi*) has been recorded from 1981 meters. A group of closely related South American species appears to be restricted to relatively high elevations (1350-3000 m) in the northern Andes.

Almost nothing is known of the host preferences, if any, of the species of *Popilius*, probably because these beetles are subcortical feeders, invading dead wood after degradation is well underway and after most of the diagnostic characters of the trees would have been lost. Even the detailed study of passalid ecology (fifteen species of ten genera) at Los Tuxtlas, Veracruz, Mexico by Castillo (1987) provides little data on *Popilius*, due to the rarity of the two species of *Popilius* encountered: *P. mysticus* was recorded from only one collection in an (unspecified) identified tree.

MATERIALS AND METHODS

Specimens

The specimens examined were provided by 24 institutions and collections, with loans of over a thousand specimens, including two types and four specimens belonging to type series. Most of the type specimens seen were examined at the institutions holding them in Paris, London and Manchester. For this review, 1406 specimens of *Popilius* from 24 collections were used. The acronyms used for the loaning institutions follow Bejsak-Collorado-Mansfeld (2004), with modifications for unlisted collections.

AMNH - American Museum of Natural History, New York, NY
ARGC - A.R. Gillogly Collection, College Station, TX
BDGC - Bruce D. Gill Collection
BMNH – The Natural History Museum [formerly British Museum (Natural History)], London, United Kingdom
CASC – California Academy of Sciences, San Francisco, CA
CFSC – Coleccion Entomologica del Colegio de la Frontera Sur, San Cristobal de Las Casas, Chiapas, Mexico
DJCC – Daniel J. Curoe Collection, Palo Alto, CA
EGRC – Edward G. Riley Collection, College Station, TX
EMEC – Essig Museum of Entomology, Berkeley, CA
FMNH – Field Museum of Natural History
FSMC – Florida Museum of Natural History, University of Florida, Gainesville, FL
HLMD – Hessisches Landesmuseum Darmstadt, Darmstadt, Germany
IDEM – Instituto de Ecologia, Xalapa, Veracruz, Mexico
INBC – Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica
JCSC - Jack C. Schuster, Guatemala City, Guatemala
LACM – Los Angeles County Museum of Natural History, Los Angeles, CA
MCZ – Museum of Comparative Zoology, Cambridge, MA
MMUE –Manchester Museum, The University, Manchester, United Kingdom

MNHN – Museum National d'Histoire Naturelle, Paris, France
MPEG – Museu Paraense Emilio Goeldi, Belem, Para, Brazil
MZSP – Museu de Zoologia da Universidade de Sao Paulo, Sao Paulo, Brazil
OSU – Ohio State University, Columbus, OH
TAMU – Texas A&M University Insect Collection, College Station, TX
UNSM – University of Nebraska State Museum, Lincoln, NE
USNM – National Museum of Natural History, Washington, DC
UVGC – Coleccion de Artropodos, Universidad del Valle de Guatemala, Guatemala City, Guatemala
ZMHB – Museum for Naturkunde der Humboldt-Universitat, Berlin, Germany

Specimen Preparation

The only dissections done for this study were to extract the male genitalia. Dried specimens were softened in warm water, the membrane posterior to the 8th abdominal segment was cut, and the genitalic capsule and spiculum were removed, severing the ejaculatory duct and intestine. For examination, the aedeagus was pushed through the genitalic capsule (9th abdominal segment, including the spiculum), to expose the sclerotized portions of the aedeagus. All of the dissected parts were placed in a hot (not boiling) solution of potassium hydroxide (KOH) until free of unwanted tissue The internal sac of the male genitalia was teased out until everted, using microforceps and insect pins with hooked tips. The genitalia were rinsed in water, placed in a plastic microvial with glycerin and pinned beneath the donor specimen.

Specimens with characters that were obscured by leg position, closed mandibles or telescoping of the body segments were softened in warm water, repositioned and dried.

Character Selection

In a preliminary morphological phylogenetic analysis of the genus *Popilius*, based on data from the primary type material that was seen, I included species of several proculine genera as out-groups to test for the monophyly of *Popilius*. The results indicated that *Popilius* was paraphyletic, regardless of the out-group(s) employed, perhaps due to the low number of number of characters. The number of characters in this preliminary dataset was approximately equal to the number of taxa. The relatively small number of characters traditionally used to differentiate the species in *Popilius* meant that two to three times as many characters would be needed to provide robust results (Bremer et al, 1999).

Due to funding and time constraints, this study is not based on data extracted from primary type material, but on the specimens at hand. The characters used were external differences that could be seen without dissection, and the male genitalia, using a dissecting microscope (6 to 50X power).

Nevertheless, I made a determined attempt to identify new character systems that might be used to differentiate taxa. Many of the differences noted were identified as the result of intraspecific variation. Also, many of the characters used in this study may be of no utility in distinguishing species, but the limited number of specimens available of many species did not permit a thorough evaluation of normal variation within those species. Further study should improve the quality of the characters used and eliminate most of those that are excessively variable.

However, some new or little used characters did prove to be useful including: position of the central tubercle relative to the parietal tubercles; surface texture between the outer tubercle and the end of the canthus; position of the outer tubercles relative to the transfrontal sulcus; form of the subocular ridge; form of the left inner tooth of the mandible; form and proportions of the antennal segments; surface texture and presence/absence of setae on the prosternal process; surface texture and presence/absence of setae in the posterior angle of mesepisternum; presence/absence of setae on the mesepimeron; form of the postmesoxal grooves: presence/absence of setae on various parts of the metasternum; surface texture and presence/absence of setae on the anterior process of the second (first visible) abdominal sternite; presence/absence of setae on the anterior face of procoxa and metacoxae; and structure of the (everted) internal sac of the male genitalia.

Preliminary examination of the internal sac of the male genitalia of a number of proculine genera has produced few characters of use, since the sac is usually completely membranous. However, a distinct pair of sclerotized tubercles is present at the base of the internal sac in species of several genera, including some *Popilius* spp.

Structures that might prove useful that were not investigated were the digestive system and epipharynx, both of which would have required dissection. While dissecting and examining specimens used in the higher taxon study (Chapter II), differences were noteed in the morphology of the epipharynx, and in the structure of the intestine among the limited exemplars of *Popilius*. Of particular interest was the presence of many sclerotized, claw-like structures on the inside of the lower intestine of *P. eclipticus* that were either not present or not evident in the other species.

Morphology

I have adopted Marshall's (2000) terminology in this study, supplemented by the few comments and observations noted above in Chapter II.

The length of specimens was measured from the middle of the labrum to the tip of the elytra. However, the total length of a single specimen can vary by over 10%, depending on the method of mounting and the degree of separation of these parts.

PHYLOGENETIC ANALYSIS

General

A determined effort was made to evaluate new species-level character systems and characters in *Popilius*, in conjunction with the search for characters useful at higher taxonomic levels that is discussed in Chapter II.

Type material and specimens identified by previous determiners (Kaup, Kuwert, Bates, Gravely, Dibb, Hincks) were examined in the MNHN, BMNH and MMUE; however, this was done using only 74 characters, before the character list was expanded. Although useful information was gathered, it was limited by the low number of characters that were examined and compared during examination of this historical material. The database assembled for evaluating the relationships within *Popilius* includes no data from primary types, but is the result of detailed examination of identified material, including a few paratypes and topotypic specimens. Critical type material of ten species of *Popilius* could not be obtained on loan from institutions in Brazil and India.

Because of these shortcomings, results of the analysis of the expanded database (232 characters) must be considered tentative. Taxonomic changes are suggested in the treatments of the respective species names (currently recognized species), but are not formally recommended at this time.

Selection of Taxa

At least one exemplar from each *Popilius* species represented was chosen. Additional exemplars were used: five exemplars of *P. eclipticus*, because of the large geographic range and morphological variation; eight exemplars of the *P. gibbosus* complex, because of the wide range of variation and the disjunct, high elevation populations/species; and duplicate exemplars of several other species, either because of previously determined specimens that had been determined as different species (*P. haagi* and *P*. "*intergeneus*", or to test for variability between conspecific specimens.

More than one exemplar was used from several taxa to take intraspecific variation into account or to try to distinguish closely related taxa. Forty-one exemplars were examined. The label data of the exemplars is included in the individual species treatments. The exemplar specimens are labeled as vouchers.

The higher-taxon phylogenetic study reported in Chapter II indicated that, as currently defined, *Heliscus*, *Odontotaenius*, *Petrejoides* and *Popilius* are paraphyletic and intermingled, *Chondrocephalus*, *Coniger*, *Pseudoarrox*. *Pseudacanthus* and *Spurius*, have also been considered closely related to *Popilius* (Dibb, 1938; Luederwaldt, 1927; Reyes-Castillo, 1970b; Schuster, 1991), and some species within the genera *Petrejoides* and *Heliscus* appear to be more closely related to species currently included within *Popilius* than to other species within the same genera (personal observations).

Selection of an optimal out-group taxon (or taxa) for evaluating *Popilius* is by no means obvious, and should result from a phylogenetic analysis of the species groups of all of the genera noted above. Addition of this many potential out-group taxa could possibly double the number of taxa in the database assembled for this study; I felt that an expansion of this size, although logical and necessary, was beyond the original scope of this study and inadvisable given the time constraints.

Character Analysis

The list of the 232 characters used to code the 41 exemplar specimens is included as Appendix D-1. Some character states are constant within *Popilius*, but are left in the matrix because they occur in related genera that can potentially be used as out-groups. There are therefore 44 invariant characters in this matrix.

Characters were coded as either binary or multistate (0-9 states). More than one character state were often encountered on the exemplar and supplementary specimens, and occasionally on opposite sides of a single specimen. Polymorphic data from a given taxon were coded with the pertinent states separated by an ampersand "&".

Males were not available for several of the taxa, and parts were missing from some taxa represented by singleton specimens. Missing data was coded as "?".

The character and character state definitions are in Appendix D-1.

Analytical Procedure

Cladistic analysis based on maximum parsimony was performed using heuristic searches (100-1000 randomized addition sequences followed by TBR branch swapping) on PAUP 4.0b10 (Swofford, 2002). The characters were initially weighted equally, and all were unordered, implying that change is equally likely between any two states. References to "distance" between taxa refer to the number of unambiguous character state changes. Due to the taxonomic problems discussed above, the characters were not polarized.

The analyses were evaluated as unrooted, examining only the relationships among the taxa, and making no assumptions about the direction of evolution.

To reduce the impact of characters of potentially poor quality and the extensive homoplasy in the datasets, successive approximations character weighting (Farris, 1969; Carpenter, 1988) was used to further evaluate phylogenetic relationships. The characters were reweighted based on the rescaled consistency index, followed by a heuristic tree search, with iterations of this procedure until the tree weights no longer changed.

Clade stability was estimated using bootstrap values (Felsenstein, 1985) and Bremer support (Bremer, 1988, 1994). Bootstrap analyses (100 bootstrap replicates, 100 random replicates per bootstrap replicate, 10 trees held at each step) were performed. Following the methodology used by Wahlberg et al (2003) support, as indicated by the resulting frequency percentages was subjectively defined as weak (50-63%, moderate (64-75%, good (76-88%) and strong 89-100%).

Decay indices (Bremer, 1988) were calculated by searching for the shortest trees not compatible with the constraint of monophyly of the taxa on selected branches; the constraint trees for these analyses were generated using either the software program TreeRot (Sorenson, 1999) or constraint statements in PAUP. Bremer support values of 3-5 were considered to indicate moderate support for a clade, and 6-10 as good support (Wahlberg et al., 2003).

RESULTS

Parsimony Analysis

Parsimony analysis resulted in six equally parsimonious trees (length 1183 steps, CI 0.280, RC 0.144) with two basic topologies. They both divide the exemplars into three monophyletic clades: the five exemplars of *P. eclipticus*, all of the remaining Mesoamerican exemplars, and all of the South American exemplars, with a monophyletic clade of nine exemplars within the South America clade (strict consensus tree at Appendix A-7). The differences between the topologies are in alternative arrangements of the apical *P. tetraphyllus* exemplars and two arrangements of the order of the *P. gibbosus* exemplars, one with the species arranged in a comb, and the other with a basal exemplar (*P. gibbosus*, Exemplar 7) and two sister clades of nine and eleven exemplars. In both topologies the three clades are about equidistant from each other, measured by the number of intervening steps (character state changes).

Successive approximations analysis of this set of trees resulted in a single tree nine steps longer than the unweighted trees. The successive approximation tree is most similar to the original trees that have the *P. gibbosus* exemplars arranged in a comb, retaining the monophyletic clade of nine exemplars (with *P. refugicornis* basal), but with *P. gibbosus* Exemplar 6 at the base of the South American clade, rather than *P. gibbosus* Exemplar 7 (Appendix A-8). The three major clades are arrayed with the basal members of each about equidistant from each other, as measured by the number of character changes, and with the *P. eclipticus* clade slightly closer to the other two than those are to each other (32 steps vs. 34 steps). Within the South American clade, *P. refugicornis* and *P*. sp. 2 Venezuela are separated from the nearest other taxa (including each other) by gaps (character state changes) about twice as wide as between most taxa in the group.

Clade Support

Bootstrap analysis of the ingroup dataset indicates strong (95-100%) support for the pairs/groups of exemplars considered to be conspecific, with the exception of the clade containing the *P. tetraphyllus* exemplars, which has good support (81%). The sister-group status of *P. lenzi* and P. *punctatissimus* is also very strongly supported (98%). Monophyly of the five exemplars of *P. eclipticus* is strongly supported (95%), of the clade containing the remaining Mesoamerican exemplars strongly supported (94%), and the clade including all of the South American taxa with good support (93%).

Decay indices (Bremer Support, BS) of the clades in the successive approximations tree of the ingroup dataset, measured by the Bremer Support Index (BS), indicate good support for all of the putative conspecific pairs/groups of exemplars, except for the *P. tetraphyllus* exemplars, the monophyly of which is supported moderately (BS=5). Good support for the sister-species status of *P. lenzi* and P. *punctatissimus* is also found (BS=6). Monophyly of the clade containing the South American taxa is quite strongly supported (BS=9), the *P. eclipticus* clade has good support (BS=6) and monophyly of the remaining Mesoamerican taxa has good support (BS=8).

DISCUSSION

Popilius Species Groups

Two clades are consistently retrieved in these analyses and they will be referred to as the Eclipticus Species Group, containing only the five exemplars of *P. eclipticus,* and Marginatus Species Group, comprised of all of the South American taxa. A third group of species is retrieved as monophyletic in the successive approximations tree (Appendix A-8),, but the monophyly is not at all supported by either the Bremer Support Index (BS=0) or bootstrap value (51%). This group of species is designated the Haagi Species Group. A fourth group containing only *P. abnormalis*, is designated the Abnormalis Species Group.

Abnormalis Species Group. This group is created for *P. abnormalis* which according to the original description (Luederwaldt, 1941) is morphologically unlike any other passalid. I have not been able to examine the unique type specimen and am unable to determine from the description if it belongs in one of the other groups, or possibly even a different genus. It is distinguished by the unique form of the pronotum, which is deeply excavate on both sides of the median line posteriorly, lack of inner tubercles, and short clypeus anterior to the transclypeal sulcus.

Eclipticus Species Group. The members of this species group can be distinguished by the presence of a low median tubercle just anterior to the posterior marginal groove of the last visible abdominal sternite, a transverse groove on each parietal ridge, and other characters as noted in Chapter IV and in the *Popilius* matrix (Appendix D-2).

I currently consider the Eclipticus Species Group to be comprised of a single variable species. However, male specimens from Panama and the lowlands of eastern Costa Rica have a pair of unusual, sclerotized tubercle-like structures at the base of the internal sac of the genitalia not found in other representatives of the Eclipticus Species Group. However, this character is shared with several other passalid taxa: the two exemplars of *P. haagi* in this analysis, the exemplars of *Chondrocephalus*, *Spurius* and *Paxillus leachi* examined during the higher taxon analysis reported in Chapter II, as well as unidentified species of Petrejoides from Mexico (personal observations). This paired structure has not been previously reported. As more taxa are examined the character may prove to be a ground plan structure useful in determining basal relationships, not only among the genera of Proculini, but between Proculini and the New World Passalini, since *Paxillus leachi* is included without reservations in Passalini (Reyes-Castillo, 1970b; Reyes-Castillo & Fonseca, 1992).

Marginatus Species Group. This species group is restricted to the South American species of *Popilius*, including *P. erotylus*, which is known from both South America and eastern Mesoamerica. They may be distinguished by the setose posterior angle of the mesepisternum, outer tubercles vertical and on the transfrontal sulcus, mesepisternum punctate and matt to the hind angle (with only a punctate anteroventral matt patch in *P. erotylus)*, and the lack of a tubercle on the last visible sternite.

Within this group are two allopatric morphotypes and two intermediate species. One morphotype is comprised of taxa related to *P. marginatus*, with the anterior margin of antennal segment 5 sharp (segment is triangular), and the anterolateral area of the metasternum setose only near the mesocoxae and in the lateral groove (occasionally not to the posterior tip); *P. marginatus*, *P. tetraphyllus*, *P. erotylus*, *P. magdalenae*, and *P*. sp. 1 Colombia). The second morphotype is comprised of taxa related to *P. gibbosus* with the lateral depression of the metasternum setose to the posterior tip, anterior margin of antennal segment 5 half as long as the posterior margin, and the entire anterolateral area of the metasternum setose to the tip of the lateral depression. This last feature was the character used by Gravely (1918) in creating *Oileoides* (the *P. gibbosus* species complex, *P*. sp. 3 Bolivia, and *P*. sp. 4 Venezuela). Two intermediate species (*P. refugicornis* and *P*. sp. 2 Venezuela) do not fall neatly into either group.

Haagi Species Group. I consider Haagi Species Group to be only a temporary construct to accommodate the species not included in the other species groups. This species group is composed only of Mesoamerican species with a distribution from central Mexico to central Panama. It is characterized by the glabrous posterior angle of the mesepisternum, outer tubercles on the transfrontal sulcus slightly surpassing the clypeal margin, mesepisternum anteroventrally impunctate or punctate and smooth (occasionally with only a punctate, anteroventral matt patch, but not punctate and matt to the hind angle), and last visible sternite not tuberculate. However, it consists of those species remaining after Reyes-Castillo’s redefinition of proculine genera

(Reyes-Castillo, 1970b) and the removal of many of the species included in *Popilius* by Gravely (1918) and after the Eclipticus and Marginatus Species Groups are distinguished (*P. haagi*, *P. hirsutus*, *P. klingelhoefferi*, *P. lenzi*, *P. mysticus*, *P. punctatissimus*, *P. scutellopunctatus*, and *P.* spp. 5-10).

Although the Haagi Species Group is not consistently monophyletic in the analyses, and is defined clearly solely as a repository for taxa with as yet unknown affinities. Their status should be resolved after analysis with appropriate out-groups. It is defined only by plesiomorphic characters, and I believe that it will not survive intact when the generic relationships within Proculini have been resolved. The taxa in this species group may eventually be assigned to as many as three or four different clades.

Both *P. haagi* and the eastern form of *P. eclipticus* have the sclerotized tubercles at the base of the internal sac of the male genitalia. This character is newly discovered and first implemented here; its presence or absence has been verified only for the taxa included in the phylogenetic studies presented in this dissertation, and it may prove useful in differentiating *Petrejoides* and other clades from *Populiu*s.

Relationships among Species Groups

The unrooted topology of the successive approximations tree has three major branches, two of which are equivalent equivalent to the Eclipticus, Marginatus and Haagi Species Groups defined above The presence of a complex structure (paired tubercles in the internal sac of the male genitalia) in *P. haagi*, the eastern form of *P. eclipticus*, and at least some species of *Chondrocephalus*, *Petrejoides*, *Spurius*, and *Paxillus*, suggests the possibility of a common ancestor and advisability of testing a wide range of potential out-group taxa.

Perhaps due to long-branch attraction (Felsenstein, 1978) or this species group being paraphyletic, anomalies are noted in this preliminary phylogeny. *P*. spp. 5 Panama and 6 Mexico are only moderately supported as sister taxa (BS=3, bootstrap of 67%); 54 unambiguous character changes separate the two species in the six most parsimonious trees, and 53 changes in the successive approximations tree, by far the greatest difference between sister taxa in the entire tree. Both species are diminutive and it is possible that parallel evolution of small size may have driven the development of homoplastic character states.

P. spp. 8-10 Guatemala appear macroscopically similar and are all from high mountains in Guatemala, but are not supported as a clade. *P*. spp. 8 Guatemala and 9 Guatemala are sister taxa, and apical in the group in all of the most parsimonious trees (Appendix A-7), and adjacent to the basal *P*. sp. 10 Guatemala in the successive approximations tree (Appendix A-8). Analyses of subsets of the full database sometimes resulted in a basal, monophyletic clade containing all three taxa, although this was not supported in the analyses reported above.

This level of instability within the Haagi Species Group suggests that not only is the group paraphyletic, but that some of the included taxa are not at all closely related to each other. Re-evaluation once more appropriate outgroups are found may resolve the status of these taxa

The Abnormalis Species Group is established for convenience until the unique and dramatically distinct type can be carefully examined and an informed decision made on whether it is a normally-developed specimen and valid species, and what the most closely related taxa might be. From the description and line drawing (Luederwaldt, 1941) it is not possible to eliminate the possibility that this is a species of *Petrejoides* or perhaps *Heliscus*.

Without a robust phylogeny of *Popilius* and neighboring genera, including at least *Petrejoide*s, it is premature to discuss relationships among the species groups.

Zoogeographic Implications

The center of diversity of Proculini is in the highlands of western Mesoamerica (Guatemala and southeastern Mexico), and number of genera represented decreases from 18 in this region to only six in South America (Reyes-Castillo, 1970b; Reyes-Castillo & Amat, 1991; Schuster et al., 2003). Only *Popilius*, *Publius* and *Veturius* are represented in South America by more than one species.

Eclipticus Species Group. The large range of this species (central Mexico to northern South America, and sea level to well over 2000 m.) is unusual in Passalidae and unique in *Populiu*s, suggesting that the taxon may be composed of more than one species. The only evidence of this is a novel structure in the male genitalia, discussed in detail above, that is shared with one species of the Haagi Species Group and species of four other genera; so far, only for the taxa examined in this study have been checked for the presence of this structure. Without a robust phylogeny, it is not possible to determine whether the structure is evidence of basal relationships, a common homoplastic apomorphy, or evidence of the reversal(s) of a complex character state, as has been demonstrated with the loss and secondary gain of wings in Phasmidae (Whiting, et al., 2003). If determined to be basal, the presence of this structure only in the eastern population (Panama and eastern lowland Costa Rica) would be counterintuitive, since the species is known from high mountains in the heart of the center of proculine diversity. This may be resolved when a more closely related outgroup can be used to polarize the character.

Marginatus Species Group. This strongly supported monophyletic clade is restricted to South America, but is widespread in both range and elevation. The number of distinct species and diverse habitats occupied suggest that the ancestral population of this species group reached South America and underwent speciation before the most recent land connection. The presence of *P. erotylus* in both South America and the coastal lowlands of eastern Mesoamerica suggests a more recent range expansion for this species, probably associated with the formation of the Isthmus of Panama.

The species in this group are arrayed by the analyses into two allopatric morphotypes and two intermediate forms (Appendix A-8). The taxa related to *P. marginatus* are distributed from Colombia to Argentina, although not recorded from the west coast (west of the Andes) of South America south of Colombia, but have not been recorded from elevations above 500 m. The forms related to *P. gibbosus* are restricted to the northern and eastern Andes at elevations from 1500-3000 m. The two species with intermediate characters also have an intermediate distribution: *P. refugicornis* is known only from low mountain rain forest along the eastern border of Brazil, and one of the paratypes is noted to have been collected at an elevation of 1100 m. (Buerhnheim, 1962); the only known specimen of *P*. sp. 2 was collected at 1600 m., but in an isolated mountain range between Caracas, Venezuela and the Atlantic Coast. These species *P. refugicornis* and *P*. sp. 2 occupy an intermediate position between the two morphotypes. When an acceptably close outgroup taxon is found for this species group, it may be determined whether these species are basal to two daughter clades or intermediate between consecutively-evolving morphotypes.

Haagi Species Group. Although the taxa included in this group are all Mesoamerican, they do not appear to form a monophyletic unit. When a supra-generic phylogeny of this section of Proculini has been accomplished and generic limits defined, some species in this species group may be moved to other genera. The resulting species groups and genera will certainly have a Mesoamerican origin and should provide considerable insight into proculine evolution.

P. lenzi of Cocos Island, is strongly supported as the sister of *P. punctatissimus* of mid-elevation Panama and Costa Rica. However, monophyly of the other sister-taxon pairs in this species group is not well supported: hirsutus+mysticus (BS=3, bootstrap of 73%), spp. 5 Panama and 6 Mexico (BS=3, bootstrap of 67%), spp. 8 Guatemala and 9 Guatemala (BS=2, bootstrap of 57%).

CONCLUSIONS

The substantial increase in the number of characters and character systems with phylogenetic value has permitted rigorous analysis of the species in hand. The analysis has provided justification for the description of ten new species, synonymy of four species names, elevation of a subspecies name to species status, and creation of species groups within *Popilius*. The genus is shown to be paraphyletic as currently defined.

No single outgroup is immediately basal to all *Popilius* species, as the genus is currently defined, and the number of possible outgroup taxa is almost as large as the total taxa currently included in *Popilius*. Because of this, evaluation of the status of the species groups and many of the species must await a re-evaluation of the supra-generic classification of this section of Proculini and re-definition of the generic limits.

This study provides a foundation for both the search for more appropriate outgroups with which to evaluate the elements within *Popilius* and for a generic-level revision of the genera closely related to *Popilius*. Most of the characters used in this analysis will be applicable in the study of other genera, and new characters and additional taxa can be added to the matrix. I intend to continue and build on this study, refining the database, obtaining the loan of more specimens, examining type material with the expanded (232-character) character set (and adding new characters as encountered), and testing the appropriateness of a range of potential outgroups.

CHAPTER IV
THE GENUS *POPILIUS*

INTRODUCTION

General

A checklist of the species currently recognized in *Popilius*, and a dichotomous identification key including all except one of the species precede the species treatments, which are arranged in the same order as they appear in the key. The species not included in the key, *P. amazonicus*, is treated following *P. marginatus*, with which I believe it will eventually be synonymized.

Descriptions

Systematists are increasingly caught between the competing constraints of the need for more precise, complete, and therefore lengthy descriptions versus the cost of increasing narrative text, page space and article length in publishing a descriptive manuscript. As more is learned about a clade of organisms and new differences found, the characters and character states used to differentiate the component taxa increase in number and complexity. Passalid descriptions have generally lengthened from the approximately fifteen characters used by Percheron (1841, 1844), thirty characters by Burmeister (1847), 12 characters by Kaup (1861), and eight to ten characters lines by Kuwert (1891), to the 54-63 characters employed by Buerhnheim (1962), Boucher (1991a), Reyes-Castillo & Castillo (1992) and Nomura et al. (1993).

This problem has been noted before and alternatives have been proposed: rapid journal publication of brief new species descriptions, supplemented by expanded descriptive information, figures, photographs, etc. placed on a server accessible through the Internet (Erwin & Johnson, 2000; Erwin, 2000b; Johnson, 2000); and use of a taxon/character data matrix to concisely summarize extensive character state data, with the character and state definitions published (Erwin, 2000a), and referred to in subsequent publications (e.g. Erwin, 2000c). Erwin defined 109 characters used in his study of *Agra* (Erwin, 2000a); I use 232 characters in this study.

The analytical procedures used to estimate phylogenies require the conversion of narrative-defined characters and character states to a matrix format; the same matrix can be used to publish extensive descriptive details to supplement a short, concise narrative description. This is the format used in the individual species treatments in this chapter; a short diagnosis and description are supplemented by the *Popilius* data matrix at Appendix D-2.

Locality Data

Locality data are presented for each species, listed alphabetically and in a descending order from largest political element to smallest, with lesser directions in parentheses. The numbers in parentheses following the country, state, province, and department names represent the number of specimens seen from each of those areas. The collection holding the specimens is noted to permit efficient access to specimens from specific taxa or specific localities for testing my conclusions, obtaining DNA from specimens of specific localities, etc. Dates are not included, except for the specific identification of exemplar specimens, because passalids have obligately overlapping generations. In a locality where a species routinely occurs, adults can be found in every week of the year.

***POPILIUS* KAUP, 1871**

(type species: *P. marginatus* (Percheron, 1835)
Oileoides Gravely, 1918

Generic description, following Reyes-Castillo (1970b). *Head.* Transclypeal sulcus present, narrow, strongly impressed, impunctate or irregularly punctate. Anterior border of clypeus dorsoventrally acute; clypeus anterior to transfrontal sulcus flat, almost linear to transversely quadrate, but not rounded and shiny; anterior angles of clypeus indistinct, acute or rounded, not directed downwards; outer tubercles small. Frontal fossae pubescent, or at least with a few setae posteriorly, not deep. Frontal ridges distinct and inner tubercles usually present and distinct (absent in *P. abnormalis*). Mediofrontal structure with the central tubercle distinct and its apex directed upward; parietal ridges angular, located at each side of the central ridge. *Legs.* Profemur with marginal sulcus on the anterior border of the ventral face. Spur of protibia with sharp tip, occasionally widened, always directed downwards. Mesotibia with the dorsal ridge distinct, not low; setal brush dense or sparse.

SPECIES INCLUDED IN *POPILIUS*

Abnormalis Species Group

abnormalis Luederwaldt, 1941

Eclipticus Species Group

- *eclipticus* (Truqui, 1857)
    - *felschei* Kuwert, 1891
    - *frantzi* Kuwert, 1897 New synonymy
    - *guatemalae* Gravely, 1918
    - *varius* Kuwert, 1891

Marginatus Species Group

- *amazonicus* Gravely, 1918
- *erotylus* Reyes-Castillo & Castillo, 1992
- *fischeri* (Pereira, 1941)
- *gibbosus* (Burmeister, 1847)
- *hebes* Kuwert, 1891
- *magdalenae* Boucher, 1986
- *marginatus* (Percheron, 1835)
    - *sieberi* (Kuwert, 1897) New synonymy
- *moritzi* Kuwert, 1897
- *novus* Kuwert, 1891
    - *thiemei* Kuwert, 1897
- *parvicornis* (Gravely, 1918)
- *refugicornis* Buehrnheim, 1962
- *tetraphyllus* (Eschscholtz, 1829)
    - *quinquelamellatus* Luederwaldt, 1927
- *villei* Kuwert, 1897
- sp. 1 Colombia
- sp. 2 Venezuela

sp. 3 Bolivia
sp. 4 Venezuela

Haagi Species Group

haagi (Kaup, 1868)
    intergeneus (Bates, 1886) New synonymy
    tau (Kaup, 1869) New synonymy
hirsutus Luederwaldt, 1941
klingelhoefferi (Kaup, 1869)
lenzi Kuwert, 1897
mysticus Bates, 1886
punctatissimus Luederwaldt, 1941 New status
scutellopunctatus Kuwert, 1897
sp. 5 Panama
sp. 6 Mexico
sp. 7 Mexico
sp. 8 Guatemala
sp. 9 Guatemala
sp. 10 Guatemala

KEY TO THE SPECIES OF *POPILIUS*

Note: *P. amazonicus* Gravely is not included in the key because no specimens were available and the distinguishing characters are not distinctive enough to permit differentiation of this species from others.

1. Posterior margin of prothorax with deep, semicircular emargination on each side of mid-line, forming rounded median lobe between them; frons without inner tubercles …………………..………………………………………...…*abnormalis* Luederwaldt

1’. Posterior margin of prothorax with margin evenly curved, rounded; frons with inner tubercles………...........………..…………..……………………………..…………2

2 (1’). Last visible sternite medioposteriorly tuberculate; each parietal ridge with transverse groove; upper surface of dorsal mandibular tooth rugose or coarsely punctate; dorsal surface of base of mandible tuberculate……………………………*eclipticus* (Truqui)

2’. Last visible sternite not tuberculate, upper surface of dorsal mandibular tooth almost always smooth, rarely rugose (*P. hirsutus*); dorsal surface of base of mandible smooth, punctate or rugose; parietal ridges rarely (sp. 10 Guatemala) with transverse groove………...…3

3 (2’). Posterior angle of mesepisternum setose; outer tubercles vertical, on transfrontal sulcus; mesepisternum punctate and matt to hind angle (tip shiny or matt), rarely (*P. erotylus)* with only a punctate anteroventral matt patch ……………………………… ……………………………..…Marginatus Species Group (South American species)…4

3’. Posterior angle of mesepisternum glabrous; outer tubercles on transfrontal sulcus, slightly surpassing clypeal margin; mesepisternum anteroventrally impunctate or punctate and smooth, occasionally with only a punctate, anteroventral matt patch, not punctate and matt to hind angle …Haagi Species Group (Mesoamerican species)…13

4 (3). Metasternum with at least some setae in lateral groove (occasionally not to posterior tip) and near mesocoxae, but not with entire anterolateral area setose to posterior tip of lateral area; 8th antennal segment at least 3.5 times as wide as long; usually with 1-2 small spurs on outer margin of meso- and metatibiae, 3-5 antennal lamellae........5

4’. Metasternum with entire anterolateral area setose to posterior tip of lateral area; 8th antennal segment no more than 3 times as wide as long; usually without spurs on outer margin of meso- and metatibiae, 3 antennal lamellae.......................................11

5 (4). Lateral margins of metasternum setose only in anterior 1/10; posterior margin of mesofemur and metafemur usually glabrous, occasionally with up to 5 setae; posterolateral area of metasternum not completely impunctate……………………....6

5’. Lateral margins of metasternum setose to posterior tip, posterior margin of mesofemur and metafemur setose, posterolateral area of metasternum impunctate...10

6 (5). Antenna with three lamellae……………………..………..…..…...............….........7

6’. Antenna with four or five lamellae…………………………………………..………..9

7 (6). Tip of central tubercle even with parietal tubercles; prosternal process glabrous posterior to procoxae; antennal segments 5 and 6 triangular, anteriorly acute…………….…………….….…………………...……*marginatus* (Percheron)

7’. Tip of central tubercle posterior to level of parietal tubercles; prosternal process anterolaterally setose just posterior to procoxae; antennal segments 5 and 6 quadrangular, anteriorly truncate…………………….……………………………….8

8 (7). Transfrontal sulcus straight or slightly concave; anterior marginal groove of pronotum punctate in lateral 2/3-4/5; mesosternum posteromedially lightly matt; connection between central tubercle and frontal ridges a single narrow ridge; subocular ridge absent or indistinct………………. *erotylus* Reyes-Castillo & Castillo

8’. Transfrontal sulcus distinctly bi-arcuate; anterior marginal groove of pronotum impunctate; mesosternum posteromedially shiny; connection between central tubercle and frontal ridges indistinctly double and usually wide; subocular ridge short (no more than 1/2 way to posterior margin of antennal fossa)…………..…sp. 1 Colombia

9 (6’). Prosternal process posteriorly shiny, matt only in transverse anterior band; left mandible bifid, right mandible trifid; profemoral groove setose; tip of terminal spur of protibia blunt; antenna with four lamellae………………....…*magdalenae* Boucher

9’. Prosternal process completely matt; mandibles apically trifid; profemoral groove glabrous; tip of terminal spur of protibia sharp; antenna with four or five lamellae ……...…………………………………….…………...…*tetraphyllus* (Eschscholtz)

10 (5). Frontal ridges arise from two close ridges from anterior base of central tubercle; dorsal tip of central tubercle posterior to parietal ridges, with structure indented medially; frontal ridges and parietal ridges about parallel; central tubercle usually high, erect; profemoral groove glabrous; lateral area of metasternum widened subapically, narrowed at very tip; left mandible bifid, right mandible trifid ………….
…………………………………………………………….*refugicornis* Buehrnheim

10’. Frontal ridges arise directly from anteromedial tip of central tubercle; dorsal tip of central tubercle anterior to parietal ridges; frontal ridges and parietal ridges divergent laterally; central tubercle low; frontal ridges arise directly from anteromedial tip of central tubercle; profemoral groove setose; lateral area of metasternum uniformly narrow posteriorly; both mandibles apically trifid……………...….…sp. 2 Venezuela

11 (4’). Anterior face of procoxa just posterior to trochanter medially glabrous; elytral humeri setose only ventrally; hypostomal process laterally convex; pronotum laterally glabrous; central tubercle even with or posterior to parietal tubercles…...sp. 3 Bolivia

11’. Anterior face of procoxa just posterior to trochanter medially setose; elytral humeri completely setose; hypostomal process longitudinally grooved or flattened; pronotum usually with a few short, fine setae laterally; central tubercle sometimes anterior to parietal tubercles……………….…………………………………….........….…...12

12 (11’). Mesosternal scars with short, fine setae, a few setae often between the scars and the posterior margin of the mesosternum; left internal tooth bifid; central tubercle distinctly anterior to parietal tubercles……………………….…..…...sp. 4 Venezuela

12’. Mesosternal scars glabrous; left internal tooth trifid; central tubercle even with, posterior to, or rarely anterior to parietal tubercles …..gibbosus (Burmeister) complex

13 (3’). Mesepimeron glabrous; clypeus anteriorly with a rugose patch at least between outer tubercle and frontogenal suture; lateral depression of metasternum glabrous or setose only in anterior 1/10………………….…………………………………………...…14

13’. Mesepimeron setose; clypeus anteriorly smooth from frontogenal suture to tip of canthus; lateral depression of metasternum setose in anterior 1/10 to 7/8 (only *P. punctatissimus* is setose in the anterior 1/10)…….………..........................……….15

14 (13) Clypeus anterior to transfrontal sulcus very short, about equal to length (anterior-posterior) of transfrontal sulcus; mandibles apically trifid; central tubercle and parietal tubercles present, but not linked by ridges; parietal ridges absent; left inner tooth bifid; mesosternum anteriorly with transverse band of setae at extreme anterior margin…......……………………...………………………………...….sp. 5 Panama

14’. Clypeus anterior to transfrontal sulcus distinctly longer (anterior-posterior) than transfrontal sulcus; mandibles apically bifid; central tubercle and parietal tubercles connected by parietal ridges; left inner tooth trifid; mesosternum anteriorly completely glabrous and shiny……………………………………..…....sp. 6 Mexico

15 (13’). Anterior process of first complete, visible abdominal sternite (between and just posterior to metacoxae) glabrous; lateral depression of metasternum uniformly

narrow posteriorly; mesosternum posteromedially finely punctate/rugose or matt; parietal ridges evenly angulate or rounded dorsally ……………….………...……...16

15’. Anterior process of first complete visible abdominal sternite (between, and just posterior to, metacoxae) setose, usually thickly (sp. 8 Guatemala has 2-3 setae); posterior portion of lateral depression of metasternum widened subapically, narrowed at very tip; mesosternum posteromedially smooth, shiny; parietal ridges usually with a transverse dorsal groove (sp.9 Guatemala has evenly angulate or rounded parietal ridges)………………………………………………………………………..…23

16 (15). Frons glabrous; mentum medially glabrous; anterior marginal groove of pronotum impunctate; pronotum laterally impunctate…………………………....…sp. 7 Mexico

16’. Frons setose anterior and posterior to parietal ridge; mentum with at least 1-3 setae medially; anterior marginal groove of pronotum punctate in lateral 2/3 to 3/4; pronotum laterally punctate at least in and around the lateral depressions……...…..17

17 (16’). Frontal ridges arise directly from anteromedial tip of central tubercle or from a short, single ridge just anterior to base of central tubercle; mentum posteromedially shiny; labrum anteriorly symmetrical; hypomeron medially with a moderately wide matt area with a concave lateral margin…...……………………………………………..….18

17’. Frontal ridges arise from a single or double ridge well anterior to base of central tubercle; labrum projecting further on left side than right; mentum posteromedially matt, rarely (some *P. punctatissimus*) shiny; hypomeron medially with a wide matt area with a straight, convex or slightly concave lateral margin……….……………19

18 (17). Frontal ridges arise directly from anteromedial tip of central tubercle, and meet posteromedially at an angle of about 120°; postmesocoxal grooves widely separate medially (greater than distance between mesocoxae); mentum posteromedially shiny; inner tubercles distinct and at least equal in height to outer tubercles; mesosternal scar posteriorly (“tail”) short, extending about halfway or less to end of mesepisternum; mesepisternum with distinct anteroventral matt patch....*haagi* (Kaup)

18’. Frontal ridges arise from a single ridge just anterior to base of central tubercle, and meet posteromedially at an angle of about 45°; postmesocoxal grooves with a depression between medial ends of the grooves; mentum posteromedially matt; inner tubercles indistinct, or distinct, but usually lower than outer tubercles; mesosternal scar posteriorly (“tail”) long, extending about to end of mesepisternum); mesepisternum with matt puncture rims, but without distinct anteroventral matt patch………...*klingelhoefferi* (Kaup)

19 (17’). Subocular ridge irregularly raised, partially obscured by strong punctures; postmesocoxal grooves with a depression between the medial ends of grooves or connected medially…………………..………………………………………………20

19’. Subocular ridge evenly raised; postmesocoxal grooves widely separate medially (greater than distance between esocoxae)……………………….....………...…...…22

20 (19). Elytral humerus sparsely setose; mesosternal scar anteriorly expanded (about 1/3 width of mesosternum) and thick; mesosternal scar anteriorly (“head”) setose; pronotal arm widely setose, matt; right dorsal mandibular tooth anteriorly (lateral view) obtuse or right-angled; canthus evenly wide, rounded or obtusely angled laterally……….……………………...………………....*scutellopunctatus* Kuwert

20’. Elytral humerus glabrous; mesosternal scar anteriorly slightly expanded medially or wide (~1/3 width of mesosternum) but narrow; mesosternal scar glabrous; pronotal arm shiny, setose only close to prosternal process or glabrous; right dorsal mandibular tooth anteriorly (lateral view) projecting; canthus narrowest medially, expanded apically, and angulate laterally……………………………………..…..21

21 (20’). Anterior margin of pronotum slightly recurved at lateral third, anterior angles very slightly projecting; pronotum (excluding the marginal grooves) anterolaterally punctate, laterally punctate above lateral depressions and onto disc (at least 3 punctures on disc on each side); lateral depression of metasternum setose only in anterior 1/10; frontal ridges diverge in concave, curved lines from origin to inner tubercles and meet medially at angle of about 180° or connected in even arc; postmesocoxal grooves with depression between medial ends of grooves …………… ……………………………………………………..….*punctatissimu*s Luederwaldt

21’. Anterior margin of pronotum straight, anterior angles rounded, not projecting; pronotum (excluding the marginal grooves) anterolaterally impunctate, laterally punctate only punctate in and around lateral depressions; lateral depression of metasternum setose in anterior 1/2; frontal ridges diverge in convex, recurved lines from central tubercle to inner tubercles and meet medially at angle of about 45°; postmesocoxal grooves connected medially………..……………..…....l*enzi* Kuwert

22 (19’). Transfrontal sulcus about straight; elytral humerus sparsely setose; prosternal process narrowly truncate posteriorly; upper surface of right dorsal mandibular tooth concave (lateral view), rugose or coarsely punctate (dorsal view)……….*hirsutus* Luederwaldt

22’. Transfrontal sulcus recurved laterally, bi-arcuate; elytral humerus glabrous; prosternal process acute posteriorly; upper surface of right dorsal mandibular tooth straight or even (lateral view), smooth (dorsal view)…...……………...*mysticus* Bates

23 (15’). Central tubercle with free tip, turned upward apically; subocular ridge short, extending about half the distance to posterior margin of the antennal fossa); mentum glabrous medially; frontal ridges diverge in straight lines from origin to inner tubercles; elytral humeri glabrous…..………..…………………….…sp. 8 Guatemala

23’. Central tubercle low and without a free tip; subocular ridge reaching posterior margin of antennal fossa in acute angle; mentum punctate and setose medially; frontal ridges diverge in convex, recurved lines from origin to inner tubercles; elytral humeri setose either dorsolaterally or ventrolaterally………………………………………………24

24 (23). Parietal ridges evenly angulate or rounded dorsally; frontal ridges arise directly from anteromedial tip of central tubercle; frontal ridges meet medially at angle of about 180°; postmesocoxal grooves connected medially; anterior marginal groove of pronotum evenly deep…………...……...sp. 9 Guatemala

24’. Parietal ridges with a transverse dorsal groove; frontal ridges arise from single or double ridge well anterior to base of central tubercle; frontal ridges meet medially a angle of about 45°; postmesocoxal grooves widely separate medially (greater than the distance between mesocoxae); anterior marginal groove of pronotum deeper anteromedially……………………………………………………….sp. 10 Guatemala

CHAPTER V

THE SPECIES OF *POPILIUS*

ABNORMALIS SPECIES GROUP

The Abnormalis Species Group is diagnosed by: frons without inner tubercles; posterior margin of prothorax with a deep, semicircular emargination on each side of the mid-line, forming a rounded median lobe between them.

This species group contains one aberrant, very distinctive species, *P. abnormalis*, which is known only from the holotype. The type was not available for examination so I was unable to evaluate other characters that might allow placement of this species in one of the other species groups or in a different genus.

Popilius abnormalis **Luederwaldt, 1941**

Popilius abnormalis Luederwaldt, 1941: 79. Type material not seen. According to Pereira (Luederwaldt, 1941; Pereira edited Luederwaldt's manuscript and published it under Luederwaldt's name after the latter's death), the holotype was deposited in the Division of Insects, MZSP, with the accession number 23.000, presumably with labels indicating the type locality as Guayabo, Costa Rica and the collector as A. Alfaro. The type material apparently consisted of a single specimen. Attempts to contact the MZSP regarding this specimen were not answered.

Original Description. A translation of Luederwaldt's description of *Popilius abnormalis* (1941) follows (italics as included in the original):

> Length 22mm. Labrum slightly concave. Antennal lamellae robust, first article 2 1/2 times as wide as long. Mandibles with three terminal teeth. Head finely rugose and punctate throughout. Lateral tubercles and frontal area finely punctate, clypeus rather narrow, anteriorly with a small concavity, posteriorly straight; lateral tubercles forming a large plate, slightly convex, ending and narrowing posteriorly. Horn indistinct, with a short prominence and curved downward, without a free tip. Frontal ridges evenly strong, arising in front of the point of the horn and tied to the point by two slightly convex ridges which form an obtuse angle at the base, very distinct and without the internal tubercles. Frontal area short and broad, ending in the clypeus. Supraocular ridge with a

> weak angle near the summit. Pronotum above finely rugose and opaque, and very shiny in the lateral margins. Anterior angles slightly rounded. Lateral and anterior grooves punctate, the former narrow, the latter somewhat longer and wider than the lateral. Marginal area above the scars strongly punctate and with some punctures on the disk. *Posterior border of the pronotum on both sides of the scutellum strongly indented in a semicircle, forming thereby a rounded lobe, with an angle in the beginning of the indentation*, where the lateral grooves end, which continue very finely to the base of the median angle. Scutellum very punctate, smooth only in the midline. Dorsal striae of elytra finely punctate and with punctation larger laterally, with all the interstriae rather wide and flat. Mentum punctate overall, with the lateral lobes pubescent and the scars indistinct. Prosternum broadly truncate behind. Mesosternum shiny, in the place of the scars with a curved mark, narrow and opaque. Metasternum in the anterior areas sparsely punctate and with a few very fine hairs. Middle and hind tibiae pubescent and with longitudinal rows of punctures placed within sulcae, and with one tooth visible anterior to the tip. Episterna narrow, poorly delineated and glabrous. One specimen. Guayabo, Costa Rica. IV 1931, A. Alfaro leg.

No specimen was available for examination, so no additional description was possible.

Diagnosis. This species is distinguished by two characters unique within *Popilius*, the frons without inner tubercles and the posterior margin of prothorax with a deep, semicircular emargination on each side of the mid-line, forming a rounded median lobe between them. Length 22mm.

Geographical Distribution and Ecology. Despite extensive collecting in the Turrialba area on the Caribbean slope of Costa Rica, this species is known only from the type locality. No ecological data were recorded.

Locality Data. According to Luederwaldt (1941), the collection locality is Guayabo, Costa Rica. Guayabo is in the vicinity of Turrialba, Cartago Province (A. Solis, personal communication).

Exemplar Material. No specimens were available for study, so an exemplar was not included in the phylogenetic analysis.

Remarks. *Popilius abnormalis* is aptly named and should be easily identifiable, as the form of the posterior margin of the pronotum is unique in the Passalidae. Despite Luederwaldt’s description and figure (line drawing) giving the impression of a specimen deformed by genetic malfunction or physical damage during the pupal stage, I am informed (Fonseca, personal communication) that the specimen is not teratoid, and that the specimen is symmetrical and shows no evidence of injury or significant wear (e.g. the central tubercle). The absence of inner tubercles in this species is unique in *Popilius*, and suggests that the species may be more appropriately placed in another genus, possibly *Petrejoides*, when the holotype (the only known specimen) can be examined. The distinguishing characters are so distinctive that the species could be included in the key, despite the lack of an exemplar.

Comparison of the description of *P. abnormalis* with specimens of *P. punctatissimus*, the only other similarly sized representative of the genus known to occur near the type locality of *P. abnormalis*, suggests that these species are probably not conspecific, although they share glabrous episterna (setose only in the anterior 1/10), an uncommon character among Mesoamerican *Popilius* spp.). They differ in the implied length of the clypeus (shorter than that of *P. hirsutus*, comparing the original descriptions of which are three pages apart), number of ridges linking the frontal ridges to the central tubercle (*P. punctatissimus* has one), the lack of inner tubercles (present in *P. punctatissimus*), and several other characters. Both taxa were described in the same paper, so the author must have been convinced of the significant differences between them (Luederwaldt, 1941).

Similarly, comparison of the description of *P. abnormalis* with that of *Petrejoides subrecticornis* (in Castillo and Reyes-Castillo, 1984), a species of similar size and shape known from Costa Rica, which does have a narrow clypeus, also reveals significant differences. *Petrejoides subrecticornis* differs in having inner tubercles, central tubercle with a free (although short) tip, supraocular ridge with two tubercles, and an impunctate scutellum, among other details.

A trip was made in early 2002 to search for this species. Much of the Turrialba area is now mixed agricultural and urban. Passalids were collected at slightly higher elevations to the north and northwest, but no *Popilius* were encountered. Specimens of *P. punctatissimus* were collected by A. Solis about 30 km to the east of Turrialba in primary forest in the Reserva Biologica Barbilla, Limon Prov., at a similar elevation to the type locality of *P. abnormalis*.

ECLIPTICUS SPECIES GROUP

The Eclipticus Species Group is diagnosed by: last visible sternite medioposteriorly tuberculate, dorsal tooth of mandible dorsally (dorsal view) rugose or coarsely punctate; dorsal surface of base of mandible tuberculate, each parietal ridge with a transverse groove; frons with inner tubercles; posterior margin of prothorax without a deep, semicircular emargination on each side of the mid-line.

This species group currently contains a single, geographically widespread and highly variable species that usually comprises most of the specimens of *Popilius* in museum collections.

***Popilius eclipticus* (Truqui, 1857)**

Passalus eclipticus Truqui, 1857:261 (sep.: 4). Holotype in MNHN with labels a) "Soranus Passalus eclipticus T. Mex. Mn" (with "Passalus" lined out), b) "Collection Mniszech", c) "Ex-Musaeo Van Langsberge". Without a type label.

Popilius felschei Kuwert, 1891:173. Holotype at MNHN with labels a) "Felschei Kuw. Guatemala", b) Ex-Musaeo A. Kuwert 1894", c) "Popilius abud Kuwert" (the third label is written in Oberthur's hand, according to S. Boucher; personal communication).

Popilius frantzi Kuwert, 1897:297. Lectotype in HLMD with labels a) Costarica Frantz (green label), b) Popilius frantzi Kuw., c) Kuwert det., d) LECTOTYPE (red label), e) LECTOTYPE frantzi Kuwert 1897, S. Boucher det. 97. Paralectotype in HLMD with labels a) 27308, b) PARALECTOTYPE (red label), c) PARALECTOTYPE frantzi Kuwert 1897, S. Boucher det. 97. New synonymy.

Popilius guatemalae Gravely, 1918: 27. Type material not seen, presumably in the collection of the Indian Museum (now Zoological Survey of India), Calcutta, India.

Popilius varius Kuwert, 1891:172. Holotype at MNHN with labels a) "varius Kuw. Am. centr", b) "Ex-Musaeo A. Kuwert 1894", c) "Popilius abud Kuwert" (the third label is written in Oberthur's hand, according to S. Boucher; personal communication).

I examined the types of *P. eclipticus, P. felschei* and *P. varius* and collected data on 74 morphological characters, and examined the lectotype and paralectotype of *P. frantzi*. Attempts to contact the Zoological Survey of India regarding the type of *P. guatemalae* were unsuccessful.

Original Description. A translation of Truqui's description of *Popilius eclipticus* (1857) follows:

> Somewhat convex, ventral margin of pronotum and mesotibia with dense, yellowish-brown hair; clypeus punctate, shiny, strongly marginate, tuberculate on both sides; central tubercle transvers, medially longitudinally carinate, carina produced as far as frontal carinae, central tubercle basally carinate, adjacent; frontal carinae jointly arcuate and distant from the transverse central tubercle, short, terminating in a small (inner) tubercle; frontal rim tri-tuberculate, external tooth of the lower tubercle dentate; ocular tooth obtuse;frontal depressions densely punctate; pronotum very smooth, on both sides posteromedially smoothly impressed; deeply, sparsely punctate in and

> around the impression; elytra strongly striate, striae punctate throughout; mesotibia armed with a spine, metatibia nearly unarmed. - Length, 32mm; elytral length 19mm; width 11.5mm.

Truqui (1857) noted that he was informed that the specimen was from Mexico.

Description. *Head*: Frons with inner tubercles; each parietal ridge with a transverse groove; dorsal tooth of mandible dorsally (dorsal view) rugose or coarsely punctate; dorsal surface of base of mandible tuberculate. *Pronotum*: Posterior margin of prothorax without a deep, semicircular emargination on each side of the mid-line. *Abdomen*: Last visible sternite medioposteriorly tuberculate. *Male Genitalia*: With or without a pair of prominent, sclerotized tubercles just inside the opening of the internal sac of the male genitalia. *Length*: 25.5-37.5 mm (25.5-32.0 mm in Panama).

For the description of all characters examined in each of the five exemplars, see the *Popilius* matrix at Appendix D-2.

Diagnosis. This species can be distinguished from all other species in the genus by the medioposterior tubercle of the last visible sternite, present in both sexes. The transverse groove on each lateral ridge is a very distinctive character shared with only two uncommon, apparently not closely related species of *Popilius* from Guatemala, *P*. spp. 8 and 10. Length 25.5-37.5 mm (25.5-32.0 mm in Panama).

Geographical Distribution and Ecology. *Popilius eclipticus* is the species with the widest distribution in the genus, known from central Mexico to northern South America, and from near sea level to at least 2438 m (Chiapas, Mexico and Suchitepeque, Guatemala).

Very little host information has been recorded, but several collections at high elevations in Mexico (Chiapas), Guatemala (Baja Verapaz) and Honduras (Comayagua) have been made from rotting pine logs. Reyes-Castillo (1970b) notes that specimens have been collected in Mexico in a wide variety of habitats, from tropical rain forest to montane tropical forest and cloud forest. Reyes-Castillo and Castillo (1992) report that this species is relatively abundant in disturbed areas, where it is often the only passalid species present.

The Panamanian form is found from near sea level to about 1000 m. In eastern Panama (east of the canal area) this form often inhabits the same logs as *P. erotylus* (personal observations); it is sympatric with *P. punctatissimus* in western Panama.

***Locality Data*.** 574 specimens examined from AMNH, ARGC, BDGC, CASC, CFSC, DJCC, EDRC, EMEC, FMNH, IDEM, INBC, LACM, MCZ, OSU, TAMU, UNSM, USNM.

BRAZIL (24). CAYO (2): Blancaneaux Cave (road to) (CMNH), Mountain Pine Ridge (ARGC). ORANGE WALK (1): Rio Bravo Conser. Area (env. La Milpa ruins) (ARGC). TOLEDO (21): Punta Gorda (1 km W), San Jose (3.5 mi. N) (ARGC).

COLOMBIA (1). S.A. Felipe Ovalle Q (AMNH).

COSTA RICA (203). ALAJUELA (1): San Ramon (Res. Biol. Alberto Brenes, Rio San Lorencito) (INBC). CARTAGO (45): Grano de Oro (Chirripo, Turrialba, A. C. Amistad) (INBC), Hamburg Farm (south slope Volcan Irazu, Reventazon) (USNM). GUANACASTE (48): A.C.G. La Cruz (Est. Biol. Maritza, P.N. Guanacaste) (INBC), Derrumbe (Estacion Cacao, W side Volcan Cacao) (INBC), Estacion Cacao (2km SW side Volcan Cacao) (INBC), Estacion Maritza (west side Volcan Orosi) (INBC), Estacion Mengo (SW side Volcan Cacao) (INBC), Estacion Pitilla (9 km S Sta. Cecilia) (INBC), Hacienda Orosi (La Maritza) (INBC), Los Almendros (P. N. Guanacaste) (INBC). HEREDIA (6): Estacion El Ceibo (P. N. Braulio Carrillo) (INBC), Estacion Magsaysay (P. N. Braulio Carrillo) (INBC). LIMON (17): Estacion Hitoy-Cerere (Rio Cerere Res. Biol.) (INBC). PUNTARENAS (64): Buen Amigo (San Luis, Monteverde, A. C. Amistad) (INBC), Estacion Biol. Las Alturas (Coto Brus) (INBC), Estacion La Casona (Res. Biol. Monteverde) (INBC), Estacion Leonel Hernandez (Res. Biol. Monteverde) (INBC), Estacion Pittier (Coto Brus) (INBC), Estacion Quebrada Bonita (R. B. Carara) (INBC), Finca Cafrosa (Est. Las Mellizas, P. N. Amistad) (INBC), Las Mellizas (INBC), Los Mogos (INBC), Monteverde (EMEC, INBC, LACM, OSU, TAMU, UNSM, USNM), Quetzal (Monteverde area) (LACM), Parrita (INBC), Rancho Quemado (Peninsula de Osa) (INBC), Rio Negro (25 mi. NE La Union) Idem), San Luis (Monteverde) (INBC), Zona Protectora Las Tablas (1.5 km NE de la Estacion) (INBC). SAN JOSE (20): Fila El Alto (road between Legua and San Francisco) (INBC), Hacienda Tiquires (Rio Tiquires) (INBC), La Palma (LACM), Rancho Redondo (IDEM), Rio Durazno (W Volcan Irazu) (USNM). NO FURTHER DATA (2) (AMNH, USNM – ex. determined as P. frantzi by J.R. Dibb).

ECUADOR (1). PICHINCHA (1): Tinalandia (12 km. SE Santo Domingo) (USNM).

GUATEMALA (55). BAJA VERAPAZ (9): Chilasco (6.6 km W) (BDGC), Purulha (ARGC, IDEM), Union Barrios (IDEM), La Cumbre (Km 138, Guatemala-Coban) (IDEM). IZABAL (1): Modesto Mendez (IDEM). PETEN (40): Piedras Negras (USNM), No further data (ARGC). SUCHITEPEQUEZ (3): Finca El Cipre (CASC), Moca (AMNH). NO FURTHER DATA (2): “Concepcion, Pinulha” (IDEM), (USNM).

HONDURAS (13). CHOLUTECA (1): Tiger Is. (peak) (EMEC). COMAYAGUA (3): Comayagua (24 mi. SE) (IDEM). CORTES (2): Lago Yojoa (Pena Blanca) (EMEC).

FRANCISCO MORAZAN (5): Cerro Uyuca (30 km E Tegucigalpa) (BGC), Zamorano (ARGC, OSU, USNM). LA PAZ (1): La Paz (USNM). OCOTEPEQUE (1): Guisayote (DJCC).

MEXICO (55). CAMPECHE (2): Escarcega (IDEM). CHIAPAS: (40): Angel Albino Corzo (above Finca Custepec) (CASC), Cate-Jitotol (9 km) (IDEM), Cinco Lagos (Lagunas de Montebello, Mpio. La Trinitaria) (CFSC), Hoja Blanca (6 km before; Mpio Escuintla) (IDEM), Huixtla (24 mi. N) (EMEC, IDEM), Lacanja Chansayab (IDEM), La Cienega (4-6 km NW, 40 km NW Las Cruces, Mpio. Cintalapa) (CASC), Lagunas de Montebello (Mpio. La Trinitaria) (IDEM), Motozintla (ridge between Cerro Boqueron and Niquivil) (CASC), Ocosingo (IDEM), Ocozocoautla-Malpaso (Km 39) (IDEM), Palenque (IDEM), Parque Laguna Belgica (20 km N Ocozocoautla) (LACM, UNSM), Rancho Alegre (San Geronimo (Mpio Motozintla) (IDEM), Reserva El Triunfo (Sendero de Finca Prusia) (ARGC), San Jeronimo (IDEM), San Jeronimo (Tacana) (IDEM), Santa Rosa (IDEM), Tuxtla Gutierrez-Acayucan Road (new road, Mile 18) (ARGC), Tziscao (2 km. before, Lagos de Montebello) (IDEM). OAXACA (2): Finca San Carlos (Mpio. Matias Romero) (CASC), San Jose Chiltepec (Naranjal) (IDEM). PUEBLA (2): Villa Juarez (IDEM), Finca Elena (Villa Juarez) (IDEM). QUINTANA ROO (6): Carrillo Puerto (IDEM). VERA CRUZ (3): Jalapa (AMNH), Tierra Blanca (FMNH).

NICARAGUA (8). JINOTEGA (2): Carretera Matagalpa-Jinotega (Km. 147.5) (IDEM), Santa Martha (18 km N Matagalpa) (CASC). RIO SAN JUAN (6): Bartolo Field Station (Rio San Juan, ca. 2mi. SE El Castillo) (ARGC), Refugio Bartolo (confluence of Rio San Juan and Rio Bartolo) (ARGC).

PANAMA (211). CHIRIQUI (13): Jaramillo Abajo (3 km E Boquete) (ARGC), Lagunas del Volcan (5 km SW Volcan) (ARGC), Reserva la Fortuna (ARGC), Santa Clara (EGRC, UNSM), Santa Clara (I km NW; 7 km NE) (ARGC), Volcan (14 km W) (ARGC). COCLE (3): Cerro Gaital (DJCC), La Mesa (N El Valle) (ARGC, DJCC). COLON (69): Gatun (5 km W) (ARGC), Maria Chiquita (5 km E; 6 km E) (ARGC), Pipeline Road (11 km NW Gamboa) (ARGC), Santa Rita Ridge (from east of Sabanitas to 4 km S Cerro Santo Domingo) (ARGC, UNSM). DARIEN (39): Cana (Pirre Ridge Trail, 720-1225 m) (ARGC). PANAMA (84): Barro Colorado Island (FMNH, OSU), Cerro Azul (ARGC, OSU), Cerro Campana (west side) (ARGC), Cerro Jefe (ARGC, UNSM), El Llano-Carti Road (Km. 7.5; Km. 8) (ARGC). VERAGUAS (3): Cerro Tute (8 km W Santa Fe) (ARGC).

VENEZUELA (1). Los Camales (no further data; possibly “Los Canales”?) (FMNH).

NO DATA (2) (USNM).

Exemplar Specimens. Five exemplars representing different body sizes and different areas within the distribution of this taxon were examined and scored for the matrix, supplemented by additional specimens.

Exemplar 1 (ecliptEx1, Appendix D-2). Western Mesoamerica, high elevation: Mexico: Sta. Rosa, Estado de Chiapas, VIII-1962 G. Halffter (male with genitalia dissected - IDEM).

Exemplar 2 (ecliptEx2, Appendix D-2).. Western Mesoamerica, low elevation: Belize: Toledo District, 3.5 mi. N. San Jose, N16°18’21” W89°06’37”, 14-16-VI-2001 (male with genitalia dissected - ARGC).

Exemplar 3 (ecliptEx3, Appendix D-2).. Central Mesoamerica, high elevation: Costa Rica: Puntarenas, Monteverde 1400’, 16-VII-1989, R.H, Pine (teneral female, INBC). Second teneral female with same data used for confirmation (INBC). Costa Rica: Punt. Monteverde, 1400m, 28 May 1990, Sikes & Longino (male with genitalia dissected - LACM).

Exemplar 4 (ecliptEx4, Appendix D-2).. Costa Rica. Costa Rica: no further data (USNM). This specimen was determined as *Popilius frantzi* by J.R. Dibb; there is evidence of old dermestid damage, and the genitalia are missing.

Exemplar 5 (ecliptEx5, Appendix D-2).. Panama, low elevation: Panama: Panama Prov., Km.7.5 El Llano-Carti Rd., elev. 350m, 6-VII-95, A.R. Gillogly (male with genitalia dissected – ARGC).

Remarks. *Popilius felschei* was described by Kuwert (1891) and then relegated to a form (Kuwert, 1897) without nomenclatorial. *Popilius guatemalae* was determined to be a synonym *of P. eclipticus* by Hincks (1953). *P. varius* was synonymized with *P. eclipticus* by Reyes-Castillo and Castillo (1992) after comparison of the holotypes. Here, I add *P. frantzi* as a synonym of *P. eclipticus*.

P. frantzi was included in the “*eclipticus* group” by Dibb (1938), who distinguished this species by its length (>30 mm), the frontal ridges that almost reach and join the outer tubercles, and by the longitudinal depression immediately at the foot of the apex of the central tubercle. Dibb (1940) differentiated *P. frantzi* from *P. eclipticus* by the frontal ridges almost reaching and joining the outer tubercles, and a longitudinal depression present immediately at the foot of the apex of the central tubercle. Both species were defined as containing specimens over 30 mm in length. There appear to be very few determined specimens of this species (none to my knowledge in the last 60 years), despite the relatively large numbers of this species group that have been collected in Costa Rica. A specimen of *P. frantzi* determined by J. R. Dibb (in the USNM) was used as an exemplar in this study. I examined the lectotype (a teneral specimen in excellent condition) and paralectotype of *P. frantzi* (in HLMD), which are from Costa Rica and

Mexico, respectively. I conclude that they are conspecific with *P. eclipticus*, and are most similar to the larger western form (see below).

Determined specimens of *P. eclipticus* from Belize (8), Costa Rica (37), Guatemala (8), Honduras (5), Nicaragua (1) and Panama (4) were checked for the characters considered to be diagnostic for *P. frantzi.* Fourteen specimens had all three characters, one specimen each from Belize, Guatemala and Mexico, and 11 from Costa Rica. The Costa Rican specimens were from only 4 of the 13 localities from that country in this sample, all from over 1100 m in elevation. Of the total of 22 specimens from these four localities, nine had either an extended frontal ridge or depression at the foot of the central tubercle, and two had neither character. Ten were over 30 mm in length, and 12 were less than 30 mm. None of the three diagnostic characters for *P. frantzi* was consistently present in any of the examined populations of this species group.

However, both the geographical and elevational distributions of *P. eclipticus* are unusually broad for passalid species, and there is great variation in the topology of the dorsal surface of the head. This strongly suggests that more than one species may be included within what is recognized as this taxon. A similar breadth of elevational distribution in the genus *Pseudepisphenus* in New Guinea has been found to involve a complex of species (Boucher 1990, 1991a, 1992, 1993).

Although there is considerable variation in size (length) among specimens of *P. eclipticus* collected from the same locality, individuals from elevations over 1000 m tend to be noticeably larger than those from lower elevations. This is evident in the material from Costa Rica, Guatemala, Mexico and Panama, the countries best represented among the specimens examined. The topology of the dorsal surface of the head is also quite variable within series. There is a tendency for specimens from higher elevations in the Monteverde area of Costa Rica to have higher central tubercles with an almost or very slightly free tip, and a few setae in the lateral depressions of the pronotum, but these characters also vary within series.

Despite the considerable variation in morphology and the long series and wide distribution of the examined specimens, I have found no external characters that will consistently separate populations.

During this study, I have noted that the male genitalia of *P. eclipticus* are quite distinct from those of all other *Popilius* species; the median lobe is rigidly attached to the parameres in the medial half, the parameres are widely fused to the basal piece, the entire capsule is strongly pigmented and sclerotized, and the temones are very short, stout and attached diagonally. However, the internal sac occurs in two distinct forms, completely membranous or with a pair of prominent, sclerotized tubercles just inside the opening.

The only character that I have found useful in distinguishing populations within *P. eclipticus* is the presence or absence of the sclerotized tubercles at the base of the internal sac of the male genitalia. Both character states are shared with other species of *Popilius* and related genera, but both have not been found in any other species, suggesting that *P. eclipticus* currently encompasses a cryptic species complex. Specimens from Mexico to Nicaragua lack these tubercles, as do Costa Rican specimens from higher elevations, whereas the tubercles are present in male specimens examined from throughout Panama and from several localities at low elevations (100-700 m) along both the Caribbean and Pacific coasts of Costa Rica. This population is uniformly small for the species (25.5-32.0 mm). The presence of these prominent tubercles is a distinctive character shared with only three species currently included in *Popilius* (*P. haagi*, sp. 5,and sp. 9). In addition, apparently homologous tubercles are present in the exemplars of *Chondrocephalus* sp. (Mexico), *Spurius* sp. (Panama), and *Paxillus leachi* (Panama) examined during the higher-taxon study reported in Chapter II, and in two species of *Petrejoides*. (personal observations). Whether it occurs in taxa not yet examined remains to be determined.

Since I am unable to distinguish the females of these populations, have only this one character to distinguish the populations, and have not made an exhaustive study of the distribution of this character, I choose not to formally separate the eastern population at this time. If this form is found to be consistently distinct from other populations of this species, the holotype of *P. varius* (27 mm in length) should be re-examined to determine to which form it belongs and if the name should be removed from synonymy. The holotype is labeled “Am. centr”, although Kuwert’s (1897) description of the species states, probably in error, “Amazonengebiet”.

It may be significant that the distribution of the larger specimens of *P. eclipticus* appears to be similar to that of endemic pines in Central America. There are no endemic pine forests in Panama (Powell & Palminteri. in press).

MARGINATUS SPECIES GROUP

The Marginatus Species Group is diagnosed by: posterior angle of mesepisternum setose; outer tubercles on transfrontal sulcus, vertical; mesepisternum punctate and matt to the hind angle, rarely (*P. erotylus)* with only a punctate anteroventral matt patch; outer tubercles on transfrontal sulcus, vertical; inner tubercles present; last visible sternite not medioposteriorly tuberculate; parietal ridges without a transverse groove; posterior margin of prothorax without a deep, semicircular emargination on each side of mid-line.

This species group includes all of the species of *Popilius* that occur in South America except for *P. eclipticus*. Within this clade, two groups of species are distinguishable, with two species intermediate between them. The intermediate species are *P. refugicornis* and *P*. sp. 2 Venezuela.

The species related to *P. marginatus* are characterized by the following diagnosis: the metasternum is setose at least anteriorly in the lateral groove, but never with the entire anterolateral area setose to the posterior tip of the lateral area; the antennal lamellae are wide, with the 8th antennal segment at least 3.5 times as wide as long; the antennae have 3-5 lamellae; the meso- and metatibiae usually have 1-2 small spurs on the outer margin; the posterior angle of the mesepisternum is setose. This portion of the group is widespread, but not known from over 500 m in elevation.

The species most closely related to *P. gibbosus* can be diagnosed as follows: the entire anterolateral area of the metasternum is setose to the posterior tip of the lateral area; the posterior angle of the mesepisternum is setose; the mesepisternum is punctate and matt to the hind angle (tip shiny or matt); the 8th antennal segment is no more than 3 times as wide as long; the meso- and metatibiae usually without spurs on the outer margin. Specimens are reliably known only from 1500-3000 m in elevation on the eastern slope of the Andes of Bolivia, and the Cordillera Oriental of Colombia, including both the western branch (Cordillera de Perija of Colombia) and eastern branch (Sierra Nevada of Venezuela). Two specimens with minimal data are reported to be from the Cauca Valley of Colombia (Gravely, 1918).

The two intermediate species, *P. refugicornis* and *P*. sp. 2 Venezuela, appear to be restricted to low, isolated mountain ranges in eastern Brazil and northern Venezuela.

Gravely created the genus *Oileoides* for two species of *Popilius* (*P. parvicornis* and *P. subrecticornis*) both of which he believed had an extensive patch of setae on the anterior and lateral portions of the metasternum. Subsequently, *O. subrecticornis* was transferred to *Popilius* (the species is now in *Petrejoides*), *O. fischeri* was described as new, and three additional species, *P. gibbosus*, *P. hebes* and *P. villei*, were added to *Oileoide*s based on a specimen of *P. gibbosus* determined by Luederwaldt and unpublished notes left by Luederwaldt (Pereira, 1941), *Oileoides* was synonymized under *Popilius* by Reyes-Castillo (1970b). However, the species of *Popilius* with an extensive patch of setae on the lateral areas of the metasternum, including the type specimens of *P. moritzi* and *P. novus* (personal observations), form a morphologically and geographically discrete array within the South American *Popilius*

***Popilius marginatus* (Percheron, 1835)**

Passalus marginatus Percheron, 1835: 89. Holotype not seen, possibly in the Chevrolat Collection (personal communication, S. Boucher).

Soranus *sieberi* Kuwert, 1897: 295. Lectotype in ZMHB with labels a) Para Sieber, b) Kuwert det. c) Soranus Sieberi Kuw. Para, d) LECTOTYPE (red label), e) LECTOTYPE sieberi Kuwert 1897, S. Boucher 97. Paralectotype in AMHB with labels a) 27311, b) PARALECTOTYPE (red label), c) PARALECTOTYPE sieberi Kuwert 1897, S. Boucher 97, d) Hist.-Coll. (COLEOPTERA) Nr. 27311, Soranus sieberi Kuwert Para, Sieber (green label). The type material was compared with determined specimens of *P. marginatus*. New synonymy.

Original Description. A rough translation of Percheron's original description of *Popilius marginatus* (1835) follows:

> Length 9 1/2 (Note: 9.5 lignes are about 21.4 mm). Body semi-convex. Disk of the head finely punctate laterally; on the vertex is raised a short, conical, elevated, sharp tubercle; at the base are two fairly long, transverse carinae; anterior to the tubercle, two other small, nearly parallel carinae serving as the foundation of a third-semicircle, the extremities of which end in a small tubercle, ending at the lateral margins of the clypeus, which is edged, armed with two small raised teeth; its anterior margin, very flattened, has a small, medial depression; the angles of the head and the ocular carinae are nearly rounded; the labrum is nearly straight. The mandibles are lightly curved, distinctly tridentate; the prementum articulates with the mentum in a sinuate line; the lobes of the mentum are strongly punctate; the lateral depressions of the mentum are obscured by this punctation such that one can not see more than the lower outline. The antennae have the last segment triangular, very depressed, obtuse at the extremity; the sixth and seventh segments have the beginning of lamellae. The pronotum is as wide as high, narrow, lightly concave at the anterior border, the angles of which are almost square; the dorsal groove does not reach all the way to the anterior border of the pronotum; the lateral depressions are rounded, rather impressed, smooth, accompanied by a few small punctures; the scutellum is strongly punctate; the mesosternal scars are absent; the disk of the metasternum has a few sparse punctations, and the abdominal scars are straight, the same breadth throughout, rugose. The elytra with their striae evenly punctate,

> the punctures of which are filled, scarcely marked, well-separated; no part of the body showing noted setation.
>
> This species comes from Brazil, and belongs to the collection of M. Chevrolat."

Kuwert (1898) published a more detailed description in the form of an identification key. An assembled translation follows:

> The transverse lateral ridges not grooved dorsally. There is no longitudinal line present anterior to the foot of the central tubercle to which both frontal ridges connect. From the tip of the central tubercle to the middle of the arc of the frontal ridges run two small, usually indistinct, parallel ridges which are about as far apart as the width of the central tubercle. Posteriorly, a groove medially at the base of the central tubercle. Prothorax punctate in and around the lateral depressions and neighboring area, especially posteriorly. The anterior marginal groove deep. The frontal ridges form an arc that is less than semicircular. The central tubercle anteriorly slightly overhanging. The anterior tooth of the mandible with strong points. Lateral punctation of the metasternum weak, interspersed with fine setae. Disk of the metasternum convex, not bordered, posteriorly margined by a few punctures. Mesosternum with a large, flat depression medially.
>
> Length 25mm. Hab. Colombia.

Description. *Head*: Tip of central tubercle longitudinally even with parietal tubercles; antenna with three lamellae, antennal segments 5 and 6 triangular, anteriorly acute. *Prosternum*: Prosternal process glabrous posterior to procoxae. *Metasternum*: Lateral margins setose only in anterior 1/10; posterolateral area with at least some shallow punctures. *Legs*: Posterior margin of mesofemur and metafemur usually glabrous, occasionally with up to 5 setae. *Length*: 18.0-23.0 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. *Popilius marginatus* appears most similar to *P. tetraphyllus*, also a species from relatively low elevations. It can be separated from the rest of the species in the Marginatus Species Group by having three lamellae, lateral margins of metasternum setose only in the anterior 1/10, tip of the central tubercle longitudinally even with the parietal tubercles, prosternal process glabrous posterior to the procoxae, and antennal segments 5 and 6 triangular and anteriorly acute. Length 18.0-23.0 mm.

Geographical Distribution and Ecology. The range of this species includes much of the Amazon Basin (Argentina, Bolivia, Brazil, Colombia, French Guiana, Peru, Surinam), with the recorded elevations being no higher than 500 m. It is sympatric with *P. magdalenae* and *P. tetraphyllus* at one site in Brazil, with all three species appearing discrete and represented by good series. No host data has been recorded.

Locality Data. 141 specimens examined from AMNH, CASC, IDEM, INPA, LACM, MPEG, USNM, ZMHB.

BOLIVIA (6). SANTA CRUZ (4): Chajare (San Antonio) (IDEM), Sierra Santa Ana (IDEM), no further data (CASC). NO FURTHER DATA (2): Lagunillas (possibly Dept. Chiquisaca?) (USNM).

BRAZIL (116). AMAZONAS (4): Br. 174 (km60) (INPA), Manaus (IDEM), Reserva Ducke (Manaus) (INPA). MARANHAO (1): Nova Olinda (Am.) (INPA). PARA (110): Altamira (10 km W) (AMNH), BOA VISTA (IDEM), Bujaru (MPEG), Obidos (IDEM), Mocajuba (Mangabeira (IDEM) Cruz Alta (Rio Trombetas) (INPA), no further data (ZMHB). NO FURTHER DATA (3): Est. Aml. (km 134, Min. Am.) (INPA), Faz. NAF 6 (km.31, Est. BR) (INPA), Faz NAF (km.174) (INPA).

COLOMBIA (4). MAGDALENA (2): NW Sierra Norte de Sta. Marta (MCZ), Vista Nieve (San Lorenzo Mt.) (USNM). META (2): Parque Nacional Natural La Macarena (IDEM).

PERU (12). CUZCO (1): Inambari (Quispicanchi (IDEM). HUANUCO (1): Tingo Maria (AMNH). JUNIN (1): Satipo (Jauja) (AMNH). LORETO (2): Callicebus Res. Station (Mishana, Rio Nanay, 25 km SW Iquitos) (USNM). MADRE DE DIOS (2): Res. Natural Tambopata (IDEM). PASCO (4): Pan de Azucar (LACM). SAN MARTIN (1): Achinamiza (IDEM).

SURINAME (1). BROKOPONDO (1): no further data (IDEM).

Exemplar Specimens. Two exemplar specimens were examined and coded separately:

Exemplar 1 (margEx1, Appendix D-2), a male (IDEM) labeled a) Colombia: Parque Nacional Natural Macarena, Meta. Alt. 500 msm, G. Garcia, col., b) (male symbol), c) Popilius marginatus (Perch.), Reyes Castillo. det.90.

Exemplar 2 (margEx2, Appendix D-2),, a specimen (IDEM) labeled Bolivia: Sta. Cruz, Sierra de Santa Ana, 63°37'W, 1720'S, Y. Cambefort, Leg.

Remarks. *P. marginatus* is a widespread lowland species with a fair amount of morphological variation. Monophyly of the two exemplars is very strongly supported by the bootstrap value (100%) and Bremer Support Index (BS=7). Some specimens from Bolivia have 2-8 punctures outside the lateral depressions of the pronotum, but are otherwise similar in the key characters to the rest. The lectotype and paralectotype of *P. sieberi* (both labeled Para) were compared with the long series of specimens of *P. marginatus* from the single locality in Para State, Brazil from INPA. The frontal ridges of the lectotype and paralectotype meet medially in a smooth arc, with a distinct ridge branching off and running to the base of the central tubercle. Both type specimens fall well within the range of variation of the series of *P. marginatus* and are considered to conspecific with it. Although I have not seen the holotype of *P. marginatus*, it is a well-characterized species and I feel confident in placing *P. sieberi* in synonymy.

The two specimens from the Department of Magdalena, Colombia noted above may represent a distinct form, although the differences from typical *P. marginatus* are slight. Both specimens have a glabrous scutellum, anterior marginal pronotal grooves reaching only halfway to the midline, and setose anterolateral corners of the prosternal process posterior to the procoxae. The typical form has the scutellum strongly punctate medially, anterior marginal pronotal grooves reaching 2/3-3/4 of the distance to the midline, and glabrous prosternal process posterior to the procoxae. These specimens were collected in the Sierra Norte de Santa Marta, an isolated range of the northernmost extension of the Andes, well separated from the main Cordillera Oriental. If the examination of additional specimens shows these minor characters to be consistent within this population, species status may be warranted.

I consider it probable that examination of the holotype of *P. amazonicus* will reveal that it falls within the range of variation of *P. marginatus*.

The analyses place this species with the other lowland South American species, and it appears to be most closely related to *P. magdalenae* and *P. tetraphyllus*.

***Popilius amazonicus* Gravely, 1918**

Popilius amazonicus Gravely, 1918: 27. Type material not seen, presumably deposited in the collection of the Indian Museum (now Zoological Survey of India), Calcutta, India. Attempts to contact the Zoological Survey of India regarding the type material of *P. parvicornis* were unsuccessful.

Original Description. Gravely’s (1918) brief description of *Popilius amazonicus* follows:

> One specimen from the Amazon, Peru. Length 20 mm. *P. amazonicus* resembles *P. marginatus* in general appearance, but the tubercles and ridges of the head resemble rather those of *P. intergeneus*, the pronotum is very sparsely punctured near the scars, the pointed posterior extremity of the prosternum is very slender, and the scars of the abdominal sterna are more extensively punctured.

In his key to the species of *Popilius*, Gravely adds:

> The clypeus more or less broadly flattened and trapezoidal...The central tubercle small, its apex not free...The antennal lamellae long, equal to about four of the immediately preceding joints in length...The frontal ridges long and approximately straight, meeting in a slightly obtuse angle.

Gravely also provides a line drawing of the head, from dorsal view - Fig. IV, 7, p.24.

No specimen was available for examination, so no additional description was possible.

Diagnosis. The distinguishing characters offered by Gravely are not distinctive enough to permit differentiation of this species from others in the genus, especially from *P. marginatus*. Length 20 mm.

Geographical Distribution and Ecology. This species is still known only from the type locality, "Amazon, Peru".

Locality Data. According to Gravely (1918) the collection locality was Amazon, Peru.

***Exemplar Material*.** No specimens were available for study.

Remarks. Gravely's (1918) figure of the frontal area of *P. amazonicus* is a simple line drawing suggesting that the frontal ridges originate at (or near) the tip of the central tubercle and are straight from the origin to the outer tubercles.

The shape and length of the frontal ridges are variable in other species of *Populiu*s, including *P. marginatus* and *P. gibbosus*; they are sometimes straight and occasionally even reach the outer tubercles. However, in no other species of *Popilius* do the frontal ridges consistently extend from the central tubercle past the inner tubercles, so I do not consider this to be a character that reliably separates species. The other characters noted by Gravely are similarly variable, and his figure does not conclusively show that the frontal ridges connect directly with the central tubercle.

Luederwaldt (1931) noted having seen a damaged specimen of *Popilius* from the Brazilian Amazon which he felt looked like *P. amazonicus*, and created his sieberi species group to include *P. sieberi* and *P. amazonicus*. The group was defined by having the central tubercle feebly developed, quite or almost without a free apex, and the frontal carinae not being joined to the central tubercle by a longitudinal ridge.

Dibb (1938) included this *P. amazonicus* with *P. sieberi* and *P. intergeneus* in his "intergeneus species group", using the same characters employed by Luederwaldt, while adding that the anterior margin of clypeus is not produced in the middle, and the lateral ridges are obsolete or not grooved. He also rephrased the frontal ridge state, noting that the frontal ridges are entirely separate to the base of the central tubercle. Dibb presumably based these comments on Gravely's sketch of *P. amazonicus* and characters noted in Gravely's key to *Popilius*.

These authors add no new information to the original description, key characters and figure of *P. amazonicus*, suggesting that neither author was able to examine a specimen, and that both authors relied on Gravely's simple figure for their interpretation of the form of the frontal ridges. I know of no specimens of this species, other than the holotype.

P. sieberi is synonymized with *P. marginatus* in the present study. Neither the lectotype nor paralectotype of *P. sieberi* has frontal ridges that run uninterrupted to the apex of the central tubercle; the frontal ridges are evenly connected medially and then connected to the apex of the central tubercle by a distinct double ridge. *P. intergeneus* is synonymized in this study with *P. haagi*. Although *P. haagi* does have the frontal ridges connected directly with the apex of the central tubercle, it is known only from Mexico, Guatemala and El Salvador, and belongs to a species group with no members in South America.

I consider it probable that when the holotype of *P. amazonicus* becomes available for study it will prove to fall within the range of variation of *P. marginatus*. It is therefore placed in the Marginatus Species Group.

Because *P. amazonicus* cannot be differentiated from other species in the genus using the characters listed by Gravely, it is not included in the key to species. However, it appears to belong to the lowland series.

Popilius erotylus **Reyes-Castillo & Castillo, 1992**

Popilius erotylus Reyes-Castillo & Castillo, 1992: 366. Holotype female in the IDEM not examined. The label data of the type series, according the authors follows (see remarks section below): Holotype female: Panama, Panama Prov., BCI, 25 APR 1962, H. Ruckers (PRC). Allotype male: San Blas (locality between El Llano and Carti), 14 FEB 1982, A. Arauz (MIUP). Paratypes: 5 females with the same collecting data as the allotype (MIUP); female, Tocumen, 4 JUL 1962, R. E. Schroeder and R. P. Eckerlin; female, BCI, 20 MAR 1952, C. W. Rettenmeyer.

Original Description. The original description, in English, is extensive and sufficiently detailed to permit discrimination of this species from its congeners, so it is not duplicated here.

Description. *Head*: Transfrontal sulcus straight or slightly concave; tip of central tubercle posterior to level of parietal tubercles; connection between central tubercle and frontal ridges a single narrow ridge; subocular ridge absent or indistinct; antenna with three lamellae; antennal segments 5 and 6 quadrangular, anteriorly truncate. *Pronotum*: Anterior marginal groove of pronotum punctate in lateral 2/3-4/5. *Prosternum*: Prosternal process anterolaterally setose just posterior to procoxae. *Mesosternum*: Posteromedially lightly matt. *Metasternum*: Lateral margins setose only in anterior 1/10; posterolateral area with at least some shallow punctures. *Legs*: Posterior margin of mesofemur and metafemur glabrous. *Length*: 22.0-26.5 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. *P. erotylus* is most similar to *P.* sp. 1 Colombia, with which it shares antennae with three lamellae, the tip of the central tubercle posterior to the level of the parietal tubercles, the prosternal process anterolaterally setose just posterior to procoxae, and antennal segments 5 and 6 quadrangular and anteriorly truncate. It is distinguished from *P.* sp. 1 Colombia by the straight or slightly concave transfrontal sulcus, anterior marginal groove of pronotum punctate in lateral 2/3-4/5, posteromedially lightly matt mesosternum, the single narrow ridge connecting the central tubercle and frontal ridges, and the absent or indistinct subocular ridge. The apical ventral tooth on the left mandible is reduced, appearing absent in most specimens due to natural wear. Length 22.0-26.5 mm.

Geographical Distribution and Ecology. This species has been collected primarily in Panama and Costa Rica, with a single specimen known from Venezuela. It is known from relatively low elevations (about sea level to 850 m, but usually below 500 m), but no host data have been recorded. It can be found in the same logs as *P. eclipticus* (personal observations), but is allopatric with the other two species of *Popilius* known from Panama, *P. punctatissimus* and *P.* sp. 5 Panama. *P. erotylus* occurs along both the Pacific and Caribbean coasts, and is known from as far west as and Pta. Uvita on the Pacific side, and Rio La Gloria (west of Chiriqui Grande), Bocas del Toro Pr., on the Caribbean side.

Locality Data. 155 specimens examined from ARGC, CASC, DJCC, EGRC, INBC, MCZ, UNSM, USNM.

COSTA RICA (12). PUNTARENAS (12): Est. Esquinas (Pen. De Osa) (INBC), Est. Quebrada Bonita (Res. Biol. Carara) (INBC), Rancho Quemado (Pen. Osa) (INBC), Pta. Uvita (DJCC).

PANAMA (142). BOCAS DEL TORO (7): Rio La Gloria (km 8.8 Rambala-Almirante Road) (ARGC). COCLE (20): La Mesa (El Valle) (DJCC). COLON (53): Gatun (5 km W) (ARGC), Maria Chiquita (6 km SE) (ARGC), Pipeline Rd. (8 km NW Gamboa) (ARGC), Rio Guanche (ARGC), Rio Piedras (2 km E Maria Chiquita) (ARGC), Santa Rita Ridge (E. Sabanitas; km 8, 17) (ARGC), Skunk Hollow (6 mi. NW Gatun Locks) (UNSM). DARIEN (1): Cana (Pirre Trail) (ARGC). PANAMA (60): Barro Colorado Island (CASC, EGRC, MCZ), Cerro Jefe (UNSM), Charco Trail (Soberania N.P. (ARGC), El Llano-Carti Road (km 7.5-8) (ARGC), Fort Clayton

(CASC), Jesus Maria Road (8 km E Las Margaritas (ARGC), K19 Road (8 km W Paraiso, Canal Area) (ARGC), K1B Road (1 mi. E Fort Kobbe, Canal Area) (ARGC). PROVINCE UNKNOWN (1): XX Plantation (USNM).

VENEZUELA (1). ZULIA (1): Los Encontados (R. Onia, E of Zulia) (MCZ).

Exemplar Specimens. The exemplar was a male (genitalia dissected, ARGC), labeled PAN.: Colon Pr., 6 km SE Maria Chiquita, 9°26'N 79°42' W, 350m, 29 Mar 92, A.R. Gillogly. It was supplemented by other specimens from western Panama and southeastern Costa Rica.

Remarks. This species is a member of the lowland series of the Marginatus Species Group, and is the only species of this clade that has a verified range reaching Mesoamerica. It appears that this species has extended its range from South America, colonizing forests at low elevations as far west as southeast Costa Rica and northwest Panama. This species is most closely related to *P.* sp.1 Colombia.

Note: The original manuscript of Reyes-Castillo and Castillo's book chapter was submitted in Spanish and translated by the editors into English (A. Aiello, personal communication). The following changes that were made, and errors in the original that were repeated, are worth noting (personal observations).

The label data of the holotype is different in the original manuscript from the published version, and was presumably changed to match currently accepted political entities and commonly used abbreviations. The data in the original manuscript undoubtedly reports the label(s) on the specimen exactly: "PANAMA: Zona del Canal, Isla de Barro Colorado, 25-IV-1962, H. Ruckers, col." The label data of the allotype, as reported in the manuscript is "San Blas, Urdibi entre El Llano y Carti". Urdibi appears to refer to a specific locality, although I cannot find this name on maps, nor in the Defense Mapping Agency Gazetteer of Panama (Anonymous, 1990). The label data of the paratype noted as from "BCI" was changed from the manuscript, which states "Zona del Canal, Isla de Barro Colorado".

Two references to "*P. refurgicornis*" are typographical errors; the correct spelling is "*P. refugicornis*".

The manuscript also describes the eyes as large, the anterior angles of the pronotum as directed anteriorly (instead of upwards), and the junction of elytral striae 1 and 10 with irregular punctation (rather than all of the striae).

Popilius sp. 1 Colombia

Description. *Head*: Transfrontal sulcus distinctly bi-arcuate; connection between the central tubercle and frontal ridges indistinctly double and usually wide; tip of central tubercle posterior to level of parietal tubercles; subocular ridge short (no more than 1/2 way to posterior margin of antennal fossa); antenna with three lamellae; antennal segments 5 and 6 quadrangular, anteriorly truncate. *Pronotum*: Anterior marginal groove impunctate. *Prosternum*: Prosternal process anterolaterally setose just posterior to procoxae. *Mesosternum*: Posteromedially shiny. *Metasternum*: Lateral margins of metasternum setose only in anterior 1/10; posterolateral area with at least some shallow punctures. *Legs*: Posterior margin of mesofemur and metafemur glabrous.

For the description of all characters examined, see Appendix **D-2** – *Popilius* Matrix. Length 22.0-26.5 mm.

Diagnosis. *P.* sp. 1 is most similar to *P. erotylus*, with which it shares antennae with three lamellae, the tip of the central tubercle posterior to the level of the parietal tubercles, the prosternal process anterolaterally setose just posterior to procoxae, and antennal segments 5 and 6 quadrangular and anteriorly truncate. It differs from *P. erotylus* in the distinctly bi-arcuate transfrontal sulcus, impunctate anterior marginal groove of the pronotum, posteromedially shiny mesosternum, indistinctly double and usually wide connection between the central tubercle and frontal ridges, and short subocular ridge (no more than 1/2 way to posterior margin of antennal fossa).

Geographical Distribution and Ecology. This species is known from a single collection from western Colombia. No ecological data accompanied the specimens.

The Western Range of the Andes in this area reaches an elevation of about 4000 m and supports forest up to about 3000 m.

Locality Data. 26 specimens examined from FMNH.

COLOMBIA (26). VALLE (26): Buenaventura (FMNH).

Exemplar Specimen. The exemplar was a male (genitalia dissected, FMNH) with the labels a) Buenaventura, Cauca, Colomb., VI-2-1938, b) Col. & pres. by Henry S. Dybas, c) (male symbol), d) Popilius marginatus Perch., det. F.S. Pereira 1959.

Remarks. This species is a member of the lowland series and most closely related to *P. erotylus*. It is the most basal of the species in the series, and is adjacent to, but not closely related to, the intermediate species *P. refugicornis*.

P. sp. 1 Colombia has a more robust form than the other species in the series.

***Popilius magdalenae* Boucher, 1986**

Popilius magdalenae Boucher, 1986: 501. Holotype in the MNHN not seen. Two paratypes in IDEM were examined, both with labels a) “GUAYANA FRANCESA; St. Georges Oyapock IX-1970”, b) “POPILIUS MAGDALENAE BOUCHER, 1986, S. Boucher det. 1986”, c) “PARATYPE”. One of the specimens also bears a small label with female symbol.

Original Description. A rough translation of Boucher’s original description of *Popilius magdalenae* (1986) follows:

> Form sub-parallel, slighty flattened. Coloration shiny black above and below.
>
> Total length - 24-25mm; length of elytra - 14-15mm; length of pronotum - 5-5.5mm; width of elytra - 9-9.5mm; width of pronotum - 7.5-8mm.
>
> Head rather depressed centrally. Anterior margin of the labrum straight or lightly concave, with an indentation in the middle for half of the depth: sides straight; anterior angles obtuse and rounded; evenly covered with fine setae on the disk, more thickly laterally. Clypeus concave medially, smooth; posterior margin higher than the anterior; anterior margin in the shape of a brace, the obtuse angles of which are obliquely projecting. Mediofrontal structure of the *marginatus* type, well-defined. Central tubercle slightly elevated, the tip vertical and blunt; lateral bases broad, extended by the lateral ridges which each form a carina which is oblique, not sharp; base posteriorly with a conical depression. Angle of the frontal ridges distant from the central tubercle and filled with a triangular raised area than does not pass the anterior level of the inner tubercles. Frontal ridges semicircular, reaching the slightly elevated inner tubercles. External tubercles flat at their tips, which are covered by the hind angles of the clypeus. Anterior angles of the head very obtuse. Ocular canthus with a highly rounded anterior angle. Frontal fossae punctate and setose, and indented to the occipital sulcus. Eyes large and globular. Mandibles with the dorsal tooth prominent, slightly widened. Mentum glabrous and flat on the disk; lateral depressions slightly marked, punctate and setose.
>
> Antennal club with four lamellae, “spongy” (finely pubescent); first segment (of the club) clearly shorter than the other three; second segment slightly longer than the last two, thicker apically; third segment sub-parallel; fourth

segment thick, with the length of the exterior margin grooved barely marked, but distinct.

Pronotum punctate in and around the lateral depressions. Marginal groove punctate and rugose, evenly dilated towards the anterior angles and extending a third of the width of the pronotum. Medial groove reaching the posterior margin.

Elytra entirely glabrous, except for the humeral margin, where two small tufts of fine setae stand one above the other. Striae finely punctate throughout.

Mesosternum with a broad matt band; lateral scars indistinct, finely punctate and matt. Metasternum with disk smooth, posterolateral areas margined or not by a few fine punctures, and the anterolateral areas margined by setigerous punctures; lateral fossae straight, glabrous and rugose.

Abdomen glabrous; third sternite with the marginal groove almost entirely evident.

Mesotibiae strongly setose, with 1-2-3 post-medial spines.

Aedeagus very similar to that of *P. tetraphyllus*, but distinctly larger, less stocky and more sclerotized. Length: 2.5mm."

Type Material. 19 specimens.

Male holotype: Montagne des Singes, Kourou, VII-1985, S. Boucher leg., S.t., in heartwood of a rotten dicotyledonous trunk. (Total length: 24mm.)

Female paratypes: Montagne des Singes, Kourou, XI-1984, F.c., 2 ex., XII-1984, F.c., 1 ex., M. Durnaton leg.; VII-1985, S. Boucher leg., S.t., 5 ex.; 23-VII-1985, F.c., 1 ex., 13-IX-1985, F.c., 1 ex., 27-IX-1985. F.c., 1 ex., P. Bleuzen leg. (Holotype and one female paratype deposited in the MNHN: one female paratype in the collection of P. Reyes-Castillo, Mexico).

5 paratypical specimens in the collection of P. Reyes-Castillo, from French Guiana, St. Georges de lOyapock. IX-1970. J. Gaston leg.

2 paratypical specimens in the collection of the MNHN; 1 specimen determined as *P. tetraphyllus* (probably determined by Dejean), from Cayenne (ex-musaeo J. Thompson); 1 specimen determined as *P. abortivus* Perty, tetraphyllus Dejean nec. Eschscholtz, from Cayenne (ex-Musaeo ED. Brown).

Comments. This is the second known species of the genus, with *P. tetraphyllus*, having four lamellae.in the antennal club. The two species share the same biotope in Guyane. It is curious to note that despite hunting through out the year and in numerous locations at the same time, we captured *P. magdalenae* only in the Montagne des Singes (southwest of Kourou), in July, August, September and December.

Description. *Head*: Antenna with four or five lamellae; left mandible bifid, right mandible trifid. *Prosternum*: Prosternal process posteriorly shiny, matt only in a transverse anterior band. *Mesosternum*: Mesosternal scars coalescent medially. *Metasternum*: Lateral margin setose only in anterior 1/10; posterolateral area of metasternum with at least some shallow punctures. *Legs*: Profemoral groove setose; tip of terminal spur of protibia blunt; mesofemur posteriorly glabrous; posterior margin of mesofemur and metafemur glabrous. *Length*: 21.5-25.5 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. *Popilius magdalenae* appears most similar to *P. tetraphyllus*, but has a posteriorly shiny prosternal process matt only in a transverse anterior band, bifid left mandible, setose profemoral groove, blunt tip to the terminal spur of the protibia, and antenna with four lamellae (never five). Length 21.5-25.5 mm.

Geographical Distribution and Ecology. This species is known only from north-central South America. Although no ecological data were recorded with these specimens, the collection localities all appear to be from elevations of less than 500m. Boucher (1986) notes that six of the nineteen specimens in the type series were collected in mist nets (“filet crylde”).

Locality Data. 32 specimens examined from CASC, IDEM, INPA.

BRAZIL (28). PARA (28): Est. Cruz Alta (Rio Trombetas) (INPA).

FRENCH GUIANA (2). St. Georges Oyapock (paratypes - IDEM).

SURINAM (2). Wilhelmina (CASC).

Exemplar Specimens. The exemplar was a female from IDEM with labels a) Guayana Francesa, St. Georges Oyapock, IX-1970, b) (female symbol), c) Popilius magdalenae Boucher 1986, S. Boucher det. 1986, c) PARATYPE (red label). The characters for the male genitalia were from a specimen from INPA with labels a) Brasil: Para, Cruz Alta, Rio Trombetas, 13-23-XI-1982, C.R.V. Fonseca, b) 0021423, c) (male symbol), d) Popilius magdalenae Boucher, Reyes Castillo, det. 88.

Remarks. P. magdalenae is a member of the lowland series and is most closely related to *P. erotylus* and *P. marginatus*.

***Popilius tetraphyllus* (Eschscholtz, 1829)**

Passalus tetraphyllus Eschscholtz, 1829: 23 (sep.:11). Holotype not seen.

Popilius quinquelamellatus Luederwaldt, 1927: 37. The holotype and eight paratypes were presumably deposited in the Division of Insects, MZSP. Attempts to contact the MZSP regarding these specimens were not answered.

Original Description. A rough translation of Eschscholtz's original description of *Popilius marginatus* (1829) follows:

> Species 13, *Passalus tetraphyllus*; anterior angles of the thorax rectangular, laterally diffusely punctate arond the depressions, elytra basally glabrous.
>
> Habitat in Guiana.
>
> Length 8 lignes (8 lignes are about 18.0 mm), black. At the vertex of the head, two anterior carinae meet in an angle, the two ridges posterior form a straight line, all of these being connected medially by a weak longitudinal carina; supraorbital carinae unarmed. Labrum truncate; mandibles apically obtusely tridentate. Antennae with four lamellae: last lamellar segments elongate, fourth segment half as long. Thorax half as long as wide, anteriorly not constricted; anterior margin medially cut short, laterally slightly sinuate on both sides, anterior angles square, not sharp; convex, grooved dorsally, lateral depression large and transversely punctate, large, sparse punctures around the depression, lateroventrally setose. Elytra dorsally not distinctly flattened, striae distinct throughout and very deeply punctate, humerus glabrous. - probably the illustrious Count Dejean called this species Passali tetraphylii in his catalog.

A translation of Luederwaldt's original description (1927a) of *Popilius quinquelamellatus* follows:

> Very similar to P. marginatus, differing from it, as well as all of the other species in this genus, by the five lamellae of the antennal club. Para. 9 specimens.

Description. *Head*: Antenna with four or five lamellae; mandibles apically trifid. *Prosternum*: Prosternal process completely matt. *Metasternum*: Lateral margins of metasternum setose only in anterior 1/10; posterolateral area of metasternum with at least some shallow punctures. *Legs*: Profemoral groove glabrous; tip of terminal spur of protibia sharp; mesofemur posteriorly glabrous; posterior margin of mesofemur and metafemur glabrous. *Length*: 17.0-21.0 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. *Popilius tetraphyllus* appears most similar to *P. marginatus*. It can be separated from the most of the species in the Marginatus Species Group by having four or five lamellae, and from *P. magdalenae* by the completely matt prosternal process, apically trifid mandibles; glabrous profemoral groove and sharp tip of the terminal spur of the protibia. Length 17.0-21.0 mm.

Geographical Distribution and Ecology. The only ecological data recorded were elevations of 100 and 325 m in Brazil, and 170 m in Colombia.

Locality Data. 58 specimens examined from CMNH, FMNH, IDEM, INPA, MPEG, USNM.

“AMAZONAS” (1). NO FURTHER DATA (1): (IDEM).

BOLIVIA (1). BENI (1): Chalcobo Indian Village (on Rio Benicito) (FMNH).

BRAZIL (30). AMAZONAS (4): Calmbe Vigia (MPEG), Manaus Campus FUA (IDEM), Reserva Locke (26 km de Manaus) (IDEM). MATO GROSSO (1): Utiariti (Rio Papagaio) (IDEM). PARA (23); Bujaru (MPEG), Est. Cruz Alta (Rio Trombetas) (INPA), Santarem (CMNH), Taruma (I km W; Manaus) (CMNH). RIO DE JANEIRO (1). No further data (CMNH). RONDONIA (1): Vilhena (INPA).

COLOMBIA (4). AMAZONAS (4): Reserva Aguas Claras (Leticia, km 18 via Tarapaca Desv. Nazareth) (IDEM).

FRENCH GUIANA (2). Maroni River (vic. Duserre) (IDEM), Montsinery (IDEM).

GUYANA (2). CUYUNI-MAZARUNI (1): Upper Mazaruni R. (IDEM). UPPER TAKUTU-UPPER ESSEQUIBO (1): Tumatumari (USNM).

TRINIDAD (11). Quare Valley (CMNH).

VENEZUELA (7). BOLIVAR (7): Chirima (La Gran Sabana) (IDEM), Luepa (IDEM).

Exemplar Specimens. Three exemplar specimens were examined and coded separately.

Exemplar 1 (tet4lam, Appendix D-2) was a male (genitalia dissected, IDEM) labeled a) Brasil - Amazonas, Reserva Locke, 26 Kms de Manaos, 3-X-1964, A. Mones, b) (male symbol).

Exemplar 2 (tet5lamAm, Appendix D-2) was a male (genitalia dissected, but damaged by dermestid, IDEM) labeled a) Amaz. b) (male symbol), c) Ex Musaeo H.W. Bates, 1892, d) nov. sp., ReyesCastillo XII-74, e) crenatus McL. (Label upside down).

Exemplar 3 (tet5lamBOL) was the female (FMNH) labeled a) BOLIVIA: Beni Prov. VII, 10-19, 1960. B. Malkin leg., b) Chacobo Indian Village on Rio Benicito, 66° -12°20’, c) (female symbol).

Remarks. *P. tetraphyllus* is a member of the lowland series and most closely related to *P. marginatus*.

Eschscholtz (1929) specifically states that his *P. tetraphyllus* has three long antennal lamellae and one shorter one. Luederwaldt (1927a) differentiates *P. quinquelamellatus* from all other species in the genus by its five lamellae, the only character noted in his description. Shortly afterwards, Luederwaldt (1927b) realized that *P. tetraphyllus* actually belonged in the genus *Popilius*, despite having been placed in three different genera and synonymized under two other species by a series of authors. He noted the similarity between Eschscholtz's species and *P. quinquelamellatus*, and placed his species in the synonymy of *P. tetraphyllus*, while amending the spelling of the generic and specific names published in his original paper. Luederwaldt did not mention whether he saw determined material of *P. tetraphyllus* or came to the conclusion after tracing the species through the literature. In synonymizing his species, Luederwaldt (1927b) reports that only the basal lamella of *P. quinquelamellatus* is rudimentary, implying that the four terminal lamellae are all long and well developed. Since Luederwaldt believed these two species to be conspecific, he did not add other distinguishing characters.

Two exemplars with five lamellae were compared with one quadrilamellate exemplar from Brazil. The 15 specimens with five lamellae examined in this study were those from "Amazonas", Bolivia, Colombia, Guyana (Upper Mazaruni R.), and Venezuela in the list above. Although no series included specimens with both 4 and 5 lamellae this was the only character that clearly differentiated them; the size ranges were similar - 18.0-21.0 mm for the specimens with five lamellae and 17.0-21.0 mm for those with four lamellae. The Bolivian and "Amazon" exemplars with five lamellae more closely resembled the exemplar with four lamellae than they did each other.

Popilius refugicornis **Buehrnheim, 1962**

Popilius refugicornis Buehrnheim, 1962. Type material not seen. According to the author, the holotype (male, Number 9.515), allotype (female, Number 9.516) and five paratypes (Numbers 9.513, 9.514, 9.517, 9.518, and 9.519) were deposited in the Collection of Coleoptera of the Instituto Oswald Cruz, Rio de Janeiro, Brazil. Three additional paratypes were deposited in the Entomological Collection of the National Museum, Rio de Janeiro, Brazil.

Original Description. A translation of Buerhnheim's original description of *Popilius refugicornis* (1962) follows:

> *Length* - 21 to 24.5mm, taken from the anterior margin of the clypeus to the posterior point of the elytra.

Head - Central tubercle small, pointed upward and with the tip not reaching the line of the anterior ridges of the lateral tubercles. Parietal tubercles hardly distinct, unlike the frontal ridges, which are prominent and long, and which do not medially reach the central tubercle, the tip of which is set back. The lateral ridges sinuate; close to the end there is a small, rounded prominence which does not impede continuation to the base of the supraocular ridges. The remaining borders of the lateral tubercles are absent, as there is a gradual slope from the frontal ridges, the highest part, to the posterior part, where they reach the level of the frontal fossae. Frontal ridges forming an open arc, semiparabolic, with a small inner tubercle at each extremity, indistinct posteriorly, while quite distinct anteriorly, leaving the frontal area much more depressed in relation to the rest of the head. The frontal ridges diverge from two almost parallel carinae which extend from the base of the tip of the central tubercle. Inner tubercles slightly evident, on the continuation of the frontal ridges and quite near the outer tubercles. Frontal area lightly rugose with a sharp elevation in the angle which begins near the union of the frontal ridges with the carinae which descend from the central tubercle. Clypeus with the surface smooth, free, separated from the frontal area by a line without notable hills and well-delineated. Inclined anteriorly, the clypeus is higher than the frontal area for the length of the line of separation that determines the distinctiveness of the latter. Outer tubercles distinct, turned slightly to the side and situated at the extremities of the line of separation of the clypeus from the frontal area. Ocular canthus posteriorly rounded and angled upward. Suprocular ridge completely formed, by a sharp edge and terminating above the anterior angle of the head. Possessing one small tubercle on the point of the ocular canthus, another more distinct on the tip of the first quarter of the ocular globe, and a third quite round and hardly distinct at the tip of the posterior part of each lateral tubercle. A bridge in the continuation of the base of the outer tubercle and not connected to the anterior angle of the head, due to a groove that flanks internally the anterior portion of the supraocular ridge. Anterior angle of the head with the vertex rounded and sightly turned upwards. Antennae with three lamellae slender apically, the terminal one appearing like an obtusely angled scalene triangle whose free side is the shortest. The two segments preceding the lamellae slightly narrowed, probably rudimentary lamellae. Mentum laterally punctate, with some setae, and with the median lobe smooth. Lateral depressions of the mentum indistinct. Lateral areas of the ventral side of the head highly punctate and pilose.

Mouthparts - Labrum punctate and pilose. Anterior margin slightly concave and with a line of deeper punctures next to it. Left mandible with two terminal teeth and with the lower anterior tooth flattened and split. Right mandible with three terminal teeth and with the lower anterior tooth sharp and without a split tip. The second segment of the labial palp distinctly more robust than the distal.

Pronotum - Anterior margin almost straight, with about 1/8 of each side lightly concave, which causes a slight prominence to the rounded tips of the lateral angles. Anterior marginal grooves wide, distinclty excavate, with the medial half dilated and arcuate, each occupying about 3/8 of the anterior margin. These are smooth, only with a few punctures in a little more than the external 1/4. Lateral marginal grooves narrow, with a row of punctures medially and extending past the middle of the posterior margin of the pronotum. Medial groove beginning at the posterior margin of the pronotum, narrower in the posterior portion, a little wider in the anterior portion and ending narrowly almost at the anterior margin of the pronotum. With a small dilation in the middle, and interiorly smooth. Lateral depressions almost smooth, with only a few, shallow punctures.

Prosternum - Prosternal process with the posterior tip of the rhomboid pointed. Rhomboid quite broad and with the margins of the anterior sides adorned with some setae. Ventrolateral areas of the pronotum punctate and setose in the anterior, lateral and posterior portions, while the internal portion is smooth. There is a dense line of hairs at the joint of the insertion of the first pair of legs. Anterior and posterior margins of the prosternum adorned with a dense line of setae.

Mesosternum - Smooth and without obvious scars. There are only shadows in the area of the scars, caused by a slight depression and roughness of the chitinous surface. Posterior margin medially with fine punctation and a feeble impressed rugosity.

Elytra - Striae with uniform punctation. Epipleurae narrow, glabrous and smooth.

Metasternum - Metsternal disk without margin and with the surface smooth. Episterna slender in the anterior portion, wider posteriorly, distinclty excavate, rough and finely setose. Intermediate areas smooth, but not in the anterior portion, at the point of insertion of the second pair of legs, where there is distinctly impressed punctation and pilosity that extends to the episterna.

Measurements - See Table 1.

(Note: Table 1 lists the accession number, various lengths and widths, and the provenance of each of the ten specimens in the type series, and is not reproduced here.)

Description. *Head*: Frontal ridges arise from two close ridges from anterior base of central tubercle; central tubercle usually high, erect; dorsal tip of central tubercle posterior to parietal ridges, with the structure indented medially; frontal ridges and parietal ridges about parallel; antenna with three lamellae; left mandible bifid, right mandible trifid; lateral lobes of the mentum about semicircular apically. *Prosternum*: Prosternal process highly convex longitudinally posterior to procoxae. *Metasternum*: Lateral margins setose to the posterior tip, widened subapically, narrowed at very tip; posterolateral area impunctate. *Legs*: Profemoral groove glabrous; posterior margin of mesofemur and metafemur setose. *Length*: 26.0-26.5 mm (21-24.5 mm in Buehrnheim, 1962).

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. This member of the Marginatus species Group is quite distinctive, distinguishable from the other species in the group by the lateral margins of metasternum setose to the posterior tip, setose posterior margins of the mesofemur and metafemur, impunctate posterolateral area of the metasternum, frontal ridges arising from two close ridges from the anterior base of the central tubercle, dorsal tip of the central tubercle posterior to the parietal ridges and with the structure indented medially, the frontal ridges and parietal ridges are about parallel, the profemoral groove is glabrous, and the left mandible is bifid. The most similar species in this species group is *P*. sp. 2, in which the frontal ridges arise directly from anteromedial tip of the central tubercle, the dorsal tip of the central tubercle is anterior to the parietal ridges, the frontal ridges and parietal ridges are about parallel, the profemoral groove is setose, and both mandibles are apically trifid. Length 26.0-26.5 mm (21-24.5 mm in Buehrnheim, 1962).

Geographical Distribution and Ecology. This species is known only from areas of Atlantic rain forest along the east coast of Brazil, from the states of Espirito Santo (the type locality is Sooretama) and Rio de Janeiro, where a series of reserves protect some of the few remaining stands of Atlantic tropical rainforest, much of which is below 50 m in elevation. The only ecological data on this species are from the published label data for the ten specimens of the type series; one specimen which was collected at 1100 m., and another was collected at light (Buehrnheim, 1962).

Locality Data. 2 specimens examined from MCZ, USNM.

BRAZIL (2). RIO DE JANEIRO (1): Guapi (USNM). NO FURTHER DATA (1) (MCZ).

Exemplar Specimen. The specimen from USNM was selected as the exemplar (sp1COL, Appendix D-2), and bears the labels a) Guapi, Braz, Mar.31, 1935, P. Sandig, b) (female symbol).

Remarks. *P. refugicornis* is one of two intermediate species in this species group. It is morphologically nearest the lowland series, but is only moderately supported as sister to that clade (BS=5, bootstrap value of 68%). It's highly restricted range in the coastal forest of far eastern Brazil suggests that it may be a relict of a more widespread ancestor, and may be one of the most basal members of this species group.

Popilius sp. 2 Venezuela

Description. *Head*: Central tubercle low; frontal ridges arise directly from anteromedial tip of central tubercle; dorsal tip of central tubercle anterior to parietal ridges; frontal ridges and parietal ridges divergent laterally; antenna with three lamellae; mandibles apically trifid; lateral lobes of the mentum apically truncate. *Prosternum*: Prosternal process broadly convex posterior to the coxae. *Mesosternum*: Mesosternal scar reaches posterior margin and is setose; fine setae between scar and posterior margin. *Metasternum*: Lateral margins setose to the posterior tip; lateral area of metasternum uniformly narrow posteriorly posterolateral area impunctate. *Legs*: Profemoral groove setose; posterior margin of mesofemur and metafemur setose.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix. Length 22.0-26.5 mm.

Diagnosis. This species is unique in the species group in having the dorsal tip of the central tubercle anterior to the parietal ridges, and frontal ridges which arise directly from the anteromedial tip of the central tubercle. With *P. refugicornis*, it shares characters differing from the other species: the lateral margins of metasternum setose to the posterior tip, setose posterior margins of the mesofemur and metafemur, and impunctate posterolateral area of the metasternum. Besides the arrangement of the central tubercle and frontal ridges, it may be distinguished from *P. refugicornis* by the frontal ridges and parietal ridges diverging laterally, low central tubercle, setose profemoral groove, and apically trifid mandibles.

Geographical Distribution and Ecology. The only known specimen was collected at 1600 m elevation in the range of mountains between Caracas and the Atlantic coast.

Locality Data. 1 specimen examined from IDEM.

VENEZUELA (1). DISTRITO FEDERAL (1): Los Venados (P. Nac. Avila) (IDEM).

Exemplar Specimen. The sole specimen seen (sp2VEN, Appendix D-2) was the exemplar (IDEM), and has the labels a) Los Venados, P. Nac. Avila, (D.F.) m.1600, b) 11-VIII-1968, Bordon leg. c) (female symbol), d) Popilius sieberi Kuwert, Reyes Castillo, 1974.

Remarks. *P*. sp. 2 Venezuela is one of two intermediate species in this species group. It is morphologically between the lowland and high-altitude series, but not closely related to either, and is only moderately supported (BS=5, bootstrap value of 82%) as being within this species group. It's alternative placement as either basal in the entire species group or internal in a comb-like series is probably due to the lack of a close outgroup with which to polarize the characters and confidently root the clade.

This species is most closely related to *P. refugicornis* and elements of the high-altitude series, but is separated from both by distinct gaps in character changes. It's apparently highly restricted range in the coastal mountains of northernmost Venezuela suggests that it may be a relict of a more widespread ancestor, and may be the most basal member of this species group. When the passalid holdings of institutions in Venezuela can be examined, it is hoped that more specimens (including males) of this interesting and possibly pivotal species may be found and the range and habitat better understood..

Popilius **sp. 3 Bolivia**

Description. *Head*: Rugose area between the central tubercle and frontal ridges; central tubercle low; central tubercle even with or posterior to parietal tubercles; hypostomal process glabrous and laterally convex; left internal tooth trifid. *Pronotum*: Anterolaterally impunctate; laterally glabrous. *Prosternum*: Prosternal process completely matt. *Elytra*: Humeri setose only ventrally. *Mesosternum*: Mesosternal scars glabrous, narrow, not reaching the posterior margin of the mesosternum. *Metasternum*: Posterolateral area of the metasternum impunctate. *Abdomen*: Apical sternite glabrous. *Legs*: Anterior face of procoxa just posterior to trochanter medially glabrous; mesofemur and metafemur posteriorly setose.

For the description of all characters examined, see Appendix D-2. Length 19.0-22.0 mm.

Diagnosis. This species may be distinguished from the other taxa in the high altitude series by its medially glabrous anterior face of the procoxa just posterior to the trochanter, ventrally (not dorsally) setose elytral humeri, laterally convex hypostomal process, laterally glabrous pronotum, central tubercle even with or posterior to the parietal tubercles, trifid left internal tooth and glabrous mesosternal scars.

Geographical Distribution and Ecology. This species is so far known only from Bolivia, at elevations of 1880-2200m. No other ecological information has been recorded. The two localities are about 150 miles apart near the easternmost edge of the Andes, and are reportedly in areas of cloud forest.

Locality Data. 5 specimens examined from ARGC, JCSC.

BOLIVIA (5). SANTA CRUZ (2): El Chape (Florida) (ARGC). COCHABAMBA (3): Khara Huasi (Carrasco).

Exemplar Specimens. The exemplar (sp3BOL, Appendix D-2) was a female (ARGC) labeled Bolivia: Sta. Cruz Florida: El Chape, Dec. 8-13-1991, 1900-2200 msnm, Coll. E.N. Smith. It was supplemented by a male (genitalia dissected) with the same label data.

Remarks. This species is the only one of the taxa closely related to *P. gibbosus* known from outside of the northern Andes of Colombia and Venezuela. No specimens of the high altitude series are known from between the Bolivian and Colombian speciers, perhaps due to a lack of collecting or habitat destruction. Although this species is distinct and highly derivative (33 character changes from the nearest other taxon) its placement within the high-altitude series is unstable. Analysis of the species group using a closely related outgroup may resolve its status.

***Popilius* sp.4 Venezuela**

Description. *Head*: Tip of central tubercle distinctly anterior to parietal tubercles; hypostomal process longitudinally grooved or flattened; left internal tooth bifid. *Pronotum*: Usually with a few short, fine setae laterally. *Elytra*: Humeri completely setose. *Mesosternum*: Mesosternal scars with short, fine setae, a few setae often between the scars and the posterior margin of the mesosternum. *Legs*: Anterior face of procoxa just posterior to trochanter medially setose.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix. Length 22.5-28.0 mm.

Diagnosis. This species may be differentiated from others in the species group by its finely setose mesosternal scars and bifid left inner tooth.

Geographical Distribution and Ecology. This species appears to be restricted to the higher elevations of the Sierra Nevada of Venezuela from 1500-2600 m. The only specimen collected below 2000 m is the example from Mosquey, Venezuela; the altitude (1500 m) on the label of this specimen may be in error, as the elevation of Mosquey is 1884 m. Except for the specimen with questionable data, this species appears to be elevationally allopatric with the Venezuelan populations of *P. gibbosus*, which have been collected at lower elevations (1500-1900 m).

The enlarged pronotum of over half of the specimens from La Carbonera suggests that this population may be brachypterous and possibly flightless, but the wings of this specimens of this population were not examined.

Locality Data. 29 specimens examined from PRC.

VENEZUELA (29): MERIDA (25): El Paramito (Jaji), Estacion Experimental Forestal ULA (Carr. Jaji-La Azulita), La Carbonera (Campo Elias and Pino Lazo), La Montana (cable car station, 2442 m), La Mucuy. TRUJILLO: (4): Laguna Bocono, Mosquey (Bocono).

Exemplar Specimens. Two exemplars were examined and analyzed separately.

Exemplar 1 (sp.4VenEx1, Appendix D-2) has labels a) Venezuela, Merida, Carbonera, 2600m, 8-X-69, b) J.&B. Bechyne leg., (male symbol), d) Popilius entre villei y gibbosus, Reyes Castillo Det. 1975.

Exemplar 2 (sp.4VenEx2, Appendix D-2) has labels a) Venezuela: La Mucuy, Edo. De Merida, 25-V-77, J. Mateu, col., b) Alt. 2300m, c) (male symbol); it was supplemented by one female and one teneral with the same label data.

Remarks. This species is part of the high altitude series and appears to be the species from the highest elevations in this species group. Every specimen has a more stocky form than the other representatives of the high altitude series. It’s placement in the high altitude series is unstable, from the most basal to apical; re-analysis with a more appropriate outgroup may resolve its placement.

***Popilius gibbosus* complex**

This species complex includes seven currently accepted species and one synonym. The seven species are listed below in order of description date.

Passalus gibbosus (Burmeister, 1847: 507). Holotype not seen, presumably in the Burmeister Collection in the Zoological Museum in Halle, Germany. A specimen from Colombia in the MNHN, determined by Kuwert, was examined.

Popilius novus Kuwert, 1891: 172. Holotype in the MNHN with the labels a) Colomb., b) novus Kuw. Amaz. (probably in Kuwert’s writing, per S. Boucher, personal communication), c) Ex-Musaeo A. Kuwert 1884, d) Popilius novus Kuwert Reyes Castillo det. 69, e) TYPE (in red).

Popilius thiemei Kuwert, 1897: 301. Lectotype in the MNHN with the labels a) Nouv. Grenade, Muzo, Dr. O. Thieme, 10.11.1877, b) Thiemei Kuw. Neu Gran (probably in Kuwert's writing, per S. Boucher, personal communication), c) Ex-Musaeo A. Kuwert 1884, d) Popilius novus Kuwert Reyes Castillo det. 1969. This species was synonymized under *P. novus* by Reyes-Castillo (1970b).

Popilius hebes Kuwert, 1891: 172. Holotype in the MNHN with the label hebes Kuw. Am. Cent. (probably in Kuwert's writing, per S. Boucher, personal communication).

Popilius moritzi Kuwert, 1897: 299. Lectotype in the MNHN with the labels a) Dr. Moritz, 1858, Venezuela, b) Moritzii Kuw. Venez. (probably in Kuwert's writing, per S. Boucher, personal communication), c) Ex-Musaeo A. Kuwert 1894, d) Popilius moritzi Kuwert Reyes Castillo det. 69.

Popilius villei Kuwert, 1897:300. Holotype in the MNHN with the label Ecuador/Villei Kuw. Ecuad (probably in Kuwert's writing, per S. Boucher, personal communication).

*Popilius parvicornis (*Gravely, 1919): 23. Type material not seen, presumably in the collection of the Indian Museum (now Zoological Survey of India), Calcutta, India. Attempts to contact the Zoological Survey of India regarding the type material of *P. parvicornis* were not answered.

Popilius fischeri (Pereira, 1941): 96. According to the author the holotype and 10 paratypes were deposited in the Collection of the Dept of Zoology, MZSP, with the accession number 22.998, presumably with labels indicating the type locality as Costa Rica and the collectors as Nevermann and A. Alfaro. More than one specimen was in the type series, as the original description includes a size range. Attempts to contact the MZSP regarding these specimens were not answered. One of four paratypes in the MNHN was examined.

I examined at the MNHN the holotypes of *P. hebes, P. novus, and P. villei*, lectotypes of *P. moritzi* and *P. thiemei*, a paratype of *P. fischeri* and a specimen of *P. gibbosus*, collecting data on 74 morphological characters.

None of the original or subsequent descriptions allows any of these species to be unequivocally differentiated from all of the others. The authors used different sets of characters, and re-descriptions often changed data from the originals or assumed character states that were not specifically stated. As a result, only a thorough revision of the species, including detailed examination of all of the type specimens will resolve the status of the these species. This complex is composed of taxa from high elevations (1350-3000 m) in disjunct, and often small and isolated, forest remnants, there is a high potential for independent evolution of populations, and a high possibility of encountering undescribed taxa in addition to the two (*P*. sp. 3 Bolivia and *P*.

sp. 4 Venezuela) addressed below. In addition to not having access to three of the seven type specimens, I had only 54 specimens of this highly variable complex available for this study, including three series of 5-18 specimens. The examination of specimens in collections in Colombia and Venezuela that probably have a significant amount of material representing this species complex, and from several major museums in North America and Europe that I expect to have specimens, will be necessary to revise these species.

Because of the disjointed treatment of this species complex by previous authors, the original descriptions of the seven recognized species are not included here. Instead, some characters and their potential for resolving the status of the species are addressed in the Remarks section, below.

Description. *Head*: Central tubercle even with, posterior to, or rarely anterior to parietal tubercles; area between the central tubercle and frontal ridges variable, with flat rugose patch, or one or two longitudinal ridges; hypostomal process longitudinally grooved or flattened and often setose; mandible apically trifid, left internal tooth trifid. *Pronotum*: Rarely punctate only in the lateral depressions, usually with a few short, fine setae laterally. *Elytra*: Humeri completely setose. *Mesosternum*: Mesosternal scars glabrous. *Abdomen*: Apical sternite occasionally with posteromedial setae, individually or in a patch. *Legs*: Anterior face of procoxa just posterior to trochanter medially setose. Abdomen: Posterior marginal groove of last abdominal sternite complete. *Length*: 19.5-31.0 mm.

Diagnosis. The *P. gibbosus* complex is quite variable, but may be distinguished from the other members in the species group by the glabrous mesosternal scars, trifid left internal tooth, completely setose elytral humeri, longitudinally grooved or flattened and often setose hypostomal process, medially setose anterior face of the procoxa just posterior to the trochanter, and the posterior marginal groove of last abdominal sternite reaches completely across the segment, rather than only 3/4 to 4/5 of the width. *Length*: 19.5-31.0 mm.

Geographical Distribution and Ecology. This highly variable species complex is known from localities in the Cordillera Oriental of the northern Andes, including both the Sierra de Perija of Colombia and Sierra Nevada of Venezuela. The only ecological data recorded were elevations. Specimens were collected in three fairly discrete, but linked areas of the Cordillera Oriental of the northern Andes; the southern section in Colombia (2000-3000 m, but only one specimen reportedly collected from below 2500 m), Serrania de Perija (1350-1500 m) and the Sierra Nevada (1600-1900 m). The absence of specimens from the Cordillera Occidental and Cordillera Central of Colombia may be an artifact of collecting; all of the specimens of the high altitude series seen during this study were from the Cordillera Oriental or eastern slope of the Andes.

Populations of this species are probably reproductively isolated from each other, as the patches of remaining cloud forest in the northern Andes are scattered and passalids are not vagile.

Locality Data. 54 specimens examined from AMNH, CAS, FMNH, FSMC, PRC.

COLOMBIA (43). Felipe Ovalle Q. (no further data; possibly the name of the collector) (19) (AMNH). BOYACA (5): Sanct. de Fauna y Flora de Iguaque (W. Arcabuco-Villa de Leyva, Municipio de Villa de Leyva, Cordillera Oriental) (PRC). CUNDINAMARCA (11): entre Mosquera y La Mesa (PRC), Granjas de Padre Luna (Mpio. Alban) (PRC), La Calera (km. 9 – from corner Mundo Nuevo) (PRC), Laguna de Catarnica (PRC), Reserva Carpanta (Sietecuerales) (PRC), Santandercito (PRC), Tequendama (PRC), Vereda Chiscal (Zipacon) (PRC). MAGDALENA (7): Finca San Jose (8 km SE Socorpa Mission, Sierra de Perija) (FMNH), forest trail from Socorpa Mission to Finca San Jose (Sierra de Perija) (FMNH), Socorpa Mission (Sierra de Perija) (FMNH). META (1): PNN Macarena (curia) (PRC).

NO FURTHER DATA (1) (PRC).

VENEZUELA (9). ARAGUA (4): Rancho Grande (Parque Nacional) (PRC).

TRUJILLO (2): Aguas Negras (Bocono) (CAS, PRC), Boca de Monte (Bocono) (PRC). NO FURTHER DATA (2) (FSMC).

NO DATA (1) (PRC).

Exemplar Specimens. Eight exemplars were examined and analyzed separately.

Exemplar 1 (gibbEx1, Appendix D-2), a male (genitalia dissected), had labels a) Colombia, Magdalena, Sierra de Perija, Socorpa Mission, b) Elev. 1350-1400 m, VIII:14-20:1968, leg. B. Malkin, c) (male symbol).

Exemplar 2 (gibbEx2, Appendix D-2), a male (genitalia dissected), had labels a) Cundinamarca, Zipacon, Vereda Chiscal, Ma. Vargas leg., b) (male symbol), c) Popilius novus (?) Kuwert 6-9.

Exemplar 3 (gibbEx3, Appendix D-2), a male (genitalia dissected), had labels a) Venezuela: Rancho Grande, Edo. Aragua, 12-11-1967, Bordon leg., b) Alt. 1700 m, c) Popilius novus Kuwert, Reyes Castillo 1974, d) (upside down) Popilius gibbosus (Burmeister), Reyes Castillo 1970, e) (red label) Compare au type par Reyes Castillo XII-74 Mus. Paris.

Exemplar 4 (gibbEx4, Appendix D-2), a male (genitalia dissected), had labels a) Santandercito, Enero-62, b) 06, c) (male symbol), d) Popilius novus Kuwert, Reyes Castillo Det. 90.

Exemplar 5 (gibbEx5, Appendix D-2) had labels a) Colombia, Tequeolana (spelling barely legible), b) 05779, c) (female symbol), d) Oileoides fischeri P. Pereira, P. Pereira det. 1947, e) Popilius fischeri (Pereira) Reyes Castillo Det. 1970.

Exemplar 6 (gibbEx6, Appendix D-2), a male (genitalia dissected), had labels a) Dr. Moritz, 1858, Venezuela, b) (male symbol), c) Popilius moritzi Kuw. ”(ipre vid)”, d) Difficilis M.B., Columbia (label folded).

Exemplar 7 (gibbEx7, Appendix D-2), a male (genitalia dissected), had labels a) Dr. Moritz, 1858, Venezuela, b) (male symbol), c) marginatus Perch. Det. Kuwert, d) (label folded) Rufilabris Columb. Moritz.

Exemplar 8 (gibbEx8, Appendix D-2), a male (genitalia dissected), had labels a) Colombia, S.A., Felipe Ovalle Q., Ac. 33501, b) (male symbol), c) Popilius parvicornis (Gravely) Reyes Castillo, det. 1970.

Remarks. This species complex belongs to the high altitude series of the Marginatus Species Group. The species within this series have been differentiated primarily by the length and robustness of the antennal lamella, degree of development of a sulcus on the central tubercle, presence or absence of a rugose patch anterior to the central tubercle, and presence/absence and shape of a raised area anteromedial to the frontal ridges (Kuwert, 1897; Pereira, 1941). Only *P. fischeri* was described from more than a single specimen, so the authors had little idea of the amount of variation occurring within most of the species.

Six series of 2-18 specimens of the *P. gibbosus* complex and representing each of the three geographic areas noted in the distribution section above were examined for intraspecific variation. Within these series antennal lamellae were uniform in length and proportions; the sulcus usually on the posterior portion of the central tubercle ranged from completely absent to a depression at the base of the central tubercle to a distinct groove on the posterior slope of the central tubercle; the area between the tip of the central and the frontal ridges varied from a single or double longitudinal ridge connecting the central tubercle and frontal ridges to a matt, rugose area with indistinguishable ridges; and the raised area anteromedial to the frontal ridges varied in shape and size.

None of the characters used by the original authors to distinguish these species provided consistent separation of the series examined.

Examination of type material in the MNHN revealed some differences, but not the extent of the variation within each species. The five type specimens (including *P. thiemei*, which is a synonym of *P. novus*) and a paratype of *P. fischeri* that were examined are very similar; the only characters found to clearly distinguish species or sub-groups are the length of the antennal lamellae, degree of pronotal punctation, degree of punctation in the posterolateral area of the metasternum, presence or absence of setae posteromedially on the last abdominal sternite, and body length.

The specimens fall into two broad morphotypes; a small form 19.5-23 mm in length and with short, thick antennal lamellae (lamellae of the 8th and 9th segments about 2-3 times as long as the length of the external/posterior margin of the segment), and a larger form 24.5-28.5 mm long and with longer antennal lamellae (lamellae of the 8th and 9th segments over three times as long as the length of the external/posterior margin of the segment).

The smaller morphotype includes the type specimens of *P. novus* (19.5 mm; 22 mm per Kuwert, 1897), *P. thiemei* (19 mm; 20 mm per Kuwert, 1897), and *P. moritzi* (20.5 mm; 23 mm per Kuwert, 1897) and the paratype of *P. fischeri* (21.5 mm; type series from 22-25 mm per Pereira, 1941). The lengths stated in the original descriptions are consistently longer than when the same specimens were measured by me, probably because the current measurement procedure by passalid specialists is to measure length from posterior tip of the elytra to anteromedial margin of the labrum; the traditional practice was to measure from tip of abdomen to furthest extension of the mandibles). The range in length is probably about 19.0- 24 mm, assuming at least 1 mm less than the 25 mm maximum recorded by Pereira (1941) for *P. fischeri*. The type specimen of *P. moritzi* has 2 shallow punctures in the posterolateral area of the metasternum, the paratype of *P. fischeri* had only a few punctures (less than 10) and the type specimen of *P. novus* had 10-15 punctures. This amount of variation is common within series of passalid species, and is not sufficient to distinguish between species, so these species are indistinguishable using the original descriptions. All except one of the specimens available on loan for this study can be placed in the first sub-group. They range in size from 19.5-24.0 mm, and the number of posterolateral metasternal punctures was from impunctate (the majority of specimens) to five shallow punctures.

The larger morphotype includes the type specimens of *P. hebes* (26.0 mm; 27 mm per Kuwert, 1897), and *P. villei* (28.5 mm; 29 mm per Kuwert, 1897). Although not mentioned by Kuwert (1897) in his description of the species, or by any subsequent author, the holotype of *P. hebes* has a posteromedial patch of setae on the last sternite. This character is rarely encountered in Passalidae (Doesburg Sr., 1942; Doesburg Jr., 1974, 1992), and would be significant here if it were consistently present in populations in the species complex. However, within the a series labeled “Colombia, Felipe Ovalle Q.”, only 14 of 18 specimens had from a few fine setae to a large patch of setae posteromedially on the last abdominal sternite, as did a smaller proportion (6 of 11) of specimens of four smaller series. The type of *P. villei* was the only specimen with an impunctate pronotum. The posterolateral area of the metasternum of the type specimens of *P. hebes*, *P. villei* and *P. thiemei* was impunctate.

The original descriptions of the two remaining species, *P. gibbosus* and *P. parvicornis*, were compared with the diagnoses of these sub-groupings.

Burmeister (1847) described P. gibbosus as having the pronotum punctate in the lateral depressions and being 12 “lignes” in length (12 lignes are about 27.1 mm), but does not specifically mention the antennal lamellae, posterolateral area of the metasternum nor the terminal abdominal sternite. However, he separated and diagnosed his groups of Passalidae in outline format, and described *P. gibbosus* within a group of species having long antennal lamellae, in contrast to the following group with the lamellae short, rounded, and only slightly longer than the base of the segment. *P. gibbosus* can be placed in the sub-group with *P. hebes* and *P. villei*, although there is not enough information in the literature to distinguish it from *P. hebes*; *P. villei* has an impunctate pronotum.

Gravely (1918) noted that *P. parvicornis* is 27-28.5 mm in length and has moderately long antennal lamellae, and that the surface of the head is smooth and glossy. Although Pereira (1941) understood this latter to mean that the surface of the head was glabrous and used this as a key character, I can not agree since Gravely was contrasting the matt and rugose area between the central tubercle and frontal ridges with the condition of the rest of the head. Gravely did not specifically note whether the surface of the head was setose or glabrous. The species of the high altitude series that I have examined all have the surface of the head at the very least sparsely setose.

The one specimen of the larger morphotype available for examination was Exemplar 8, determined by Reyes-Castillo as *P. parvicornis*. It is 31.0 mm in length, has lamellae about 3.4 times the length of the external/posterior margin of the segment), impunctate posterolateral area of the metasternum and the pronotum shallowly punctate in the lateral depressions. The label on this specimen (Colombia, S.A., Felipe Ovalle Q.) is the identical to those on 18 other specimens (22-23 mm long, with 14 of the 18 specimens having a setose terminal sternite), which belong in the first sub-group. Since no other locality has more than one form of this species complex and no locality “Ovalle” can be found in Colombia, the label information may indicate the name of the collector rather than a specific collecting locality.

With the addition of the original descriptions of *P. gibbosus* and *P. parvicornis*, and of the single specimen of this subgroup available for examination, the size range of the second group is about 26.0-31.0 mm. The only one of the four species included that can be distinguished from the others is *P. villei*, with its impunctate pronotum. However, the punctation of the pronotum of the specimen determined by Reyes-Castillo as *P. parvicornis* is so shallowly punctate as to be almost impunctate, The proliferation of species in this group appears to be due to an unfortunate combination of problems; the relative rarity of this species complex in collections, inadequate and careless descriptions, and a lack of familiarity with the previously described species. Kuwert had a propensity for extreme taxonomic splitting, and large numbers of his genera and species have since been synonymized. Arrow (1906) suggests that Kuwert was led "…to include hasty determinations and descriptions based upon single, imperfect or abnormal specimens and to ignore the facts of geographical distribution and the rules of nomenclature.", and adds that Kuwert subdivided most of the common species of previous authors without recognizing the existence of natural variation, including the normal wear through abrasion of protruding structures (cephalic tubercles, mandibular dentition, etc.). Kuwert consistently offers only a single length, rather than range, even for common species. He (Kuwert, 1891) notes that he has seen *P. gibbosus*, describes *P. novus* as having the metasternum impunctate and glabrous (the only characters besides length in the description, both of which are the opposite of the states present on the holotype), and describes *P. hebes* with two vague characters, useless unless a person has specimens of the other species mentioned. Kuwert (1897) then changes the length of *P. gibbosus*, states that *P. novus* has the metasternum widely punctate (though glabrous) laterally and changes the type locality from "Columbia" to "Amazon.", and describes three additional species (*P. moritzi*, *P. villei* and *P. thiemei*), noting that two are very similar to *P. novus* and *P. hebes*.

Gravely (1918) described *P. parvicornis*, designating it as the type species of a new genus, *Oileoides*, based on the expanded clypeus "as in the more primitive species of Popilius," and the laterally widely setose metasternum. All members of the high altitude series share these characters, yet none of the other species in this series is included in Gravely's keys to *Oileoides* or *Popilius*. I conclude that he was not familiar with any of the high altitude species described by Burmeister and Kuwert that are now included in the Marginatus Species Group.

Pereira was apparently introduced to Passalidae through preparing Luederwaldt's unpublished manuscripts (including new species descriptions) for publication and appears not to have been familiar with the literature or the type material of Passalidae in European museums (Luederwaldt, 1941). As a result, he described *P. fischeri*, not realizing that Kuwert had already described three small species in this species complex. He also prepared a key to the five species that he recognized as belonging to this species group without having seen three of them, while making assumptions on character states based on unsupportable evidence, e.g. the presumed form of the central tubercle and absence of setae in the frontal fossae, based on Gravely's description and line drawing of *P. parvicornis* (Gravely, 1918). I tested Pereira's key using type material (two holotypes and a paratype) representing three of the species in his key; the only specimen that could be correctly identified using the key characters was Pereira's species. The key was then tested using the lectotypes of *P. moritzi* and *P. thiemei*, and a specimen of *P. gibbosus* determined by Kuwert; both of Kuwert's small species keyed out to *P. fischeri*, and the specimen of *P. gibbosus* keyed to *P. hebes*. The key is unworkable, except to separate the two sub-groups noted above.

Reyes-Castillo (1970b) synonymized *Oileoides* under *Popilius*, uniting all the species of the *P. gibbosus* species complex for the first time. However, his work addressed the higher categories of New World Passalidae, and he did not discuss relationships among the species of *Popilius*.

In summary, although this complex of species can be separated into two morphotypes; none of these species can be unequivocally distinguished from the other members of its morphotype, and specimens cannot be reliably identified to species. A more thorough examination of the species in this complex, with detailed examination of the type material and using more specimens and long series must be conducted. It appears very likely that several of the species in the complex must eventually be placed in synonymy. It is also possible that examination of additional specimens may bridge all of the currently evident differences, reducing the complex to a single, highly variable species.

HAAGI SPECIES GROUP

The Haagi Species Group is diagnosed by: posterior angle of mesepisternum glabrous; outer tubercles on the transfrontal sulcus, slightly surpassing clypeal margin; mesepisternum anteroventrally impunctate or punctate and smooth, occasionally with only a punctate, anteroventral matt patch, but not punctate and matt to the hind angle; parietal ridges occasionally (*P*. sp. 10 Guatemala) with a transverse groove; inner tubercles present; posterior margin of prothorax without a deep, semicircular emargination on each side of the mid-line; frons with inner tubercles; meso- and metatibiae usually without spurs.

This species group appears to be artificial, with species (e.g. *P. haagi and P.* spp. 5 Panama and 6 Mexico) possibly being more closely related to species currently placed in *Petrejoides* than to the other members within this group. Revision of the generic limits within Proculini should clarify the relationships of the species in this group (personal observations). The three undescribed species from Guatemala (*P*. spp. 8-10 Guatemala) may eventually be found to form a clade, although in this analysis they did not consistently group together.

***Popilius* sp. 5 Panama**

Description. *Head*: Clypeus anterior to the transfrontal sulcus very short, about equal to the length (anterior-posterior) of the transfrontal sulcus; clypeus anteriorly with a matt border from outer tubercle to tip of canthus; parietal ridges absent; mandibles apically trifid; left inner tooth bifid. *Mesosternum*: Anteriorly with a transverse band of setae at extreme anterior margin. *Mesepimeron*: Glabrous. *Metasternum*: Completely glabrous.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix. Length 15.0-17.0 mm.

Diagnosis. This species is immediately recognizable by its size, as it is the smallest in the genus. It also possesses a suite of other characters unique within the genus; the clypeus anterior to the transfrontal sulcus is very short, about equal to the length (anterior-posterior) of the transfrontal sulcus, the metasternum is completely glabrous, the parietal ridges are absent, the mesosternum anteriorly has a transverse band of setae at the extreme anterior margin, and the clypeus has a matt anterior border from the outer tubercle to the tip of the canthus. It shares with only *P*. sp. 6 Mexico a completely glabrous mesepimeron.

Geographical Distribution and Ecology. This is the smallest species in the genus, and is known only from elevations from 100-1300m along a 1-kilometer section of ridge on the northeast slope of Cerro Guayabo in Panama. The ridge rises up to and then follows the Continental Divide just to the west of the point where the highway between Chiriqui and Chiriqui Grande crosses the border between Bocas del Toro and Chiriqui Provinces. The Continental Divide Trail runs up the ridge for about two kilometers. Although the distribution data includes sites in both provinces, the province noted on a label reflects the side of the trail on which a given specimen was collected, with none being collected more than 150 m from the crest of the ridge.

The site is high, wet, evergreen rain forest, but is being cleared for orchards and pasture up to the Chiriqui border, which is also the edge of the protected watershed (Reserva la Fortuna) of the Fortuna Dam. Specimens were collected in dead wood ranging from rather freshly cut (less than six months old) to dark and thoroughly decayed, and from small standing stumps, small dead sticks (as small as two centimeters in diameter and less than a foot long), and larger, rotten pieces. None of the host trees has been identified, but the species appears to be a generalist feeder.

The extremely limited known distribution of this species is possibly an artifact of collecting, as there are very few roads that cross the Cordillera Talamanca in western Panama or eastern Costa Rica, and few areas above 200 meters elevation on the Caribbean slope of the cordillera in Panama are accessible without considerable hiking.

Locality Data. 42 specimens examined from ARGC.

PANAMA (42). BOCAS DEL TORO (29): Continental Divide area (3 km west or northwest of Fortuna Highway at border) (ARGC). CHIRIQUI (13): Continental Divide area (3 km west or northwest of Fortuna Highway at border) (ARGC).

Exemplar Specimen. The exemplar is a male from ARGC with genitalia dissected and labels a) Panama: Bocas del Toro Prov. 3 km. w. Fortuna Hwy. at Continental Divide border. El. 1050m, 13-VII-95, A.R. Gillogly, b) male symbol.

Remarks. Although this diminutive species has the general appearance of the species of the Haagi Species Group other than P. spp. 8-10 Guatemala, it is separated from P. sp. 6 Mexico, the nearest other taxon, by 53 unambiguous character state changes, and is not well supported as the sister to P. sp. 6 Mexico (BS=2, bootstrap frequency of 67%). It has several autapomorphies, including novel modifications in the form of the mediofrontal structure, and a very short clypeus anterior to the transclypeal sulcus, that suggest that it is either highly derived or basal in the species group. The phylogenetic analysis places it as the sister taxon to P. sp. 6 Mexico but both have a number of autapomorphies and are the smallest species in the genus. It may be that the evolution of smaller size is driving modification of these morphological characters.

The restricted known range in northwest Panama and distance from the center of diversity of this species group weigh against this species being basal in the species group, but are balanced by synapomorphies with other species in the group, particularly *P. punctatissimus* and *P. lenzi*. Analysis of a dataset expanded to include representatives of the species groups of *Petrejoides* and the other genera related to *Popilius* should resolve the placement of this interesting species.

***Popilius* sp. 6 Mexico**

Description. *Head*: Clypeus anterior to the transfrontal sulcus distinctly longer (anterior-posterior) than the transfrontal sulcus; clypeus anteriorly with a rugose patch between outer tubercle and frontogenal suture; central tubercle and parietal tubercles connected by parietal ridges; mandibles apically bifid; left inner tooth trifid. *Mesosternum*: Anteriorly completely glabrous and shiny. *Mesepimeron*: Glabrous. *Metasternum*: Lateral depression setose in anterior 1/10.

For the description of all characters examined, see Appendix D-2. Length 19.0-21.0 mm.

Diagnosis. This is the only species of *Populiu*s with the apices of both mandibles bifid. This and *P*. sp. 5 Panama are the only members of the genus that have a completely glabrous mesepimeron. This species can also be distinguished from *P*. sp. 5 Panama by the lateral depression of the metasternum being setose in its anterior 1/10; in *P*. sp. 5 Panama the lateral depression of the metasternum is completely glabrous.

Geographical Distribution and Ecology. This small species is known from only two locations in south-central Mexico, near Cerro Baul (elevation 1615 m.), Chiapas at the westernmost tip of the Sierra Madre de Chiapas, and from El Palmar (elevation 600’) Veracruz (presumably the vicinity of the forestry station, Campo Experimental El Palmar, Municipio de Tezonapa), near the southeast end of the Sierra Madre Oriental. These are on opposite sides of the Isthmus of Tehuantepec. Although these probably represent isolated populations, there were no significant differences among the five specimens.

Locality Data. 5 specimens examined from CASC and MCZ.

MEXICO (5). CHIAPAS: (4): ridge SE of Cerro Baul (21 km N. Rizo de Oro, formerly Nueva Tenochtitlan) (CASC). VERA CRUZ (1): El Palmar (16 km W. Tetzonapa) (MCZ).

Exemplar Specimen. The most sclerotized (darkest) of the three male CASC specimens from Cerro Baul was used as the exemplar, with the other four specimens used to supplement the observations.

Remarks. This species shares an unusual character, a glabrous mesepimeron, with *P*. sp. 5 Panama, and is placed as the sister to this species in the phylogenetic analysis. The small size of these two species may have forced non-homologous loss of characters, resulting in an apparent closer relationship than in actuality. The results of the successive approximations procedure suggest that this species and *P*. sp. 5 Panama are just as closely related to the outgroup taxa (*Petrejoides* spp.) as to the other members of this species group.

Popilius **sp. 7 Mexico**

Description. *Head*: Clypeus anteriorly smooth from frontogenal suture to tip of canthus; parietal ridges evenly angulate or rounded dorsally; frons glabrous; mentum medially glabrous. *Pronotum*: Anterior marginal groove of pronotum impunctate; pronotum laterally impunctate. *Mesosternum*: Mesosternum posteromedially finely punctate/rugose or matt. *Mesepimeron*: Mesepimeron setose. *Metasternum*: Lateral depression of metasternum uniformly narrow posteriorly; lateral depression of metasternum setose at least in anterior 3/4. *Abdomen*: Anterior process of first complete, visible abdominal sternite (between and just posterior to metacoxae) glabrous. *Leg*s. Profemora expanded.

For the description of all characters examined, see Appendix D-2. Length 27.5-30.0 mm.

Diagnosis. This very distinctive species can be identified by its glabrous frons, medially glabrous mentum, laterally impunctate anterior marginal groove of the pronotum, glabrous anterior process of the first visible abdominal sternite, widely separate postmesocoxal grooves and setose mesepimeron, and expanded profemora.

Geographical Distribution and Ecology. This uncommonly collected species occurs in an unusually broad elevational range for passalids (100-600m and 1230-1340 m), in the states of Oaxaca and Veracruz, Mexico. It has been collected in a clearing in low tropical forest, and from intermediate evergreen and mesophilic montane forests. No host data have been recorded.

***Locality Data*.** 6 specimens examined from IDEM.

MEXICO (6). OAXACA: (3): Metates (6.4 km. S), Valle Nacional (15 km S). VERA CRUZ (3): Dos Amates (Catemaco), Est. Biol. Trop. “Los Tuxtlas” (Mpio San Andres Tuxtla), Pipiapan (Parque de la Flora y Fauna Silvestre Tropical, Catemaco).

***Exemplar Specimen*.** The exemplar was a male from IDEM, with genitalia dissected, and with labels a) Mexico: 6.4 km S Metates, Oaxaca, 24-II-1984, Alt. 1340m, P. Reyes col., b) bosque mesofilo de montana.

Remarks. This species is “*Popilius* sp. nov.” in Castillo (1987) and “*Popilius* sp. A” in Castillo & Reyes-Castillo (1997), in which the authors note the expanded protibia of this hardwood-burrowing species, and speculate that the rarity of the species may be due to an unusual microhabitat, which they suggest might be in detritus, epiphytes, or the interface between log and soil. The wide protibia is not a common character state in passalids, and the presence appears not to be homologous. Other taxa with expanded protibiae are: a species of *Cylindrocaulus*, specialist in the root masses of arboreal ferns (Kabakov, 1967); *Taeniocerus bicanthatus* which reported colonizes only the log/ground interface (Kon & Johki, 1987); *Odontotaenius floridanus* which appears to be restricted to relictual sand dunes in Florida (Schuster, 1994); and an undescribed species of *Odontotaenius* from Panama. The glabrous frons and lack of punctation on the pronotum are also unusual within *Popilius*, and may also be related to a specialized lifestyle.

Although this species is grouped with *P. mysticus* and *P. hirsutus* in the analyses, this relationship is not supported by the branch stability measures (BS=2, bootstrap frequency of 54%).

Popilius haagi (Kaup, 1868)

Passalus haagi Kaup, 1868: 21. The single type specimen was noted by Kaup to be in the collection of Dr. Haag. The type was not seen, and may be in the Museum fur Naturkunde of the Humboldt University in Berlin, Germany.

Soranus intergeneus Bates, 1886: 21. Holotype in the BMNH, with labels a) round, with red border "Type", b) "Mexico, Salle Coll.", c) "Orizaba", d) "BCA Col. II (2). Soranus", e) "1739", f) "Soranus intergeneus Bates". Four paratypes: one in the BMNH with labels a) "Guatemala, Salle Coll.", b) "Soranus intergeneus Bates", c) "BCA Col. II (2). Soranus", d) "P. intergeneus Bates det. J.R. Dibb"; one in the BMNH with labels a) "Guatemala", b) "Salle Coll.", c) "Soranus intergeneus Bates"; two in the MNHN with labels a) "Guatemala", b) "Salle Coll.", c) "Soranus intergeneus Bates", d) "H.W. Bates Biol. Cent. Amer.", e) "PARALECTOTYPE". New synonymy.

Pertinax tau Kaup, 1869:26. Holotype in the MNHN with labels a) Popilius tau Kp. Columbia (in Kaup's writing, per S. Boucher, personal communication), b) EX-Musaeo Van Lansberge (Darmstadt), c) TYPE (in red), d) (folded label) Type du (illegible) Colombia, e) Holotypus (in red). The author noted that only one specimen was seen. New synonymy.

I examined the holotype and all paratypes of *P. intergeneus* at the BMNH and MNHN, and the holotype of *P. tau* at the MNHN, collecting data on 74 morphological characters from the holotypes. I also examined a specimen in the MNHN bearing the labels a) "Soranus Haagi Mexico" (probably in Kuwert's handwriting), b) klingelhoferi (Kp1869) (longhand, in Boucher's writing), collecting data on 74 morphological characters.

Original Description. A translation of Kaup's original description of *Popilius haagi* (1868b) follows:

> Length 9 1/2''' (Note: 9.5 lignes are about 21.4 mm). Elytra 5 1/2 '' (about 11.6mm). A compact, broad form. Clypeus wide, slanting downward, in the form of a weak, convex arc, medially weakly notched, and separated from the frons by a sulcus. At the end of this (sulcus), a small (outer) tubercle. Central tubercle with a broad base, arched with two broad, triangular lateral tubercles. At the base of the steeply sloped, not free, central tubercle, the frontal ridges are attached in an arc, and end in (inner) tubercles before the clypeal (outer) tubercles. From the two discrete tubercles, a bridge goes to the inner margin of the inner supraocular ridge. From the middle of the ridge of the supraocular

ridge, the ridge slopes anteriorly and posteriorly. The central tubercle is surrounded by a somewhat uneven depression up to the bridge.

Mentum with the lateral lobes almost completely deeply punctate, with small, oval, almost obsolete lateral depressions. Pronotum with obtuse angles, weakly concave, with punctate anterior marginal groove, which reaches to the middle of the ocular ridge. A large group of punctures in the anterior corners, and above and around the deeply punctate pronotal scars, with isolated punctures almost reaching the midline. A vestige of a scar along the suture of the mesosternum. Metasternal disk indistinct, without punctures in the posterior intermediate areas. Punctation of the elytra distinct; those laterally formed by small ridges. Two small spines on the mesotibiae, one on the metatibiae. Sparsely setose, only a short crest on the ridge of the mesotibia.

Mexico. One example from the collection of Dr. Haag,the assiduous collector for whom this species is named.

Description. *Head*: Labrum anteriorly symmetrical. *Pronotum*: Anterior marginal groove punctate in lateral 2/3 to 3/4; laterally punctate at least in and around the lateral depressions; clypeus anteriorly smooth from frontogenal suture to tip of canthus; inner tubercle distinct, linear, very close to the outer tubercle, and at least equal in height to outer tubercle; frontal ridges arise directly from anteromedial tip of central tubercle, and meet posteromedially at an angle of about 120°; parietal ridges evenly angulate or rounded dorsally; frons setose anterior and posterior to parietal ridges; mentum with at least 1-3 setae medially; mentum posteromedially shiny. *Prosternum*: Prosternal process widely truncate posteriorly. *Mesosternum*: Mesosternal scar posteriorly (“tail”) short, extending about halfway or less to end of mesepisternum; posteromedially finely punctate/rugose and shiny *Mesepisternum*: With an anteroventral matt patch. *Mesepimeron*: Setose. *Metasternum*: Postmesocoxal grooves widely separate medially (greater than distance between mesocoxae); lateral depression setose at least in anterior 3/4, uniformly narrow posteriorly. *Abdomen*: Anterior process of first complete, visible sternite (between and just posterior to metacoxae) glabrous. *Length*: 20.5-22.0 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. This species is distinct from all other species in the Haagi Species Group. It is distinguished by the frontal ridges arising directly from the anteromedial tip of the central tubercle to the linear inner tubercles and meeting posteromedially in an angle of about 120°, posteriorly short mesosternal scar (extending about halfway or less to the end of the mesepisternum), mesepisternum with an anteroventral matt patch, widely separate postmesocoxal grooves, posteromedially shiny mentum, mesosternum finely punctate/rugose and shiny posteromedially, glabrous anterior process of first visible abdominal sternite (between and just posterior to metacoxae), and the lateral depression of metasternum setose at least in its anterior 3/4. Length 20.5-22.0 mm.

Geographical Distribution and Ecology. Label data indicates that this species is widespread but uncommonly collected, and known from intermediate elevations (500-1400 m) from El Salvador to southeastern Mexico. A specimen from Purulha, Guatemala was encountered in cloud forest and specimens from Veracruz, Mexico were collected in liquidambar forest and in a coffee plantation.

Locality Data. 13 specimens examined from AMNH, FMNH, FSMC, IDEM.

EL SALVADOR (1). S. Salvador (NO FURTHER DATA) (FSMC).

GUATEMALA (7). ALTA VERAPAZ (4): Coban (AMNH), Tactic (IDEM), Tontem (IDEM). BAJA VERAPAZ (1): Purulha (IDEM). NO FURTHER DATA (2): FMNH, IDEM.

MEXICO (5). CHIAPAS: (1): Santa Rosa (IDEM). VERACRUZ (4): Carr. Huatusco-Jalapa (km 7) (IDEM), Cerro El Vigia (San Martin Tuxtla) (IDEM), Las Juntas (Teocelo) (IDEM), Rio Jamapa (Coscomatepec) (IDEM).

Exemplar Specimens. Two exemplar specimens were examined and coded separately:

Exemplar 1 (haagi, Appendix D-2), was a male specimen from IDEM, with the genitalia dissected and bearing the labels a) Guatemala, b) (male symbol), c) Ex Musaeo A. Kuwert, 1894. It was supplemented by a late teneral female specimen from IDEM with labels a) Mexico. Rio Jamapa, Coscomatepec, Edo. de Veracruz, II-VII-75, H. Brailovsky, col, b) (female symbol), c) Popilius haagi (Kaup) Reyes Castillo det.92.

Exemplar 2 (haagiint, Appendix D-2), was a male specimen from FSMC, with the genitalia dissected and bearing the labels a) S. Salvador 1877.XII, b) intergenius det. Kuwert.

Remarks. *P. haagi* is a widespread but uncommonly collected species, which has led to identification errors by a number of passalid specialists. Kaup (1868b) described this species as *Passalus haagi* from a single specimen from Mexico in the Haag Collection, which he did not retain. He described *Pertinax tau* in 1869 for a single specimen from “Columbia” in the Mniszech Collection, which he also did not retain. In his reclassification of the family, using his quinary system, Kaup (1871) transferred *Passalus haagi* into his new genus *Soranus*, and *Pertinax tau* into *Popilius*, also new. Kaup apparently did not recognize the great similarity between the descriptions of these two species nor remember details of the specimens.

Bates commented (1886) on his great difficulty with Kaup’s higher classification and that he was not familiar with *Soranus haagi*. He then described *Soranus intergeneus* for specimens from Mexico which he felt were intermediate between the genera *Soranus* and *Popilius*, noting unspecified characters on the head that placed his species closest to those in *Soranus*.

Kuwert (1897) retained the two genera as distinct, noting that the difference between them was unclear and redefining them such that *Soranus* contained species with the frontal ridges arising directly from the apex of the central tubercle, with the rest of the species being placed in *Popilius*. He also noted that he had not seen specimens of *P. tau* nor any of Bates' species, including *Soranus intergeneus*. However, in order to include the species in his key without having seen them, Kuwert had to make assumptions as to the form of characters that he had not observed and which had not been reported in the literature.

When Gravely (1918) united three other genera under *Popilius*, however, his key to the genus only included 9 of the 37 species then in the genus, omitting *P. haagi* and *P. tau*, and his discussion of *P. intergeneus* is too short and vague to determine the species he was examining.

These actions by Kuwert and Gravely were done with minimal changes in species status, and *P. haagi*, *P. intergeneus* and *P. tau* were united in the same genus for the first time. In his revision of the higher classification of the New World passalids Reyes-Castillo (1970b) split the genus, again, but these three species remained in *Popilius*.

My examination of the holotypes of *P. intergeneus* and *P. tau* determined that they are conspecific, and that they closely match the description of *P. haagi*, including characters that are unusual within the genus, the frontal ridges arising directly from the apex of the central tubercle and diverging widely, and the presence of very small scars on the mesosternum. Examination of the specimen in the MNHN determined as *Soranus haagi* by Kuwert convinced me that the three species are inseparable, and I feel confident in synonymizing *P. intergeneus* and *P. tau* under *P. haagi*, even though I have not yet seen the type of the latter.

Despite its apical position in the successive approximations trees, this species is not well supported as a member of this species group (BS=3, bootstrap frequency of 51%) and does not appear to be closely related to any species in either the species group or the genus. It shares paired tubercles in the internal sac of the male genitalia with three of the outgroup exemplars (*Petrejoides* spp.), and may be moved to a different species group or genus after the generic limits within Proculini are revised.

***Popilius klingelhoefferi* (Kaup, 1869)**

Popilius klingelhoefferi (Kaup, 1869): 5. The holotype was not seen, but is presumably in the HLMD (per S. Boucher). I examined a specimen in the MNHN with the labels a) Popilius klingelhoferi Guatem. Sg., b) Collection Mniszech, c) Ex-Musaeo van Lansberge, d) klingelhofferi Kp., compare au type, e) S. Boucher det. 94. Data on 74 morphological characters were collected.

Original Description. Kaup's description of *Popilius klingelhoefferi*, roughly translated from the original (1869), follows:

> Length 9 1/2''' (Note: 9.5 lignes are about 21.4 mm). Elytra 5 1/2 ''' (= about 12.4 mm). Easily distinguished from the the previous and following species by the smooth, anteriorly deplanate clypeal margin, on the dorsal side of which is a weak sulcus with two small tubercles at the ends. The central tubercle has, attached to its middle, two long, transverse ridges which are prolonged lobe-like posteriorly and are forked at the base of the central tubercle. From the tip of the central tubercle the frontal ridges fall down in an acute angle, forming at the base of the central tubercle two small arcs with a small (inner) tubercle at the end. The lateral ridges of the central tubercle run almost parallel with the frontal ridges. In the middle of the frons, between the frontal ridges, is a small, longitudinal tubercle. the back of the head forms a convex bulge with fine, sparse punctures and a weak longitudinal groove in the middle.
>
> the depressions of the lateral portions of the surface of the head somewhat rough. Mentum weakly convex, smooth and projecting medially, with small, defined scars (depressions). Both this and the lateral lobes punctate. Prothorax (pronotum) with small, punctate lateral depressions with sparse punctures above them.
>
> Anterior marginal groove narrow, reaching to the middle of the ocular ridge. Mesosternum anteriorly convex and medially grooved, posteriorly widened and rugose. Under the sulcus with matt colored, weak scars, forming a deep hook to the middle of the mesosternum. The scutellum is convex; longitudinally, medially, thickly punctate. The metsternal disk weakly margined, with a few indistinct punctures in the hind angles. One spine, possibly two, on the mesotibiae.
>
> Prothorax (prosternum) and mesotibiae sparsely setose; finely but very distinctly punctate in the grooves of the elytra.
>
> Mexico. I have named this slender and elongate species after my friend, Colonel Klingelhoffer, who is well known to European entomologists as a diligent collector.

Description. *Head*: Labrum anteriorly symmetrical; clypeus anteriorly smooth from frontogenal suture to tip of canthus; inner tubercles indistinct, or distinct, but usually lower than outer tubercles; outer tubercle closer to anterior tubercle of supraocular ridge than to inner tubercle; frontal ridges arise from a single ridge just anterior to base of central tubercle, and meet medially at an angle of about 45°; parietal ridges evenly angulate or rounded dorsally; frons setose anterior and posterior to parietal ridge; subocular ridge moderately long, reaching about half the distance to the antennal fossa, irregular; mentum with at least 1-3 setae medially, posteromedially matt. *Pronotum*: Anterior marginal groove punctate in lateral 2/3 to 3/4; laterally punctate at least in and around the lateral depressions. *Prosternum*: Prosternal process narrowly truncate posteriorly; hypomeron medially with a moderately wide matt area with a concave lateral margin. *Elytra*: Humerus setose ventrolaterally adjacent to mesepimeron. *Mesosternum*: Mesosternal scar posteriorly ("tail") long, extending about to end of mesepisternum); posteromedially finely punctate/rugose or matt. *Mesepisternum*: With matt puncture rims, but without a distinct anteroventral matt patch. *Mesepimeron*: Setose. *Metasternum*: Postmesocoxal grooves with a depression between the medial ends of the grooves; lateral depression setose at least in anterior 3/4, uniformly narrow posteriorly.
Abdomen: Anterior process of first complete, visible sternite (between and just posterior to metacoxae) glabrous. *Length*: 19.0-23.0 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. *P. klingelhoefferi* belongs to a complex of similar species that are distinct from the rest of the species group, including *P. scutellopunctatus*, *P. punctatissimus*, *P. lenzi*, *P. mysticus* and *P. hirsutus*. It is distinguished by the depression between the medial ends of the postmesocoxal grooves, a single short ridge connecting the frontal ridges with the central tubercle, posteromedially matt mentum, a long mesosternal scar extending about to the posterior margin of the mesepisternum, and the elytral humerus setose ventrolaterally adjacent to the mesepimeron. Length 19.0-23.0 mm.

Geographical Distribution and Ecology. This species is known only from moderately high elevations (1219-1981 m) in Guatemala and far eastern Mexico, and has been recorded from primitive forest, mesophilic forest, and pine-oak-liquidambar forest. Specimens were collected in liquidambar and pine.

Locality Data. 37 specimens examined from ARGC, CASC, CFSC, FMNH, IDEM, USNM, UVGC.

GUATEMALA (3). NO FURTHER DATA (3) (FMNH, USNM).

MEXICO (34). CHIAPAS: (34): Cate-Jititol (4 kms) (IDEM), El Suspiro (Berriozabal, km 8) (IDEM), Cinco Lagos (cerca de; Lagunas de Montebello, Municipio La Trinitaria) (CFSC, IDEM), Comitan (29 km NW) (UVGC), Dos Lagos (14km E, paved road at Lagos de Dolores, Municipio de La Trinitaria) (CASC), Lagos de Montebello (ARGC), Lagos de Montebello (near Cinco Lagos) (ARGC), Municipio Mikontik (11 km N Tzontehuitz on road to Pueblo Viejo) (CASC), Municipio Tapalapa (CFSC), Ocosingo (IDEM), Oxchuc (USNM), Santa Rosa (CASC, IDEM), San Cristobal (3.5 km NE, Municipio San Cristobal de Las Casas) (CFSC).

Exemplar Specimen. The exemplar was a male specimen in the IDEM, with the genitalia dissected and bearing the labels a) Ocosingo, Chis. 1200m, zona montanosa, bosque primitivo, VI-IX-47, M. del Toro, b) Popilius klingelhofferi (Kaup) Reyes Castillo, det. 1968, c) (placed upside down) Popilius mysticus Bat., P. Pereira det. 968, d) Compare au type par Reyes Castillo, XII-74, Museo Paris.

Remarks. *P. klingelhoefferi* is very similar in size and form to *P. haagi*, which has led to considerable confusion among passalid specialists in determining specimens. The placement of this species within the Haagi species Group is variable, but it seems to be most closely related to *P. mysticus* and *P. scutellopunctatus*. *P. klingelhoefferi* and *P. mysticus* appear to be sympatric, and both are allopatric with respect to *P. scutellopunctatus* which is known only from El Salvador. It is quite possible that if additional specimens of *P. scutellopunctatus* can be collected, the differences between it and *P. klingelhoefferi* may be bridged.

Popilius scutellopunctatus **Kuwert, 1897**

Popilius scutellopunctatus Kuwert, 1897: 301. Holotype probably mislaid in the MNHN. A specimen of *Petrejoides subrecticornis* (Kuwert, 1897) in the MNHN bears the labels a) S. Salvador 1877 XII.34, b) scutellopunctatus Kuw. S. Salvador (in Kuwert's handwriting, per S. Boucher), c) Ex-Musaeo A. Kuwert 1894, d) Holotipo, e) Popilius scutelopunctatus (sic) Kuwert, Reyes Castillo det. 69, f) Petrejoides (male symbol) subrecticornis Kuwert, C. Castillo, det. 1981. There may be another specimen in a European museum, but none has yet been located (S. Boucher, personal communication).

I examined the specimen of Petrejoides subrecticornis (Burmeister) bearing the holotype label of *P. scutellopunctatus* at the MNHN and collected data on 74 morphological characters.

Original Description. A rough translation of Kuwert's description of *P. scutellopunctatus,* assembled from the key format in which it was published (1897), follows:

> The transverse lateral ridges not grooved dorsally. Without a short longitudinal line anterior to the foot of the central tubercle which connects both frontal ridges. From the tip of the central tubercle to the middle of the arc of the frontal ridges there is either a simple longitudinal ridge or there is no ridge, but only a matt, rough area. The frontal area never with two small ridges uniting in an acute angle, but almost always with a more or less shortened longitudinal ridge which does not reach the transfrontal sulcus. Scutellum punctate, with a wide, smooth midline. Meso- and metatibiae without small spines. From the tip of the more or less acutely keeled central tubercle a single ridge reaches to the slightly arched frontal ridges which join together in an obtuse angle, and which end in weak tubercles two-fifths of the distance from the clypeal teeth. The wide anterior marginal grooves of the pronotum coarsely, the lateral marginal grooves of the pronotum finely, and the lateral scars coarsely and thickly punctate; the latter with a large group of punctures above it. Mesosternum without scars. The smoothly striate elytra without strongly swollen intervals, not strongly punctate. Clypeus straight, medially with or without a groove or depression. There is neither a longitudinal keel or groove within the arc of the frontal ridges. Depressions of the head smooth. Abdominal sternites without scars, equally highly rounded. Posterior angles of the metasternum punctate.
>
> Length 22mm. Hab. San Salvador.

Description. *Head*: Labrum projecting further on left side than right; clypeus anteriorly smooth from frontogenal suture to tip of canthus; canthus evenly wide, rounded or obtusely angled laterally; frontal ridges arise from a single ridge well anterior to base of central tubercle; frons setose anterior and posterior to parietal ridges; parietal ridges evenly angulate or rounded dorsally; subocular ridge long, reaching over half the distance to the antennal fossa, partially obscured by strong punctures; right dorsal mandibular tooth anteriorly (lateral view) obtuse or right-angled; mentum posteromedially matt. *Pronotum*: Anterior marginal groove punctate in lateral 2/3 to 3/4; punctate onto disc (at least 3 punctures on each side). *Prosternum*: Hypomeron medially with a wide matt area with a straight, convex or slightly concave lateral margin; pronotal arm widely setose, matt. *Elytra*: Humerus sparsely setose. *Mesosternum*: Mesosternal scar anteriorly (“head”) setose, wide (about 1/3 width of mesosternum); posteromedially finely punctate/rugose or matt. *Mesepimeron*: Setose. *Metasternum*: Postmesocoxal grooves connected medially; lateral depression setose at least in anterior 3/4, uniformly narrow posteriorly. *Abdomen*: Anterior process of first complete, visible abdominal sternite (between and just posterior to metacoxae) glabrous.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix. Length 21.0 mm.

The character states used in Appendix D-2 are from the exemplar, and not from the specimen bearing the type label, for the reasons discussed in the remarks section, below.

Diagnosis. This species is most similar to *P. klingelhoefferi* and *P. lenzi*, and is distinguishable within the species group by the medially connected postmesocoxal grooves, sparsely setose elytral humerus, widely setose and matt pronotal arm, posteriorly matt and punctate or setose mentum, and the frontal ridges arising from a single connecting ridge well anterior to the base of the central tubercle.

Geographical Distribution and Ecology. This species is known only from El Salvador. There are no ecological data with the specimens.

Locality Data. 2 specimens examined from FSMC, IDEM.

EL SALVADOR (2): No further data (FSMC, IDEM).

***Exemplar Specimen*s.** Two exemplars were examined and analyzed.

Exemplar 1 (scutEx1, Appendix D-2) was a female specimen (FSMC) with labels a) S. Salvador 1877 XII.6, b) (female symbol), c) scutellopunctatus det. Kuwert. The collection label suggests that it was collected within one or two days of the holotype, and was possibly part of the series examined by the describer.

Exemplar 2 (scutEx2, Appendix D-2) was a male specimen (IDEM) with labels a) America de Staudinger 1929, b) MZUSP, c) 05882, d) male sex symbol, e) Popilius scutellopunctatus Kuw. Lueder. Det. 1931, f) (label folded) Popilius mysticus Bates Kuwert det.

Remarks. I examined the holotype of *P. scutellopunctatus* and compared it with the holotype of *Petrejoides subrecticornis* Burmeister, which is also in the MNHN. The latter bears two locality labels, a) Moritz Venez, and b) subrecticornis Kuwert Guatemala (in Kuwert's handwriting). I agree with C. Castillo, whose determination label is on the type of *P. scutellopunctatus,* that the two specimens are conspecific and belong to the genus *Petrejoides* (Castillo & Reyes-Castillo, 1984).

However, several lines of evidence suggest that the specimen bearing the holotype label of *P. scutellopunctatus* may not belong to the species described by Kuwert, specifically, the moving of labels among specimens, the mismatch between the original description of *P. scutellopunctatus* and the morphology of the specimen now bearing the holotype label ("holotipo"), and the presence of two specimens that may have been seen by Kuwert, one of which is quite possibly part of the series used to prepare the original description. *P. scutellopunctatus* and *Petrejoides subrecticornis* are very similar in size and shape, so it is also possible that Kuwert's series included specimens of both species, and that the type label was placed on one that did not match the description prepared during examination of the others.

The two locality labels associated with the holotype of *Petrejoides subrecticornis* provide evidence that labels have been moved, as the genus *Petrejoides* is not known from Venezuela and *Petrejoides subrecticornis* is from western Mesoamerica. The specimen bearing the holotype label of *P. scutellopunctatus* belongs to a species currently placed in a different genus and does not match Kuwert's original description.

The labels on Exemplar 1, the specimen obtained on loan from FSMC, suggest that this specimen was collected within a day of the specimen originally bearing the type label, and it appears likely to have been part of the original series examined by Kuwert in describing *P. scutellopunctatus.* That a series was examined by Kuwert is indicated by his description of the clypeus of *P. scutellopunctatus* as either having or not having a medial groove or impression, character states not possible to be present on a single specimen.

The specimen on loan from IDEM, Exemplar 2, bears labels a) America de Staudinger 1929, b) MZUSP, c) 05882, d) male sex symbol, e) Popilius scutellopunctatus Kuw. Lueder. Det. 1931, f) (label folded) Popilius mysticus Bates Kuwert det. This specimen also has had at least one label moved, as it is not possible to have been obtained from Staudinger in 1929, determined by Luederwaldt in 1931, and also have been determined by Kuwert, who died in 1894 (Anonymous, 1895). Luederwaldt was familiar with *Popilius* (see Luederwaldt, 1941), which had considerably wider limits until divided by Reyes-Castillo (1970b). Luederwaldt evidently recognized that this specimen matched Kuwert's description (or the original holotype) of *P. scutellopunctatus*, and added his determination label.

Both the FSMC and IDEM specimens belong to the genus *Popilius*, not *Petrejoides*, and appear to be conspecific. There are minor, but constant differences between these two specimens and the nearest other species, *Popilius klingelhoefferi*, as noted in the diagnosis above and in the key to *Popilius*.

Kuwert's (1897) original description of *P. scutellopunctatus* fits well with both *Petrejoides subrecticornis* and the two exemplar specimens of *P. scutellopunctatus*, except for his statement that the mesosternum is without scars (both of these species have mesosternal scars) and that there is neither a longitudinal keel or groove within the arc of the frontal ridges (the exemplar of *P. scutellopunctatus* from IDEM has a small raised area in the frontal angle). However, Kuwert specifically states that "From the tip of the more or less acutely keeled central tubercle a single ridge reaches to the slightly arched frontal ridges which join together in an obtuse angle…". Both exemplars of *P. scutellopunctatus* have this ridge. *Petrejoides subrecticornis* does not have a longitudinal connecting ridge; the frontal ridges end at the anterior base of the central tubercle (Castillo & Reyes-Castillo, 1984).

Because Kuwert's original description of *P. scutellopunctatus* more closely matches the exemplar specimens labeled *P. scutellopunctatus* and there is evidence of the transfer of labels among specimens, I conclude that *P. scutellopunctatus* has been prematurely synonymized under *Petrejoides subrecticornis,* and that the name should be considered valid until a thorough search of the MNHN holdings can be made for a specimen conspecific with the two exemplars of *P. scutellopunctatus* in this study.

Petrejoides subrecticornis is similar in size and form to the two exemplars of *P. scutellopunctatus*. It is possible that the specimen bearing the type label of *P. scutellopunctatus* and Exemplar 1 (scutEx1) of this study were part of a mixed series that was subsequently split up among collections.

P. scutellopunctatus is therefore treated as a valid species. The type specimen of *P. scutellopunctatus* has apparently been mislaid within the MNHN, and the holotype label (which appears to be in Spanish, which is not a language expected to be used on a label by Kuwert, a German) was placed on a specimen of *Petrejoides subrecticornis* in error.

***Popilius punctatissimus* Luederwaldt, 1941, New status**

Popilius tau punctatissimus Luederwaldt, 1941: 82. The author noted that three cotypes were deposited in the MZSP, with accession numbers of 23.002, 23.003, 23.004. Attempts to contact the MZSP regarding these specimens were not answered.

I examined the type of *P. tau* at the MNHN and collected data on 74 morphological characters.

Original Description. A translation of Luederwaldt's brief description of *P. tau punctatissimus* (1941) follows:

> Differs from *P. tau* Kaup by having the anterior marginal groove of the pronotum quite longer and wider, with a strongly punctate sinuosity; almost all of the lateral area with rich, dense punctation, with punctures as far as on the disk, and sometimes as far as the median groove. Frontal ridges in a very wide arc, almost parallel to the lateral ridges. Frontal area as in *P. tau* Kaup and *P. klingelhoefferi* Kaup. Costa Rica. Nevermann and A. Alfaro, coll.

Pereira added at the end of Luederwaldt's description that, in his view, these did not constitute a variety distinct from the typical species.

A translation of Kaup's original description of *P. tau* (1869) follows:

> Length 9''' (Note: 9 lignes are about 20.3 mm). Similar to the previous species (Note: the species addressed just previous to *P. tau* was *P. marginatus*) but has a T-formed shape on the frons and the frontal ridges originate directly divergent from the base of the central tubercle. The prothorax has a deep, wide, punctate anterior marginal groove. The medial groove goes up to the anterior margin. Numerous punctures above the lateral depressions and a few on the anterior corners. The prosternal process slopes sharply anteriorly to the plate, has no shiny margins and a wide tip posteriorly. The mesosternum is convex, smooth, and without medial, longitudinal grooves. The lateral scars anteriorly moderately distinct and very flat. A few punctures in the hind angles of the metasternal disk. Scutellum sparsely punctate. One distinct, and anteriorly one indistinct spine on the mesotibia. A vestige of a small spine on the metatibia.
>
> Columbia. One specimen in the Mniszech Collection.
>
> In 1871, Kaup redescribed the species. A translation of that description follows: Length 22mm, elytra 13mm, width 7-7.5mm.
>
> A somewhat narrower form than *marginatus*. The flat, rounded central tubercle is dorsally grooved to the base, and the somewhat elevated tip is abruptly brought to a point. The acutely developed transverse ridges end in a point. At the base of the central tubercle are the sharp frontal ridges, which diverge greatly in a weak arc. The raised clypeal ridge separated from the frons by a groove. In the middle of the frons is a ridge, which is connected anteriorly to a transverse ridge, forming a Latin T. Deepened between these ridges, on both sides of the frons. The depression between the supraocular ridge and the central tubercle and frontal ridges finely punctate, otherwise smooth on the rest of the head surface. Prothorax with groups of punctures above the lateral depressions and on the anteriorly rounded corners. The small, posteriorly-widened anterior marginal groove punctate, as is the margin of the groove. Lateral margin of the metasternum finely shagreened and glabrous; the latter generally sparse. Meso- and metatibiae with two fine spines.
>
> Colombia. One specimen in the Mniszech Collection.

Kuwert’s description (1897), in key form, repeats the characters used in Kaup’s 1871 description, though adding that only a single ridge connects the tip of the central tubercle to the frontal ridges and there is no transverse groove on the lateral ridges, but failing to mention that the frontal ridges diverge directly from the base of the central tubercle. This suggests that Kuwert may not have seen the type of *P. tau*, or he would probably have placed this species in the genus *Soranus* Kaup, for which the frontal ridges springing directly from the base of the central tubercle is a diagnostic character.

Description. *Head*: Labrum projecting further on left side than right; clypeus anteriorly smooth from frontogenal suture to tip of canthus; canthus narrowest medially, expanded apically, and angulate laterally; frontal ridges arise from a single or double ridge well anterior to base of central tubercle; frontal ridges diverge in concave, curved lines from origin to inner tubercles and meet medially at an angle of about 180° or connected in an even arc; frons setose anterior and posterior to parietal ridge; subocular ridge long, reaching over half the distance to the antennal fossa, irregularly raised, partially obscured by strong punctures; right dorsal mandibular tooth anteriorly (lateral view) projecting; mentum punctate and setose medially. *Pronotum*: Anterior margin slightly recurved at lateral third, anterior angles very slightly projecting; anterior marginal groove punctate in lateral 2/3 to 3/4; anterolaterally (excluding the marginal grooves) punctate, laterally punctate above lateral depressions and onto disc (at least 3 punctures on disc on each side). *Prosternum*: Hypomeron medially with a wide matt area with a straight, convex or slightly concave lateral margin; pronotal arm glabrous, shiny. *Elytra*: Humerus glabrous. *Mesosternum*: Mesosternal scar anteriorly slightly or distinctly (~1/3 width of mesosternum) expanded medially, but narrow; mesosternal scar glabrous. *Mesepimeron*: Setose. *Metasternum*: Postmesocoxal grooves with a depression between the medial ends of grooves; lateral depression of metasternum setose only in anterior 1/10. *Length*: 20.0-23.0 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. This species belongs to the complex of species including *P. lenzi*, *P. klingelhoefferi*, *P. scutellopunctatus*, *P. mysticus* and *P. hirsutus*. It can be distinguished by the depression between the medial ends of the postmesocoxal grooves, glabrous pronotal arm, the pronotum (excluding the marginal grooves) anterolaterally and laterally punctate above the lateral depressions and onto the disc (at least 3 punctures on the disc on each side), the lateral depression of the metasternum setose only in its anterior 1/10, and the tip of the central tubercle about even with the parietal tubercles. Length 20.0-23.0 mm.

Geographical Distribution and Ecology. This species occurs in Costa Rica and Panama at generally intermediate elevations (usually from 480-1340 m) from the northernmost Cordillera de

Guanacaste to the easternmost mountains of the Cordillera Talamanca, about 60 miles west of the Isthmus of Panama. The elevational and geographical outlier is a series of four specimens from the Barra del Colorado area (15 m), in extreme northeastern Costa Rica near the border with Nicaragua. The species is found on both Atlantic and Pacific slopes of the cordilleras as far east as Bocas del Toro, Panama on the Caribbean side and Cocle Province, Panama on the Pacific slope. In western Panama, it occurs in high dry forest (1000-1340 m) on the Pacific slope and in wet tropical forest (935 m) at the single collection locality in Bocas del Toro. No host associations have been made.

Locality Data. 104 specimens examined from ARGC, DJCC, EMEC, IDEM, INBC, PRC, UNSM, USNM, UVGC.

COSTA RICA (36). ALAJUELA (4): Rio San Lorencito (R.F. San Ramon, 5 km N Colonia Palmarena) (INBC). Rio Sarapiqui (2 km SE Cariblanco) (EMEC), San Ramon (Rio San Lorencito) (INBC). CARTAGO (1): Guayabo (Turrialba area) (IDEM).

GUANACASTE (8): Est. Pitilla (9 km S Sta. Cecilia) (INBC), Rio San Lorenzo (Tierras Morenas, Z.P. Tenorio) (INBC). LIMON (18): La Palma (no further data, presumably Limon Prov.) (USNM), Reserva Biologica Barbilla (INBC), Sardinas (Barra de Colorado) (INBC), Sector Cerro Cocori (Finca de E. Rojas) (INBC). PUNTARENAS (4): Finca Cafrosa (Est. Las Mellizas, P.N. Amistad) (INBC), Las Mellizas (INBC).

SAN JOSE (1): Est. Bijagual (600 m N Bijagualito) (INBC).

PANAMA (68). BOCAS DEL TORO (1): Fortuna Hwy border station (ridge end, 4 km NW) (ARGC). CHIRIQUI (25): Lagunas del Volcan (near city of Volcan) (ARGC), Las Lagunas (4-5 km W and SW Volcan) (ARGC), Rio Sereno (5 km E) (ARGC), Santa Clara (Dist. Renacimiento) (UNSM, UVGC). COCLE (42): Cerro Gaital (DJCC), Cerro Gaital (3 km N La Mesa) (ARGC), La Mesa (El Valle) (ARGC, DJCC). La Mesa (NE side Cerro Gaital) (ARGC).

Exemplar Specimens. The exemplar was a male specimen in the ARGC, with the genitalia dissected and with labels a) PANAMA: Chiriqui Pr., Lagunas del Volcan near city of Volcan, July 4, 1996, 1300 m, Gillogly & Schaffner, b) (male symbol). This specimen was supplemented by a female specimen in the IDEM bearing the labels a) Costa Rica Guayabo, VI 931, Alfaro leg., b) 05893, c) (female symbol), d) Popilius tau (Kaup), Reyes Castillo det.1968, e) XII-1974, Compare au type, par Reyes Castillo, 74, Mus. Paris, NEC klingelhoeferi, f) Popilius tau Kaup, P. Pereira det 946.

Remarks. Based on Kaup's original description, this species appears to be quite similar to *P. haagi*, and the holotype appears to be conspecific with *P. haagi*, a species which is not known to occur east of Guatemala. There is no species of *Popilius* currently known to occur in Colombia or Panama (part of Colombia until 1903) that fits this description.

During this study, the holotype of *P. tau* was found to be conspecific with the holotype of *P. haagi* (Kaup), and *P. tau* is here synonymized under *P. haagi*. Luederwaldt (1941) published the trinomial name " *Popilius tau punctatissimus var. n.*" describing three specimens from Costa Rica as a variety that he felt was distinct from the type. Under Article 45.6.4 of the International Code of Zoological Nomenclature (ICZN, 1999), the name *punctatissimus* is considered to be subspecific, and therefore an available name. Luederwaldt's brief description includes several of the distinctive characters separating this species from the others in the genus, so the valid name of this taxon is *P. punctatissimus* Luederwaldt.

Pereira added remarks to Luederwaldt's description which he edited and published after the latter's death, and noted that he did not consider this taxon to constitute a distinct form of the species. He did not note whether he based his opinion just on the quality of the characters and shortness of the description, or from comparison with the holotype of *P. tau*.

This species is most closely related to *P. lenzi* (BS=6, bootstrap frequency of 93%), the two of which appear most similar to *P. mysticus*, *P. hirsutus*, *P. klingelhoefferi* and *P. scutellopunctatus*.

***Popilius lenzi* Kuwert, 1897**

Popilius lenzi Kuwert, 1897: 301. Holotype in MNHN with labels a) Cocos I., b) Ex Musaeo A. Kuwert 1894, c) Lendzii Kuw. Cocos-Ins., d) (female symbol) Type (in red). I examined the holotype of *P* lenzi at the MNHN and collected data on 74 morphological characters.

Original Description. A rough translation of Kuwert's description of *Popilius lenzi*, assembled from the key format in which it was published (1897), follows:

> The transverse lateral ridges not grooved dorsally. There is no longitudinal line present anterior to the foot of the central tubercle to which both frontal ridges connect. From the tip of the central tubercle to the middle of the arc of the frontal ridges with either a simple longitudinal ridge or there is no ridge, but only a matt, rough area. The frontal area never with two small ridges uniting in an acute angle, but almost always with a more or less shortened longitudinal ridge which does not reach the transfrontal sulcus. Scutellum punctate, with a wide, smooth midline. Meso- and metatibiae with one small

> spine. From the tip of the central tubercle to the base a split ridge goes down, to which are connected the quite transverse, highly convex frontal ridges, which on their ends bear strong (inner) tubercles. The clypeal ridge raised up at its ends to high teeth (outer tubercles). Pronotal anterior and lateral marginal grooves and the lateral depressions punctate, also a few punctures above the latter. In place of the mesosternal scars, on either side is one longitudinal row of weak punctures. Hind angles of the metasternum not deeply punctate. There is no longitudinal keel within the arc of the frontal ridges. Depressions of the head completely smooth. Length 26mm. Hab. Cocos Island.

Description. *Head*: Labrum projecting further on left side than right; clypeus anteriorly smooth from frontogenal suture to tip of canthus; canthus narrowest medially, expanded apically, and angulate laterally; frontal ridges arise from arise from a single or double ridge well anterior to base of central tubercle; frontal ridges diverge in convex, recurved lines from central tubercle to inner tubercles and meet medially at an angle of about 45°; parietal ridges evenly angulate or rounded dorsally; frons setose anterior and posterior to parietal ridge; subocular ridge long, irregularly raised, partially obscured by strong punctures; right dorsal mandibular tooth anteriorly (lateral view) projecting; mentum punctate or setose only posteriorly. *Pronotum*: Anterior margin straight, anterior angles rounded, not projecting; anterior marginal groove punctate in lateral 2/3 to 3/4; anterolaterally impunctate (excluding the marginal grooves); laterally punctate only in and around lateral depressions. *Prosternum*: Pronotal arm shiny, setose only close to the prosternal process or glabrous; hypomeron medially with a wide matt area and straight, convex or slightly concave lateral margin. *Elytra*: Humerus glabrous. *Mesosternum*: Mesosternal scar glabrous, anteriorly slightly expanded medially or wide (~1/3 width of mesosternum) but thin. *Mesepimeron*: Setose. *Metasternum*: Postmesocoxal grooves connected medially; lateral depression setose in anterior 1/2.

Abdomen: Anterior process of first complete, visible sternite (between and just posterior to metacoxae) glabrous. *Length*: 23.0-26.5 mm.

For the description of all characters examined, see Appendix D-2– *Popilius* Matrix.

Diagnosis. *P. lenzi* is most similar to *P. punctatissimus* and *P. klingelhoefferi*. It can be distinguished from other species in the Haagi Species Group by the medially connected postmesocoxal grooves, pronotum anterolaterally impunctate (excluding the marginal grooves), pronotum laterally punctate only in and around the lateral depressions, and lateral depression of metasternum setose only in the anterior half.

Geographical Distribution and Ecology. This species is known only from Cocos Island, 532 km southeast of the Nicoya Peninsula of Costa Rica, and almost halfway to the Galapagos Islands. The land surface of the island is 24 square km and the highest elevation is 638 m. Locality data indicate that specimens have been collected at elevations from 10-260 m from rotting logs and in a malaise trap (one specimen). One specimen was collected from the trunk of a rotting *Rooseveltia*, a genus of palms endemic to the island. On some labels the locality is confused with the Cocos (Keeling) Islands in the Indian Ocean.

***Locality Data*.** 82 specimens examined from AMNH, CASC, CMNH, FMNH, INBC, LACM, PRC, USNM.

COSTA RICA (82). PUNTARENAS (82): Bahia de Chatham (CASC, INBC), Bahia Yglesias a la catarata (Yglesias por el Sendero) (INBC), Cocos Id. Indian Ocean (sic) (AMNH), Cocos Island (AMNH, CASC, CMNH, FMNH, INBC, LACM, PRC, USNM), El Guarumal (send. Wafer-Chatham) (INBC), Los Llanos (INBC). Orilla del Rio Gienio (INBC).

Exemplar Specimens. The exemplar was the specimen in the IDEM with labels a) Isla de Coco IX-13-1905, F.X. Williams, b) TOPOTIPO (red paper), c) Compare au type par Reyes-Castillo XII-1974 (red paper), Mus. Hist. Nat. Paris. It was supplemented by two specimens in the CASC, a teneral specimen with the same locality data except for a date of IX-12-05, and a male specimen with genitalia dissected with a locality label the same as the exemplar.

Remarks. The number of specimens available for study is extraordinarily large for a species of *Popilius* with such a small range, but Cocos Island has been the subject of a number of scientific expeditions, and has undoubtedly been studied in far more detail than most other forest areas of similar size within the range of *Popilius*. Cocos Island is now a national park and World Heritage Site.

This species appears to be most closely related to *P. punctatissimus* (BS=6, bootstrap frequency of 93%), the range of which includes the Pacific slope of the Cordillera Talamanca in Costa Rica and Panama, the portion of mainland Mesoamerica closest to Cocos Island. This species may be derived from a founding individual or small population of a common ancestor that drifted on vegetation from the mainland to Cocos Island and differentiated in isolation.

Popilius hirsutus **Luederwaldt, 1941**

Popilius hirsutus Luederwaldt, 1941:82. Type material not seen. According to the author the holotype was deposited in the Division of Insects, MZSP, with the accession number 22.998, presumably with labels indicating the type locality as Costa Rica and the collectors as

Nevermann and A. Alfaro. Attempts to contact the MZSP regarding this specimen were unsuccessful

Original Description. A translation of Luederwaldt's original description of *Popilius hirsutus* (1941) follows:

> Length 25-28mm. Mandibles with three terminal teeth. Clypeus like that of *P. marginatus* (Perch.), rather wide and dilated. Central tubercle without a free tip, lightly widened posteriorly, low and ridged for its entire length. Lateral tubercles large and planar, rising immediately behind the tip of the central tubercle, forming a right angle with it, and directed slightly anteriorly, the anterior part being quite declivitous with the tips armed with a tooth-like tubercle. Frontal ridges slightly arcuate, distinct to the inner tubercles, united with the central tubercle by two carinae, or a single one grooved in the middle. Frontal angle obtuse, with or without a rounded, medial tumidity. Frontal area smooth. Clypeal sulcus marked and almost straight. External tubercles strong, the inner tubercles weak and situated almost near the sulcus. Frontal fossae rugose and setose. Supraocular ridges with two angles. Pronotum with the median sulcus distinctly widened anteriorly, the laterals very narrow and punctate, the exteriors somewhat widened, almost reaching the median sulcus; anterior angles rounded, scars with a few punctures, with a group of punctures above which sometimes extends up to the disk, ventral border with dense hair. Elytra not fused, with dorsal striae finely, and the laterally more strongly, punctate. Humeri and epiplurae glabrous. Lobes of the mentum with deep punctures and setose. Prosternum terminating posteriorly in a point. Mesosternum without well delimited scars. Disk of the metasternum posteriorly indistinctly margined; intermediate and anterior areas punctate and setose, posteriorly sparsely punctate. Metepisterna narrow, not widened, punctate and with weak pubescence. Meso- and metatibiae with one lateral spine. Costa Rica, IV. 1925, F. Nevermann, leg.

Description. *Head*: Labrum projecting further on left side than right; clypeus anteriorly smooth from frontogenal suture to tip of canthus; transfrontal sulcus about straight; frontal ridges connected to the base of the central tubercle by a double ridge with a narrow medial groove; parietal ridges evenly angulate or rounded dorsally; frons setose anterior and posterior to parietal ridge; subocular ridge long, reaching over half the distance to the antennal fossa, evenly raised;

right dorsal mandibular tooth dorsally (lateral view) concave, dorsally (dorsal view) rugose or coarsely punctate;

mentum punctate and setose medially. *Pronotum*: Anterior marginal groove punctate in lateral 2/3 to 3/4; laterally punctate at least in and around the lateral depressions. *Prosternum*: Prosternal process narrowly truncate posteriorly; hypomeron medially with a wide matt area with a straight, convex or slightly concave lateral margin. *Elytra*: Humerus sparsely setose. *Mesosternum*: Posteromedially finely punctate/rugose or matt. *Mesepimeron*: Setose. *Metasternum*: Postmesocoxal grooves widely separate medially (greater than distance between mesocoxae; lateral depression setose at least in anterior 3/4, uniformly narrow posteriorly. *Abdomen*: Anterior process of first complete, visible abdominal sternite (between and just posterior to metacoxae) glabrous. *Length*: 25.0-28.5 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. *P. hirsutus* is distinguishable by its sparsely setose elytral humerus, straight transfrontal sulcus, widely separate postmesocoxal grooves, frontal ridges connected to the base of the central tubercle by a double ridge with a narrow medial groove, setose mesepimeron, and glabrous anterior process of the first visible abdominal sternite. Length 25.0-28.5 mm.

Geographical Distribution and Ecology. Very little is known about this large species of *Popilius*. It is uncommon in collections, with only four known specimens. The only ecological data with the specimens were elevations, 640 m. at Est. Cacao and 1000-1400 m. at Est. San Ramos, and the reference to “Ebene Limon” on the label of the specimen from Hamburg Farm suggests the eastern slope of the cordillera. It appears that this species is widespread at intermediate elevations in northern and eastern Costa Rica, although very uncommonly collected.

Locality Data. 3 specimens examined from INBC, USNM.

COSTA RICA (3). ALAJUELA (1): Est. San Ramon Oeste (INBC). LIMON (1): Hamburg Farm (Reventazon, Ebene) (USNM). GUANACASTE (1): Estacion Cacao (2km SW side Volcan Cacao) (INBC).

Exemplar Specimens. The USNM specimen (male, with genitalia dissected) from Limon Province was selected as the exemplar, for reasons discussed in the remarks below. The labels on the specimen are a) Hamburg Farm, Reventazon, Ebene Limon, b) Costa Rica, F. Nevermann 12 V 25, c) Popilius hirsutus Lueder. Lueder. Det. 1932, d) Popilius hirsutus Luederwaldt, Reyes Castillo. Det. 1970. The specimens from Alajuela Pr. (male, genitalia dissected) and Guanacaste Prov. (female) were used to supplement observations of the exemplar.

Remarks. This appears to be a valid species, but is quite rare in collections. Although Luederwaldt mentioned no specimens in addition to the holotype, the length in the description was recorded as a range, suggesting that the author examined more than one specimen. The USNM specimen bears labels indicating that the collector was F. Nevermann (12 V 25) and that the specimen was determined as *Popilius hirsutus* by Luederwaldt in 1932 and again by Reyes-Castillo in 1970. Luederwaldt determined this specimen using a manuscript name nine years before the species was formally described. The date of collection is only a month later than that of the type specimen, and the collector was one of those mentioned in the original description. It appears highly probable that the USNM specimen is one of at least two used by Luederwaldt to prepare his description.

P. hirsutus is placed by the analyses closest to *P. mysticus,* although their sister group relationship is not well supported (BS=3, bootstrap frequency of 73%). It appears to be most closely related to *P. mysticus*, *P. klingelhoefferi* and *P. scutellopunctatus and P. punctatissimus*.

***Popilius mysticus* Bates, 1886**

Popilius mysticus Bates, 1886: 11. Holotype in BMNH with labels a) round, red-bordered “Type”, b) “Cubilguitz, VeraPaz, Champion”, c) “Popilius mysticus Bates” (in same handwriting as holotype of *P. intergeneus*), d) “B.C.A. II.2”, e) B.C.A. Col. II (2) Popilius mysticus. Seven paratypes in BMNH with labels a) “Cubilguitz, VeraPaz, Champion”, b) “Popilius mysticus Bates”, one with an additional determination label by J.R. Dibb, and another with the additional label “B.C.A. II.2”. One paratype in BMNH with labels a) “Guatemala”, b) “Izabal”, c) 1732”, d) “B.C.A. Col. II (2)”, e) Popilius mysticus, f) “B.C.A., II.2”.

I examined the holotype at the BMNH and collected data on 74 morphological characters.

Original Description. A rough translation of Bates’ description of *Popilius mysticus* (1886) follows:

> Rather narrow, moderately depressed; central tubercle compressed, lateral tubercles wide basally, anteriorly vertical; frontal ridges close to base of central tubercle, not springing from it, but tied by a longitudinal line; pronotal margin anteriorly on both sides with nearly sinuate angles (but angles not acute), anterior marginal groove widened and punctate, laterally half more weakly punctate; elytra punctate-striate, interstices moderately convex; base and wide lateral depression of metasternum punctate and rugose, apically punctate on both sides, very few or none; mesotibiae with one spine, dorsal carina gradually elevated, ciliate.

> Length 25mm; thorax 6, elytra 15mm long. Hab. GUATEMALA, Cubilguitz 1000 feet (Champion), Yzabal (Salle).
>
> Bates also adds that the frontal ridges:
>
> …instead of originating at the apex of the central tubercle (which in *P. mysticus* is almost vertical, and on early the same level as its broad flanking tubercles), commence lower down, and describing a short curve end in a small tubercle long before the clypeal suture; at the same time they are joined to the base of the central tubercle by a longitudinal wheal, which shows traces of being composed of two obscure parallel keels, and is continued a short distance within and beyond the angle of the frontal carinae.
>
> Mr. Champion collected a good series of specimens at Cubilguitz, in the low forest-region of northern Vera Paz.

Description. *Head*: Labrum projecting further on left side than right; transfrontal sulcus lightly recurved laterally, bi-arcuate; clypeus anteriorly smooth from frontogenal suture to tip of canthus; frontal ridges arise from a single or double ridge well anterior to base of central tubercle; parietal ridges evenly angulate or rounded dorsally; frons setose anterior and posterior to parietal ridge; subocular ridge long, reaching over half the distance to the antennal fossa, evenly raised; mentum with at least 1-3 setae medially; right dorsal mandibular tooth dorsally (lateral view) straight or even, dorsally (dorsal view) smooth; mentum posteromedially matt. *Pronotum*: Anterior marginal groove punctate in lateral 2/3 to 3/4; laterally punctate at least in and around the lateral depressions. *Prosternum*: Prosternal process acute posteriorly; hypomeron medially with a wide matt area with a straight, convex or slightly concave lateral margin. *Elytra*: Humerus glabrous. *Mesosternum*: Mesosternum posteromedially finely punctate/rugose or matt. *Mesepimeron*: Setose. *Metasternum*: Postmesocoxal grooves widely separate medially (greater than distance between mesocoxae; lateral depression of metasternum setose at least in anterior 3/4, uniformly narrow posteriorly. *Abdomen*: Anterior process of first complete, visible sternite (between and just posterior to metacoxae) glabrous. *Length*: 21.5-27.0 mm.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix.

Diagnosis. This species belongs to the complex of species including *P. klingelhoefferi*, *P. scutellopunctatus*, *P. punctatissimus*, *P. lenzi* and *P. hirsutus*. It differs from the other members of the Haagi Species Group by its biarcuate transfrontal sulcus, glabrous elytral humerus, widely separate postmesocoxal grooves, posteromedially matt mentum, dorsally longitudinally keeled or ridged central tubercle, setose mesepimeron, and glabrous anterior process of the first visible abdominal sternite. Length 21.5-27.0 mm.

Geographical Distribution and Ecology. This species is known from relatively low elevations (100-1000 m) along the Caribbean slope from Honduras to Belize, northern Guatemala and southeastern Mexico. It is known from high evergreen and high mesophilic forests (150-800 m) in Mexico and low rain forest in Belize and Honduras. One specimen was attracted to light. No host data has been collected.

Locality Data. 21 specimens examined from ARGC, IDEM, UVGC, USNM.

BELIZE (3). CAYO (1): Blue Hole State (sic, read "National") Park (nr. St. Hermans Cave) (ARGC). TOLEDO (2): San Jose (3.5 mi. N) (ARGC).

GUATEMALA (8). ALTA VERAPAZ (4): Secanquin (USNM), Telemann (20 km S) (UVGC). IZABAL (2): Chocon Machacas (Livingstone) (UVGC), Sierra de Caral (Camino Quebradas-La Firmeza) (UVGC). PETEN (1): Aldea Bethel (UVGC). NO FURTHER DATA (1): (USNM).

HONDURAS (1). ATLANTIDA (1): Rio Secate (P.N. Pico Blanco, La Ceiba) (ARGC).

MEXICO (9). CHIAPAS: (2): Diaz Ordaz (2 km SW, Mpio Cintalapa) (IDEM). OAXACA (2): Finca San Carlos (Col. Agricola Progreso, Mpio. Matias Romero) (IDEM), Metates (Sierra de Juarez) (IDEM). VERA CRUZ (5): Est. Biol. Los Tuxtlas (IDEM), Laguna Escondida (Mpio San Andres Tuxtla) (IDEM), Teocelo (IDEM), Uxpanapa (IDEM).

Exemplar Specimens. The exemplar was a male specimen in the IDEM with the genitalia dissected and bearing the labels a) Teocelo, Ver., 8-III-1975, J. Llorente, Zoo. Fac. Cie. UNAM, b) (male symbol), c) Popilius mysticus Bates, Reyes Castillo, det. 92. It was supplemented by a specimen from IDEM with the labels a) Mexico: Finca
Sn Carlos, Col. Agricola Progreso, Mpio Matias Romero, 25,28-V-59, F. Medellin. b) (in red) Compare au Serie Paralectotypes par Reyes Castillo, XII-74, Mus. Paris, c) Popilius mysticus Bates, Reyes Castillo, det. 1970.

Remarks. Although their sister group relationship is not well supported (BS=3, bootstrap frequency of 73%), *P.hirsutus* is placed by the analyses closest to *P. mysticus. P.hirsutus* appears to belong to a group of species including *P. mysticus, P. klingelhoefferi* and *P. scutellopunctatus and P. punctatissimus*. This species is especially similar to *P. klingelhoefferi*, but is generally larger and occurs at lower elevations.

Popilius sp. 8 Guatemala

Description. *Head*: Clypeus anteriorly smooth from frontogenal suture to tip of canthus; central tubercle with a free tip, turned upward apically; frontal ridges arise directly from anteromedial tip of central tubercle and diverge in straight lines from the origin to the inner tubercles; parietal ridges with a transverse dorsal groove (sometimes indistinct); subocular ridge short, extending about half the distance to the posterior margin of the antennal fossa; mentum glabrous medially.

Elytra: Humeri glabrous.

Mesosternum: Mesosternum posteromedially smooth, shiny. *Mesepimeron*: Setose.

Metasternum: Lateral depression of metasternum setose at least in anterior 3/4; posterior portion of lateral depression of metasternum widened subapically, narrowed at very tip.

Abdomen: Anterior process of first complete, visible abdominal sternite (between, and just posterior to, metacoxae) setose (2-3 setae).

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix. Length 24.5-27.0 mm.

Diagnosis. This is one of three large species of the *Popilius* so far known only from mountainous areas of Guatemala (designated *P*. spp. 8-10 Guatemala). This taxon can be distinguished from other species in the Haagi Species Group by the frontal ridges diverging in straight lines from the origin to the inner tubercles, glabrous elytral humeri, medially glabrous mentum, subocular ridge extending only about half the distance to the posterior margin of the antennal fossa, central tubercle with a free tip which is turned upward apically, transversely grooved parietal ridges (sometimes indistinct), posteromedially smooth and shiny mesosternum, setose (2-3 setae) anterior process of the first visible abdominal sternite, setose mesepimeron and lateral depression of the metasternum setose about to its tip.

Geographical Distribution and Ecology. This species is known only from the area around Purulha, Baja Verapaz, Guatemala, presumably from high elevation.

Locality Data*.* 6 specimens examined from JCSC.

GUATEMALA (5). BAJA VERAPAZ (5): Coban (km 156 a), Purulha, Purulha (5 mi. E).

NO DATA (1).

Exemplar Specimen**.** The exemplar was a male (sp.8GUAT, Appendix D-2; genitalia dissected) from JCSC with labels a) Guatemala, Baja Verapaz, km. 156 a Coban, 20-V-1991, Peter Hubbell, b) yellow dot, c) (male symbol).

Remarks. This species is placed in the analyses as the sister taxon of *P*. sp. 9 Guatemala, although the relationship is very weakly supported (BS=2, bootstrap frequency of 57%. The placement of this pair in the tree is variable, either apical or basal and adjacent to *P*. sp. 10 Guatemala, with which they macroscopically have the most similarity. This extreme difference is presumed to be due to the analysis of disparate, distantly related taxa using a suboptimal outgroup, and the topology of the tree and placement of these species is expected to change when an acceptable outgroup can be determined.

***Popilius* sp. 9 Guatemala**

Description. *Head*: Clypeus anteriorly smooth from frontogenal suture to tip of canthus; central tubercle low and without a free tip; frontal ridges arise directly from anteromedial tip of central tubercle and meet medially at an angle of about 180°; frontal ridges diverge in convex, recurved lines from origin to inner tubercles; parietal ridges evenly angulate or rounded dorsally; subocular ridge reaching posterior margin of antennal fossa in acute angle; mentum punctate and setose medially. *Pronotum*: Anterior marginal groove evenly deep. *Elytra*: Humeri setose ventrolaterally (opposite mesepimeron). *Mesosternum*; Posteromedially smooth, shiny. *Mesepimeron*: Setose.
Metasternum: Postmesocoxal grooves connected medially; lateral depression setose at least in anterior 3/4, widened subapically, narrowed at very tip. *Abdomen*: Anterior process of first complete, visible abdominal sternite (between, and just posterior to, metacoxae) thickly setose.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix. Length 27.5-29.0 mm.

Diagnosis. This species is one of three large *Popilius* taxa so far known only from mountainous areas of Guatemala (designated *P*. spp. 8-10 Guatemala). It can be differentiated from other species of the Haagi Species Group by its medially connected postmesocoxal grooves, dorsally evenly angulate or rounded parietal ridges, frontal ridges arising directly from the anteromedial tip of central tubercle, frontal ridges meeting medially at an angle of about 180°, evenly deep anterior marginal groove of the pronotum, medially punctate and setose mentum, elytral humerus setose ventrolaterally adjacent to the mesepimeron, central tubercle low and without a free tip, subocular ridge reaching the posterior margin of the antennal fossa in acute angle, frontal ridges recurved from their origin to the inner tubercles, posteromedially smooth and shiny mesosternum, thickly setose anterior process of the first visible abdominal sternite and lateral depression of the metasternum setose about to its tip.

Geographical Distribution and Ecology. This species is known only from high elevations in far western Guatemala. The only ecological data recorded for this species is that it occurs at elevations of 1500 and 1900 m, and that the specimen from La Fraternidad is from cloud forest (1900 m).

***Locality Data*.** 2 specimens examined from JCSC and UVGC .

GUATEMALA (2). QUETZALTENANGO (1): Santa Maria de Jesus (UVGC). SAN MARCOS (1): La Fraternidad (JCSC).

Exemplar Specimen. The exemplar was a female (sp.9GUAT, Appendix D-2; UVGC) labeled Guatemala, Quetzaltenango, Santa Maria de Jesus, 24-25 Abril 1993, J. Monzon, 1500m.
Remarks. This species is placed in the analyses as the sister taxon of *P*. sp. 8 Guatemala, although the relationship is very weakly supported (BS=2, bootstrap frequency of 57%. The placement of this pair in the tree is variable, either apical or basal and adjacent to *P*. sp. 10 Guatemala, with which they macroscopically have the most similarity. This extreme difference is presumed to be due to the analysis of disparate, distantly related taxa using a suboptimal outgroup, and the topology of the tree and placement of these species is expected to change when an acceptable outgroup can be determined.

***Popilius* sp. 10 Guatemala**

Description. *Head*: Frontal ridges arise from a single or double ridge well anterior to base of central tubercle and meet medially at an angle of about 45°; frontal ridges diverge in convex, recurved lines from origin to inner tubercles; central tubercle low and without a free tip; parietal ridges with a transverse dorsal groove; subocular ridge reaching posterior margin of antennal fossa in acute angle; mentum punctate and setose medially. *Pronotum*: Anterior marginal groove of pronotum deeper anteromedially, *Elytra*: Humeri setose dorsolaterally. *Mesosternum*: Posteromedially smooth, shiny. *Mesepimeron*: Mesepimeron setose. *Metasternum*: Postmesocoxal grooves widely separate medially (greater than the distance between mesocoxae); lateral depression of metasternum setose at least in anterior 3/4. *Abdomen*: Anterior process of first complete, visible sternite (between, and just posterior to, metacoxae) thickly setose.

For the description of all characters examined, see Appendix D-2 – *Popilius* Matrix. Length 32.0-34.5 mm.

Diagnosis. This species is one of three large *Popilius* taxa so far known only from mountainous areas of Guatemala, *P*. spp. 8-10. It can be differentiated from other species of the Haagi Species Group by its transversely grooved parietal ridges, dorsolaterally setose elytral humerus, frontal ridges arising from a single or double ridge well anterior to base of central tubercle and meeting medially at an angle of about 45°, widely separate postmesocoxal grooves, anteromedially deeper marginal groove of the pronotum, medially punctate and setose mentum, central tubercle low and without a free tip, subocular ridge reaching the posterior margin of the antennal fossa in an acute angle, posteromedially smooth and shiny mesosternum, setose anterior process of the first visible abdominal sternite, setose mesepimeron and lateral depression of the metasternum setose about to its tip.

Geographical Distribution and Ecology. This species is fairly widespread in Guatemala, although not commonly collected. It is known from elevations of 1300-1500 m, and one specimen was caught in a light trap.

Locality Data. 6 specimens examined from JCSC.

GUATEMALA (6). BAJA VERAPAZ (1): Purulha (7 km NE). HUEHUETENANGO (1): Buena Vista Chiblac (Barillas). ZACAPA (4): La Union (near; 2 km N).

Exemplar Specimen**.** The exemplar (sp.10GUAT, Appendix D-2) was a male specimen (with genitalia dissected; JCSC) with the labels a) Guatemala, Zacapa Dept., nr. La Union, 1-V-1992, 1500 m, J. Monzon (male symbol), b) yellow circular dot, c) (male symbol).

Remarks. This species is placed by the analyses at or close to the base of the Haagi Species Group, however, the presence of this species in the group is not at all supported (BS=0, bootstrap frequency of 51%). It appears most similar to P. spp. 8 and 9 Guatemala, but also shares autapomorphies with *P. eclipticus*. Confident analysis of the placement of this species will hinge on finding the most appropriate outgroup to use for a broad analysis of species groups from all of the genera most closely related to *Popilius*.

CHAPTER VI

SUMMARY

The objective of this study was to make a phylogenetic analysis of the genus *Popilius* (Passalidae) and use it as a basis for revising the genus. In order to identify the relation of the passalid genus *Popilius* to other genera in the Proculini, and test for an acceptable out-group a phylogenetic analysis of the higher taxonomic levels in Passalidae was done.

This higher-taxon analysis suggests that the New World species form a monophyletic clade, contrary to the traditionally held view, and that the African taxa and Southeast Asian taxa also form monophyletic clades. This is strong evidence that passalids, an old group considered to be near the base of the Scarabaeoidea, are not very successful in vicariant movement, but tend to ride continental masses.

The results of the phylogenetic analysis of the species of *Popilius* strongly suggest that the genus is not monophyletic and that the species within it are intermingled with several closely related, also paraphyletic and intertwined genera (*Heliscus*, *Odontotaenius*, *Petrejoides* and possibly *Spurius*). A phylogenetic analysis of these genera and redefinition of their boundaries is necessary before an out-group for the analysis of *Popilius* can objectively be chosen. Although clarifying the relationships is critically important for phylogenetic studies, the effort that would be required was beyond the limited scope of this study and will be addressed in the future.

Because no closest out-group could be chosen, an unrooted analysis of *Popilius* was conducted. Four species groups were defined, the species available were described and their natural history summarized, and ten undescribed species were identified. Much of the type material was unavailable, so these species are described, but formal names are not proposed at this time.

New character systems were investigated in a search for adult characters that could be useful in differentiating taxa. New or under-utilized systems that provide good characters and show the most promise for phylogenetic study include the metendosternite, eversible internal sac of the male genitalia, prostheca of the right mandible, epipharynx, and hypopharynx.

A new autapomorphy for the family is reported here, an organ on the inner surface of both elytral humeri. The structure has a membranous covering and appears to contact an apophysis on the base of the wing. I suggest that it may be a sound receptor, but this hypothesis has not yet been tested.

I consider this study to be open-ended, and plan to expand it with the intent of resolving the taxonomic confusion surrounding *Popilius*.

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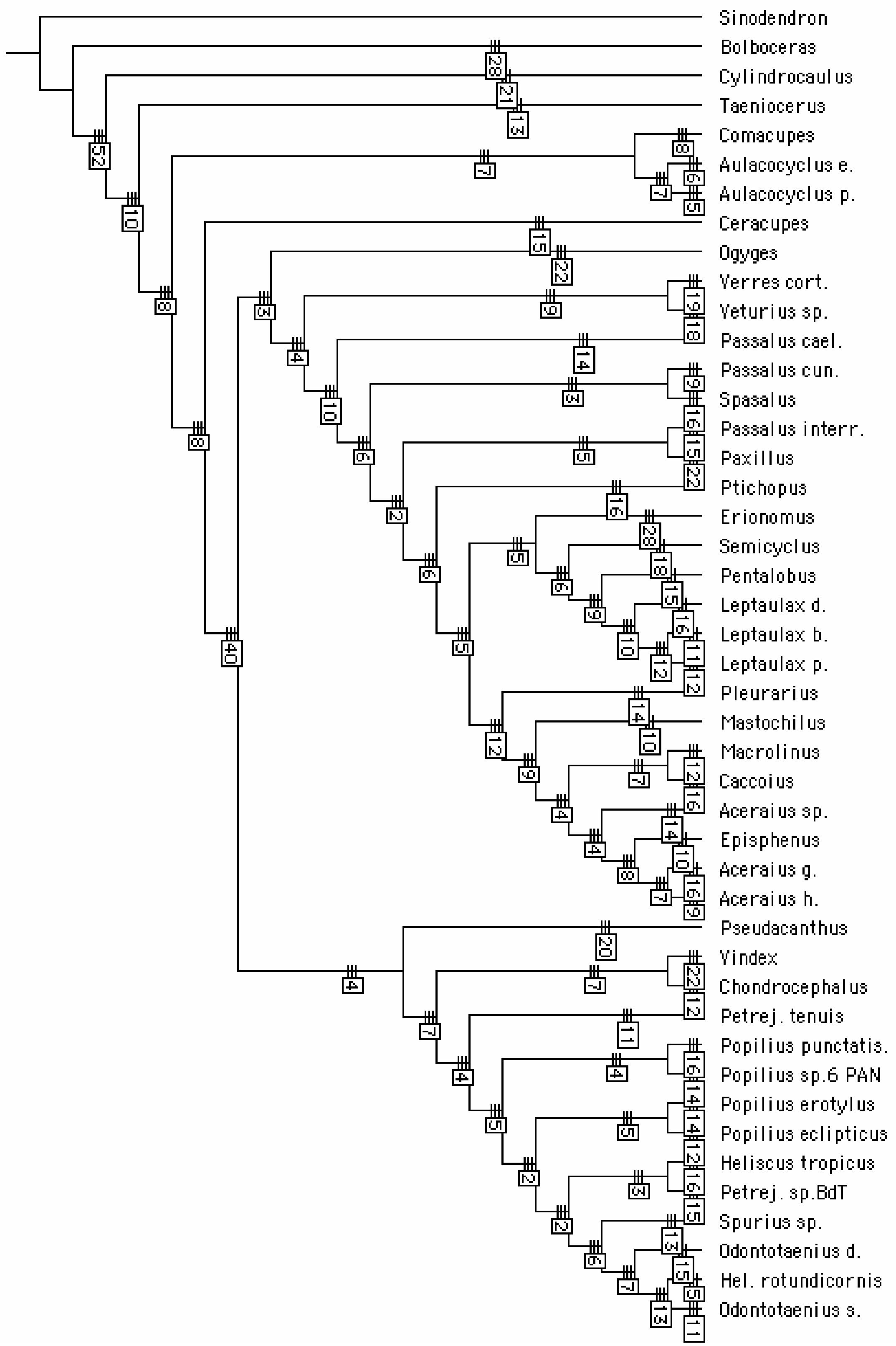
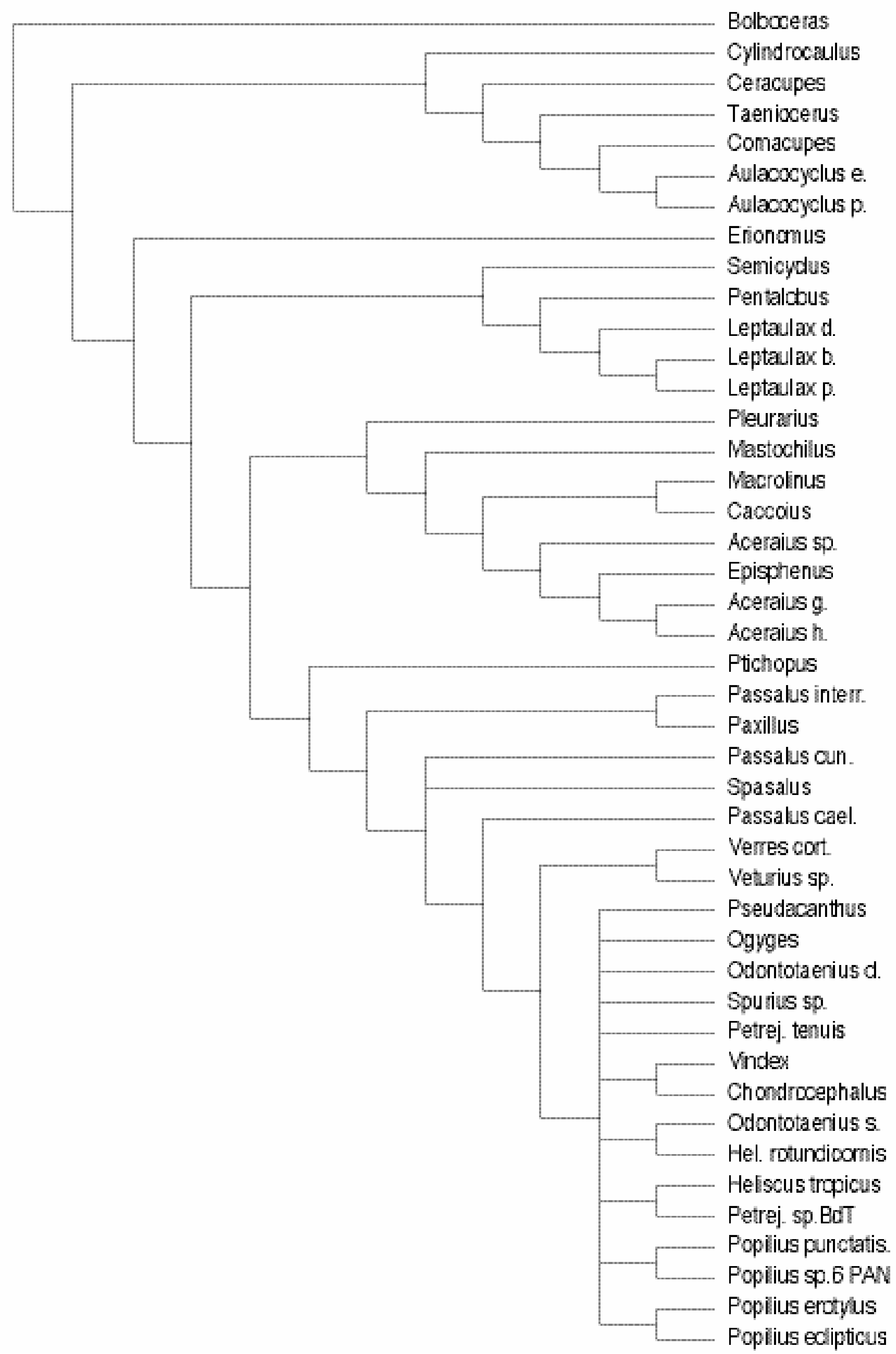
APPENDIX A

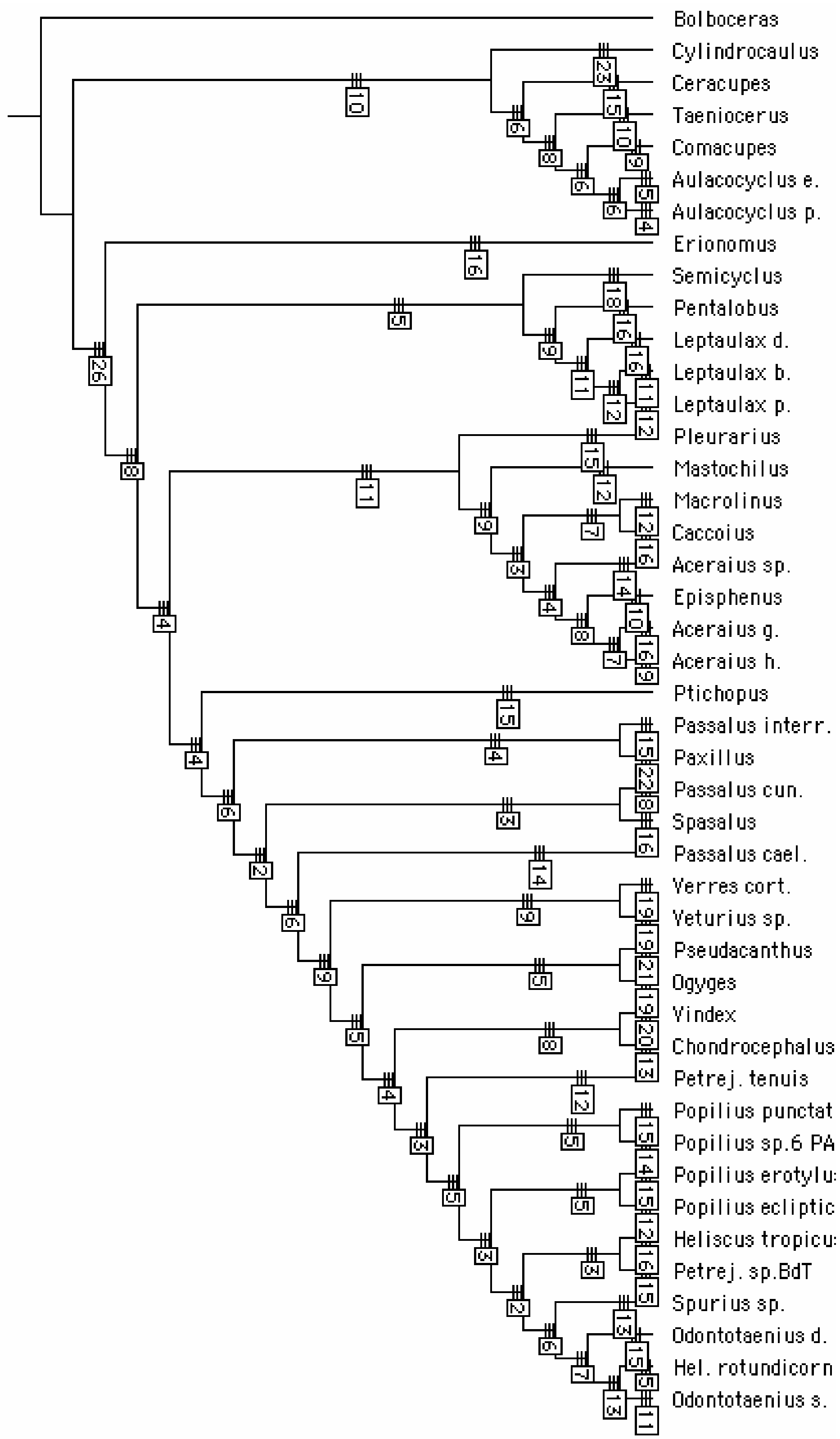
FIGURES



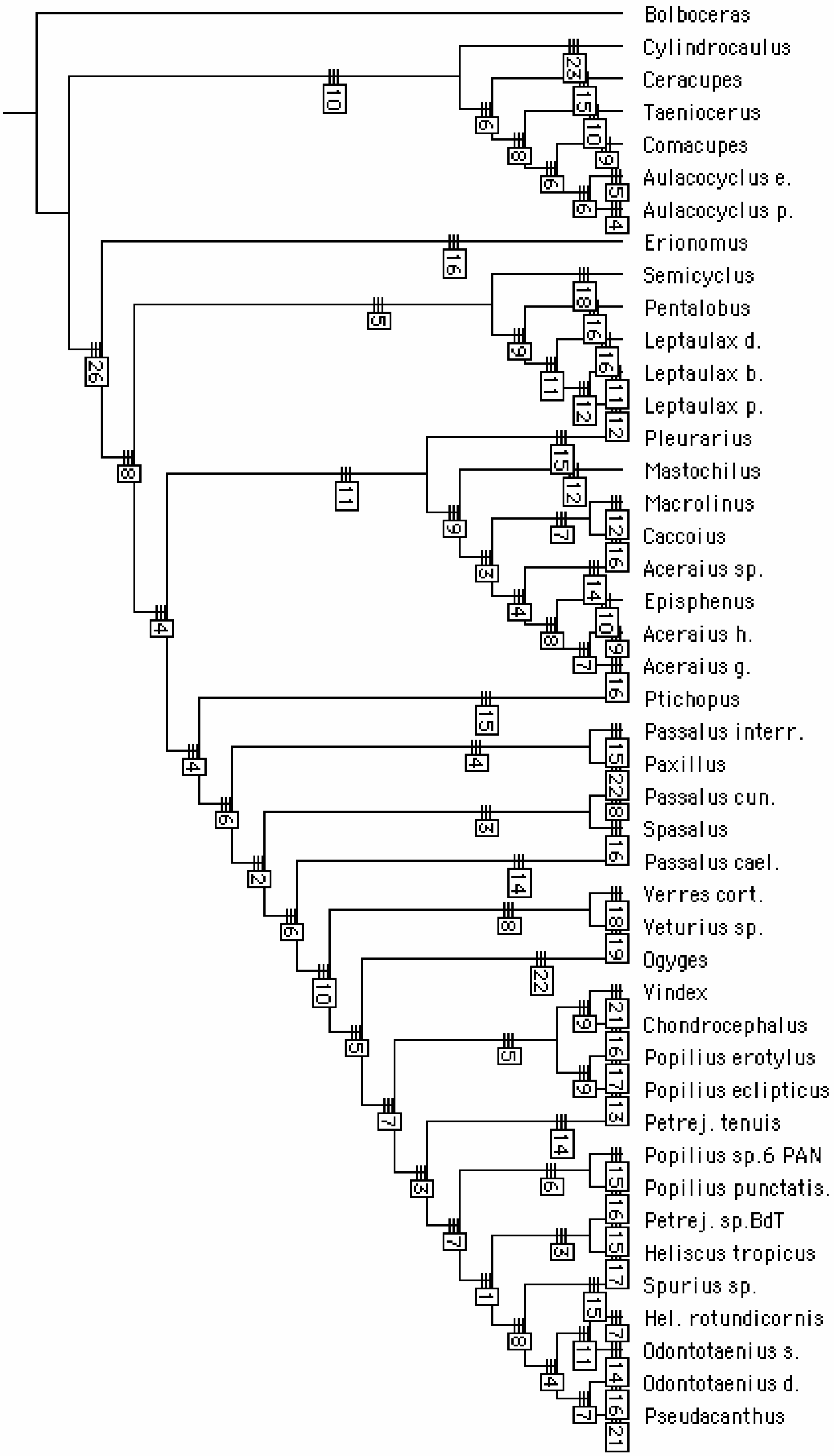
Appendix A-1. The single tree resulting from parsimony analysis of Passalidae with *Bolboceras* and *Sinodendron* out-groups. Branch lengths noted with the number of unambiguous changes.



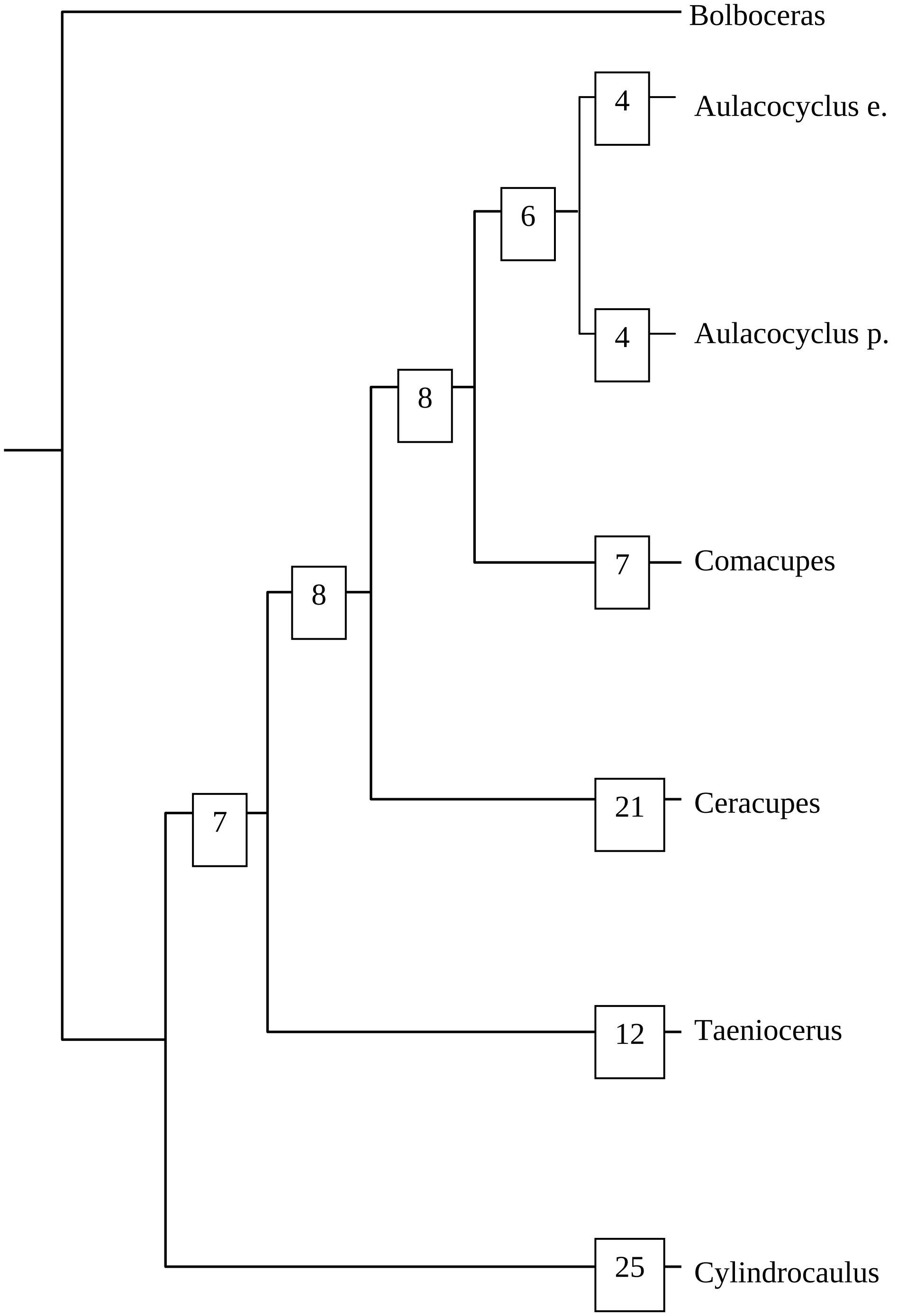
Appendix A-2. Strict concensus of the six trees resulting from parsimony analysis of Passalidae with *Bolboceras* as the out-group.



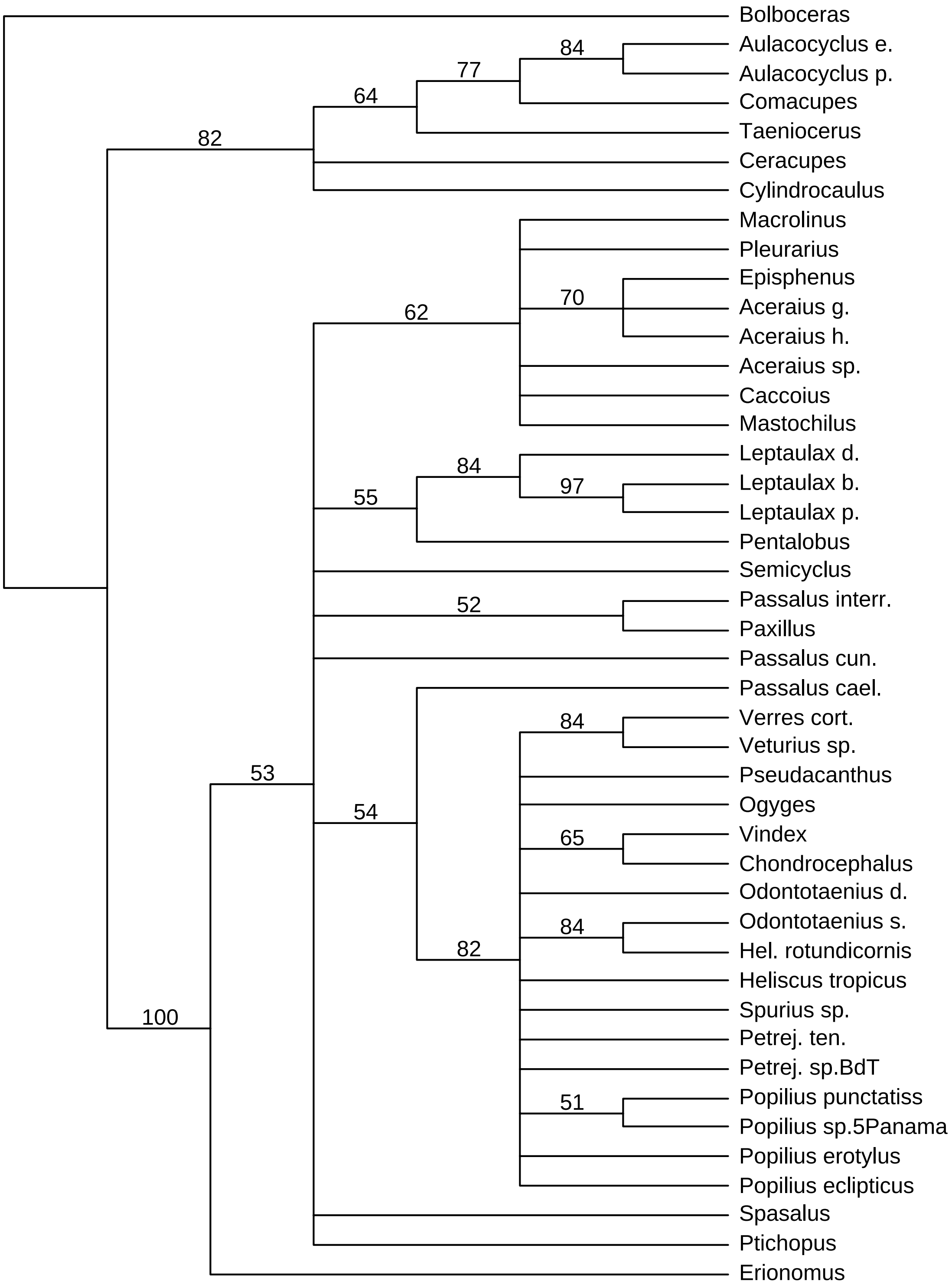
Appendix A-3. The preferred tree, one of six trees resulting from parsimony analysis of Passalidae with *Bolboceras* as the out-group. *Pseudacanthus* is placed basally. Branch lengths are noted.



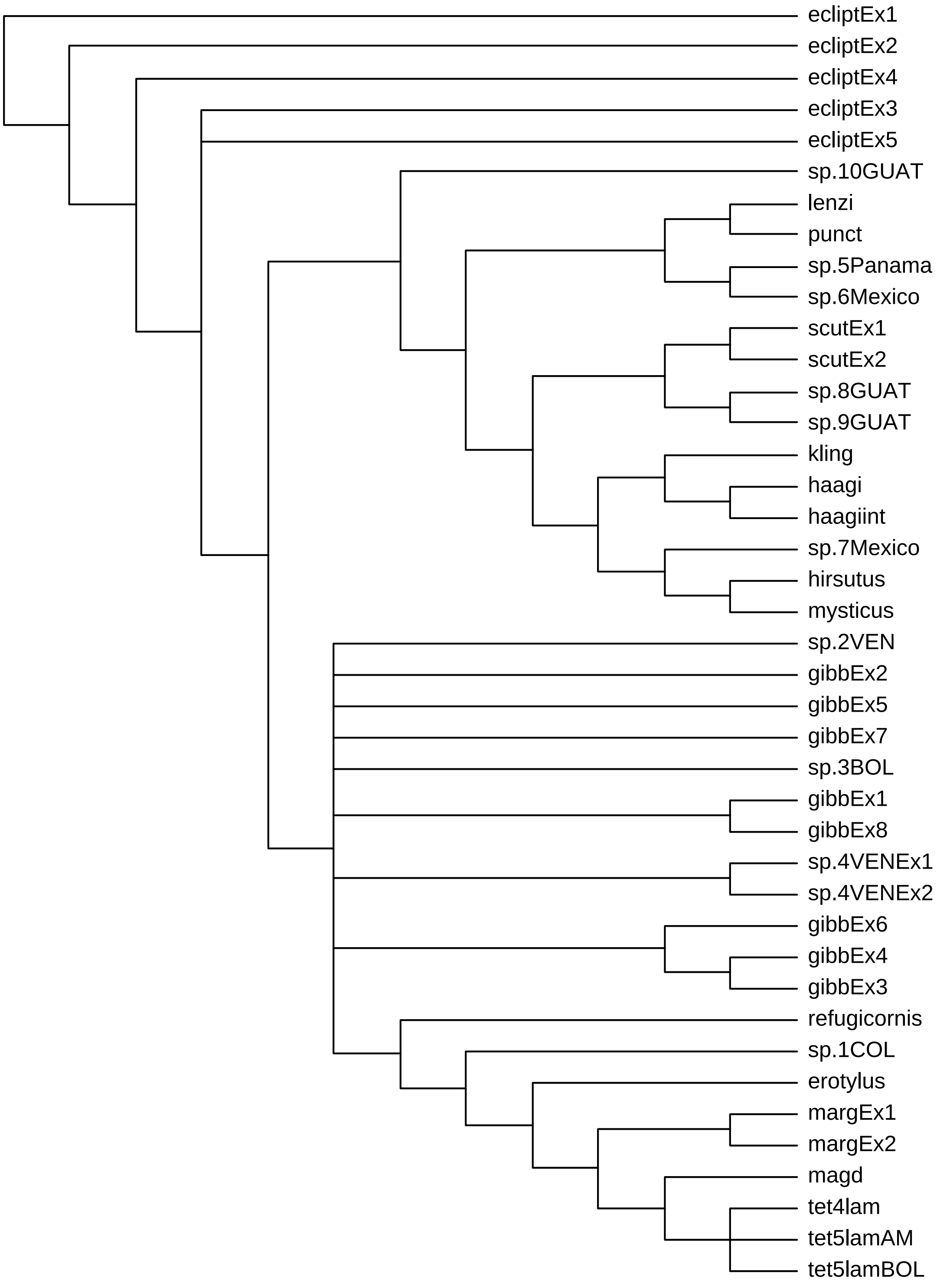
Appendix A-4. One of six trees resulting from parsimony analysis of Passalidae with *Bolboceras* out-group; *Pseudacanthus* placed apically. Branch lengths are number of unambiguous changes.



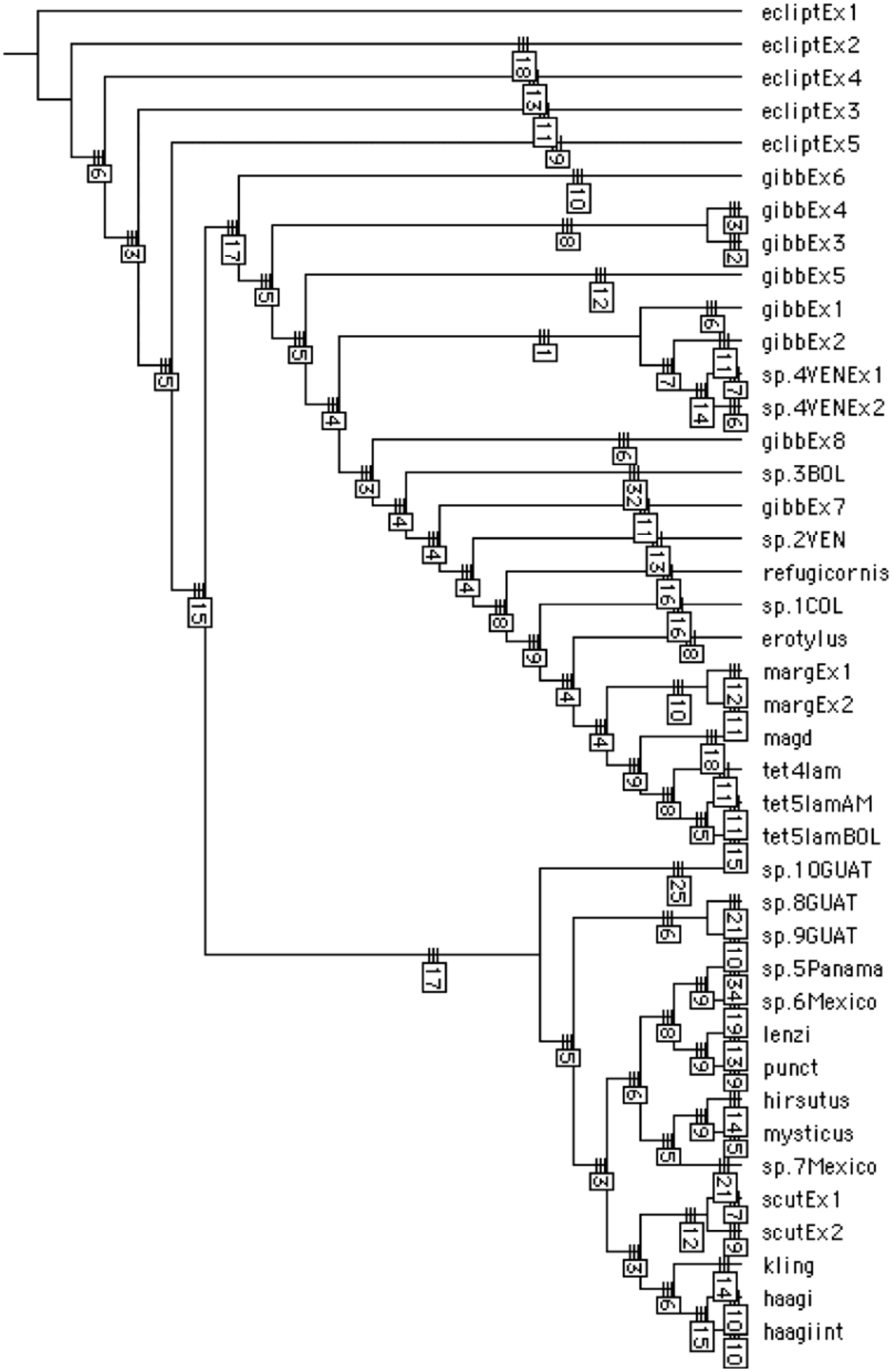
Appendix A-5. The single tree resulting from parsimony analysis of Aulacocyclinae with *Bolboceras* as the out-group. Branch lengths are noted with the number of unambiguous changes.



Appendix A-6. Bootstrap clade support of the preferred tree of the preliminary phylogeny of Passalidae, with *Bolboceras* as the out-group. Support values are shown.



Appendix A-7. Strict consensus of the six most parsimonious trees of the analysis of the Popilius dataset.



Appendix A-8. Successive approximations tree of six equally parsimonious trees resulting from parsimony analysis of the 41-OTU *Popilius* dataset. Branch lengths are noted with the number of unambiguous changes.

APPENDIX B

TABLES

Table B-1. Spearman's Rank Correlations of partitioned Bremer support indices from the analysis of Passalidae with *Bolboceras* as the out-group. ** Correlation is significant at the .01 level (2-tailed). * Correlation is significant at the .05 level (2-tailed).

Spearman's rho	N=40	MOUTH-PARTS	MANDI-BLES	FRONTO-CLYPEUS	ANTENNAE/ LEGS	WINGS/ ELYTRA	EXTERNAL	INTERNAL	MALE GENITALIA
MOUTH-PARTS	Correlation Coefficient	1.000	-0.020	-0.433**	-0.290	0.286	0.048	0.189	0.206
	Significance	.	0.901	0.005	0.069	0.073	0.767	0.243	0.201
MANDI -BLES	Correlation Coefficient	-0.020	1.000	0.124	0.174	0.012	-0.080	-0.333*	.167
	Significance	0.901	.	0.444	0.282	0.943	0.623	0.036	0.303
FRONTO-CLYPEUS	Correlation Coefficient	-.433	-0.124	1.000	-0.074	-0.374*	-0.326	0.236	-0.416**
	Significance	0.005**	0.444	.	0.649	0.017	0.040	0.143	0.008
ANTENNAE/ LEGS	Correlation Coefficient	-0.290	0.174	-0.074	1.000	-0.131	0.354*	-0.103	-0.122
	Significance	0.069	0.282	0.649	.	0.420	0.025	0.525	0.453
WINGS/ ELYTRA	Correlation Coefficient	0.286	0.012	-0.374*	-0.131	1.000	0.263	0.263	-0.144
	Significance	0.073	0.943	0.017	0.420	.	0.102	0.102	0.374
EXTERNAL	Correlation Coefficient	0.048	-0.080	-0.326	0.354*	0.263	1.000	-0.326	-0.144
	Significance	0.767	0.623	0.040	0.025	0.102	.	0.040	0.374
INTERNAL	Correlation Coefficient	0.189	-0.333*	0.236	-0.103	0.263	-0.326	1.000	0.058
	Significance	0.243	0.036	0.143	0.525	0.102	0.040	.	0.723
MALE GENITALIA	Correlation Coefficient	0.206	0.167	-0.416**	-0.122	-0.144	-0.144	0.058	1.000
	Significance	0.201	0.303	0.008	0.453	0.374	0.374	0.723	.

Table B-2. Spearman’s rank correlations of partitioned Bremer support indices from the analysis of Passalinae with *Erionomus* as a functional out-group. ** Correlation is significant at the .01 level (2-tailed). * Correlation is significant at the .05 level (2-tailed).

Spearman’s rho	N=35	MOUTH-PARTS	MANDI-BLES	FRONTO-CLYPEUS	ANTENNAE/ LEGS	WINGS/ ELYTRA	EXTERNAL	INTERNAL	MALE GENITALIA
MOUTH-PARTS	Correlation Coefficient	1.000	0.528**	0.508**	0.288	0.211	0.052	-0.321	1.000
	Significance	.	0.001	0.002	0.099	0.232	0.771	0.064	.
MANDI-BLES	Correlation Coefficient	0.528**	1.000	--0.645**	0.519**	0.355*	-0.180	-0.231	0.310
	Significance	0.001	.	0.000	0.002	0.039	0.309	0.189	0.074
FRONTO-CLYPEUS	Correlation Coefficient	0.508**	--0.645**	1.000	-0.708**	-0.425*	-0.184	0.265	0.125
	Significance	0.002	0.000	.	0.000	0.012	0.298	0.130	0.481
ANTENNAE/ LEGS	Correlation Coefficient	0.288	0.519**	-0.708**	1.000	0.376*	0.369*	-0.390*	-0.370*
	Significance	0.099	0.002	0.000	.	0.029	0.032	0.023	0.031
WINGS/ ELYTRA	Correlation Coefficient	0.211	0.355*	-0.425*	0.376*	1.000	0.007	-0.138	0.013
	Significance	0.232	0.039	0.012	0.029	.	0.970	0.437	0.944
EXTERNAL	Correlation Coefficient	0.052	-0.180	-0.184	0.369*	0.007	1.000	-0.531**	-0.494**
	Significance	0.771	0.309	0.298	0.032	0.970	.	0.001	0.003
INTERNAL	Correlation Coefficient	-0.321	-0.231	0.265	-0.390*	-0.138	-0.531**	1.000	0.469**
	Significance	0.064	0.189	0.130	0.023	0.437	0.001	.	0.005
MALE GENITALIA	Correlation Coefficient	1.000	0.310	0.125	-0.370*	0.013	-0.494**	0.469**	1.000
	Significance	.	0.074	0.481	0.031	0.944	0.003	0.005	.

APPENDIX C

DATA FOR THE PRELIMINARY PHYLOGENY OF PASSALIDAE

Appendix C-1. CHARACTER ANALYSIS FOR THE PRELIMINARY PHYLOGENY OF PASSALIDAE

Head

Labrum

1. Anterior margin of labrum symmetrical (0), or asymmetrical (1).

2. Labrum widest in anterior third (0), in medial third (1), or in basal third (2).

Epipharynx

3. Median anterior tormal process of epipharynx n/a (not distinguishable) (0), entirely pigmented (1), or less pigmented medially in basal third to three-quarters (2.

4. Number of pores in anterior medial, longitudinal pore patch of median anterior tormal process n/a (not distinguishable) (0), 0-18 (1), ~33-59 (2), ~65-80 (3), or at least 108 (4).

5. Medial pore patch of median anterior tormal process n/a (not distinguishable) (0), single, narrow (1), single, longitudinal, wide (2), or double, longitudinally parallel (3).

6. Medial pore patch of median anterior tormal process n/a (not distinguishable) (0), a single patch, reaching base or basal depression (1), a single patch, not reaching base or basal depression (2), or two patches, anterior and posterior (3).

7. Number of pores in posterior longitudinal pore patch of median anterior tormal process (just anterior to basal depression) n/a (not distinguishable) (0), 0 (1), 2-4 (2), or 9 (3).

8. Base of epipharynx n/a (not distinguishable) (0.5), without supplementary pore patches (1), or with supplementary pore patches (2).

9. Base of epipharynx medially n/a (not distinguishable) (0), planar (1), with transverse carina (2), or with medial depression (3).

10. Basal membranous area of epipharynx without sclerites (0), or with thin, paired sclerites (1).

Frontoclypeal region

11. Central tubercle absent (0), present, with a double or horseshoe-shaped ridge (1), present, with single ridge/point (2), or secondarily lost (3).

12. Central tubercle absent (0), low, without a free tip (1), erect, without a free, anteriorly-directed tip (2), with a free, anteriorly-directed tip (3), with a free, posteriorly-directed tip (4), or secondarily lost (5).

13. Central tubercle highest point absent (no central tubercle) (0), present, lateral tubercles absent (1), anterior to highest point of lateral tubercles (2), even with highest point of lateral tubercles (3), posterior to highest point of lateral tubercles (4), or secondarily lost (5).

14. Lateral tubercles absent (0), obsolete, represented only by laterally sloping ridges (1), distinct, linked by ridges to central tubercle or to each other (2), or distinct, not linked to central tubercle or to each other (3).

15. Lateral tubercles absent, dorsally angulate, or dorsally evenly convex (0), or present, with a transverse groove on the crest (1).

16. Frontal ridges absent (0), present, without a tubercle between the mediofrontal structure and the inner tubercle (1), present, with at least one tubercle between the mediofrontal structure and the inner tubercle (2), or secondarily lost (3).

17. Frontal ridges absent (0), arise from a single ridge from anterior base of central tubercle (1), arise from two ridges from anterior base of central tubercle (2), without a distinct carina linking to the central tubercle (3), or secondarily lost (4).

18. Frontal ridges absent (0), diverge in straight lines from origin (1), diverge in concave, curved lines from origin (2), diverge in convex, recurved lines from origin to inner tubercles (3), or secondarily lost (4).

19. Frontal ridges absent (0), present, but not reaching inner tubercles (or inner tubercles absent) (1), evident only between central tubercle and inner tubercles (2), evident from central tubercle to outer tubercles (3), or secondarily lost (4).

20. Inner tubercles absent (0), present, highest point closer to base of central tubercle than to anterior margin of clypeus (1), present, highest point about equidistant from base of central tubercle and anterior margin of clypeus (2), present, closer to anterior margin of clypeus than to base of central tubercle (3), present on or immediately posterior to anterior margin (4), or secondarily lost (5).

21. Inner tubercles absent (0), posterior to outer tubercles (1), about even with outer tubercles (2), or secondarily lost (3).

22. Inner tubercles absent (0), connected anterior to frontal ridge by a rounded, transverse carina (1), connected anterior to frontal ridge by a sharp, transverse carina (2), not connected anterior to frontal ridge by a transverse carina (3), or secondarily lost (4).

23. Inner tubercle absent (0), not on same structure as outer tubercle and anterolateral clypeal margin (1), on same structure as outer tubercle and anterolateral clypeal margin (2), or secondarily lost (3).

24. Clypeus anteromedially without ring-like punctures (0), or with ring-like punctures (1).

25. Frontal area, anterior to the frontal ridges or mediofrontal structure, glabrous (0), or setose (1).

26. Frontal area, anterior to the frontal ridges or mediofrontal structure, even (0), or with a medial elevation or longitudinal ridge (1).

27. Outer tubercles absent (0), present, symmetrical (1), or present, asymmetrical (2).

28. Outer tubercles absent (0), present, horizontal, distinctly surpassing margin of clypeus (1), present, horizontal, slightly surpassing margin of clypeus (2), or present, vertical, on anterior margin of clypeus (3).

29. Outer tubercles absent (0), separated from the anterolateral clypeal margin by the anterior clypeal marginal sulcus (1), or fused with the anterolateral clypeal margin, completely interrupting the anterior clypeal marginal sulcus (2).

30. Anterior face of outer tubercles n/a (tubercles absent) (0), multiply, horizontally grooved (appearing layered) (1), with single, horizontal groove (2), or not grooved (3).

31. Posterolateral ridge (of right side) absent (0), present, posterolateral to outer tubercle, without a tubercle at end of ridge (1), or present, posterolateral to outer tubercle, with a tubercle at lateral end of ridge (2).

32. Transfrontal sulcus absent (0), present (1), or secondarily lost (2).

33. Transfrontal sulcus absent (0), complete (1), interrupted by the inner tubercles or frontal ridges (2), obsolete or absent in the medial third (3), or secondarily lost (4).

34. Transfrontal sulcus absent (0), arcuate, convex anteriorly (1), about straight, transverse (2), concave anteriorly (3), recurved (4), or secondarily lost (5).

35. Clypeus anteriorly without a transfrontal sulcus (0), flat anterior to the transfrontal sulcus (1), convexly rounded from the transfrontal sulcus to the anterior margin (2), or about vertical anterior to the transfrontal sulcus (3).

36. Anterior margin of clypeus with a secondary tubercle just medial to each frontogenal suture (0), without secondary tubercles (1), with one, medial secondary tubercle (2), or with two medial secondary tubercles (3).

37. Anteroventral margin of clypeus not visible (0), obtuse (1), ~right-angled (2), acute (30°-80°) (3), or sharp (<30°) (4).

38. Clypeus anterior face without a vertical medial ridge (0), or with a vertical medial ridge (1).

39. Anterior face of clypeus with medial setae absent (0), on anterior face, only medially (1), or on anterior face, only along ventral margin (2).

40. Anterior marginal sulcus of clypeus absent (0), anterior, concave, hidden beneath the anterior margin of the clypeus (1), anterior, medially visible from above; laterally concave, hidden beneath the anterior margin (2), anterior, entirely visible from above (3), or dorsal (4).

41. Ventral margin of anterior marginal sulcus transversely concave or straight (0), or projecting medially, the projection often medially shallowly emarginate (1).

42. Anterolateral angles of clypeus (viewed from above) not projecting (0), projecting, obtuse (1), or projecting, acute (2).

43. Anterolateral angles of clypeus (viewed from side) obtuse (0), ~right-angled (1), or acute (2).

Parietal-occipital region

44. Anterior angles of supra-orbital ridge not projecting (0), projecting, broadly rounded (1), obtuse (2), about right-angled (3), or acute (4).

45. Canthus absent (0), even, rounded laterally (1), narrowest medially, expanded and angulate laterally (2), or complete (3).

46. Canthus absent (0), without medial, longitudinal ridge (1), with one medial, longitudinal ridge (2), or with two medial, longitudinal ridges (3).

47. Supraorbital ridge higher than mediofrontal structure (MFS) (0), about same height MFS (1), or lower than MFS (2).

48. Supraorbital ridgeline with 3 dorsal points (including a raised tubercle at anterior tip (0), with 2 dorsal points (1), with 1 dorsal point (2), straight (3), or evenly rounded (4).

49. Supraorbital ridgeline with a single ridge (0), forked posteriorly (1), or forked anteriorly, lateral to frontoclypeal suture (2).

50. Supraorbital ridge not connected by a ridge with the lateral tubercle (0), or connected by a ridge with the lateral tubercle (1).

51. Supraorbital ridge anteriorly separated from frontal ridge by depression (0), or connected to frontal ridge by a ridge (1).

52. Postocular depression without distinct margins (0), with distinct lateral margin only (1), or with distinct lateral and medial margins (2).

53. Postocular depression with medial longitudinal ridge absent (0), or present (1).

54. Area posterior to postocular ridge glabrous (0), or setose (1).

55. Circum-occipital sulcus absent (0), extending only to medial margin of supraorbital ridge (1), or extending posterior to supraorbital ridge (2).

Hypostomal process

56. Hypostomal process (ventral view) absent (0), uniformly very narrow (1), wide, parallel-sided (2), very wide medially (3), or spindle-shaped (4).

57. Anterior tip of hypostomal process (ventral view) absent (0), truncate/blunt (1), or acute or narrowly rounded (2).

58. Hypostomal process laterally (ventral view) absent (0), convex (1), flattened (2), or concave (3).

59. Hypostomal process laterally (ventral view) absent (0), glabrous (1), or setose (2).

60. Ratio of basal length to apical length from a line across posteriomedial margin of mentum n/a (0), 3.1-11.6 (1), 2.0-2.6 (2), or 1.3-1.9 (3).

61. Ratio of space between mentum and hypostomal process at narrowest point to width of hypostomal process at that point n/a (no hypostomal process) (0), 2.3-7.0 (1), 0.9-1.1 (2), 0.15-0.67 (3), or appressed/touching or overlapping (4).

Tentorium

62. Anterior tentorial arm in the form of a slender, free, strut (0), or narrow, vertical flange, attached dorsally to the head capsule for its entire length (1).

Mouthparts

Mandibles

63. Mandible with a medial prostheca (0), or without a medial prostheca (1).

64. Internal dentition of mandible symmetrical (0), or asymmetrical (1).

65. Lower anterior tooth of mandible in ~vertical plane (0), or ~horizontal plane (1).

66. Mandible without a movable tooth (0), or with a movable tooth (1).

67. Right mandible without a basal prostheca 0), or with a narrowly rounded, finger-like prostheca (dientecillo of Reyes-Castillo, 1970b) (1).

68. Dorsal mandibular acetabulum without anterior notch (0), or with anterior notch (1).

69. Base of mandible dorsally ~evenly curved (0), or with deep depression (1).

70. Mandible externally with even margin (0), or with distinct outer angle (1).

71. Mandible externally with concave surface (0), or with strong depression (1).

72. Right, dorsal mandibular tooth anteriorly (lateral view) obtuse (0), about right-angled (1), acute (2), projecting (3), or n/a - short, dorsally acute (4).

73. Right, dorsal mandibular tooth posteriorly (lateral view) obtuse or gradually sloping (0), about right-angled (1), or n/a - short, dorsally acute (2).

74. Right, dorsal mandibular tooth posteriorly (lateral view) straight or even (0), medially concave (1), evenly convex (2), or acute (3).

75. Right, dorsal mandibular tooth dorsally (dorsal view) smooth (0), or rugose or coarsely punctate (1).

76. Right, dorsal mandibular tooth dorsally (dorsal view) narrow (0), or widened medially (1).

77. Right, dorsal mandibular tooth dorsally (dorsal view) evenly ridged (0), or rounded laterally and angulate medially, with appearance of being rolled over (1).

78. Ventrobasal depression of mandible with 2 distinct margins basally (0), with at least lateral margin indistinct (1), or absent (2).

79. Ventrobasal depression of mandible apically directed towards base of lower inner tooth (0), towards apex of mandible (1), or n/a, without basal depression (2).

80. Setae in the ventrobasal depression of mandibles (both mandibles summed; examine dry) no more than 54 (0), or more than 65 (1).

Maxillary palpae

81. Second segment slightly longer than third segment (0), or much longer than third segment (1).

Lacinia

82. Number of lacinial teeth one (0), two, with basal tooth simple (1), or two, with basal tooth with broad base (2), none (3).

83. Apical tooth of lacinia with simple tip (0), truncate tip (1), bifid tip (2), or absent (3).

84. Base of lacinia acute, oblique (0), truncate (1), or rounded (2).

Labium

85. Medial, anterior margin of mentum laterally emarginate (0), or not emarginate laterally (1).

86. Mentum medially emarginate (0), or not emarginate (1).

87. Mentum medially without depressions or keels (0), with lateral, basal depressions (1), with a wide longitudinal depression (2), or with a single, longitudinal keel (3).

88. Prementum with subapical carina and transverse setal line present (0), carina absent, setal line present (1), or both absent (2).

89. Prementum with medial, longitudinal carina present (0), or absent (1).

Labial palpae

90. Labial palpae inserted at tip of prementum (0), or at base of prementum (1).

91. Bases of labial palpae close together (0), or far apart (1).

92. First segment of labial palp easily visible (0), or barely visible (1).

93. Second segment of labial palp ~ as wide as third segment (0), much wider than third segment, third segment reduced (1), or much wider than third segment, third segment not reduced (2).

Hypopharynx

94. Paraglossae separate, discrete, not pigmented or sclerotized (0), or fused to and not distinguishable from hypopharynx, forming a pigmented, sclerotized “ligula” (1).

95. Anteromedial area of hypopharynx absent (0) longitudinally carinate, tip not concave (1), longitudinally carinate, tip slightly concave (2), with straight, or slightly anteriorly curved, transverse carina (3), with strongly arcuate transverse carina reaching anterior margin (4), or with arcuate transverse carina not reaching anterior margin (5).

96. Anterior arcuate carina of hypopharynx n/a (without a sclerotized ligula) (0), absent (1), present, each side evenly curved (2), or present, each side flared laterally in apical half (3).

97. Hypopharynx anteromedially n/a (without a sclerotized ligula) (0), without a transverse, arcuate carina (1), with only a transverse, arcuate carina (2), with an additional buttress on each inner side of an arcuate carina (3), with a medial transverse carina joining the sides of an arcuate carina (4), with a medial transverse carina joining the sides of an arcuate carina, and a tubercle at the midpoint of the carina (5), with a medial tubercle between the sides of an arcuate carina (6), or with a doubly arcuate transverse carina, and a longitudinal carina from tip of ligula to tip of anterior angle of transverse carina (7).

98. Hypopharynx medially n/a (without a sclerotized ligula) (0), narrowly, longitudinally ridged (1), with wide, convex or flat, longitudinal ridge (2), with circular/oval depression (3), with “U”-shaped depression (4), or with transverse depression (5).

99. Medial transverse ridge of hypopharynx n/a (without a sclerotized ligula) (0), absent (1), straight (2), or U-shaped (open anteriorly) (3).

100. Hypopharynx posteriorly n/a (without a sclerotized ligula) (0), longitudinally ridged (1), with round, flattened area (2), or with transverse depression (3).

101. Hypopharynx basally n/a (without a sclerotized ligula) (0), medially raised (1), medially raised with medial, posteriorly directed tubercle not reaching basal margin (2), medially raised with emarginate anterior margin and medial, posteriorly directed tubercle reaching basal margin

(3), medially raised with emarginate anterior margin and medial, posteriorly directed tubercle extending past basal margin (4).

102. Posterior margin of hypopharynx not separated by a sulcus from membranous base (0), or margined posteriorly by a distinct sulcus (1).

Antennae

103. Number of antennal segments 11 (0), or 10 (1).

104. Number of antennal lamellae 3 (0), 4 (1), 5 (2), or 6 (3).

105. Antennal segments 5-7 that are not lamellate are entire (rounded) apicomedially (0), that are not lamellate are emarginate apicomedially (1), or are all lamellate (2).

Pronotum

106. Pronotum dorsally evenly rounded (0), or raised medially (1).

107. Pronotal marginal grooves complete (0), or interrupted medially, both anteriorly and posteriorly (1).

Prosternum

108. Prosternal process greatly expanded posterior to prosternal margin, posteriomedially tuberculate (0), or posteriorly narrow, not greatly expanded posterior to prosternal margin, not tuberculate (1).

109. Ratio of width of prosternal process at posterior margin of prosternum to length of process from widest point to posterior margin of prosternum 1.1-2.6 (~pentagonal) (0), 0.54-0.95

(~widely truncate posteriorly) (1), 0.24-0.45 (~narrowly truncate posteriorly) (2), or 0.04-0.18 (~acute posteriorly) (3).

110. Prosternal process medially even (0), or with a transverse fold (1).

111. Prosternal process medially flat (0), or with a longitudinal, convex ridge (1).

112. Prosternal process glabrous (0), setose along anterior margin (1), setose along posterior margin (2) or setose medially (3).

113. Pronotal arms (posterior to coxae) shiny (0), or matt (1).

Elytra

114. Internal costal margin of elytron glabrous (0), setose linearly (~single, closely spaced) in narrow groove, beginning about the length of the basal binding patch apical to the patch (1), or setose in wide band (2).

115. Distal binding patch of elytron absent (0), or present (1).

116. Inner face of elytral humerus appearing similar to adjoining surfaces, without a membrane-covered patch of tissue (0), or with a membrane-covered patch of tissue (possible hearing organ) (1).

Wings

117. Surface of wing covered with fine setae (0), covered with short, stocky setae (as if stippled) (1) or membranous (2).

118. Relative numbers of dorsal/ventral costal setae dorsal>ventral (difference >3 setae) (0), dorsal ~equal to ventral (within 2 setae) (1), or dorsal<ventral (difference >3 setae) (2).

119. Subcosta joins costa distal to point of closest approach of CuA and AA (0), about the same distance from the wing base as to the point of closest approach of CuA and AA (1), proximal to point of closest approach of CuA and AA (2), or not distinguishable (flightless species) (3).

120. Number of free MP veins between MP1+2 and CuA, 2 (0), 1 (1), or 0 (2) (flightless species).

121. Free MP vein(s) between MP1+2 and CuA arise distal to point of closest approach of CuA and AA (0), about the same distance from the wing base as to the point of closest approach of CuA and AA (1), proximal to point of closest approach of CuA and AA (2), or not distinguishable (flightless species) (3).

122. Vein AA forked (into AA1+2 and AA3+4) (0), not forked (1), or not distinguishable (flightless species) (2).

123. Vein AA, at closest point to CuA, far from CuA (farther apart than width of CuA) (0), close to CuA (within width of CuA) (1), touches CuA (2), or
not distinguishable (flightless species) (3).

124. Vein RP present proximal to the radial spring (0), absent (1), or not distinguishable (flightless species) (2).

125. Vein MP apically appearing single (0), double (RP3+4 + MP 1+2) (1), or not distinguishable (flightless species) (2).

Mesosternum

126. Mesosternum anteriorly wide (~1/2 width of mesothorax) (0), or narrow (~1/5-1/3 width of mesothorax) (1).

127. Mesosternum anteriorly (just posterior to anterior margin) completely setose (0), completely glabrous and matt (1), completely glabrous and shiny (2), with a single, medial, longitudinal patch of setae (3), with an even, medial, transverse band of setae (4), with an anteriorly

emarginate, medial, band of setae (5), with a medial patch of setae in “Y” shape (6), with an anterior band of setae, emarginate posteriorly (7), with two separate, medial patches of setae joined in a “V’ shape, or joined and anteriorly emarginate (8), or with two small, medial, setose pits (9).
Note: this area is usually obscured by the prosternum in mounted specimens.

128. Sternacosta of mesosternum absent (0), parallel to anterior margin of metasternum, lateral to mesocoxa, not reaching metasternum (1), or meeting metasternum in acute or right angle lateral to mesocoxa (and usually continuing beneath or along anterior metasternal margin to lateral margin) (2).

Mesepisternum

129. Posterior corner of mesepisternum shiny (0), or matt (1).

130. Posterior corner of mesepisternum glabrous (0), or setose (1).

131. Mesepisternum posteriorly does not reach metasternum (0), or reaches metasternum (1).

Mesepimeron

132. Mesepimeron setose (0), or glabrous (1).

Metasternum

133. Postmesocoxal grooves connected medially (0), narrowly separate medially (<distance between mesocoxae) (1), moderately separate medially (~distance between mesocoxae) (2), or widely separate medially (>distance between mesocoxae) (3).

Metanotum

134. Metanotal membrane widest anteriorly (0), ~parallel-sided (1), widest posteriorly, with straight sides (2), or widest posteriorly, with arcuate sides (3).

135. Metanotal membrane ~horizontal (0), or ~ vertical (1).

136. Anterior transverse suture transverse (0), or oblique (1).

137. Alacrista dorsal to metascutellar ridge (with metascutellar ridge invaginated like a phragma) (0), or anteriorly confluent with metascutellar ridge (1).

138. Metascutellar ridge with a lateral transverse ridge (ventral metascutellar ridge) at posterior one-third (0), or at midpoint (1).

139. Ventral metascutellar ridge reaches posterior margin of metascutellum ~one-third to one-half distance to the lateral margin (0), does not reach the posterior margin, but extends ~four-fifths distance to lateral margin (1), or absent (2).

140. Lateral, transverse carina of postnotum short, thick (0), long, forked laterally (1), or long, thin, light, forked medially (2).

141. Metascutellar ridges not connected posteriorly, not reaching posterior margin of metanotum (0), connected posteriorly, with short, medial, longitudinal sulcus from posterior end of metascutellar groove to posterior edge of postnotum (1), connected posteriorly, metascutellar groove reaching posterior margin of postnotum in a point (2), or connected posteriorly, metascutellar groove reaching posterior margin of postnotum widely (3).

142. Metascutellar groove tapering posteriorly (0), or parallel-sided (1).

143. Posterior margin of metanotum medially straight (0), or medially produced posteriorly (1).

Abdomen

144. Anterior margin of abdominal tergite VI projecting medially (0), or not projecting medially (1).

145. Medial braces of abdominal tergite VI strong, meeting posteriorly (0), not meeting posteriorly (1), or absent (2).

145. Medial braces of abdominal tergite VI not forked posteriorly (0), forked posteriorly (1), forked anteriorly (2), or absent (3).

147. Anterolateral struts of abdominal tergite VI far anterior (0), medial (1), or absent (2).

148. Anterolateral struts of abdominal tergite VI straight (0), doubly recurved (1), or absent (2).

149. Number of visible abdominal sternites 7 (0), 6 (the anterior sternite visible only laterally (1), or 5 (2).

150. Posterior bulge of abdominal sternite lII (internally) absent (0), reaches the posterior margin of sternite lII (1), comes close to the posterior margin of sternite lII (within same distance as width of the sclerotized anterior border of sternite IV) (2), or is far from the posterior margin of sternite lIl (more than the width of sclerotized anterior border of sternite IV) (3).

Prothoracic Leg

151. Procoxae protruding well past level of intervening prosternal process, almost touching medially (0), or about level with intervening prosternal process, distinctly separate (1).

152. Profemoral groove present (0), or absent (1).

153. Anterodorsal setal patch of profemur ~one-half length of femur (0), or at least two-thirds length of femur (1).

154. Anterodorsal setal patch of profemur (antennal brush of Marshall, 2000) ~one-half width of femur (0), ~one-third to one-quarter width of femur (1), or ~one-sixth to one-eighth width of femur (2).

155. Tip of protibia, at base of terminal spur, without apical stout setal comb (0), with stout comb not reaching anterodorsal ridge (1), or with stout comb reaching anterodorsal ridge (2).

156. Tip of terminal protibial spur sharp (0), blunt (1), or bifid (2).

157. Tip of terminal protibial spur directed ventrally (0), anteriorly (1), or dorsally (2).

158. Terminal protibial spur shorter than terminal spine (0), ~same length as terminal spine (1), or longer than terminal spine (2).

Mesothoracic Leg

159. Mesotrochantin present, visible (0), or not visible (fused/hidden) (1).

160. Mesocoxa transverse (closed laterally by mesepimeron) (0), or globose (closed laterally by mesosternum/metasternum) (1).

161. Meso- and metatibiae with transverse comb of setae (0), transverse pair(s) of spines (1), or single, or no, marginal spine(s) (2).

Metathoracic Leg

162. Metacoxa open laterally (0), or closed laterally by metepisternum and first visible abdominal sternite (1)

163. Metacoxa with two distinct, transverse ridges (0), or with one distinct and one obsolete ridge (wider apart) (1).

164. Posterior margin of metafemur glabrous (0), with 1-10 setae (1), or with >10 setae (2).

165. Metacoxa medially glabrous (0), or setose (1).

Mesendosternite

166. Number of intercoxal bridges 1 (0), 2 (1), 3 and anterior longest (2), 3 and posterior longest (3), 3 and medial longest (4).

167. Mesendosternite separate anteriorly (0), joined and evenly convex anteriorly (1), or joined and emarginate/concave anteriorly (2).

168. Mesendosternite anteriorly not connected (0), connected, without median keel (0), or connected, with median, longitudinal keel/ridge (1).

169. Mesendosternite with 1 transverse bridge (0), 2 transverse bridges (1), 3 transverse bridges, with ratio of lengths of anterior/middle bridges 0.59-0.86 (2), 3 transverse bridges, with ratio of lengths of anterior/middle bridges 1.19-1.25 (3), or 3 transverse bridges, with ratio of lengths of anterior/middle bridges 1.83-8.71 (4).

Metendosternite

170. Tip of anterior arm of metendosternite rounded (0), acute (1), or concave/bifid (2).

171. Anterior arm of metendosternite dorsally (between flanges), medially, longitudinally concave (0), flat (1), or longitudinally ridged (2).

172. Anterior flange of metendosternite meets furca (medial piece) dorsally (0), or laterally (1).

173. Anterior flange of metendosternite evenly triangular to tip (0), margin recurved (triangular basally, roughly parallel-sided anteriorly), reaching tip (1), or does not reach tip (2).

174. Anterior flange of metendosternite meets furcal arm anteriorly (0), or meets furcal arm ventrally (1).

175. Anterior flange of metendosternite in higher plane than posterior flange (0), in same plane as posterior flange (1), or in lower plane than posterior flange (2).

176. Furcal arms of metendosternite straight, rising well above coxae (0), or recurved in wide, very shallow U, little or no higher than coxae (1).

177. Furcal arms of metendosternite diverge in ~180° angle (0), or ~100-145° angle (1).

178. Furcal arms of metendosternite medially recurved to join anterior arm in even curve (0), or angle (1).

179. Furcal arms of metendosternite basally recurved in ~180° angle (0), or in ~90-165° angle (1).

180. Posterior flange of metendosternite ~one-fourth width of furcal arm (0), ~0ne-third width of furcal arm (1), or ~one-half width of furcal arm (2).

181. Posterior flange of metendosternite meets furcal arm ventrally (0), or posteriorly (1).

Male Genitalia

182. Male terminalia capsule-like (0), or in the shape of a lyre or horseshoe (spiculum) (1).

183. Aedeagus widest across basal piece (0), parameres (1), or median lobe (2).

184. Ratio of width to length of aedeagus <0.33 (0), 0.40-0.54 (1), 0.62-0.91 (2), or >1.01 (3).

185. Ratio of width to length of median lobe of aedeagus <0.09 (0), or > 0.30 (1).

186. Ratio of width of median lobe of aedeagus to width of mesosternum (between mesocoxae) <1.20 (0), 1.71-3.73 (1), 4.30-5.00 (2), or >5.71 (3).

187. Median lobe of aedeagus dorsally strongly sclerotized, rigid, (narrow) (0), lightly sclerotized, flexible, (moderate to large in size) (1), or lightly sclerotized, flexible, (greatly reduced) (2).

188. Median lobe of aedeagus dorsally completely sclerotized (0), with medial, longitudinal, membranous area in basal 1/2-7/8 (1), or with medial, longitudinal, membranous area complete (2).

189. Median lobe of aedeagus laterally wrapping around and meeting in plane ventrally (0), wrapping around and meeting in angular shelf ventrally (1), or not meeting ventrally (2).

190. Margins of median lobe of aedeagus evenly rounded (0), produced as dorsolateral lobes/tubercles (1), or produced laterally as spines (2).

191. Median lobe of aedeagus without basal, dorsomedial tubercles (0), or with distinct basal, dorsomedial tubercles (1).

192. Median lobe of aedeagus fused to parameres (0), not fused to parameres (1), or hidden within fused parameres (2).

193. Parameres strongly sclerotized, rigid (0), lightly sclerotized, flexible, meeting ventrally (1), lightly sclerotized, flexible, not meeting ventrally (2), or lightly sclerotized, flexible, with large, triangular sclerite between the tips ventrally (3).

194. Parameres not prolonged laterally (0), prolonged in finger-shaped lobes anterolaterally (1), prolonged in hooks laterally (tips flat) (2), or prolonged in hooks basolaterally (tips free) (3).

195. Parameres dorsally fused medially (0), or dorsally separate medially (1).

196. Parameres indistinguishable from basal piece (medially completely fused to basal piece) (0), very long (about twice as long as basal piece) (1), moderately long (~length of basal piece) (2), or short (less than or equal to one-half length of basal piece) (3).

197. Parameres completely fused to basal piece (0), partially fused to basal piece (1), or not fused to basal piece (2).

198. Basal piece of aedeagus laterally wrapping around and meeting ventrally (0), wrapping around and almost meeting ventrally (1), or not wrapping around or meeting ventrally (2).

199. Basal piece of aedeagus mediodorsally joined (0), or separate (1).

200. Genital opening apical, or nearly apical and on ventral face (0), medial on ventral face (1), or on lower half of ventral face (basal margin on shelf) (2).

201. Genital opening at end of very narrow, sclerotized, tubular median lobe, with a flagellum (0), at end of very narrow, sclerotized, tubular median lobe, without a flagellum (1), with an eversible, membranous sac (2), with an eversible sac covered with short, pigmented scales (3), with an eversible sac with short spicules (4), or with an eversible sac with patch(es) of long setae (5).

202. Genital opening basally without lateral pore patches (0), or with two, lateral pore patches at base of eversible sac (1).

203. Genital opening basally, internally sclerotized (0), membranous (1), membranous, with an erect, membranous, stiff, tooth-shaped protuberance on each side (2), or membranous, with a prominent, erect, tooth-like sclerite on each side (3).

204. Genital opening basally without a triangular sclerite on each side (0), or with a triangular sclerite on each side (1).

205. Eversible sac absent (0), present, subapically unmodified (1), present, with a subapical, ventral, sclerotized scoop-shaped structure (2), or present, with a subapical, ventral, sclerotized, double scoop-shaped structure (3).

206. Temones absent (0), present, straight, longitudinal (1), present, straight, diagonal (2), present, curved medially (3), or present, hooked basally (4).

207. Temones absent (0), short, not reaching apex of basal piece (1), reaching apex of basal piece (2), ending between apex and base of basal piece (3), reaching base of basal piece (4), or passing base of basal piece (5).

Appendix C-2. TAXON/CHARACTER MATRIX FOR THE PRELIMINARY PHYLOGENY OF PASSALIDAE.

Diphyllostoma	0	2	0	0	0	0	0	0	0	0
Sinodendron	0	0	0	0	0	0	0	0	0	0
Bolboceras	0	2	0	0	0	0	0	1	3	0
Aulacocyclus e.	0	2	1	1	2	1	1	1	2	0
Aulacocyclus p.	0	2	1	2	2	1	1	1	1	0
Comacupes	0	0	1	1	2	2	1	1	1	0
Taeniocerus	1	1	2	1	2	2	1	1	2	1
Ceracupes	1	0	2	1	2	2	1	1	3	0
Cylindrocaulus	0	0	2	1	0	0	1	1	3	0
Macrolinus	1	1	2	1	1	3	2	1	3	0
Pleurarius	1	1	2	1	1	3	2	1	3	0
Episphenus	1	0	2	1	2	2	1	1	3	0
Aceraius g.	1	0	2	1	1	2	2	1	3	1
Aceraius h.	1	0	2	1	1	3	2	1	3	0
Aceraius sp.	1	1	2	1	1	2	1	1	3	?
Caccoius	1	0	2	1	1	3	2	1	3	0
Mastochilus	1	1	2	1	1	3	2	1	3	0
Leptaulax d.	1	2	2	1	2	3	2	2	3	0
Leptaulax b.	0	2	2	1	1	3	2	1	3	1
Leptaulax p.	1	2	2	1	1	3	2	1	3	0
Pentalobus	1	1	2	1	1	3	2	1	3	0

Character #	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Erionomus	1	1	2	1	1	2	1	1	3	0
Semicyclus	1	1	2	1	1	3	2	1	3	0
Passalus interr.	1	1	2	2	2	3	2	1	3	0
Passalus cun.	1	2	2	2	2	3	2	1	3	1
Passalus cael.	1	2	2	1	2	3	2	1	3	0
Paxillus	1	1	2	1	2	3	2	1	3	0
Spasalus	0	1	2	1	2	3	2	1	3	0
Ptichopus	1	1	2	1	1	3	2	1	3	0
Verres cort.	1	2	2	2	2	1	1	1	3	0
Veturius sp.	1	0	2	2	2	3	3	1	3	0
Pseudacanthus	0	0	?	?	?	?	?	1	?	?
Ogyges	1	0	2	3	2	2	1	1	3	0
Vindex	1	2	2	4	3	2	1	1	3	0
Chondrocephalus	0	1	2	1	1	2	1	1	3	0
Odontotaenius d.	0	2	2	3	2	1	1	1	3	0
Odontotaenius s.	1	1	2	2	1	1	1	1	3	0
Heliscus tropicus	1	2	2	3	2	2	1	1	3	0
Hel. rotundicornis	1	0	2	2	1	1	1	1	3	0
Spurius sp.	1	0	2	3	2	2	1	1	3	0
Petrej. ten.	1	1	2	3	2	2	1	1	3	0
Petrej. sp.BdT	0	2	2	2	2	2	1	1	3	0
Popilius punctatis	1	2	2	1	1	2	1	1	3	0
Popilius erotylus	1	0	2	4	2	1	1	1	3	0

Character #	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Diphyllostoma	0	0	0	0	0	0	0	0	0	0
Sinodendron	1	3	1	0	0	1	2	1	1	0
Bolboceras	1	4	1	0	0	1	2	1	1	0
Aulacocyclus e.	2	2	1	0	0	1	2	1	1	0
Aulacocyclus p.	2	2	1	0	0	1	2	1	1	0
Comacupes	2	1	1	0	0	1	2	1	1	0
Taeniocerus	1	3	1	0	0	1	2	1	1	0
Ceracupes	2	2	1	0	0	1	2	1	1	0
Cylindrocaulus	0	0	0	0	0	0	0	0	0	0
Macrolinus	1	1	2	2	0	1	2	3	3	3
Pleurarius	1	1	2	1	0	1	2	3	3	3
Episphenus	1	1	2	2	0	1	2	3	3	3
Aceraius g.	1	1	2	1	0	1	2	3	2	3
Aceraius h.	1	1	2	2	0	1	2	3	3	3
Aceraius sp.	1	1	2	2	0	1	2	3	3	3
Caccoius	1	1	2	2	0	1	1	3	3	3
Mastochilus	1	1	2	2	0	1	2	3	3	1
Leptaulax d.	1	1	2	2	0	2	2	3	2	4
Leptaulax b.	1	1	2	1	0	2	1	3	2	4
Leptaulax p.	1	1	3	1	0	2	1	3	2	4
Pentalobus	1	1	2	2	0	2	1	3	2	4

Character #	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Erionomus	1	1	2	2	0	2	2	3	2	3
Semicyclus	1	3	2	2	0	3	4	4	0	4
Passalus interr.	1	3	2	2	0	2	2	2	3	3
Passalus cun.	1	1	2	2	0	2	2	2	3	3
Passalus cael.	1	1	2	2	0	1	2	2	2	3
Paxillus	1	1	2	2	0	2	2	2	3	2
Spasalus	1	1	2	2	0	2	2	2	3	3
Ptichopus	1	1	2	2	0	2	2	3	3	3
Verres cort.	1	1	3	2	0	1	3	2	2	4
Veturius sp.	1	1	2	1	0	1	2	3	1	3
Pseudacanthus	1	3	2	1	0	3	4	4	4	4
Ogyges	1	1	2	2	0	1	2	2	2	3
Vindex	1	1	2	2	0	1	1	2	2	4
Chondrocephalus	1	1	2	2	0	1	1	2	2	3
Odontotaenius d.	1	3	2	1	0	3	4	4	4	5
Odontotaenius s.	1	3	2	1	0	1	2	1	2	1
Heliscus tropicus	1	3	2	2	0	1	2	2	2	2
Hel. rotundicornis	1	3	2	1	0	3	4	4	4	5
Spurius sp.	3	0	5	2	0	3	4	4	4	3
Petrej. ten.	1	3	2	2	0	1	2	2	2	3
Petrej. sp.BdT	1	3	2	2	0	1	2	2	2	1
Popilius punctatis	1	1	2	2	0	1	1	3	2	3
Popilius erotylus	1	1	4	2	0	1	3	1	2	3
Popilius eclipticus	1	1	3	2	1	1	1	2	2	2
Popilius sp.5PAN	1	1	2	3	0	1	2	2	2	2

Character #	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Diphyllostoma	0	0	0	0	0	0	0	0	0	0
Sinodendron	0	0	0	0	0	0	0	0	0	0
Bolboceras	0	0	0	0	0	1	0	0	0	0
Aulacocyclus e.	0	0	0	0	0	0	0	0	0	0
Aulacocyclus p.	0	0	0	0	0	0	0	0	0	0
Comacupes	0	0	0	0	1	0	0	0	0	0
Taeniocerus	0	0	0	0	1	1	0	0	0	0
Ceracupes	0	0	0	0	0	0	0	0	0	0
Cylindrocaulus	0	0	0	0	0	0	0	0	0	0
Macrolinus	1	2	1	0	1	1	1	1	1	1
Pleurarius	1	3	1	0	1	1	2	1	1	1
Episphenus	1	2	1	0	0	0	2	1	1	1
Aceraius g.	1	2	1	0	1	1	2	1	1	1
Aceraius h.	1	2	1	0	1	0	2	1	1	1
Aceraius sp.	1	2	1	0	0	1	2	1	1	1
Caccoius	1	2	1	0	1	0	1	1	1	1
Mastochilus	1	2	1	0	0	0	1	1	1	1
Leptaulax d.	2	2	1	1	1	1	1	1	1	2
Leptaulax b.	2	2	1	0	1	1	1	1	1	2
Leptaulax p.	2	2	1	0	1	1	1	1	1	2
Pentalobus	2	2	1	1	0	1	1	1	1	2

Character #	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
Erionomus	1	1	1	0	0	1	1	1	1	2
Semicyclus	2	1	1	1	0	0	1	1	1	2
Passalus interr.	1	3	1	1	0	1	1	1	1	2
Passalus cun.	1	3	1	1	0	1	1	1	1	2
Passalus cael.	1	3	1	1	0	1	1	1	1	2
Paxillus	1	3	1	1	0	1	1	1	1	2
Spasalus	1	3	1	1	0	1	1	1	1	2
Ptichopus	1	3	1	0	0	{01}	1	1	1	2
Verres cort.	1	3	2	0	0	0	1	1	2	3
Veturius sp.	1	3	1	0	0	1	1	1	2	3
Pseudacanthus	1	1	1	0	0	0	1	1	2	3
Ogyges	1	3	1	0	0	0	1	3	2	3
Vindex	2	1	1	0	0	0	1	1	2	2
Chondrocephalus	1	1	1	0	0	0	1	1	2	2
Odontotaenius d.	3	4	3	0	0	0	1	2	2	2
Odontotaenius s.	1	3	1	0	0	0	1	3	2	2
Heliscus tropicus	1	3	1	0	1	0	1	3	2	2
Hel. rotundicornis	3	4	3	0	0	0	1	3	2	2
Spurius sp.	1	3	1	0	1	0	1	2	2	2
Petrej. ten.	1	3	1	0	0	0	1	3	2	2
Petrej. sp.BdT	1	3	1	0	1	0	1	2	2	2
Popilius punctatis	1	3	1	0	1	1	1	2	2	2
Popilius erotylus	1	3	1	0	1	1	1	3	2	2
Popilius eclipticus	1	3	1	0	1	0	1	2	2	2
Popilius sp.5PAN	1	3	1	0	0	0	1	2	2	2

Character #	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Diphyllostoma	1	0	0	0	0	1	0	0	0	0
Sinodendron	0	0	0	0	0	1	0	0	0	3
Bolboceras	0	0	0	0	0	1	3	0	2	1
Aulacocyclus e.	0	0	0	0	0	0	3	0	2	1
Aulacocyclus p.	0	0	0	0	0	0	3	0	2	1
Comacupes	0	0	0	0	0	0	4	0	2	1
Taeniocerus	0	0	0	0	0	0	3	0	2	1
Ceracupes	0	0	0	0	0	0	4	0	1	1
Cylindrocaulus	0	0	0	0	0	0	3	0	1	3
Macrolinus	1	0	0	0	0	1	4	0	0	1
Pleurarius	0	0	0	0	0	1	4	0	0	1
Episphenus	0	0	0	0	0	1	4	0	0	2
Aceraius g.	0	0	0	0	0	1	4	1	0	2
Aceraius h.	0	0	0	0	0	1	4	1	0	2
Aceraius sp.	0	0	0	0	0	1	4	1	0	2
Caccoius	1	0	0	0	0	1	4	1	0	1
Mastochilus	0	0	0	0	0	1	4	0	0	1
Leptaulax d.	1	0	0	0	0	2	3	0	0	1
Leptaulax b.	2	0	0	0	0	2	3	0	0	2
Leptaulax p.	2	0	0	0	0	2	3	0	0	1
Pentalobus	2	0	0	0	0	3	3	0	2	1

30	Character #	31	32	33	34	35	36	37	38	39	40
2	Erionomus	2	0	0	0	0	3	4	0	0	1
2	Semicyclus	2	0	0	0	0	1	3	0	0	1
2	Passalus interr.	0	0	0	0	0	3	3	0	2	1
2	Passalus cun.	0	0	0	0	0	1	3	0	2	1
2	Passalus cael.	0	0	0	0	0	3	1	0	2	1
2	Paxillus	0	0	0	0	0	1	3	0	2	1
2	Spasalus	0	0	0	0	0	1	1	0	2	1
2	Ptichopus	0	0	0	0	0	1	1	0	2	1
3	Verres cort.	0	0	0	0	0	1	3	0	2	4
3	Veturius sp.	0	0	0	0	0	1	1	0	2	4
3	Pseudacanthus	1	1	2	2	2	1	1	0	2	1
3	Ogyges	1	0	0	0	0	1	2	0	0	4
2	Vindex	1	1	2	3	3	1	1	0	2	3
2	Chondrocephalus	1	1	2	3	1	1	1	0	2	4
2	Odontotaenius d.	0	1	1	2	2	1	1	0	2	4
2	Odontotaenius s.	0	1	1	4	2	1	1	0	2	4
2	Heliscus tropicus	0	1	1	1	2	1	1	0	2	4
2	Hel. rotundicornis	0	1	1	1	2	1	1	0	2	4
2	Spurius sp.	1	1	1	3	1	1	1	0	2	4
2	Petrej. ten.	0	1	1	2	3	1	1	0	2	4
2	Petrej. sp.BdT	0	1	1	1	2	1	1	0	2	4
2	Popilius punctatis	0	1	1	4	1	1	1	0	2	4
2	Popilius erotylus	0	1	1	2	1	1	1	0	2	4
2	Popilius eclipticus	0	1	1	4	1	1	1	0	2	4
2	Popilius sp.5PAN	0	1	1	1	1	1	1	0	2	4

Character #	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
Diphyllostoma	0	0	?	1	0	0	0	3	0	0
Sinodendron	0	1	0	0	1	1	2	2	0	0
Bolboceras	0	0	2	0	3	2	2	3	0	0
Aulacocyclus e.	0	0	0	1	2	1	2	2	0	0
Aulacocyclus p.	0	0	0	0	2	1	2	{24}	0	0
Comacupes	0	0	0	0	2	1	2	1	0	0
Taeniocerus	0	0	0	0	2	1	2	0	0	0
Ceracupes	0	1	2	0	2	1	2	1	0	0
Cylindrocaulus	0	0	0	0	1	1	0	0	0	0
Macrolinus	0	1	2	2	1	2	2	1	2	0
Pleurarius	0	1	2	3	2	2	2	1	2	0
Episphenus	0	1	2	{34}	1	2	2	1	0	0
Aceraius g.	0	0	0	4	1	2	2	1	0	0
Aceraius h.	0	1	2	2	1	2	2	1	2	0
Aceraius sp.	0	1	2	2	2	2	2	1	2	0
Caccoius	0	1	2	2	1	2	2	1	2	0
Mastochilus	0	1	2	2	1	2	2	1	2	0
Leptaulax d.	0	2	2	2	2	2	2	1	0	0
Leptaulax b.	0	2	2	1	2	2	2	1	0	1
Leptaulax p.	0	2	2	1	2	2	2	1	0	1
Pentalobus	0	2	2	1	2	2	2	1	0	0

Character #	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
Erionomus	0	2	2	0	2	2	2	1	0	0
Semicyclus	0	2	2	0	2	1	2	1	0	0
Passalus interr.	0	1	2	3	1	2	2	1	0	0
Passalus cun.	0	2	1	1	2	2	2	1	0	0
Passalus cael.	0	2	2	1	1	1	2	1	0	0
Paxillus	0	2	2	2	2	2	2	1	0	0
Spasalus	0	2	2	4	2	2	2	1	1	0
Ptichopus	0	2	2	2	2	2	2	1	0	0
Verres cort.	0	2	2	1	2	1	2	1	0	1
Veturius sp.	0	0	0	1	1	1	2	1	0	0
Pseudacanthus	0	1	2	1	2	1	2	0	0	0
Ogyges	0	1	2	0	2	1	2	4	1	0
Vindex	0	1	2	1	2	1	2	2	0	1
Chondrocephalus	0	1	2	1	1	2	2	0	1	0
Odontotaenius d.	1	2	2	1	1	1	2	1	1	0
Odontotaenius s.	1	2	2	1	1	2	2	0	1	0
Heliscus tropicus	1	2	2	1	2	1	2	0	0	0
Hel. rotundicornis	1	2	2	1	2	2	2	0	1	0
Spurius sp.	0	1	2	1	1	1	2	0	1	0
Petrej. ten.	0	1	2	1	2	1	2	0	0	0
Petrej. sp.BdT	1	1	2	1	2	2	2	0	0	0
Popilius punctatis	0	1	2	1	2	1	2	2	1	0
Popilius erotylus	0	2	2	1	1	1	2	0	0	0
Popilius eclipticus	0	2	2	1	2	1	2	0	0	0
Popilius sp.5PAN	0	1	2	2	2	2	2	0	0	0

Character #	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
Diphyllostoma	0	0	0	1	0	0	0	0	0	0
Sinodendron	0	0	0	1	0	1	1	2	1	3
Bolboceras	0	0	0	1	1	1	2	2	1	0
Aulacocyclus e.	0	0	0	1	0	1	2	1	1	1
Aulacocyclus p.	0	0	0	1	0	1	2	1	1	1
Comacupes	0	1	0	1	0	1	2	1	1	1
Taeniocerus	0	0	0	1	0	1	2	1	2	2
Ceracupes	0	1	1	1	0	1	2	1	1	3
Cylindrocaulus	0	0	0	0	0	1	2	1	1	3
Macrolinus	0	0	0	1	2	2	2	1	1	1
Pleurarius	1	2	0	0	1	4	2	1	1	3
Episphenus	0	0	0	1	1	2	2	1	1	2
Aceraius g.	0	0	0	1	1	4	2	3	2	3
Aceraius h.	0	0	0	1	1	2	2	3	2	2
Aceraius sp.	0	0	0	1	1	2	2	1	1	3
Caccoius	0	0	0	1	1	2	2	3	1	3
Mastochilus	1	1	0	0	1	2	2	1	1	1
Leptaulax d.	0	0	0	1	1	2	1	3	1	3
Leptaulax b.	0	0	0	1	1	2	1	1	1	3
Leptaulax p.	0	0	0	1	1	2	1	1	1	3
Pentalobus	1	2	0	1	1	4	2	1	1	3

Character #	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
Erionomus	1	2	1	0	1	4	2	3	1	2
Semicyclus	0	0	0	1	1	4	2	1	1	2
Passalus interr.	1	0	0	0	1	4	2	1	1	2
Passalus cun.	1	0	0	0	1	4	2	1	2	1
Passalus cael.	1	0	0	0	1	4	2	1	1	3
Paxillus	1	1	0	1	1	4	2	1	2	3
Spasalus	0	1	0	0	1	4	2	1	1	2
Ptichopus	1	2	0	0	1	4	2	1	1	2
Verres cort.	1	2	0	0	1	3	2	2	1	1
Veturius sp.	1	2	0	0	1	3	2	3	1	1
Pseudacanthus	1	1	0	0	1	4	2	1	1	2
Ogyges	1	2	0	0	1	4	2	1	2	2
Vindex	1	2	0	0	1	3	2	1	1	2
Chondrocephalus	1	1	0	0	1	3	2	3	1	2
Odontotaenius d.	1	1	0	0	1	4	2	3	1	3
Odontotaenius s.	1	2	1	0	1	4	2	2	1	3
Heliscus tropicus	0	2	1	0	1	4	2	2	2	3
Hel. rotundicornis	0	2	0	0	1	4	2	3	1	3
Spurius sp.	1	2	1	0	1	4	2	3	1	2
Petrej. ten.	0	1	0	0	1	4	2	3	1	2
Petrej. sp.BdT	1	2	1	0	1	4	2	3	1	3
Popilius punctatis	1	0	0	1	1	4	2	2	1	3
Popilius erotylus	1	2	1	0	1	4	2	3	1	3
Popilius eclipticus	1	1	0	0	1	4	2	3	1	3
Popilius sp.5PAN	1	1	0	0	1	4	2	2	1	3

Character #	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**
Diphyllostoma	0	1	1	0	?	0	0	0	0	0
Sinodendron	1	1	1	0	?	0	0	0	0	1
Bolboceras	1	0	0	1	?	0	0	0	0	0
Aulacocyclus e.	1	0	1	1	0	0	0	0	0	0
Aulacocyclus p.	1	0	1	1	0	0	0	0	0	0
Comacupes	1	0	1	1	0	0	0	0	0	0
Taeniocerus	1	0	1	1	0	0	0	0	0	0
Ceracupes	1	1	1	1	0	1	0	0	0	0
Cylindrocaulus	1	1	1	1	0	1	1	0	0	0
Macrolinus	4	0	1	1	1	1	1	1	0	1
Pleurarius	3	0	1	1	1	1	1	1	0	0
Episphenus	3	0	1	1	1	1	1	1	0	0
Aceraius g.	4	0	1	1	1	1	1	1	0	0
Aceraius h.	4	0	1	1	1	1	1	1	0	0
Aceraius sp.	3	0	1	1	1	1	1	1	0	1
Caccoius	3	0	1	1	1	1	1	1	0	0
Mastochilus	2	0	1	0	1	1	1	1	0	1
Leptaulax d.	4	0	1	1	1	1	1	1	0	1
Leptaulax b.	4	0	1	1	1	1	1	1	0	1
Leptaulax p.	4	0	1	1	1	1	1	1	0	1
Pentalobus	4	0	1	0	1	1	1	1	0	1

Character #	61	62	63	64	65	66	67	68	69	70
Erionomus	4	0	1	1	1	1	1	1	0	0
Semicyclus	4	0	1	1	1	1	1	1	0	0
Passalus interr.	3	0	1	1	0	1	1	1	0	0
Passalus cun.	3	0	1	1	0	1	1	1	0	0
Passalus cael.	4	0	1	1	0	1	1	1	0	0
Paxillus	4	0	1	1	0	1	1	1	1	0
Spasalus	4	0	1	1	0	1	1	1	0	0
Ptichopus	3	0	1	1	1	1	1	1	0	0
Verres cort.	2	0	1	1	0	1	1	1	0	0
Veturius sp.	3	0	1	1	0	1	1	1	0	0
Pseudacanthus	3	0	1	1	0	1	1	1	0	0
Ogyges	3	0	1	0	0	1	1	1	0	1
Vindex	3	0	1	1	0	1	1	1	0	1
Chondrocephalus	3	0	1	1	0	1	1	1	0	0
Odontotaenius d.	2	0	1	1	0	1	1	1	0	0
Odontotaenius s.	2	0	1	1	0	1	1	1	0	0
Heliscus tropicus	3	0	1	1	0	1	1	1	0	0
Hel. rotundicornis	3	0	1	?	0	1	1	1	0	0
Spurius sp.	4	0	1	1	0	1	1	1	0	0
Petrej. ten.	2	0	1	1	0	1	1	1	0	0
Petrej. sp.BdT	4	0	1	1	0	1	1	1	0	0
Popilius punctatis	3	0	1	1	0	1	1	1	0	0
Popilius erotylus	3	0	1	1	0	1	1	1	0	0
Popilius eclipticus	3	0	1	1	0	1	1	1	0	0
Popilius sp.5PAN	3	0	1	1	0	1	1	1	0	0

Character #	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
Diphyllostoma	0	4	2	3	0	0	0	2	2	0
Sinodendron	0	4	2	3	0	0	0	1	1	1
Bolboceras	0	4	2	3	0	1	0	2	2	0
Aulacocyclus e.	0	0	0	2	0	0	1	0	0	1
Aulacocyclus p.	0	0	0	2	0	0	1	0	0	1
Comacupes	0	0	0	0	1	1	1	1	1	2
Taeniocerus	0	0	0	0	0	0	0	0	0	1
Ceracupes	1	3	1	1	1	1	1	1	1	1
Cylindrocaulus	0	0	0	2	0	0	0	1	1	1
Macrolinus	0	0	0	1	0	0	1	1	0	1
Pleurarius	0	2	0	1	0	0	0	1	1	1
Episphenus	0	0	1	1	0	1	1	1	1	2
Aceraius g.	1	0	1	1	0	1	1	1	1	2
Aceraius h.	0	1	1	0	0	1	1	1	1	2
Aceraius sp.	0	0	1	0	0	0	1	1	0	1
Caccoius	0	0	0	1	0	0	1	1	0	2
Mastochilus	0	1	0	1	0	0	1	1	1	1
Leptaulax d.	1	3	0	1	0	0	1	0	0	2
Leptaulax b.	1	0	0	1	0	0	0	0	0	2
Leptaulax p.	0	2	0	1	0	1	1	0	0	1
Pentalobus	0	0	0	2	0	0	0	1	0	2

Character #	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
Erionomus	0	1	0	1	1	1	1	1	1	2
Semicyclus	0	1	0	0	0	0	0	1	1	1
Passalus interr.	0	0	0	1	0	0	0	1	1	1
Passalus cun.	0	0	0	0	0	0	0	1	1	1
Passalus cael.	0	0	0	0	0	0	0	1	1	1
Paxillus	0	0	0	1	0	1	1	1	1	1
Spasalus	0	2	0	1	0	0	0	1	1	1
Ptichopus	0	0	0	0	0	0	0	1	1	1
Verres cort.	0	1	0	0	0	0	0	1	1	1
Veturius sp.	0	1	0	0	0	0	0	1	1	1
Pseudacanthus	0	0	0	0	0	0	1	1	1	1
Ogyges	0	0	0	1	0	1	1	1	1	1
Vindex	0	0	0	0	0	0	1	1	1	1
Chondrocephalus	0	0	0	0	0	0	0	1	1	1
Odontotaenius d.	0	3	0	1	0	0	1	1	1	1
Odontotaenius s.	0	0	0	0	1	0	1	1	1	0
Heliscus tropicus	0	0	0	1	1	0	1	1	1	1
Hel. rotundicornis	0	0	0	0	0	0	1	1	1	0
Spurius sp.	0	0	0	1	1	0	0	1	1	1
Petrej. ten.	0	0	0	0	0	0	1	1	1	1
Petrej. sp.BdT	0	3	0	1	1	0	0	1	1	1
Popilius punctatis	0	2	0	1	0	0	1	1	1	1
Popilius erotylus	0	3	0	1	0	0	0	1	1	1
Popilius eclipticus	0	1	0	0	0	1	1	1	1	1
Popilius sp.5PAN	0	0	0	1	0	0	0	1	1	1

Character #	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
Diphyllostoma	1	3	2	2	1	1	0	2	0	0
Sinodendron	1	3	2	0	1	1	0	2	0	0
Bolboceras	1	2	1	2	0	0	0	2	0	0
Aulacocyclus e.	0	2	2	0	0	1	2	2	1	1
Aulacocyclus p.	0	2	0	0	0	1	2	2	1	1
Comacupes	0	2	2	0	0	1	2	2	1	1
Taeniocerus	1	2	0	0	0	1	3	2	1	1
Ceracupes	1	2	2	0	0	0	0	2	1	1
Cylindrocaulus	0	2	2	1	1	1	0	2	1	1
Macrolinus	0	1	0	0	0	1	0	2	1	1
Pleurarius	0	1	0	0	1	0	1	0	1	1
Episphenus	0	0	0	0	0	1	0	2	2	1
Aceraius g.	0	0	0	0	0	1	0	1	1	1
Aceraius h.	0	0	0	0	0	1	0	0	1	1
Aceraius sp.	0	0	0	0	0	1	0	2	1	1
Caccoius	0	0	0	0	0	0	0	2	1	1
Mastochilus	0	1	0	0	1	1	1	2	1	1
Leptaulax d.	0	0	0	1	1	1	0	2	1	1
Leptaulax b.	0	0	0	0	0	0	0	2	2	1
Leptaulax p.	0	0	0	0	0	1	0	1	1	1
Pentalobus	0	1	0	0	0	1	0	0	1	1

Character #	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
Erionomus	0	0	0	0	0	0	0	2	1	1
Semicyclus	1	1	0	0	0	0	0	1	2	1
Passalus interr.	1	1	0	0	0	1	0	2	1	1
Passalus cun.	0	1	0	0	1	1	0	2	1	1
Passalus cael.	0	1	0	0	0	0	0	0	1	1
Paxillus	0	0	0	0	0	1	0	2	1	1
Spasalus	0	0	0	0	1	1	0	2	2	1
Ptichopus	1	1	0	0	0	0	0	2	2	1
Verres cort.	1	1	0	0	0	0	0	0	2	1
Veturius sp.	1	1	0	0	0	0	0	1	2	1
Pseudacanthus	0	1	0	0	0	1	0	2	1	1
Ogyges	0	1	0	0	0	0	0	0	1	1
Vindex	0	1	0	1	0	0	0	0	2	1
Chondrocephalus	0	1	0	0	0	0	0	0	2	1
Odontotaenius d.	1	1	0	0	1	1	0	0	1	1
Odontotaenius s.	0	1	0	0	0	1	0	0	1	1
Heliscus tropicus	1	1	0	0	0	1	0	2	1	1
Hel. rotundicornis	0	1	0	0	0	1	0	2	1	1
Spurius sp.	0	1	0	0	0	1	0	2	1	1
Petrej. ten.	0	1	0	0	0	0	0	2	2	1
Petrej. sp.BdT	1	1	0	0	0	1	0	2	1	1
Popilius punctatis	0	1	0	0	0	1	0	1	2	1
Popilius erotylus	0	1	0	0	0	1	0	1	1	1
Popilius eclipticus	0	1	0	0	0	1	0	0	1	1
Popilius sp.5PAN	0	1	0	0	0	1	0	2	2	1

Character #	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**
Diphyllostoma	0	0	0	0	0	0	0	0	0	0
Sinodendron	0	0	0	0	0	0	0	0	0	0
Bolboceras	1	0	0	0	0	0	0	0	0	0
Aulacocyclus e.	0	0	0	1	2	1	1	1	1	1
Aulacocyclus p.	0	0	0	1	2	1	1	1	1	1
Comacupes	0	0	0	1	2	1	1	1	1	1
Taeniocerus	0	0	0	1	3	2	1	1	1	3
Ceracupes	0	0	0	1	3	1	1	1	1	2
Cylindrocaulus	0	0	0	1	5	2	1	1	1	3
Macrolinus	1	1	1	1	4	2	1	2	1	2
Pleurarius	1	1	1	1	4	3	2	2	1	3
Episphenus	1	1	1	1	4	2	5	2	1	3
Aceraius g.	1	0	1	1	4	3	5	2	1	3
Aceraius h.	1	1	1	1	4	3	5	2	2	3
Aceraius sp.	1	0	1	1	4	3	1	2	1	3
Caccoius	1	0	1	1	4	2	6	3	2	3
Mastochilus	1	1	1	1	4	3	1	2	1	3
Leptaulax d.	1	1	1	1	4	3	1	2	1	3
Leptaulax b.	1	1	0	1	4	3	1	4	3	3
Leptaulax p.	1	0	0	1	4	2	2	5	3	3
Pentalobus	1	1	0	1	5	2	1	1	1	3

Character #	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**
Erionomus	1	1	0	1	5	3	7	1	1	3
Semicyclus	1	1	0	1	5	3	1	2	1	3
Passalus interr.	1	0	1	1	4	3	1	2	1	3
Passalus cun.	1	0	0	1	5	3	1	2	1	3
Passalus cael.	1	0	1	1	5	3	1	3	3	3
Paxillus	1	0	0	1	5	3	1	3	1	3
Spasalus	1	0	0	1	5	3	1	4	3	3
Ptichopus	1	0	0	1	3	1	1	2	1	3
Verres cort.	1	0	1	1	4	3	3	2	1	3
Veturius sp.	1	0	1	1	4	3	1	2	1	3
Pseudacanthus	1	0	0	1	5	3	7	3	?	3
Ogyges	1	0	0	1	4	3	1	2	1	3
Vindex	1	0	0	1	4	3	1	2	1	3
Chondrocephalus	1	0	0	1	5	2	1	2	1	3
Odontotaenius d.	1	0	0	1	4	3	1	4	3	3
Odontotaenius s.	1	0	0	1	4	3	2	4	3	3
Heliscus tropicus	1	0	0	1	5	3	1	4	3	3
Hel. rotundicornis	1	0	0	1	4	2	2	3	3	3
Spurius sp.	1	0	0	1	4	2	1	4	3	3
Petrej. ten.	1	0	0	1	5	3	1	2	1	3
Petrej. sp.BdT	1	0	0	1	5	2	1	4	3	3
Popilius punctatis	1	0	0	1	5	2	1	4	3	3
Popilius erotylus	1	0	0	1	4	2	1	3	3	3
Popilius eclipticus	1	0	0	1	4	3	1	3	3	3
Popilius sp.5PAN	1	0	0	1	5	2	1	4	3	3

Character #	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**
Diphyllostoma	0	0	1	0	0	0	0	0	0	0
Sinodendron	0	0	1	0	0	1	0	0	0	0
Bolboceras	0	0	0	0	0	1	0	0	0	0
Aulacocyclus e.	1	0	1	0	1	0	0	1	3	0
Aulacocyclus p.	1	0	1	0	1	0	0	1	3	1
Comacupes	1	0	1	0	1	0	0	1	3	1
Taeniocerus	1	0	1	0	1	0	0	1	3	1
Ceracupes	4	?	1	0	1	0	0	1	2	0
Cylindrocaulus	1	0	1	0	1	1	0	1	1	0
Macrolinus	2	1	1	3	2	0	1	1	1	1
Pleurarius	2	1	1	0	0	0	1	1	1	0
Episphenus	2	1	1	2	0	0	1	1	1	0
Aceraius g.	3	1	1	3	2	0	1	1	1	0
Aceraius h.	3	1	1	3	2	0	1	1	1	1
Aceraius sp.	2	1	1	1	0	0	1	1	1	1
Caccoius	3	1	1	3	2	0	1	1	1	1
Mastochilus	2	1	1	3	2	0	1	1	1	1
Leptaulax d.	3	1	1	0	0	0	1	1	0	0
Leptaulax b.	3	1	1	0	0	0	1	1	0	0
Leptaulax p.	3	1	1	0	0	0	1	1	0	0

Character #	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**
Erionomus	4	1	1	1	{01}	0	1	1	1	0
Semicyclus	2	1	1	0	0	0	1	1	0	0
Passalus interr.	4	1	1	0	0	0	1	1	2	0
Passalus cun.	4	1	1	0	0	0	1	1	2	0
Passalus cael.	4	1	1	0	0	0	1	1	2	1
Paxillus	4	1	1	2	0	0	1	1	0	0
Spasalus	3	1	1	2	0	0	1	1	2	0
Ptichopus	4	1	1	0	0	0	1	1	3	1
Verres cort.	3	1	1	0	0	0	1	1	3	1
Veturius sp.	4	1	1	0	0	0	1	1	2	1
Pseudacanthus	?	?	1	0	0	0	1	1	2	1
Ogyges	1	1	1	0	0	0	1	1	1	1
Vindex	2	1	1	0	0	0	1	1	2	0
Chondrocephalus	4	1	1	0	0	0	1	1	2	0
Odontotaenius d.	2	1	1	0	0	0	1	1	2	0
Odontotaenius s.	2	1	1	0	0	0	1	1	2	1
Heliscus tropicus	3	1	1	0	0	0	1	1	3	0
Hel. rotundicornis	3	1	1	0	0	0	1	1	2	0
Spurius sp.	3	1	1	0	0	0	1	1	3	0
Petrej. ten.	3	1	1	0	0	0	1	1	3	1
Petrej. sp.BdT	1	1	1	0	0	0	1	1	2	1
Popilius punctatis	3	1	1	0	0	0	1	1	2	1
Popilius erotylus	3	1	1	0	0	0	1	1	3	0
Popilius eclipticus	3	1	1	0	0	0	1	1	3	0
Popilius sp.5PAN	1	1	1	0	0	0	1	1	1	1

Character #	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**
Diphyllostoma	1	3	1	0	0	0	1	0	0	1
Sinodendron	1	3	1	1	0	0	1	0	0	0
Bolboceras	1	3	1	2	0	0	0	0	2	0
Aulacocyclus e.	0	0	1	2	1	1	2	0	1	0
Aulacocyclus p.	1	0	1	2	1	1	2	0	0	0
Comacupes	0	0	0	2	1	1	2	0	2	0
Taeniocerus	0	0	1	2	1	1	2	2	0	0
Ceracupes	0	0	1	2	1	1	2	0	0	0
Cylindrocaulus	1	0	1	2	1	1	2	1	?	?
Macrolinus	1	2	1	2	1	1	2	0	0	1
Pleurarius	1	0	1	2	1	1	2	0	0	1
Episphenus	1	0	1	2	1	1	2	0	1	1
Aceraius g.	1	3	1	2	1	1	2	0	1	1
Aceraius h.	1	{03}	1	2	1	1	2	0	0	1
Aceraius sp.	1	3	1	2	1	1	2	1	1	1
Caccoius	1	0	1	2	1	1	2	0	1	1
Mastochilus	1	0	1	2	1	1	2	2	0	1
Leptaulax d.	1	0	0	2	1	1	2	2	0	1
Leptaulax b.	0	0	0	2	1	1	2	0	0	1
Leptaulax p.	1	0	1	2	1	1	2	0	0	1
Pentalobus	0	0	1	2	1	1	2	0	1	1

Character #	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**
Erionomus	1	3	1	2	1	1	2	0	1	1
Semicyclus	1	1	1	2	1	1	2	0	0	1
Passalus interr.	1	0	0	2	1	1	2	0	1	1
Passalus cun.	1	0	1	2	1	1	2	2	0	1
Passalus cael.	1	0	1	2	1	1	2	2	0	1
Paxillus	0	0	0	2	1	1	2	2	0	1
Spasalus	1	0	1	2	1	1	2	1	0	1
Ptichopus	1	0	0	2	1	1	2	0	0	1
Verres cort.	1	0	1	2	1	1	2	2	1	1
Veturius sp.	1	0	1	2	1	1	2	2	0	1
Pseudacanthus	1	0	1	2	1	1	2	0	1	1
Ogyges	1	0	1	2	1	1	2	0	?	?
Vindex	1	0	1	2	1	1	2	0	0	1
Chondrocephalus	1	0	1	2	1	1	2	0	0	1
Odontotaenius d.	1	0	1	2	1	1	2	0	0	1
Odontotaenius s.	1	0	1	2	1	1	2	2	0	1
Heliscus tropicus	1	1	1	2	1	1	2	2	0	1
Hel. rotundicornis	0	0	1	2	1	1	2	0	0	1
Spurius sp.	0	0	1	2	1	1	2	0	0	1
Petrej. ten.	1	0	1	2	1	1	2	1	0	1
Petrej. sp.BdT	1	0	1	2	1	1	2	0	1	1
Popilius punctatis	0	0	1	2	1	1	2	0	0	1
Popilius erotylus	1	1	1	2	1	1	2	1	0	1
Popilius eclipticus	1	1	1	2	1	1	2	2	0	1
Popilius sp.5PAN	1	0	1	2	1	1	2	0	0	1

Character #	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**
Diphyllostoma	0	0	3	2	1	0	3	0	0	0
Sinodendron	1	0	0	2	1	0	0	0	0	0
Bolboceras	1	0	0	2	1	1	0	0	0	0
Aulacocyclus e.	0	0	0	3	0	1	1	1	1	1
Aulacocyclus p.	0	0	0	3	0	1	1	1	1	1
Comacupes	0	0	0	3	0	1	1	1	1	1
Taeniocerus	0	0	0	3	0	1	1	1	1	1
Ceracupes	0	0	1	3	0	1	1	1	1	1
Cylindrocaulus	0	1	0	2	0	0	1	1	2	1
Macrolinus	1	1	3	2	0	1	1	1	1	1
Pleurarius	1	0	2	3	0	1	1	1	1	1
Episphenus	0	0	3	2	0	1	1	1	1	1
Aceraius g.	0	0	3	2	0	1	1	1	1	2
Aceraius h.	1	0	3	2	0	1	1	1	1	{12}
Aceraius sp.	0	0	1	3	0	1	1	1	1	2
Caccoius	1	1	3	2	0	1	1	1	0	1
Mastochilus	0	0	3	3	0	1	1	1	1	1
Leptaulax d.	1	1	3	3	0	1	1	1	0	1
Leptaulax b.	1	1	{13}	2	0	1	1	1	1	1
Leptaulax p.	1	0	3	2	0	1	1	1	0	1
Pentalobus	0	0	3	3	0	1	1	1	1	1

Character #	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**
Erionomus	0	0	3	2	0	1	1	1	1	1
Semicyclus	0	0	3	3	0	1	1	1	1	1
Passalus interr.	0	0	3	3	0	1	1	1	0	1
Passalus cun.	0	1	3	3	0	1	1	1	1	1
Passalus cael.	0	1	3	3	0	1	1	1	1	1
Paxillus	1	0	3	3	0	1	1	1	0	1
Spasalus	0	0	1	3	0	1	1	1	1	1
Ptichopus	0	1	3	3	0	1	1	1	1	0
Verres cort.	0	0	0	2	0	1	1	1	1	1
Veturius sp.	0	0	3	?	0	1	1	1	0	0
Pseudacanthus	0	1	3	3	0	1	1	1	1	1
Ogyges	0	1	3	3	0	1	1	1	1	1
Vindex	0	1	3	2	0	1	1	1	0	1
Chondrocephalus	0	0	3	2	0	0	1	1	0	1
Odontotaenius d.	0	0	3	3	0	1	1	1	0	1
Odontotaenius s.	0	0	3	2	0	1	1	1	1	1
Heliscus tropicus	0	0	3	2	0	1	1	1	1	1
Hel. rotundicornis	1	0	3	2	0	1	1	1	1	1
Spurius sp.	0	0	3	3	0	1	1	1	0	1
Petrej. ten.	0	0	3	3	0	1	1	1	0	0
Petrej. sp.BdT	0	0	3	3	0	1	1	1	0	0
Popilius punctatis	0	0	3	2	0	1	1	1	1	1
Popilius erotylus	0	0	3	2	0	1	1	1	1	1
Popilius eclipticus	0	0	3	2	0	1	1	1	0	1
Popilius sp.5PAN	0	1	3	3	0	1	1	1	1	1

Diphyllostoma	2	0	0	1	2	3	2	2	0	0
Sinodendron	0	0	0	1	2	3	2	2	1	0
Bolboceras	2	0	0	1	2	3	2	2	1	1
Aulacocyclus e.	3	0	1	1	1	1	1	0	2	1
Aulacocyclus p.	3	0	1	?	?	?	?	?	2	1
Comacupes	3	0	1	0	1	1	1	0	2	1
Taeniocerus	3	0	1	0	1	1	1	0	2	1
Ceracupes	3	0	1	0	1	0	1	0	2	1
Cylindrocaulus	0	1	1	0	1	0	1	0	2	0
Macrolinus	2	0	1	0	1	0	1	1	1	1
Pleurarius	3	0	1	0	1	0	0	1	1	1
Episphenus	2	0	1	0	1	0	0	?	1	1
Aceraius g.	3	0	1	0	1	1	0	1	1	1
Aceraius h.	{13}	0	1	0	1	0	0	1	1	1
Aceraius sp.	3	0	1	0	1	0	0	1	1	1
Caccoius	1	0	1	0	1	0	0	1	1	1
Mastochilus	2	0	1	0	1	2	0	1	1	1
Leptaulax d.	2	0	1	0	0	0	0	1	1	1
Leptaulax b.	2	0	1	0	1	2	0	1	1	1
Leptaulax p.	3	0	1	0	1	0	0	1	1	1
Pentalobus	2	0	1	0	1	0	0	1	1	1

Character #	**141**	**142**	**143**	**144**	**145**	**146**	**147**	**148**	**149**	**150**
Erionomus	0	0	1	0	1	0	0	1	1	1
Semicyclus	3	0	1	0	1	0	0	1	1	1
Passalus interr.	1	0	1	0	0	0	0	1	1	1
Passalus cun.	2	0	1	0	1	0	0	1	1	1
Passalus cael.	1	0	1	0	1	0	0	1	1	1
Paxillus	1	0	1	0	0	0	0	1	1	1
Spasalus	1	0	1	0	1	0	0	1	1	1
Ptichopus	2	0	1	0	1	0	0	1	1	1
Verres cort.	3	0	1	0	1	0	0	1	1	1
Veturius sp.	3	0	1	0	0	0	0	1	1	1
Pseudacanthus	3	0	1	0	0	0	0	1	1	1
Ogyges	0	0	1	0	0	1	0	1	1	1
Vindex	2	0	1	0	1	0	0	1	1	1
Chondrocephalus	1	0	1	0	0	0	0	1	1	1
Odontotaenius d.	3	0	1	0	0	0	0	1	1	1
Odontotaenius s.	1	0	1	0	0	0	0	1	1	1
Heliscus tropicus	3	0	1	0	1	0	0	1	1	1
Hel. rotundicornis	1	0	1	0	1	0	0	1	1	1
Spurius sp.	1	0	1	0	1	0	0	1	1	1
Petrej. ten.	2	0	1	0	1	0	0	1	1	1
Petrej. sp.BdT	1	0	1	0	1	2	0	1	1	1
Popilius punctatis	1	0	1	0	1	0	0	1	1	1
Popilius erotylus	1	0	1	0	0	0	0	1	1	1
Popilius eclipticus	2	0	1	0	1	0	0	1	1	1
Popilius sp.5PAN	3	0	1	0	1	0	0	1	1	1

Character #	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**
Diphyllostoma	0	1	1	0	0	1	0	0	0	0
Sinodendron	0	1	0	0	0	0	0	2	0	0
Bolboceras	0	1	1	2	1	1	0	1	0	0
Aulacocyclus e.	0	0	1	1	1	0	0	0	1	1
Aulacocyclus p.	0	0	1	1	1	0	0	0	1	1
Comacupes	0	0	1	0	1	0	0	0	1	1
Taeniocerus	0	0	1	0	1	0	0	0	1	1
Ceracupes	0	0	1	1	1	0	0	0	1	1
Cylindrocaulus	0	0	1	0	2	0	0	2	1	1
Macrolinus	1	0	1	1	2	1	2	0	1	1
Pleurarius	1	0	1	2	1	1	1	0	1	1
Episphenus	1	0	1	2	2	0	1	0	1	1
Aceraius g.	1	0	1	1	2	1	1	0	1	1
Aceraius h.	1	0	1	2	1	0	0	0	1	1
Aceraius sp.	1	0	1	1	1	1	2	0	1	1
Caccoius	1	0	1	2	2	1	1	0	1	1
Mastochilus	1	0	1	2	2	1	2	0	1	1
Leptaulax d.	1	0	1	1	2	1	1	0	1	1
Leptaulax b.	1	1	1	1	1	1	1	0	1	1
Leptaulax p.	1	1	1	2	1	1	1	0	1	1
Pentalobus	1	0	1	2	1	1	1	1	1	1

Character #	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**
Erionomus	1	1	1	2	1	2	0	0	1	1
Semicyclus	1	0	1	1	2	1	2	1	1	1
Passalus interr.	1	0	1	2	2	1	2	0	1	1
Passalus cun.	1	0	1	2	2	1	1	0	1	1
Passalus cael.	1	0	1	2	1	0	1	0	1	1
Paxillus	1	1	1	2	2	1	1	0	1	1
Spasalus	1	0	1	2	1	1	1	0	1	1
Ptichopus	1	0	1	2	2	0	1	2	1	1
Verres cort.	1	0	1	2	1	0	0	0	1	1
Veturius sp.	1	1	1	2	{12}	0	0	0	1	1
Pseudacanthus	1	0	1	2	1	0	0	0	1	1
Ogyges	1	0	1	2	1	0	1	1	1	1
Vindex	1	1	1	2	2	1	2	{12}	1	1
Chondrocephalus	1	0	1	2	2	0	0	0	1	1
Odontotaenius d.	1	0	1	1	2	0	0	0	1	1
Odontotaenius s.	1	0	1	2	2	0	0	0	1	1
Heliscus tropicus	1	0	1	2	2	0	0	0	1	1
Hel. rotundicornis	1	0	1	2	2	0	0	0	1	1
Spurius sp.	1	0	1	2	2	0	0	0	1	1
Petrej. ten.	1	0	1	2	2	0	0	0	1	1
Petrej. sp.BdT	1	0	1	2	1	0	0	0	1	1
Popilius punctatis	1	0	1	2	2	0	0	0	1	1
Popilius erotylus	1	0	1	2	2	0	0	0	1	1
Popilius eclipticus	1	0	1	2	2	0	0	0	1	1
Popilius sp.5PAN	1	0	1	2	1	0	0	0	1	1

Character #	**161**	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**
Diphyllostoma	0	0	1	2	1	0	0	0	0	0
Sinodendron	1	0	0	0	1	0	0	0	0	0
Bolboceras	0	0	0	2	1	0	0	0	0	0
Aulacocyclus e.	2	1	1	0	1	4	2	2	2	1
Aulacocyclus p.	2	1	1	1	1	4	2	1	2	1
Comacupes	2	1	1	0	0	3	2	2	2	1
Taeniocerus	2	1	1	1	1	4	1	2	2	1
Ceracupes	2	1	1	1	1	2	2	2	3	1
Cylindrocaulus	2	1	1	0	0	2	1	2	4	0
Macrolinus	2	1	1	1	0	2	2	2	4	1
Pleurarius	2	1	1	1	0	2	2	2	4	2
Episphenus	2	1	1	1	0	2	2	2	4	2
Aceraius g.	2	1	0	2	0	1	2	1	1	0
Aceraius h.	2	1	0	1	0	1	2	2	1	1
Aceraius sp.	2	1	0	1	0	2	1	2	4	1
Caccoius	2	1	0	1	0	2	2	1	4	1
Mastochilus	2	1	0	1	0	2	2	2	4	0
Leptaulax d.	2	1	0	0	0	2	2	2	4	1
Leptaulax b.	2	1	1	2	0	1	2	2	1	0
Leptaulax p.	2	1	1	1	0	1	2	1	1	1
Pentalobus	2	1	1	1	0	2	2	2	4	1

Character #	**161**	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**
Erionomus	2	1	1	0	1	2	1	2	4	1
Semicyclus	2	1	0	0	0	2	2	2	4	1
Passalus interr.	2	1	1	1	1	2	1	2	4	1
Passalus cun.	2	1	0	0	0	2	1	2	4	1
Passalus cael.	2	1	0	0	0	2	2	2	4	1
Paxillus	2	1	1	0	0	2	2	2	4	1
Spasalus	2	1	0	0	0	2	1	1	4	1
Ptichopus	2	1	1	0	0	2	2	1	3	2
Verres cort.	2	1	0	1	0	2	2	2	4	0
Veturius sp.	2	1	0	1	1	2	2	2	4	1
Pseudacanthus	2	1	0	1	1	2	2	2	4	1
Ogyges	2	1	0	0	0	2	2	2	4	0
Vindex	2	1	0	0	0	2	2	1	4	0
Chondrocephalus	2	1	0	0	0	2	2	1	4	0
Odontotaenius d.	2	1	1	1	0	2	1	2	4	1
Odontotaenius s.	2	1	1	0	1	2	2	2	4	1
Heliscus tropicus	2	1	0	1	1	2	2	1	4	1
Hel. rotundicornis	2	1	1	{01}	0	2	2	1	4	1
Spurius sp.	2	1	0	0	0	2	2	1	4	1
Petrej. ten.	2	1	0	1	0	2	2	1	4	1
Petrej. sp.BdT	2	1	0	1	0	2	1	1	4	1
Popilius punctatis	2	1	0	0	0	2	2	1	4	2
Popilius erotylus	2	1	0	1	0	2	1	1	4	1
Popilius eclipticus	2	1	0	0	1	2	1	2	4	1
Popilius sp.5PAN	2	1	0	0	0	2	2	1	4	0

Character #	**171**	**172**	**173**	**174**	**175**	**176**	**177**	**178**	**179**	**180**
Diphyllostoma	0	0	0	1	0	1	0	0	0	0
Sinodendron	0	0	0	0	1	0	0	0	0	0
Bolboceras	0	0	0	0	0	0	0	0	0	2
Aulacocyclus e.	2	1	2	1	1	1	1	1	1	1
Aulacocyclus p.	2	1	2	1	2	1	1	1	1	1
Comacupes	1	1	2	1	2	1	1	1	1	1
Taeniocerus	1	1	0	0	0	1	1	0	1	0
Ceracupes	1	0	2	1	1	1	1	0	1	0
Cylindrocaulus	1	1	0	0	0	1	1	0	1	2
Macrolinus	1	0	0	0	0	1	1	1	1	1
Pleurarius	1	0	1	0	0	1	1	0	1	0
Episphenus	1	0	1	0	1	1	1	0	1	1
Aceraius g.	1	0	1	0	0	1	1	0	1	1
Aceraius h.	1	0	1	0	0	1	1	0	1	0
Aceraius sp.	0	0	1	0	1	1	1	1	1	1
Caccoius	1	0	0	0	2	1	1	1	1	1
Mastochilus	1	0	1	0	0	1	1	1	1	0
Leptaulax d.	1	0	1	0	1	1	1	1	1	1
Leptaulax b.	1	0	1	0	1	1	1	1	1	1
Leptaulax p.	1	0	1	0	1	1	1	1	1	0
Pentalobus	1	0	2	1	1	1	1	1	1	1

Character #	**171**	**172**	**173**	**174**	**175**	**176**	**177**	**178**	**179**	**180**
Erionomus	2	0	0	0	0	1	1	0	1	1
Semicyclus	1	0	1	0	0	1	1	1	1	1
Passalus interr.	1	0	1	0	0	1	1	0	1	1
Passalus cun.	1	0	1	0	0	1	1	1	1	1
Passalus cael.	0	0	2	0	0	1	1	1	1	2
Paxillus	1	0	1	0	1	1	1	0	1	1
Spasalus	1	0	2	0	0	1	1	1	1	1
Ptichopus	1	0	1	0	0	1	1	1	1	1
Verres cort.	1	1	2	1	1	1	1	0	1	1
Veturius sp.	2	1	2	1	1	1	1	1	1	1
Pseudacanthus	1	0	2	1	1	1	1	0	1	1
Ogyges	1	1	2	1	2	1	1	1	1	1
Vindex	1	0	2	1	2	1	1	0	1	1
Chondrocephalus	1	0	0	1	1	1	1	0	1	1
Odontotaenius d.	0	0	2	1	1	1	1	1	1	1
Odontotaenius s.	0	1	2	1	0	1	1	1	1	0
Heliscus tropicus	2	1	2	1	0	1	1	0	1	1
Hel. rotundicornis	1	1	2	1	0	1	1	1	1	0
Spurius sp.	1	0	2	1	0	1	1	0	1	1
Petrej. ten.	0	0	2	1	1	1	1	1	1	0
Petrej. sp.BdT	1	0	2	1	0	1	1	0	1	1
Popilius punctatis	1	1	2	1	1	1	1	1	1	0
Popilius erotylus	1	1	2	1	1	1	1	0	1	1
Popilius eclipticus	1	1	2	1	1	1	1	0	1	1
Popilius sp.5PAN	1	0	2	1	1	1	1	1	1	1

Character #	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**
Diphyllostoma	0	0	1	0	0	1	0	0	0	0
Sinodendron	0	0	0	1	1	1	0	0	0	0
Bolboceras	0	0	0	0	0	0	0	0	0	0
Aulacocyclus e.	0	?	?	?	?	?	?	?	?	?
Aulacocyclus p.	0	?	?	?	?	?	?	?	?	?
Comacupes	0	1	2	1	1	0	1	0	1	0
Taeniocerus	0	1	2	1	1	1	1	0	1	0
Ceracupes	0	1	2	1	1	1	1	0	0	1
Cylindrocaulus	1	1	1	2	1	1	1	0	0	0
Macrolinus	1	1	2	2	1	1	1	1	2	2
Pleurarius	0	1	{12}	2	1	1	1	2	2	0
Episphenus	1	1	2	1	1	1	1	2	1	0
Aceraius g.	0	1	1	1	1	1	1	0	1	0
Aceraius h.	1	1	1	1	1	1	1	0	1	0
Aceraius sp.	1	1	1	2	1	0	2	0	2	0
Caccoius	0	1	2	2	1	1	1	0	2	0
Mastochilus	0	1	1	2	1	3	1	2	2	1
Leptaulax d.	1	1	1	1	1	1	1	1	2	0
Leptaulax b.	1	1	1	2	1	1	1	1	0	1
Leptaulax p.	1	1	1	2	1	1	1	1	0	1
Pentalobus	1	1	1	2	1	1	1	1	2	0

Character #	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**
Erionomus	0	1	2	2	1	3	1	0	0	0
Semicyclus	0	1	2	2	1	1	1	1	2	0
Passalus interr.	0	1	1	2	1	1	1	2	2	0
Passalus cun.	0	1	2	2	1	2	1	2	0	0
Passalus cael.	1	1	1	2	1	1	1	2	2	0
Paxillus	1	1	1	2	1	1	1	2	2	0
Spasalus	0	?	?	?	?	?	?	?	?	?
Ptichopus	1	1	1	2	1	1	1	1	2	0
Verres cort.	0	1	2	2	1	2	1	1	0	0
Veturius sp.	0	1	1	2	1	?	1	2	0	0
Pseudacanthus	1	1	{12}	2	1	3	1	2	2	0
Ogyges	0	1	1	2	1	3	1	2	2	0
Vindex	0	1	1	1	1	1	1	1	2	0
Chondrocephalus	0	1	1	2	1	1	1	2	2	0
Odontotaenius d.	0	1	{01}	2	1	2	1	2	2	0
Odontotaenius s.	0	1	1	2	1	1	1	2	2	0
Heliscus tropicus	0	1	2	2	1	3	1	2	2	1
Hel. rotundicornis	0	1	0	2	1	1	1	2	2	0
Spurius sp.	0	1	2	3	1	2	1	2	2	0
Petrej. ten.	0	1	2	2	1	2	1	2	2	0
Petrej. sp.BdT	0	1	2	2	1	2	1	2	2	0
Popilius punctatis	0	1	2	2	1	2	1	2	2	0
Popilius erotylus	0	1	1	3	1	2	1	2	2	0
Popilius eclipticus	0	1	{12}	2	1	2	1	2	2	0
Popilius sp.5PAN	1	1	2	2	1	2	1	2	2	0

Character #	**191**	**192**	**193**	**194**	**195**	**196**	**197**	**198**	**199**	**200**
Diphyllostoma	0	0	0	1	0	1	0	0	0	0
Sinodendron	0	1	0	1	1	3	2	0	0	0
Bolboceras	0	1	2	1	0	0	0	2	0	0
Aulacocyclus e.	?	?	?	?	?	?	?	?	?	?
Aulacocyclus p.	?	?	?	?	?	?	?	?	?	?
Comacupes	0	0	2	1	0	0	0	1	0	2
Taeniocerus	0	0	2	0	0	0	0	2	0	2
Ceracupes	0	0	2	0	0	2	2	2	0	1
Cylindrocaulus	0	0	2	0	0	2	2	2	0	1
Macrolinus	0	1	2	0	0	3	2	2	0	1
Pleurarius	0	1	2	0	0	2	2	2	0	1
Episphenus	0	0	2	0	0	1	2	2	0	2
Aceraius g.	0	1	2	0	0	2	2	2	0	2
Aceraius h.	0	1	2	0	0	1	2	2	0	2
Aceraius sp.	0	1	2	1	0	3	2	2	0	0
Caccoius	0	1	2	0	0	2	2	1	1	0
Mastochilus	0	1	2	3	0	2	2	2	0	0
Leptaulax d.	0	1	1	0	0	1	2	2	0	0
Leptaulax b.	0	2	1	1	1	3	2	2	0	0
Leptaulax p.	0	2	1	0	0	3	2	1	0	0
Pentalobus	0	1	2	0	1	1	1	1	1	0

Character #	**191**	**192**	**193**	**194**	**195**	**196**	**197**	**198**	**199**	**200**
Erionomus	0	1	2	0	1	0	0	2	1	1
Semicyclus	0	1	2	0	1	1	2	0	0	1
Passalus interr.	0	1	2	2	1	2	0	1	0	1
Passalus cun.	0	1	2	2	1	2	1	2	0	1
Passalus cael.	0	1	2	1	1	2	1	2	0	1
Paxillus	0	1	3	2	1	0	0	2	0	1
Spasalus	?	?	?	?	?	?	?	?	?	?
Ptichopus	0	1	2	0	1	2	1	2	0	1
Verres cort.	0	1	2	0	1	1	1	2	0	1
Veturius sp.	0	1	2	0	1	2	1	2	0	1
Pseudacanthus	0	1	2	2	1	2	2	2	0	1
Ogyges	0	1	2	2	1	2	0	2	0	1
Vindex	0	1	2	2	1	3	2	2	0	1
Chondrocephalus	0	1	1	2	1	2	2	2	0	1
Odontotaenius d.	0	0	2	2	1	2	2	2	1	1
Odontotaenius s.	0	1	2	0	1	3	0	2	0	1
Heliscus tropicus	0	1	2	2	1	2	0	2	0	1
Hel. rotundicornis	0	1	2	2	1	3	1	2	0	1
Spurius sp.	0	1	2	0	1	3	2	2	0	0
Petrej. ten.	0	1	2	0	1	3	1	2	0	1
Petrej. sp.BdT	1	1	2	2	0	3	1	2	0	1
Popilius punctatis	0	1	2	0	1	2	1	1	0	1
Popilius erotylus	0	1	2	2	0	3	1	2	0	1
Popilius eclipticus	0	1	2	2	1	3	1	2	0	1
Popilius sp.5PAN	0	1	2	0	1	2	2	1	0	1

Character #	**201**	**202**	**203**	**204**	**205**	**206**	**207**
Diphyllostoma	0	0	0	0	0	?	?
Sinodendron	?	0	0	0	?	0	0
Bolboceras	0	0	0	0	0	?	?
Aulacocyclus e.	?	?	?	0	?	?	?
Aulacocyclus p.	?	?	?	0	?	?	?
Comacupes	2	0	1	0	1	1	4
Taeniocerus	2	0	1	0	1	1	{23}
Ceracupes	3	0	1	0	1	3	3
Cylindrocaulus	2	0	1	0	1	1	3
Macrolinus	4	0	1	0	1	3	3
Pleurarius	4	0	1	0	1	3	3
Episphenus	2	0	1	0	1	3	2
Aceraius g.	2	0	1	0	1	3	2
Aceraius h.	2	0	1	0	1	3	3
Aceraius sp.	2	0	1	0	1	1	3
Caccoius	2	0	1	0	1	3	3
Mastochilus	5	0	1	0	1	3	3
Leptaulax d.	4	1	1	0	2	3	2
Leptaulax b.	5	0	1	0	3	3	3
Leptaulax p.	5	0	1	0	1	1	2
Pentalobus	5	0	1	0	1	1	1

Character #	**201**	**202**	**203**	**204**	**205**	**206**	**207**
Erionomus	4	0	1	0	1	2	2
Semicyclus	2	0	1	0	1	2	1
Passalus interr.	5	0	1	0	1	?	?
Passalus cun.	5	0	1	0	1	4	3
Passalus cael.	5	0	1	1	1	2	2
Paxillus	5	0	3	0	2	2	3
Spasalus	?	?	?	0	?	?	?
Ptichopus	3	0	1	0	1	1	4
Verres cort.	2	0	1	0	1	1	3
Veturius sp.	2	?	?	0	?	3	4
Pseudacanthus	4	0	1	1	1	1	3
Ogyges	4	0	1	0	1	3	3
Vindex	5	0	1	1	1	2	2
Chondrocephalus	2	0	3	1	1	3	3
Odontotaenius d.	2	0	2	0	1	3	{45}
Odontotaenius s.	4	0	1	0	1	3	3
Heliscus tropicus	2	0	1	0	1	1	3
Hel. rotundicornis	4	0	1	0	1	3	3
Spurius sp.	4	0	3	0	1	3	5
Petrej. ten.	2	0	1	0	1	3	4
Petrej. sp.BdT	2	0	1	0	1	1	3
Popilius punctatis	4	0	1	1	1	3	5
Popilius erotylus	2	0	1	1	1	3	4
Popilius eclipticus	4	0	3	0	1	3	3
Popilius sp.5PAN	2	0	1	1	1	3	5

APPENDIX D

DATA FOR THE ANALYSIS OF *POPILIUS*

Appendix D-1. CHARACTER ANALYSIS FOR THE ANALYSIS OF *POPILIUS*

Head

1. Central tubercle absent (0), low and without a free tip (1), high, erect, and without a free tip (2), with a free, straight, anteriorly-directed tip (3), or with a free tip, turned upward apically (4).

2. Central tubercle highest point not applicable (no central tubercle) (0), the highest point of the mediofrontal structure (1), even with top of lateral tubercles (2), or the lowest point of the mediofrontal structure (3).

3. Dorsal tip of central tubercle anterior to, but not connected to, the parietal ridges (0), anterior to and connected to the parietal ridges (1), even with the parietal ridges (2), posterior to the parietal ridges, with the structure not indented anteromedially (3), or posterior to parietal ridges, with the structure indented medially (4).

4. Basal depression absent (0), slightly evident (1), or distinct (2).

5. Parietal ridges absent (0), in a straight line (1), in an anteriorly concave arc (2), or in an anteriorly biconcave arc (3).

6. Parietal tubercles absent, obsolete or indistinct (0), low and linear (1), low and tuberculate (2), high and tuberculate, but not apically acute (3), or high and barely apically acute(4).

7. Parietal ridges absent (0), present and evenly angulate or rounded dorsally (1), present and with a transverse dorsal groove (2).

8. Parietal tubercles absent (0), linked by ridges to the central tubercle or to each other (1), or not linked to the central tubercle or to each other (2).

9. Width across eyes <4.10mm (0), 4.10-4.88mm (1), 4.92-5.66mm (2), 5.74-6.40mm (3), or >6.40mm (4).

10. Small tubercle posterior to parietal tubercle absent (0) or present (1).

11. Frontal ridges and parietal ridges divergent laterally (0), about parallel (1), or at least one of the ridges absent (2).

12. Frontal ridges absent (0), evident for 2/3 of distance between the central tubercle and inner tubercles (1), evident only between the central tubercle and inner tubercles (2), evident from the central tubercle to the outer tubercles (3), or evident from central tubercle to secondary tubercles (4).

13. Frontal ridges absent (0), arise from a single ridge just anterior to base of central tubercle (1), arise from a single or double ridge well anterior to base of central tubercle (2), arise from two close ridges from anterior base of central tubercle (3), arise from two widely separate ridges from anterior base of central tubercle, smooth between ridges (4), arise from two widely separate ridges from anterior base of central tubercle, rugose between ridges (5), arise from two close ridges from anterior base of central tubercle, matt/rugose between and lateral to ridges (6), arise directly from anteromedial tip of central tubercle (7), or arise from single ridge from anterior base of central tubercle, rugose around the ridge (8).

14. Frontal ridges meet medially at an angle of about 90° (0), about 120° (1), about 135° (2), about 180° or connected in an even arc (3), about 45° (4), or are absent (5).

15. Frontal ridges absent (0), diverge in straight lines from origin to inner tubercles (1), diverge in concave, curved lines from origin to inner tubercles (2), or diverge in convex, recurved lines from central tubercle to inner tubercles (3).

16. Frontal ridges absent (0), present and smooth (1), or present and rugose (2).

17. Frontal ridge separated from the supraocular ridge by a depression (0) or connected to the supraocular ridge by a transverse ridge (1).

18. Inner tubercles absent (0), present, with highest point closer to base of central tubercle than to anterior margin of clypeus (1), present, with highest point about equidistant from base of central tubercle and anterior margin of clypeus (2), present, with highest point closer to anterior margin of clypeus than to base of central tubercle (3), or present, with highest point immediately posterior to anterior margin of clypeus (4).

19. Inner tubercles absent (0), closer together than outer tubercles (1), about equally far apart as outer tubercles (2), or farther apart than outer tubercles (3).

20. Inner tubercles absent (0), posterior to outer tubercles (1), or about even with outer tubercles (2).

21. Inner tubercles rounded (0), linear (1), or absent (2).

22. Inner tubercles absent or indistinct (0), distinct, but lower than outer tubercles (1), distinct and about equal in height to outer tubercles (2), or distinct and higher than outer tubercles (3).

23. Frons glabrous (0), setose only posterior to parietal ridge (1), setose anterior and posterior to parietal ridge, but posterior to inner tubercles (2), or setose anterior to inner tubercles (3).

24. Area anterior to frontal ridges even (0) or with a medial elevation or longitudinal ridge (1).

25. Plane anterior to frontal ridges and inner tubercles about the same level as plane posterior to frontal ridges (0) or depressed (1).

26. Clypeus longer than transfrontal sulcus (0), about as long as transfrontal sulcus (1), or transfrontal sulcus absent (2).

27. Ratio of distance between inner tubercles/width of head (at external margin of eye) <0.26 (0), 0.26-0.30 (1), 0.31-0.33 (2), or >0.33 (3).

28. Clypeus anteromedially without ring-shaped punctures (0) or with ring-shaped punctures (1).

29. Outer tubercles absent (0), present and closer to central tubercle than to anterior margin of clypeus (1), present and closer to anterior margin of clypeus than to central tubercle, but not on the transfrontal sulcus (2), present and closer to anterior margin of clypeus than to central tubercle; on transfrontal sulcus; vertical (3), present and closer to anterior margin of clypeus than to central tubercle; on the transfrontal sulcus; slightly surpassing clypeal margin (4), present,

vertical, on anterior margin of clypeus (5), present and slightly surpassing margin of clypeus (6), or present, horizontal, surpassing margin of clypeus (7).

30. Outer tubercle closer to inner tubercle than to anterior tubercle of supraocular ridge (0), about equidistant from inner tubercle and anterior tubercle of supraocular ridge (1), closer to anterior tubercle of supraocular ridge than to inner tubercle (2), or absent (3).

31. Outer tubercles erect, ~symmetrical (0), directed somewhat laterally (1), with rugose, vertical face or basal notch laterally (2), or absent (3).

32. Outer tubercles absent (0), medial to lateral clypeal margin (1), directly posterior or dorsal to lateral clypeal margin (2), or lateral to lateral clypeal margin (3).

33. Outer tubercle absent (0), not on same structure as secondary tubercle and lateral clypeal margin (1), or on same structure as secondary tubercle and/or lateral clypeal margin (2).

34. Posterolateral ridge absent (0), present, posterolateral, connected to outer tubercle, without a tubercle at the end of the ridge (1), or present, posterolateral, connected to outer tubercle, with a tubercle at the end of the ridge (2).

35. Transfrontal sulcus absent (0), arcuate, convex anteriorly (1), present, about straight (2), present concave (3), present, lightly recurved laterally, bi-arcuate (4), or present, distinctly tri-arcuate (5).

36. Transfrontal sulcus absent (0), complete (1), interrupted by outer tubercles and/or frontal ridge (2), obsolete/missing in medial third (4), or prolonged posteriorly to inner tubercles or tip of central tubercle (5).

37. Transfrontal sulcus absent (0), ridged (1), grooved and impunctate (2), or grooved, punctate and irregular (3).

38. Transfrontal sulcus absent (0), ends at base of outer tubercle (1), on outer tubercle (2), passes posterior to outer tubercle (3), or interrupted by outer tubercles (4).

39. Clypeus with transfrontal sulcus absent (0), flat anterior to transfrontal sulcus, in same plane as just posterior to the sulcus (1), flat anterior to sulcus, sloping anteroventrally (2), about vertical anterior sulcus (3), or rounded (convex) anterior to sulcus (4).

40. Clypeus anterior to transfrontal sulcus not distinctly separated from frons (without a transfrontal sulcus) (0), ends at outer tubercles (1), or extends posterolaterally from outer tubercles (2).

41. Clypeus dorsally, anterior to transfrontal sulcus or near apex, glabrous (0) or with several long setae (1).

42. Anterior face of clypeus high (0), low (1), or sharp (2).

43. Apicodorsal margin of clypeus obtuse (0), about right-angled (1), acute (30°-80°) (2), or sharp (<30°) (3).

44. Anterior face of clypeus slanted back (0), about vertical (1), or slanted forward (2).

45. Clypeus anterior to transfrontal sulcus with lateral margins concave (0), straight (1), convex (2), or with sulcus absent (3).

46. Anterolateral margins of clypeus distinctly turned ventrally (0), about in same plane as face (1), or turned dorsally or anteriorly (2).

47. Anterolateral corners of clypeus acute (0), narrowly rounded (1), broadly rounded (semicircular margin) (2), obtusely or right-angled (3), or obsolete/indistinct (4).

48. Anterolateral corners of clypeus (viewed from side) obtuse (0), about right-angled (1), acute (2), fused to secondary tubercle and indistinguishable (3), or obsolete (4).

49. Anterior margin of clypeus medially straight (0), with concave emargination (1), lightly convex (2), projecting (or unidentate) (3), projecting (or unidentate) with concave tip (4), or triply emarginate (or bidentate) (5).

50. Anteromedial notch (or margin) of clypeus visible from above (0) or not visible from above (1).

51. Clypeus anteriorly smooth from frontogenal suture to tip of canthus (0), with rugose patch halfway from clypeus to frontogenal suture (1), with rugose patch to frontogenal suture (2), or with rugose patch from frontogenal suture to tip of canthus (3).

52. Clypeus anteriorly glabrous, shiny from frontogenal suture to outer angle of head (0) or with matt patch from frontogenal suture to outer angle of head (1).

53. Clypeus evenly dorsoventrally rounded anteriorly between outer tubercle and outer angle (0), with an anterior ledge in medial half between outer tubercle and outer angle (1), with a transverse, anterior ledge between outer tubercle and outer angle (2), or with a transverse, anterior ledge between outer tubercle and outer angle, connected to a short longitudinal ridge along frontogenal suture (3).

54. Outer angles of head not projecting (0), projecting and broadly rounded (1), obtuse (2), about right-angled (3), or acute (4).

55. Canthus evenly wide, rounded laterally (0), evenly wide, obtusely angled laterally (1), or narrowest medially, expanded apically, and angulate laterally (2).

56. Canthus dorsally without medial, longitudinal ridge (0), with one medial, longitudinal ridge (1), or with two medial, longitudinal ridges (2).

57. Canthus laterally not projecting (0), projecting as far as margin of eye (1), or distinctly projecting beyond margin of eye (2).

58. Supraocular ridge evenly ridged, evenly rounded anteriorly and posteriorly (0), lightly concave posteriorly (1), forked posteriorly (2), or forked anteriorly, lateral to transfrontal sulcus (3).

59. Supraocular ridge posteriorly setose to base of eye (0) or to middle of inner margin of eye (1).

60. Supraocular ridge higher than central tubercle/mediofrontal structure (0), about same height as central tubercle/mediofrontal structure (1), or lower than central tubercle/mediofrontal structure (2).

61. Supraocular ridgeline with 3 dorsal points (raised tubercle at anterior tip (0), with 2 dorsal points, anterior most distinct (1), with 2 dorsal points, ~ equally distinct (2), with 2 dorsal points, posterior most distinct (3), with 1 dorsal point (4), straight (5), or evenly convex (6).

62. Supraocular ridge posterodorsally evenly rounded laterally (0) or most prominent next to inner margin of eye (1).

63. Supraocular ridge posterior face sloped at about 45° (0) or about vertical (1).

64. Hypostomal process (ventral view) spindle-shaped (0), wide and parallel-sided (1), or very wide medially (2).

65. Hypostomal process anterior tip (ventral view) acute or narrowly rounded (0), or truncate/blunt (1).

66. Hypostomal process laterally (ventral view) convex (0), flattened (1), or concave (2).

67. Hypostomal process laterally (ventral view) glabrous (0) or setose (1).

68. Subocular ridge absent or indistinct (0), short (< or = to 1/2 way to posterior margin of antennal fossa) (1), long (>1/2 way to posterior margin of antennal fossa) and irregular (2), long and even (3), reaching posterior margin of antennal fossa in acute angle (4), or reaching posterior margin of antennal fossa in rounded connection (5).

Antenna

69. Anterior margin of antennal segment 5 two-thirds as long as posterior margin (0), half as long (1), or sharp (segment is triangular) (2).

70. Ratio of width/length of 6th antennal segment (across segment at widest point/length of posterior margin) 0.9-1.4 (0), 1.6-1.9 (1), or >1.9 (2).

71. Ratio of width/length of 7th antennal segment (across segment at widest point/length of posterior margin) 0.9-1.7 (0) or >2.5 (1).

72. Ratio of width/length of 8th antennal segment (across segment at widest point/length of posterior margin) <2.1 (0), 2.1-2.3 (1), 2.4-2.8 (2), 2.9-3.1 (3), 3.6-3.8 (4), or >3.8 (5).

73. Ratio of width/length of 9th antennal segment (across segment at widest point/length of posterior margin) <2.5 (0), 2.5-2.8 (1), 2.9-3.2 (2), 3.5-4.3 (3), or >4.7 (4).

74. Ratio of width/length of 10th antennal segment (widest point/tip to outer base) <0.40 (0), 0.40-0.47 (1), or >0.47 (2).

75. Tip of terminal antennal lamella rounded (0) or acute (1).

76. Setae on antennal segments 8-10 short (0) or long (~ as long as width of lamellae 8 or 9) (1).

77. Number of antennal lamellae 3 (0), 4 (1), or 5 (2).

Mouthparts

78. Labrum anteriorly symmetrical (0) or projecting further on left side than right (1).

79. Anterior margin of labrum straight (0), concave (1), deeply concave (2), or deeply concave and impressed (3).

80. Labrum dorsally uniformly setose (0) or with basomedial glabrous patch (1).

81. Labrum evenly thick (0) or thinned basolaterally (1).

82. Hypopharynx anteromedial area with strongly arcuate transverse carina reaching anterior margin (0) or arcuate transverse carina not reaching anterior margin (1).

83. Hypopharynx anterior arcuate carina with each side evenly curved (0) or each side flared laterally in apical half (1).

84. Hypopharynx anteromedially without a tranverse/arcuate carina or medial tubercle (0), with a small medial tubercle (1), with only a transverse/arcuate carina (2), with additional buttress on each inner side of an arcuate carina (3), or with medial transverse carina joining the sides of an arcuate carina (4).

85. Hypopharynx anteromedial depression smooth, shiny (0) or punctate or rugose (1).

86. Gular anterior margin broadly rounded/arcuate (0), laterally recurved (1), or obtusely angled (2).

87. Mentum punctate and setose medially (0), 1-3 setae medially (1), punctate or setose only posteriorly (2), or glabrous medially (3).

88. Mentum medially emarginate (0) or not emarginate (1).

89. Mentum posteromedially shiny (0) or matt (1).

90. Basolateral depressions of mentum shiny (0) or matt (1).

91. Lateral lobes of mentum anteriorly narrow, tapering (0), semicircular (1), broadly rounded (2), or obliquely truncate (3).

92. Prementum apically with medial tooth longest (0), teeth subequal (1), or medial tooth shortest (2).

93. Tip of prementum tridentate (0), quinquedentate (1), or bidentate (2).

94. Prementum medially glabrous (0) or setose (1).

95. Prementum with medial, longitudinal carina present (0) or absent (1).

96. Labial palp first (basal) segment easily visible (0) or barely visible (1).

97. Ratio of length/width (middle of apical margin to posterior point/width at widest point) of second segment of labial palp <1.9 (0), 1.9-2.2 (1), or >2.2 (2).

98. Labial palp second segment externally setose in apical third (0), in apical half (1), in apical two-thirds (2) or to the base (3).

99. Ratio of length of second segment of labial palp second segment/length of third segment <0.75 (0), 0.75-<1 (1), 1 (2), or >1 (3).

100. Third segment of labial palp apically narrowly rounded (0) or broadly rounded (1).

101. Ratio of length/width (mid ant. to post. point/width at widest point) of third (terminal) segment of labial palp <2.1 (0), 2.1-2.4 (1), 2.5-2.9 (2), or >2.9 (3).

102. Maxillary palp second segment slightly longer than third segment (0) or much longer (at least 1.5 times) than third segment (1).

103. Number of lacinial teeth one (0) or two (1).

104. Apical tooth of lacinia simple (0) or bifid (1).

105. Mandibles apically trifid (0), bifid (1), or left mandible bifid, right mandible trifid (2).

106. Dorsal surface of upper apical tooth of mandible with inner and outer margins subequal in height (0), inner margin higher than outer margin (1), or outer margin higher than inner margin (2).

107. Internal dentition of mandible (anterior to molar area) symmetrical (0) or asymmetrical (1).

108. Internal tooth base without small accessory tubercle (0), with small, simple, accessory tubercle (1), or with bifid accessory tubercle (2).

109. Left inner tooth simple (0), bifid (1), trifid in triangle (2), trifid in line (3), or quadrifid (triangle plus one) (4).

110. Base of left inner tooth shiny (0) or punctate/rugose (1).

111. Left inner tooth apical half wider than right (0) or about equal to right (1).

112. Dorsal tooth of mandible (lateral view) truncate (0) or triangular (1).

113. Right dorsal mandibular tooth anteriorly (lateral view) obtuse (0), about right-angled (1), acute (2), projecting (3), or not applicable - short, dorsally acute (4).

114. Right dorsal mandibular tooth dorsally (lateral view) straight or even (0), medially concave (1), or evenly convex (2).

115. Right dorsal mandibular tooth posteriorly (lateral view) obtuse or gradually sloping (0) or about right-angled (1).

116. Dorsal tooth of mandible dorsally (dorsal view) smooth (0) or rugose or coarsely punctate (1).

117. Dorsal tooth of mandible dorsally (dorsal view) narrow (0), widened medially (1), or posteriorly (2).

118. Dorsal tooth of mandible dorsally (dorsal view) evenly ridged (0) or rounded laterally and angulate medially, with appearance of being rolled over (1).

119. Dorsal surface of base of mandible smooth, glabrous (0), punctate (1), rugose (2), or tuberculate (3).

120. Base of mandible dorsally ~evenly curved (0) or with deep depression (1).

121. Lateral margin of mandible setose short of, or just to, the tip of the dorsal tooth (0) or past the tip of the dorsal tooth (1).

122. Lateral margin of mandible with even margin (0) or with distinct angle 1).

123. Base of mandible laterally with concave surface (0) or with strong depression (1).

Pronotum

124. Anterior margin of pronotum recurved laterally (0), slightly recurved at lateral third (1), or straight (2).

125. Anterior angles of pronotum somewhat projecting (about right-angled) (0), very slightly projecting (1), or rounded, not projecting (2).

126. Anterior marginal groove of pronotum impunctate (0), punctate in lateral 1/4 (1), punctate in lateral 1/3 (2), punctate in lateral 1/2 (3), punctate in lateral 2/3 (4), punctate in lateral 3/4 (5), punctate for more than lateral 3/4 (6), or punctate to midline (7).

127. Anterior marginal groove of pronotum evenly deep (0), distinctly deeper laterally (1) deeper anteriorly and laterally (2), or deeper anteromedially (3).

128. Medial groove of pronotum shallowly, slightly impressed (0), impressed in a point (1), impressed linearly (2), or impressed linearly, with a deeper point medially (3).

129. Pronotal humerus evenly convex (0) or with dorsal bulge (1).

130. Pronotum (excluding the marginal grooves) anterolaterally impunctate (0). punctate (1), or punctate, plus a diagonal groove (2).

131. Pronotum (excluding the marginal grooves) laterally impunctate (0), punctate only in lateral depressions (1), punctate in and around lateral depressions (2), punctate in and around lateral depressions, and with a diagonal groove (3), or punctate above lateral depressions and onto disc (at least 3 punctures on disc on each side) (4).

132. Lateral depressions of pronotum marked (0) or slightly evident (1).

133. Lateral depressions of pronotum glabrous (0) or setose (1).

134. Posterior face of pronotum medially setose (0) or glabrous (1).

Prosternum

135. Prosternum, anteromedial to coxae, with transverse anterior fold (0) or without transverse anterior fold (1).

136. Prosternum, anteromedial to coxae, matt (0) or shiny (1).

137. Prosternum, anteromedial to coxae and anterior to transverse sulcus, setose (0) or glabrous (1).

138. Prosternum, just anterior to procoxa, with a long line of long setae (0), with a short line of long setae (1), or without a line of setae (2).

139. Hypomeron anteromedially with single structure halfway to margin (0) or double structure halfway to margin (1).

140. Hypomeron medially without matt area (0), narrow matt area (1), moderate matt area (2), or wide matt area (3).

141. Hypomeron laterally with matt area including setae (0) or without setae (1).

142. Prosternal process pentagonal, truncate posteriorly (0), rhomboidal, narrowly truncate posteriorly (1), or rhomboidal, acute posteriorly (2).

143. Ratio of length of left side of prosternal process/width of process at tip of prosternum <2 (0), 2.0-3.9 (1). 4.0-7.5 (2), or >8.6 (3).

144. Prosternal process posteromedially even (0) or with transverse fold (1).

145. Prosternal process posteromedially flat (0) or with a longitudinal, convex ridge (1).

146. Prosternal process completely matt (0), with long, longitudinal, medial, shiny patch (1), or posteromedially shiny (2).

147. Prosternal process glabrous (0) or setose (1).

148. Pronotal arm, posterior to coxae, widely setose (0), setose only close to the prosternal process (1), or glabrous (2). (the posterior pronotal bridge of authors)

149. Pronotal arm, posterior to coxae, shiny (0) or matt (1). (the posterior pronotal bridge of authors)

Scutellum

150. Scutellum punctate overall (0), with glabrous median line (1), glabrous medially and laterally (2), sparsely punctate (3), glabrous (4), or punctate in medial line/patch (5).

Elytra

151. Base of elytra, lateral to scutellum, glabrous (0) or sparsely setose (1).

152. Anterior face of elytra glabrous (0) or setose (1).

153. Elytral humerus glabrous (0), tuft of setae ventrolaterally (opposite mesepimeron) (1), tuft of setae dorsolaterally (2), or sparsely setose (3).

154. Elytral epipleuron glabrous (0) or setose opposite anterior metasternum (1).

155. Elytra laterally glabrous (0) or setose (1).

156. Elytral striae posteriorly discrete (0) or coalescent (1).

157. Lateral striae of elytra finely punctate (0), strongly punctate (1), or transversely punctate (2).

Mesosternum

158. Mesosternum anteriorly completely setose (0), completely glabrous and matt (1), completely glabrous and shiny (2), single, medial, longitudinal patch of setae (3), even, medial, transverse band of setae (4), anteriorly emarginate, medial, band of setae (5), medial patch of setae in “Y” shape (6), anterior band of setae, emarginate posteriorly (7), two medial patches of setae; separate, joined in “V’ shape, or joined and anteriorly emarginate (8), or transverse band of setae at anterior margin (9).

159. Mesosternal scar anteriorly (“head”) absent (0), narrow (not enlarged medially) (1), moderate (slightly enlarged medially) (2), wide (~1/3 width of mesosternum) and narrow (3), wide (~1/3 width of mesosternum) and expanded (4), or coalescent medially (5).

160. Mesosternal scar posteriorly (“tail”) absent (0), short (1), or long (about to end of mesepisternum) (2).

161. Mesosternal scar glabrous (0), anteriorly (“head”) setose (1), posteriorly (“tail”) setose (2), or generally setose (3).

162. Mesosternum posteromedially glabrous, shiny (0), punctate or rugose, shiny (1), matt (2), or generally setose over much of the mesosternum (3).

163 Mesosternum, anterolaterally to mesocoxae, setose (0) or glabrous (1).

Mesepisternum

164. Mesepisternum anteroventrally impunctate (0), punctate, not matt (1), punctate, matt puncture rims, no distinct matt patch (2), punctate, with distinct, anteroventral matt patch (3), punctate, matt to posterior angle (shiny tip) (4), or punctate, matt to posterior angle (matt tip) (5).

165. Posterior angle of mesepisternum glabrous (0) or setose (1).

166. Posterior corner of mesepisternum shiny (0) or matt (1).

Mesepimeron

167. Mesepimeron medially thickly setose (0), sparsely setose (1), or glabrous (2).

Metasternum

168. Postmesocoxal grooves widely separate medially (>distance between mesocoxae) (0), moderately separate medially (~distance between mesocoxae) (1), narrowly separate medially (<distance between mesocoxae) (2), with a depression between the medial ends of grooves (3), or connected medially (4).

169. Metasternum completely glabrous (0), with at least some setae anterolaterally (1), entire anterolateral area setose to tip of lateral depression (2), or setose onto medial disc (3).

170. Width of lateral depression of metasternum, just posterior to coxa, narrower than mesosternal process; about as wide as first mesotarsal segment (0) or about as wide as mesosternal process (1).

171. Posterior portion of lateral depression of metasternum uniformly narrow (0), widened apically (1), or widened subapically, narrowed at very tip (2).

172. Lateral depression of metasternum setose about to posterior tip (0), setose in anterior 2/3 to 7/8 (1), setose in anterior 1/2 (2), setose only in anterior 1/10 (3), or glabrous (4).

173. Punctures in each metasternal posterolateral area always 0 on both sides (0), 1 (on at least one side) to 5 (1), 6-17 (2), or >17 (3).

174. Metasternal lateral depression distinctly margined (0) or smooth internally (1).

Abdomen

175. Anterior process process of first complete, visible abdominal sternite (between, and just posterior to, metacoxae) glabrous (0), with 2-3 setae (1), or thickly setose (2).

176. Anterior process process of first complete, visible abdominal sternite (between, and just posterior to, metacoxae) shiny (0) or matt (1).

177. Anterior process of first complete, visible abdominal sternite (between metacoxae) apically turned ventrally (0) or ~ flat (1).

178. Anterior process of first complete, visible abdominal sternite (between metacoxae) with margin anteriomedially beaded/raised (0) or not distinctly beaded/raised (1).

179. Posterior, vertical margin of second completely visible abdominal sternite glabrous and shiny (0) or thickly punctate or rugose (1).

180. Last visible sternite posteriorly not tuberculate (0) or medially tuberculate just anterior to posterior marginal sulcus (1).

Prothoracic Leg

181. Procoxa between posteromedial trochanter and medial femur glabrous (0) or setose (1).

182. Protrochanter anterolaterally glabrous (0) or setose (1).

183. Profemoral groove (anteriorly on ventral face) present, glabrous (0), present, setose (1) or absent (2).

184. Profemur (medially on ventral face) glabrous proximally, next to the trochanter (0) or setose (1).

185. Posterior margin of profemur thickly setose (0) or almost glabrous (3-4 setae) (1).

186. Tip of terminal spur of protibia sharp (0), blunt (1) or bifid (2).

187. Tip of terminal spur of protibia directed ventrally (0), anteriorly (1), or dorsally (2).

188. Tip of tibia, at base of terminal spur, without stout apical setal comb (0), stout comb not reaching anterodorsal ridge (1), or stout comb reaching anterodorsal ridge (2).

189. Dorsal surface of protibia with setae in two longitudinal lines (0) or uniformly distributed (1).

Mesothoracic Leg

190. Anterior face of mesocoxa medially and posteriorly (next to trochanter) setose (0) or glabrous (1).

191. Mesotrochanter glabrous posteriorly (0) or setose (1).

192. Ratio of length/width of mesofemur (measured from anterior point of trochanter to distal tip/medially widest part, at right angle to length) <2.6 (0), 2.6-3.0 (1), or >3.0 (2).

193. Anterior face of mesofemur without setae ventrally near posterior edge of distal end (0) or with 2 setae (1).

194. Posterior margin of mesofemur setose (0) or glabrous (1).

195. Length of dorsal ridge of mesotibia (viewed laterally) ~1/3 length of mesotibia (0), ~1/2 length of mesotibia (1), >1/2 to ~2/3 length of mesotibia (2), or >2/3 length of mesotibia (3).

196. Height of dorsal ridge of mesotibia (viewed laterally) low (0), moderate (1), or high (2).

197. Shape of dorsal ridge of mesotibia (viewed laterally) even in medial half (0), lightly arched (1), arched (2), or distinctly arched (3).

198. Elevation of dorsal ridge of mesotibia (viewed laterally) even (0), highest medially (1), or highest anteriorly (2).

199. Dorsal ridge of mesotibia (viewed laterally) sparsely setose (0), evenly setose (1), thickly setose, especially in posterior half (2), thickly setose, especially medially (3), or with a long brush of setae (4).

200. Length of setae on of dorsal ridge of mesotibia (viewed laterally) ~1/3 width of tibia (0), ~1/2 width of tibia (1), <width of tibia (about 3/4 to 9/10) (2), setose, ~width of tibia (3), or setose, >width of tibia (4).

201. Dorsal ridge of mesotibia (viewed dorsally) straight (0), lightly curved (1), curved (2), distinctly curved (3), very distinctly curved (overhanging lobe) (4), or recurved (5).

202. Mesotibia externally (lateral margin) with no spines (0), small spines (1), both small and strong spines (2), or strong spines (3).

203. Mesotibia, in distal half of ventral side (viewed from anterior) with 2 lines of setae ventrally (0) or without distinct lines (more setae) (1).

204. Dorsal, movable terminal spur of mesotibia shorter than first tarsal segment (0), equal to first tarsal segment (1), or longer than first tarsal segment (2).

205. Inner (medial) side of apex of mesotibia and metatibia without setae (0), with simple setae (1), or with comb of scale-like setae (2).

206. Penultimate segment of mesotarsus with at least one dorsal seta (0) or without dorsal setae (1).

Metathoracic Leg

207. Ventral face of metacoxa with two distinct, transverse ridges (0) or with one distinct and one obsolete ridge (wider apart) (1).

208. Base of metacoxa anteromedially glabrous (0) or setose (1).

209. Posterior margin of metatrochanter no more than 1 seta (0) or with tuft of ~3-5 setae (1).

210. Posterior margin of metafemur glabrous (0), with 1-10 setae (1), or with >10 setae (2).

211. Metatibia with distinct dorsoposterior ridge (0) or without distinct dorsoposterior ridge (1).

212. Metatibial dorsomedial terminal spur shorter than first tarsal segment (0), equal to first tarsal segment (1), or longer than first tarsal segment (2).

213. Metatibia externally (lateral margin) with no spines (0), with one or more small spines (1), or with strong spines (2).

214. Penultimate segment of metatarsus with at least one dorsal seta (0) or without dorsal setae (1).

Male Genitalia

215. Genitalic capsule (ventral view) widest across basal piece (0), parameres (1), or median lobe (2).

216. Ratio of median lobe width (ventral view) to mesosternal width (between mesocoxae) <3.8 (0), 3.8-4.4 (1), 4.5-5.0 (2), 5.1-5.4 (3), or >5.4 (4).

217. Median lobe (ventral view) completely sclerotized (0), with medial membranous area in basal 1/2 - 7/8 (1), or with medial membranous area complete (2).

218. Median lobe (ventral view) widely fused to parameres (0), rigid in medial 1/2, but not fused (1), or not fused to parameres (2).

219. Lateral margins of medial lobe (lateral view) evenly rounded (0), produced as dorsolateral lobes/tubercles (1), or produced laterally as spines (2).

220. Median lobe ventrally (lateral view) evenly rounded (0) or angulate (1).

221. Parameres (ventral view) fused medially (0) or separate medially (1).

222. Parameres (ventral view) long (~length of basal piece) (0) or short (<1/3 length of basal piece) (1).

223. Parameres (ventral view) not fused to basal piece (0), fused to basal piece laterally (1), or fused to basal piece medially (2).

224. Parameres (lateral view) laterally laterally rounded (0), acute (1), or hooked towards base (2).

225. Parameres (dorsal view) not meeting ventrally (0), with large, triangular sclerite between the tips ventrally (1), or meeting ventrally (2).

226. Basal piece (ventral view) distal margin straight (0), emarginate in “V” shape (1), or divided by narrow slit (2).

227. Basal piece (ventral view) medially long (0) or short (1).

228. Basal piece (ventral view) medially joined (0) or separate (1).

229. Internal sac membranous (0), covered with short, pigmented scales (1), with short spicules (2), or with patch(es) of long setae (3).

230. Internal sac, just inside opening, membranous (0), with two basal patches of asperities (1), or with two basal, erect sclerotized tubercles (2).

231. Temones straight, longitudinal (0), short, straight, diagonal (1), curved medially (2), or hooked basally (3).

232. Temones short, not reaching apex of basal piece (0), reaching apex of basal piece (1), ending between apex and base of basal piece (2), reaching base of basal piece (3), or passing base of basal piece (4).

Appendix D-2. TAXON/CHARACTER MATRIX FOR *POPILIUS*.

Character #	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
ecliptEx1	1	1	2	0	1	2	2	1	4	1
ecliptEx2	1	1	1	1	1	2	2	1	4	0
ecliptEx3	4	1	1	{12}	2	1	2	1	4	0
ecliptEx4	1	1	2	0	2	1	2	1	4	1
ecliptEx5	1	1	2	0	2	1	2	1	3	0
erotylus	1	1	4	{12}	2	1	1	1	2	0
magd	1	1	4	1	2	1	1	1	{23}	1
margEx1	1	1	1	2	3	1	1	1	1	1
margEx2	1	1	2	1	2	1	1	1	1	1
refugicornis	2	1	4	2	2	1	1	1	4	1
tet4lam	1	1	3	0	1	1	1	1	1	1
tet5lamAM	1	1	3	1	1	1	1	1	1	0
tet5lamBOL	1	1	4	1	2	1	1	1	1	0
sp.1COL	1	1	4	2	2	1	1	1	3	{01}
sp.2VEN	1	1	1	0	1	1	1	1	2	1
gibbEx1	1	1	{12}	2	1	1	1	1	2	{01}
gibbEx4	1	1	4	1	2	1	1	1	{12}	0
gibbEx3	1	1	3	1	2	1	1	1	2	0
gibbEx6	1	1	3	1	2	1	1	1	1	1
gibbEx2	1	1	4	1	2	1	1	1	{12}	1
gibbEx5	1	1	{34}	1	1	1	1	1	2	0
gibbEx7	1	1	2	1	1	1	1	1	2	0
gibbEx8	1	1	4	2	1	1	1	1	3	0
sp.3BOL	1	1	4	1	2	3	1	1	1	0
sp.4VENEx1	{12}	1	1	2	1	1	1	1	{23}	0
sp.4VENEx2	2	1	1	2	1	1	1	1	2	1
haagi	1	1	1	{01}	1	2	1	1	1	0
haagiint	1	1	1	1	1	2	1	1	1	1
hirsutus	1	1	2	0	1	2	1	1	3	1
kling	1	1	1	0	1	2	1	1	1	1

lenzi	1	1	1	0	1	2	1	1	2	0
mysticus	1	1	2	0	1	2	1	1	3	0
punct	1	1	1	0	1	2	1	1	2	0
scutEx1	1	1	2	0	1	2	1	1	1	1
scutEx2	1	1	1	0	1	1	1	1	1	1
sp.5Panama	1	1	0	0	0	4	0	2	0	0
sp.6Mexico	1	1	1	0	1	2	1	1	1	0
sp.7Mexico	1	1	1	2	1	1	1	1	3	1
sp.8GUAT	4	1	1	0	1	2	2	1	3	0
sp.9GUAT	1	1	1	0	1	2	1	1	3	0
sp.10GUAT	1	1	1	0	1	2	2	1	4	0

Appendix D-2. TAXON/CHARACTER MATRIX FOR *POPILIUS*.

Character #	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
ecliptEx1	0	2	1	2	3	1	0	3	1	1
ecliptEx2	0	2	3	3	2	1	0	2	1	1
ecliptEx3	0	2	3	3	3	1	0	3	1	1
ecliptEx4	1	2	3	3	2	1	0	3	1	1
ecliptEx5	0	2	2	2	2	1	0	3	1	1
erotylus	{01}	2	4	3	2	1	0	3	1	1
magd	0	2	{46}	3	3	1	0	3	1	1
margEx1	0	2	4	3	3	1	0	3	1	1
margEx2	0	2	4	3	3	1	0	3	1	1
refugicornis	1	2	6	3	2	1	0	3	1	1
tet4lam	0	2	{23}	3	3	1	0	3	1	1
tet5lamAM	0	2	{23}	3	2	1	0	3	1	1
tet5lamBOL	0	2	2	3	2	1	0	3	1	1
sp.1COL	0	1	4	3	2	1	0	3	1	1
sp.2VEN	0	2	7	3	2	1	0	2	1	1
gibbEx1	0	3	{568}	3	2	1	0	3	1	1
gibbEx4	0	2	6	3	2	1	0	3	1	1
gibbEx3	0	2	6	3	2	1	0	3	1	1
gibbEx6	0	2	6	2	2	1	0	3	1	1
gibbEx2	0	{12}	6	3	2	1	0	3	1	1
gibbEx5	0	2	{568}	3	2	1	0	3	1	1
gibbEx7	0	2	{568}	3	2	1	0	2	1	1
gibbEx8	0	2	{568}	3	2	1	0	3	1	1
sp.3BOL	1	2	5	3	2	1	0	3	1	1
sp.4VENEx1	0	2	4	{23}	2	1	0	{23}	1	1
sp.4VENEx2	0	2	4	2	1	1	0	3	1	1
haagi	0	2	7	1	1	1	0	3	1	1
haagiint	0	2	7	1	1	1	0	3	1	1
hirsutus	0	2	2	4	3	1	0	3	1	1

kling	0	2	1	4	1	1	0	2	1	1
lenzi	0	2	2	3	2	1	0	2	1	1
mysticus	0	2	2	4	3	1	0	3	1	1
punct	0	2	2	3	2	1	0	1	1	1
scutEx1	0	2	2	1	1	1	0	3	1	1
scutEx2	0	2	2	1	1	1	0	3	1	1
sp.5Panama	2	2	1	2	2	1	0	3	1	1
sp.6Mexico	0	2	2	2	2	1	0	3	1	1
sp.7Mexico	0	2	2	4	3	1	0	2	1	1
sp.8GUAT	0	2	{17}	2	1	1	0	2	1	1
sp.9GUAT	0	2	7	4	3	1	0	1	1	1
sp.10GUAT	0	2	2	3	3	1	0	1	1	1

Character #	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
ecliptEx1	0	2	2	0	1	0	0	0	3	0
ecliptEx2	1	1	2	1	1	0	1	0	3	0
ecliptEx3	{01}	1	2	0	1	0	3	0	4	0
ecliptEx4	1	1	2	1	1	0	2	0	3	0
ecliptEx5	1	{123}	2	1	1	0	1	0	4	0
erotylus	0	1	2	1	0	0	{01}	0	3	0
magd	0	2	2	1	1	0	1	0	3	0
margEx1	0	2	2	1	1	0	0	0	3	0
margEx2	0	2	2	1	1	0	1	0	3	0
refugicornis	0	1	2	1	1	0	1	0	3	0
tet4lam	1	2	2	1	1	0	0	0	3	0
tet5lamAM	1	1	2	1	1	0	{01}	0	3	0
tet5lamBOL	1	1	2	1	1	0	0	0	3	0
sp.1COL	0	2	2	1	1	0	1	0	3	0
sp.2VEN	1	1	2	1	1	0	1	0	3	0
gibbEx1	1	1	2	1	1	0	2	0	3	0
gibbEx4	0	1	2	1	1	0	1	0	3	0
gibbEx3	0	1	2	1	1	0	{12}	0	3	0
gibbEx6	1	1	2	0	1	0	0	0	3	0
gibbEx2	{01}	1	2	1	{01}	0	2	0	3	0
gibbEx5	1	1	2	1	1	0	3	0	3	0
gibbEx7	1	1	2	1	1	0	3	0	3	0
gibbEx8	1	1	2	1	1	0	2	0	3	0
sp.3BOL	0	1	2	0	1	0	1	0	3	0
sp.4VENEx1	{01}	1	2	1	1	0	3	0	3	0
sp.4VENEx2	0	2	2	1	1	0	2	0	3	0
haagi	0	2	2	1	1	0	2	0	4	0
haagiint	0	3	2	0	1	0	3	0	4	0
hirsutus	0	1	2	1	0	0	{12}	0	4	0

kling	{01}	{01}	2	1	1	0	0	0	4	{01}
lenzi	0	1	1	1	1	0	1	0	4	0
mysticus	0	1	2	1	0	0	2	0	4	0
punct	0	1	2	1	1	0	1	0	4	1
scutEx1	0	3	2	0	1	0	2	0	4	0
scutEx2	0	1	2	1	0	0	1	0	4	0
sp.5Panama	0	{23}	1	0	1	1	0	0	4	2
sp.6Mexico	0	3	2	0	1	0	1	0	4	0
sp.7Mexico	0	3	0	0	1	0	{12}	0	4	0
sp.8GUAT	0	2	{01}	0	1	0	2	0	4	0
sp.9GUAT	0	1	2	1	0	0	1	0	4	1
sp.10GUAT	0	1	1	{01}	{01}	0	2	0	4	2

Character #	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
ecliptEx1	2	3	2	0	4	1	2	2	2	1
ecliptEx2	2	3	2	1	2	1	2	2	1	1
ecliptEx3	2	3	2	0	2	1	2	{12}	2	1
ecliptEx4	2	3	2	0	2	1	3	2	2	1
ecliptEx5	2	3	2	0	1	1	2	2	2	1
erotylus	0	3	2	0	{23}	1	2	2	2	1
magd	2	{23}	2	0	2	1	2	2	2	1
margEx1	0	{23}	2	0	{23}	1	2	2	2	1
margEx2	2	3	2	0	2	1	2	2	1	1
refugicornis	0	3	2	0	3	1	2	2	2	1
tet4lam	0	3	2	0	2	1	2	2	1	1
tet5lamAM	0	3	2	0	3	1	2	2	1	1
tet5lamBOL	0	3	2	0	2	1	2	2	1	1
sp.1COL	0	3	2	0	4	1	2	{12}	1	1
sp.2VEN	0	3	2	0	2	1	2	2	1	1
gibbEx1	0	3	2	0	2	1	2	2	1	1
gibbEx4	0	3	2	0	2	1	2	2	1	1
gibbEx3	0	3	2	0	{124}	1	2	2	1	1
gibbEx6	0	2	2	0	1	1	2	2	1	1
gibbEx2	0	3	2	0	4	1	2	2	2	1
gibbEx5	0	3	2	0	2	1	2	2	2	1
gibbEx7	0	3	2	0	2	1	3	{12}	2	1
gibbEx8	0	3	2	0	2	1	2	2	1	1
sp.3BOL	0	3	2	0	2	1	2	2	1	1
sp.4VENEx1	0	3	2	0	2	1	2	2	2	1
sp.4VENEx2	0	3	2	0	2	1	2	2	2	1
haagi	2	3	2	0	4	1	3	1	1	1
haagiint	2	3	2	0	3	1	3	2	1	1
hirsutus	2	3	2	0	2	1	3	{12}	1	1

kling	2	3	2	0	4	1	3	2	1	1
lenzi	2	3	2	0	2	1	3	2	1	1
mysticus	2	3	2	0	4	1	3	2	1	1
punct	2	3	2	0	{24}	1	3	2	1	1
scutEx1	2	3	2	0	2	1	3	2	1	1
scutEx2	2	3	2	0	2	1	3	2	1	1
sp.5Panama	2	3	2	0	2	1	3	2	1	1
sp.6Mexico	2	3	2	0	4	1	3	{23}	1	1
sp.7Mexico	2	3	2	0	4	1	3	2	1	1
sp.8GUAT	2	3	2	0	2	1	3	2	2	1
sp.9GUAT	2	3	2	0	4	1	3	2	1	1
sp.10GUAT	2	3	2	0	1	1	2	2	1	1

Character #	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
ecliptEx1	0	2	3	0	0	2	1	2	1	0
ecliptEx2	0	2	3	0	0	0	2	2	1	0
ecliptEx3	{01}	2	3	0	0	0	1	2	1	0
ecliptEx4	0	2	3	0	0	0	1	2	1	0
ecliptEx5	0	2	3	0	0	2	1	2	1	0
erotylus	0	2	3	0	{01}	1	1	2	1	0
magd	{01}	2	3	0	0	0	1	2	1	0
margEx1	0	2	3	0	0	0	1	2	1	0
margEx2	0	2	3	0	0	0	1	2	1	0
refugicornis	0	2	3	0	1	1	1	2	1	0
tet4lam	0	2	3	0	{01}	1	1	2	1	0
tet5lamAM	0	2	3	0	{01}	2	2	2	{01}	0
tet5lamBOL	0	2	3	0	0	0	1	2	1	0
sp.1COL	0	2	3	0	0	1	1	2	1	0
sp.2VEN	0	2	3	0	0	1	1	2	0	0
gibbEx1	0	2	3	0	1	1	2	2	1	0
gibbEx4	0	2	3	0	0	2	1	2	1	0
gibbEx3	0	2	3	0	0	2	1	2	{01}	0
gibbEx6	0	2	3	0	0	1	1	2	3	0
gibbEx2	0	2	3	0	{01}	1	{12}	2	{01}	0
gibbEx5	0	2	3	0	0	2	1	2	0	0
gibbEx7	0	2	3	0	{01}	1	1	2	1	0
gibbEx8	0	2	3	0	0	1	2	2	1	0
sp.3BOL	0	2	3	0	2	2	1	2	0	0
sp.4VENEx1	0	2	3	0	{02}	2	{01}	2	0	0
sp.4VENEx2	0	2	3	0	2	2	2	2	0	0
haagi	0	2	3	0	0	0	1	2	1	0
haagiint	0	2	3	0	0	0	1	2	?	0
hirsutus	0	2	3	0	0	{01}	1	2	1	0

kling	0	2	3	0	0	0	1	2	1	0
lenzi	0	2	3	0	0	2	1	0	1	0
mysticus	0	2	3	0	0	0	2	2	1	0
punct	0	2	3	0	0	2	2	0	1	0
scutEx1	0	2	3	0	0	2	1	2	1	0
scutEx2	0	2	3	0	0	2	1	2	1	0
sp.5Panama	0	2	3	0	{01}	0	2	2	1	0
sp.6Mexico	0	2	3	0	0	0	2	2	1	0
sp.7Mexico	0	2	3	0	0	0	2	2	1	0
sp.8GUAT	0	2	3	0	0	1	{01}	2	0	0
sp.9GUAT	0	2	3	0	0	0	1	1	1	0
sp.10GUAT	0	2	3	0	0	1	{12}	0	1	0

Character #	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
ecliptEx1	0	0	0	1	1	0	0	0	{01}	2
ecliptEx2	0	0	0	2	1	1	0	1	0	2
ecliptEx3	0	0	0	1	2	0	1	0	0	2
ecliptEx4	0	0	0	1	2	1	1	1	0	2
ecliptEx5	0	0	0	{14}	1	0	0	0	0	2
erotylus	0	0	2	1	0	0	0	0	0	2
magd	0	0	2	1	0	0	0	0	0	2
margEx1	0	0	3	1	0	0	1	1	0	2
margEx2	0	0	3	1	0	0	1	0	0	2
refugicornis	0	0	1	1	0	0	0	0	0	2
tet4lam	0	0	3	1	0	1	0	0	0	2
tet5lamAM	0	0	3	1	0	0	{01}	0	0	2
tet5lamBOL	0	0	3	1	0	0	0	0	0	2
sp.1COL	0	0	2	{12}	0	0	0	0	0	2
sp.2VEN	0	0	3	1	0	0	0	0	1	2
gibbEx1	0	0	2	1	0	0	0	0	0	2
gibbEx4	0	0	{01}	4	0	0	0	1	0	2
gibbEx3	0	0	{02}	4	0	0	0	1	0	2
gibbEx6	0	0	0	4	0	0	0	1	0	2
gibbEx2	0	0	{02}	2	0	0	0	0	0	2
gibbEx5	0	0	0	1	0	0	0	1	0	2
gibbEx7	0	0	2	1	0	0	0	0	0	2
gibbEx8	0	0	1	1	0	0	0	0	0	2
sp.3BOL	0	0	1	1	0	0	0	1	0	2
sp.4VENEx1	0	0	2	1	0	0	0	0	1	2
sp.4VENEx2	1	0	2	1	0	0	0	1	1	2
haagi	0	0	0	1	0	0	{01}	{01}	0	2
haagiint	0	0	0	0	1	0	1	0	0	2
hirsutus	0	0	0	{12}	2	{01}	{12}	1	0	2

kling	0	0	0	1	1	0	0	1	0	2
lenzi	0	0	0	1	2	1	0	0	0	2
mysticus	0	0	0	1	2	0	1	0	0	2
punct	0	0	0	{12}	2	1	{01}	1	0	2
scutEx1	0	0	0	1	1	0	1	2	0	2
scutEx2	0	0	0	2	0	0	0	2	0	2
sp.5Panama	2	1	0	{01}	{12}	0	{01}	0	0	2
sp.6Mexico	1	0	0	2	2	0	0	0	0	2
sp.7Mexico	0	0	0	1	0	0	2	0	0	2
sp.8GUAT	0	0	0	1	2	1	{01}	1	0	2
sp.9GUAT	0	0	0	1	2	1	{12}	1	0	2
sp.10GUAT	0	0	0	{12}	2	0	2	0	0	2

Character #	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**
ecliptEx1	2	0	0	0	0	2	0	4	0	0
ecliptEx2	2	0	0	0	0	2	0	4	1	0
ecliptEx3	2	1	0	0	0	2	{01}	4	1	0
ecliptEx4	2	0	0	0	0	2	0	4	?	?
ecliptEx5	2	0	0	0	0	2	0	4	1	0
erotylus	2	0	0	0	0	2	0	0	2	0
magd	3	0	0	0	0	2	1	0	2	1
margEx1	2	1	0	0	0	2	0	0	2	0
margEx2	2	0	0	0	0	2	1	0	2	1
refugicornis	2	0	0	0	0	2	0	0	2	0
tet4lam	3	{01}	0	0	0	2	0	0	2	0
tet5lamAM	3	0	0	0	0	2	0	0	2	{12}
tet5lamBOL	3	0	0	0	0	2	0	0	2	2
sp.1COL	1	0	0	0	0	2	0	1	2	0
sp.2VEN	2	0	0	0	0	2	1	0	1	0
gibbEx1	3	0	0	0	0	2	1	0	1	0
gibbEx4	3	{01}	0	0	0	2	1	0	1	0
gibbEx3	3	{01}	0	0	0	2	1	0	1	0
gibbEx6	3	1	0	0	0	2	1	0	1	0
gibbEx2	{23}	0	0	0	0	2	0	0	1	0
gibbEx5	2	0	0	0	0	2	1	0	1	0
gibbEx7	{13}	0	0	0	0	2	0	0	1	0
gibbEx8	3	0	0	0	0	2	1	0	1	0
sp.3BOL	2	1	0	0	0	0	0	0	1	0
sp.4VENEx1	3	0	0	0	0	2	1	0	1	0
sp.4VENEx2	3	0	0	0	0	2	1	0	1	0
haagi	{123}	0	0	0	0	1	0	2	1	0
haagiint	2	0	0	0	0	1	0	2	1	0
hirsutus	2	0	0	0	0	2	0	3	1	0

kling	1	0	0	0	0	0	0	2	1	0
lenzi	2	0	0	0	0	1	0	2	1	0
mysticus	1	0	0	0	0	2	0	3	1	0
punct	2	1	0	0	0	1	0	2	1	0
scutEx1	1	1	0	0	0	2	0	2	1	0
scutEx2	1	1	0	0	0	2	0	2	1	0
sp.5Panama	{12}	0	0	0	0	2	0	2	1	0
sp.6Mexico	3	0	0	0	0	0	0	2	1	0
sp.7Mexico	1	0	0	0	0	0	0	2	1	0
sp.8GUAT	{12}	1	0	0	0	0	0	1	1	0
sp.9GUAT	1	1	0	0	0	0	0	4	1	0
sp.10GUAT	{23}	0	0	0	0	{01}	0	4	0	0

Character #	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
ecliptEx1	0	1	0	2	0	1	0	1	1	0
ecliptEx2	0	1	0	2	0	1	0	1	1	0
ecliptEx3	0	1	1	2	0	1	0	{01}	1	0
ecliptEx4	?	?	?	?	?	?	?	0	1	0
ecliptEx5	0	2	1	1	0	1	0	1	{01}	0
erotylus	0	4	3	1	0	1	0	1	1	0
magd	1	5	3	1	0	1	1	0	1	0
margEx1	0	5	4	0	0	1	0	1	0	0
margEx2	0	4	3	0	0	1	0	1	0	0
refugicornis	0	5	4	2	0	0	0	1	1	0
tet4lam	1	5	3	0	0	1	1	1	0	0
tet5lamAM	1	5	3	1	0	1	2	0	0	0
tet5lamBOL	1	5	3	1	0	0	2	1	1	0
sp.1COL	0	5	3	0	0	1	0	0	1	0
sp.2VEN	0	4	3	1	0	1	0	0	1	0
gibbEx1	0	3	2	1	0	0	0	1	1	0
gibbEx4	0	2	2	2	0	1	0	1	{01}	0
gibbEx3	0	3	2	1	0	1	0	1	1	0
gibbEx6	0	3	3	1	0	1	0	1	1	0
gibbEx2	0	2	2	2	0	1	0	0	1	0
gibbEx5	0	2	2	2	0	1	0	1	1	0
gibbEx7	0	3	3	1	0	1	0	0	1	0
gibbEx8	0	2	2	1	0	1	0	1	1	0
sp.3BOL	0	3	2	1	0	1	0	1	1	0
sp.4VENEx1	0	2	2	2	0	0	0	1	1	0
sp.4VENEx2	0	2	2	2	0	1	0	0	1	0
haagi	0	2	2	2	0	1	0	0	{01}	0
haagiint	0	2	1	2	0	1	0	0	0	0
hirsutus	0	3	2	1	0	1	0	1	1	0

kling	0	2	2	1	0	1	0	0	1	0
lenzi	0	3	2	2	0	0	0	1	0	0
mysticus	0	3	2	1	0	1	0	1	1	0
punct	0	3	1	1	0	0	0	1	0	0
scutEx1	0	3	2	1	0	1	0	1	1	0
scutEx2	0	2	2	1	0	1	0	1	1	0
sp.5Panama	0	0	0	2	0	1	0	0	0	0
sp.6Mexico	0	1	0	2	0	1	0	1	0	0
sp.7Mexico	0	2	2	1	0	1	0	1	1	0
sp.8GUAT	0	2	2	2	0	1	0	1	1	0
sp.9GUAT	0	2	2	1	0	1	0	1	0	0
sp.10GUAT	0	0	0	2	0	1	0	1	1	0

Character #	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
ecliptEx1	0	0	0	0	0	1	3	1	1	0
ecliptEx2	0	0	0	0	0	2	3	1	1	0
ecliptEx3	0	1	0	{01}	1	1	3	0	1	0
ecliptEx4	?	0	0	0	1	1	3	1	1	0
ecliptEx5	0	1	0	0	0	1	3	0	1	0
erotylus	0	0	0	0	1	1	3	1	0	0
magd	0	1	0	0	1	1	2	1	0	0
margEx1	0	0	0	1	0	1	3	1	0	0
margEx2	0	0	0	0	0	1	3	1	0	0
refugicornis	0	1	0	0	1	1	3	1	0	0
tet4lam	0	1	0	1	1	1	{012}	1	0	0
tet5lamAM	0	1	0	0	{01}	1	3	1	0	0
tet5lamBOL	0	1	0	0	1	1	{12}	1	0	0
sp.1COL	0	0	0	0	{01}	1	2	1	0	0
sp.2VEN	0	1	0	0	1	{12}	2	1	0	0
gibbEx1	0	1	0	0	1	1	3	{01}	0	0
gibbEx4	0	1	0	0	1	1	2	1	1	0
gibbEx3	0	1	0	0	1	1	2	1	1	0
gibbEx6	0	1	0	0	1	1	3	1	0	0
gibbEx2	0	1	0	0	1	1	3	1	0	0
gibbEx5	0	1	0	0	1	1	1	1	0	0
gibbEx7	0	?	0	0	1	1	3	1	0	0
gibbEx8	0	1	0	0	1	1	3	0	0	0
sp.3BOL	?	1	0	1	1	1	2	1	0	0
sp.4VENEx1	0	0	0	0	1	1	0	{01}	0	0
sp.4VENEx2	0	1	0	0	1	1	2	1	1	0
haagi	0	0	0	0	0	1	0	0	0	0
haagiint	0	0	0	0	0	1	0	0	0	1
hirsutus	0	0	0	0	0	1	0	1	1	1

kling	0	1	0	0	0	0	0	1	1	1
lenzi	0	1	0	0	0	0	1	1	0	1
mysticus	0	1	0	0	0	1	0	1	1	{01}
punct	0	1	0	0	0	0	0	1	1	1
scutEx1	0	1	0	0	0	{01}	2	1	1	1
scutEx2	0	1	0	0	0	0	2	1	1	1
sp.5Panama	0	1	0	0	0	{12}	3	{01}	1	0
sp.6Mexico	0	1	0	0	0	0	3	1	1	0
sp.7Mexico	0	1	0	0	0	1	3	1	1	{01}
sp.8GUAT	0	0	0	0	1	0	3	1	1	1
sp.9GUAT	0	1	0	0	1	0	0	1	1	1
sp.10GUAT	0	1	0	0	0	1	0	{01}	0	0

Character #	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**
ecliptEx1	1	2	0	0	1	0	2	1	1	0
ecliptEx2	1	1	0	1	0	0	2	1	1	0
ecliptEx3	1	2	0	0	0	0	1	1	1	0
ecliptEx4	1	2	0	1	0	0	1	1	3	0
ecliptEx5	1	2	0	1	0	0	1	{01}	1	0
erotylus	2	2	0	1	1	0	0	{12}	1	0
magd	2	2	0	1	0	0	0	2	1	1
margEx1	2	2	0	1	0	0	0	2	1	1
margEx2	2	2	0	1	1	0	1	2	1	1
refugicornis	2	2	0	1	1	0	1	{23}	1	0
tet4lam	2	{12}	0	1	0	0	0	1	3	0
tet5lamAM	2	2	0	{01}	1	0	0	{12}	{23}	0
tet5lamBOL	2	1	0	1	1	0	0	2	1	0
sp.1COL	1	2	0	1	1	0	1	2	2	0
sp.2VEN	3	2	0	1	1	0	0	2	1	0
gibbEx1	2	{01}	0	1	1	0	0	{01}	1	0
gibbEx4	2	2	0	1	1	0	0	1	2	0
gibbEx3	2	{01}	0	1	1	0	0	1	1	0
gibbEx6	2	0	0	1	1	0	0	1	2	0
gibbEx2	2	{01}	0	1	1	0	1	{23}	1	0
gibbEx5	2	0	0	1	1	0	1	{01}	1	0
gibbEx7	2	2	0	1	1	0	1	2	1	0
gibbEx8	2	2	0	1	1	0	0	{12}	2	0
sp.3BOL	2	1	0	1	0	0	1	1	1	0
sp.4VENEx1	{12}	{01}	0	1	1	0	0	{12}	2	0
sp.4VENEx2	1	0	0	1	1	0	0	2	2	0
haagi	1	0	0	1	1	0	1	{12}	1	0
haagiint	1	0	0	1	1	0	1	1	1	0
hirsutus	1	0	0	1	1	0	2	0	1	0

kling	1	0	0	1	0	0	1	0	1	0
lenzi	2	0	0	1	0	0	2	1	1	0
mysticus	1	0	0	1	0	0	2	0	0	0
punct	1	0	0	1	1	0	1	1	2	0
scutEx1	1	0	0	1	0	0	1	1	1	0
scutEx2	1	0	0	1	0	0	1	1	1	0
sp.5Panama	2	0	0	1	1	0	1	{01}	3	0
sp.6Mexico	1	0	0	1	1	0	1	0	2	0
sp.7Mexico	0	0	0	1	1	0	2	1	0	0
sp.8GUAT	1	0	0	1	0	0	1	0	2	0
sp.9GUAT	1	0	0	1	1	0	1	1	1	0
sp.10GUAT	{01}	0	0	1	0	0	1	2	0	0

Character #	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**
ecliptEx1	2	1	1	0	0	1	1	0	2	0
ecliptEx2	1	1	1	0	0	1	1	0	2	0
ecliptEx3	1	1	1	0	0	1	1	0	2	0
ecliptEx4	1	1	1	0	0	1	1	0	2	0
ecliptEx5	2	1	1	0	0	1	1	0	2	0
erotylus	0	1	1	0	0	1	1	0	2	0
magd	0	0	1	0	2	1	1	0	2	0
margEx1	0	1	1	0	0	1	1	0	2	0
margEx2	1	1	1	0	0	1	1	0	2	0
refugicornis	1	0	1	0	2	1	1	0	2	0
tet4lam	0	1	1	0	0	1	1	0	2	0
tet5lamAM	0	0	1	0	0	1	1	0	2	0
tet5lamBOL	0	0	1	0	0	1	1	0	1	0
sp.1COL	2	1	1	0	0	1	1	0	2	0
sp.2VEN	1	0	1	0	0	1	1	0	2	0
gibbEx1	1	1	1	0	0	1	1	0	2	0
gibbEx4	1	{01}	1	0	0	1	1	0	2	0
gibbEx3	1	1	1	0	0	1	1	0	2	0
gibbEx6	2	1	1	0	0	0	1	0	2	0
gibbEx2	1	1	1	0	0	1	1	0	1	0
gibbEx5	2	1	1	0	0	1	1	0	{12}	0
gibbEx7	1	1	1	0	0	1	1	0	2	0
gibbEx8	1	1	1	0	0	1	1	0	2	0
sp.3BOL	2	1	1	0	0	1	1	0	1	0
sp.4VENEx1	2	1	1	0	0	0	1	0	1	0
sp.4VENEx2	2	1	1	0	0	1	1	0	1	0
haagi	2	1	1	0	0	0	1	0	2	0
haagiint	2	1	1	0	0	1	1	0	2	0
hirsutus	1	1	1	0	0	2	1	0	2	0

kling	1	1	1	0	0	1	1	0	2	0
lenzi	2	0	1	0	0	0	1	0	2	0
mysticus	1	1	1	0	0	0	1	0	2	0
punct	{23}	0	1	0	0	0	1	0	2	0
scutEx1	2	1	1	0	0	1	1	0	2	0
scutEx2	2	1	1	0	0	0	1	0	2	0
sp.5Panama	3	0	1	0	0	{01}	1	0	1	0
sp.6Mexico	2	0	1	0	1	1	1	0	1	0
sp.7Mexico	2	1	1	0	0	0	1	0	2	0
sp.8GUAT	2	1	1	0	0	0	1	0	2	0
sp.9GUAT	1	1	1	0	0	0	1	0	2	0
sp.10GUAT	2	1	1	0	0	2	1	0	1	0

Character #	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**
icliptEx1	1	0	3	1	0	1	0	1	3	0
ecliptEx2	0	0	3	1	0	1	0	1	3	0
ecliptEx3	0	0	3	1	0	1	0	1	3	0
ecliptEx4	0	0	2	0	0	1	1	1	3	0
ecliptEx5	0	0	2	1	0	1	1	1	3	0
erotylus	0	0	2	0	0	0	0	1	0	0
magd	0	0	1	0	0	0	0	1	1	0
margEx1	0	0	3	0	0	0	0	1	1	0
margEx2	0	0	1	1	0	0	0	1	1	0
refugicornis	0	0	2	0	0	0	0	1	1	0
tet4lam	0	0	1	0	0	0	{01}	1	0	0
tet5lamAM	0	0	1	0	0	0	0	1	1	0
tet5lamBOL	0	0	3	1	0	0	0	1	{01}	0
sp.1COL	0	0	0	0	0	0	0	1	1	0
sp.2VEN	0	0	0	0	0	0	0	1	1	0
gibbEx1	0	0	{12}	1	0	0	0	1	1	0
gibbEx4	0	0	1	1	0	0	0	1	0	0
gibbEx3	0	0	1	1	0	0	0	1	0	0
gibbEx6	0	0	2	1	0	0	0	1	1	0
gibbEx2	0	0	{01}	0	0	0	0	1	0	0
gibbEx5	0	0	1	0	0	0	0	1	1	0
gibbEx7	0	0	1	0	0	0	0	1	0	0
gibbEx8	0	0	2	0	0	0	0	1	1	0
sp.3BOL	0	0	1	0	0	0	0	1	1	0
sp.4VENEx1	0	0	1	0	0	0	0	1	0	0
sp.4VENEx2	0	0	1	0	0	0	0	1	0	0
haagi	0	0	{013}	1	0	0	0	1	{12}	0
haagiint	0	0	0	1	0	0	0	1	{12}	0
hirsutus	0	0	0	1	0	1	0	1	0	0

kling	0	0	1	1	0	0	0	1	0	0
lenzi	0	0	1	0	0	0	0	1	0	0
mysticus	0	0	0	0	0	0	0	1	0	0
punct	0	0	1	0	0	0	0	1	1	0
scutEx1	0	0	0	1	0	0	0	1	1	0
scutEx2	0	0	1	1	0	0	0	1	1	0
sp.5Panama	0	0	0	1	0	0	0	1	0	0
sp.6Mexico	0	0	2	1	0	0	0	1	0	0
sp.7Mexico	0	0	0	0	0	0	0	1	0	0
sp.8GUAT	0	0	2	1	0	0	0	1	1	0
sp.9GUAT	0	0	{01}	0	0	0	0	1	1	0
sp.10GUAT	0	0	0	1	0	0	0	1	0	0

Character #	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**
ecliptEx1	0	0	0	1	2	0	0	3	0	0
ecliptEx2	0	0	0	1	1	0	0	3	0	0
ecliptEx3	1	0	0	{12}	{12}	0	0	3	0	0
ecliptEx4	{01}	0	0	2	2	0	0	3	0	0
ecliptEx5	0	0	0	0	0	0	0	3	0	0
erotylus	0	0	0	2	0	{45}	0	3	0	0
magd	0	0	0	2	2	2	0	3	0	0
margEx1	0	0	0	1	1	4	0	3	0	2
margEx2	0	0	0	1	1	{45}	0	3	0	1
refugicornis	0	0	0	2	2	0	0	3	0	0
tet4lam	0	0	0	0	0	{34}	0	3	0	{02}
tet5lamAM	0	0	0	1	0	4	0	2	0	0
tet5lamBOL	0	0	0	1	1	4	0	3	0	1
sp.1COL	0	0	0	1	0	0	0	3	0	0
sp.2VEN	0	0	0	1	2	0	0	3	0	0
gibbEx1	0	0	0	1	2	0	0	3	0	0
gibbEx4	0	0	0	0	2	0	0	3	0	{01}
gibbEx3	0	0	0	0	2	0	0	3	0	{01}
gibbEx6	0	0	0	1	2	0	0	3	0	0
gibbEx2	0	0	0	1	2	0	0	{12}	0	0
gibbEx5	0	0	0	2	2	0	0	3	0	0
gibbEx7	0	0	0	1	1	0	0	3	0	0
gibbEx8	0	0	0	1	2	0	0	3	0	0
sp.3BOL	0	0	0	1	2	0	0	2	0	0
sp.4VENEx1	1	0	0	1	2	0	0	2	0	0
sp.4VENEx2	1	0	0	1	2	0	0	3	0	0
haagi	0	0	0	2	2	{34}	0	2	0	{01}
haagiint	0	0	0	1	2	4	0	3	0	1
hirsutus	{01}	0	0	1	1	6	0	2	0	{12}

kling	0	0	0	1	2	3	0	3	0	{12}
lenzi	0	0	0	2	2	4	0	3	0	0
mysticus	0	0	0	{12}	{12}	5	0	3	0	1
punct	0	0	0	1	1	4	0	3	0	1
scutEx1	0	0	0	2	2	4	0	3	0	0
scutEx2	0	0	0	2	2	4	0	3	0	0
sp.5Panama	0	0	0	{12}	2	{23}	0	2	0	{01}
sp.6Mexico	0	0	0	1	{01}	{45}	0	3	0	2
sp.7Mexico	0	0	0	2	2	0	0	3	0	0
sp.8GUAT	0	0	0	2	2	4	0	3	0	0
sp.9GUAT	0	0	0	2	2	4	0	3	0	0
sp.10GUAT	0	0	0	1	2	{45}	3	3	0	0

Character #	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**
ecliptEx1	2	0	0	0	0	1	0	0	0	2
ecliptEx2	2	0	0	0	0	1	0	0	0	1
ecliptEx3	1	0	1	0	0	0	0	0	0	2
ecliptEx4	2	0	{01}	0	0	0	0	0	0	1
ecliptEx5	2	0	0	0	0	0	0	0	0	2
erotylus	2	0	0	0	0	0	1	0	0	1
magd	2	0	0	0	0	0	1	0	0	1
margEx1	3	0	0	0	0	0	0	0	0	1
margEx2	3	0	0	0	0	0	1	0	0	2
refugicornis	2	1	0	0	0	0	0	0	0	1
tet4lam	2	0	0	0	0	1	0	0	0	0
tet5lamAM	2	0	0	0	0	0	{01}	0	0	0
tet5lamBOL	2	0	0	0	0	1	0	0	0	0
sp.1COL	1	0	0	0	0	0	1	0	0	0
sp.2VEN	2	0	0	0	0	0	0	0	0	1
gibbEx1	2	0	1	0	0	0	0	0	0	1
gibbEx4	4	0	0	0	0	0	1	0	0	2
gibbEx3	{24}	0	0	0	0	0	1	0	0	{12}
gibbEx6	2	0	0	0	0	0	0	0	0	2
gibbEx2	2	0	1	0	0	1	1	0	0	1
gibbEx5	2	0	0	0	0	1	1	0	0	3
gibbEx7	2	0	0	0	0	1	1	0	0	1
gibbEx8	2	0	0	0	0	0	0	0	0	1
sp.3BOL	4	0	0	0	0	1	0	0	0	0
sp.4VENEx1	2	0	1	0	0	1	0	0	0	{12}
sp.4VENEx2	2	0	1	0	0	1	0	0	0	?
haagi	{24}	0	0	0	0	0	1	0	0	2
haagiint	4	0	0	0	0	0	1	0	0	2
hirsutus	4	0	{01}	0	0	0	0	0	0	3

kling	4	0	0	0	0	0	0	0	0	2
lenzi	2	0	0	0	0	0	{01}	0	0	3
mysticus	4	0	0	0	0	0	0	0	0	3
punct	4	0	0	0	0	0	1	0	0	3
scutEx1	4	0	0	0	0	0	0	0	0	3
scutEx2	4	0	0	0	0	0	0	0	0	3
sp.5Panama	4	0	0	1	0	0	1	2	0	1
sp.6Mexico	2	0	0	0	0	0	1	0	0	2
sp.7Mexico	0	0	0	0	0	0	0	0	0	1
sp.8GUAT	2	0	0	0	0	0	0	0	0	{23}
sp.9GUAT	2	0	0	0	0	0	0	1	0	3
sp.10GUAT	2	0	0	0	0	1	0	0	1	3

Character #	**141**	**142**	**143**	**144**	**145**	**146**	**147**	**148**	**149**	**150**
ecliptEx1	0	2	3	0	1	2	1	0	0	4
ecliptEx2	0	2	3	0	1	0	1	0	0	4
ecliptEx3	0	2	3	0	1	2	1	0	0	4
ecliptEx4	0	2	3	0	1	2	1	0	0	4
ecliptEx5	0	{12}	{23}	0	1	2	1	0	0	{145}
erotylus	1	2	{23}	0	{01}	0	1	0	0	5
magd	1	2	2	0	1	2	0	0	0	1
margEx1	1	2	3	0	0	0	0	0	0	0
margEx2	1	1	3	0	0	0	0	0	0	0
refugicornis	1	2	2	0	1	2	1	0	0	1
tet4lam	1	?	3	0	1	0	0	0	0	{15}
tet5lamAM	1	2	2	0	1	0	0	0	0	0
tet5lamBOL	1	1	1	0	1	0	0	0	0	1
sp.1COL	1	1	2	0	{01}	0	1	0	0	5
sp.2VEN	0	2	2	0	1	2	1	0	0	5
gibbEx1	1	2	2	0	0	1	1	0	0	4
gibbEx4	0	1	2	0	1	2	1	0	0	4
gibbEx3	0	1	2	0	0	2	1	0	0	4
gibbEx6	0	1	2	0	0	2	1	0	0	4
gibbEx2	1	2	2	0	0	2	1	0	0	4
gibbEx5	0	1	1	0	1	2	1	0	0	4
gibbEx7	0	2	3	0	0	1	1	0	0	?
gibbEx8	1	2	3	0	1	1	1	0	0	5
sp.3BOL	0	2	2	0	0	0	1	0	0	5
sp.4VENEx1	{01}	{12}	1	0	1	1	1	0	0	4
sp.4VENEx2	?	2	3	0	1	1	1	0	0	4
haagi	0	0	1	0	{01}	0	0	0	0	1
haagiint	0	0	0	1	0	0	0	0	0	5
hirsutus	0	1	2	0	0	0	0	0	0	1

kling	0	1	1	0	0	0	0	0	0	5
lenzi	0	1	1	0	1	0	0	2	0	1
mysticus	0	2	2	0	0	0	0	0	0	1
punct	0	1	1	0	1	0	0	2	0	1
scutEx1	0	0	1	0	1	0	0	0	1	1
scutEx2	0	0	1	0	0	0	0	0	1	1
sp.5Panama	1	0	1	0	0	0	0	2	0	{01}
sp.6Mexico	0	1	1	0	0	0	0	0	0	3
sp.7Mexico	1	2	2	0	0	0	0	0	0	1
sp.8GUAT	0	1	1	0	{01}	0	0	0	0	1
sp.9GUAT	0	1	1	0	{01}	0	0	0	0	1
sp.10GUAT	0	1	1	0	1	0	0	{12}	0	1

Character #	**151**	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**
ecliptEx1	0	1	1	0	0	0	0	8	4	2
ecliptEx2	0	1	1	0	0	0	0	8	3	2
ecliptEx3	0	1	1	1	0	0	0	8	4	2
ecliptEx4	0	1	1	0	0	0	0	8	4	2
ecliptEx5	0	1	{12}	0	0	0	0	8	{34}	2
erotylus	0	1	1	0	0	0	0	8	1	2
magd	0	1	1	0	0	0	0	8	1	2
margEx1	0	0	3	0	0	0	0	9	1	2
margEx2	0	1	1	0	0	0	0	9	1	2
refugicornis	0	1	1	0	0	0	0	8	2	2
tet4lam	0	0	0	0	0	0	0	8	1	1
tet5lamAM	0	0	3	0	0	0	0	8	{01}	2
tet5lamBOL	0	0	0	0	0	0	1	8	1	1
sp.1COL	0	1	1	0	0	0	0	8	1	2
sp.2VEN	0	1	1	0	0	0	0	8	3	2
gibbEx1	{01}	1	1	0	0	0	0	8	2	2
gibbEx4	0	1	1	0	0	0	0	8	1	1
gibbEx3	0	1	1	0	0	0	0	8	{14}	1
gibbEx6	0	1	1	0	0	0	0	8	4	1
gibbEx2	0	1	1	0	0	0	1	?	1	2
gibbEx5	0	0	1	0	0	0	0	8	2	2
gibbEx7	0	1	1	0	0	0	0	8	2	2
gibbEx8	0	1	1	0	0	0	0	8	1	2
sp.3BOL	0	1	1	0	0	0	0	8	0	1
sp.4VENEx1	0	1	1	0	0	0	0	8	{14}	2
sp.4VENEx2	0	1	1	0	0	0	0	8	1	2
haagi	0	1	1	0	0	0	1	8	3	1
haagiint	0	1	1	0	0	0	1	?	2	1
hirsutus	0	1	3	0	0	0	0	8	{23}	1

kling	0	1	1	0	0	0	1	8	4	2
lenzi	0	1	0	0	0	0	1	8	4	2
mysticus	0	1	0	0	0	0	0	8	3	2
punct	0	1	0	0	0	0	1	8	4	2
scutEx1	0	1	3	0	0	0	1	8	4	2
scutEx2	0	1	3	0	0	0	1	?	4	2
sp.5Panama	0	0	0	0	0	0	0	8	2	2
sp.6Mexico	0	1	0	0	0	0	0	2	1	2
sp.7Mexico	0	1	0	0	0	0	0	8	4	1
sp.8GUAT	0	1	0	0	0	0	0	8	2	2
sp.9GUAT	0	1	1	0	0	0	0	8	3	2
sp.10GUAT	0	1	2	0	0	0	0	8	4	1

Character #	**161**	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**
ecliptEx1	2	2	1	4	1	0	0	0	1	0
ecliptEx2	1	1	1	5	1	1	0	0	1	1
ecliptEx3	{01}	1	1	4	1	0	0	0	1	0
ecliptEx4	1	2	1	4	1	0	0	0	1	1
ecliptEx5	0	2	1	5	1	1	0	0	1	0
erotylus	0	2	1	3	1	0	0	{24}	1	0
magd	0	1	1	4	1	0	0	0	1	0
margEx1	0	1	1	4	1	0	0	0	1	0
margEx2	0	1	1	5	1	1	0	0	1	0
refugicornis	0	0	1	5	1	1	0	0	1	0
tet4lam	0	2	1	4	1	0	0	0	1	0
tet5lamAM	0	2	1	4	1	0	0	0	1	0
tet5lamBOL	0	1	1	4	1	0	0	0	1	0
sp.1COL	0	1	1	4	1	0	0	0	1	0
sp.2VEN	0	0	1	4	1	0	0	0	1	0
gibbEx1	0	2	1	4	1	0	0	0	2	0
gibbEx4	0	2	0	4	1	0	0	{01}	2	0
gibbEx3	0	2	0	4	1	0	0	{01}	2	0
gibbEx6	0	0	1	5	1	1	0	0	2	0
gibbEx2	0	1	1	4	1	0	0	{012}	2	0
gibbEx5	0	0	1	4	1	0	0	2	2	0
gibbEx7	0	0	1	4	1	0	0	1	2	0
gibbEx8	0	2	1	4	1	0	0	0	2	0
sp.3BOL	0	0	1	4	1	0	0	0	2	0
sp.4VENEx1	3	1	0	4	1	0	0	{02}	2	0
sp.4VENEx2	3	1	0	4	1	0	0	0	2	0
haagi	1	1	1	3	0	0	0	0	1	0
haagiint	?	1	1	3	0	0	0	0	1	0
hirsutus	1	1	1	2	0	1	0	0	1	0

kling	0	1	1	2	0	0	0	3	1	0
lenzi	0	1	1	2	0	0	0	4	1	0
mysticus	0	1	1	2	0	0	0	0	1	1
punct	0	2	1	3	0	0	0	4	1	0
scutEx1	1	2	1	2	0	1	0	4	1	0
scutEx2	1	2	1	2	0	0	0	{34}	1	0
sp.5Panama	0	2	1	2	0	0	2	0	0	0
sp.6Mexico	0	2	1	3	0	0	2	0	1	0
sp.7Mexico	0	2	1	2	0	1	0	0	1	0
sp.8GUAT	1	0	1	2	0	1	0	0	1	1
sp.9GUAT	1	0	1	{23}	0	0	0	4	1	0
sp.10GUAT	1	0	1	{123}	0	0	0	0	1	0

Character #	**171**	**172**	**173**	**174**	**175**	**176**	**177**	**178**	**179**	**180**
ecliptEx1	0	0	0	0	2	1	1	0	1	1
ecliptEx2	0	0	0	0	2	1	0	0	1	1
ecliptEx3	0	0	0	0	2	1	0	0	1	1
ecliptEx4	0	0	3	0	2	1	0	0	1	1
ecliptEx5	0	{01}	{12}	0	2	{01}	0	0	1	1
erotylus	0	3	{12}	0	2	1	0	0	0	0
magd	2	3	{23}	0	2	1	0	0	1	0
margEx1	0	{34}	3	0	0	1	0	0	0	0
margEx2	0	3	2	0	0	1	0	0	0	0
refugicornis	2	0	0	0	2	1	0	0	0	0
tet4lam	0	3	2	0	0	1	0	0	0	0
tet5lamAM	0	3	{0123}	0	{01}	1	0	0	0	0
tet5lamBOL	0	3	3	0	0	1	0	0	1	0
sp.1COL	0	3	{01}	0	1	{01}	0	0	0	0
sp.2VEN	0	0	1	0	0	0	0	0	0	0
gibbEx1	0	0	{01}	0	1	0	0	1	0	0
gibbEx4	0	0	1	0	1	1	0	0	0	0
gibbEx3	0	0	1	0	1	1	0	0	0	0
gibbEx6	0	0	1	0	1	0	0	0	0	0
gibbEx2	0	0	0	1	1	1	0	0	0	0
gibbEx5	0	0	0	0	0	0	0	0	0	0
gibbEx7	0	0	0	1	2	0	0	0	0	0
gibbEx8	0	0	0	0	0	0	0	0	0	0
sp.3BOL	0	0	0	0	0	0	1	1	0	0
sp.4VENEx1	0	0	0	0	1	0	0	0	0	0
sp.4VENEx2	0	0	0	0	1	1	0	0	0	0
haagi	0	0	{01}	0	0	1	0	0	0	0
haagiint	0	0	3	0	0	1	0	0	0	0
hirsutus	0	1	{12}	0	0	0	0	0	0	0

kling	0	0	1	0	0	1	0	0	0	0
lenzi	0	3	3	0	0	0	0	0	0	0
mysticus	0	1	2	0	0	1	0	0	0	0
punct	0	3	{23}	0	0	0	0	0	0	0
scutEx1	0	0	3	0	0	0	0	0	0	0
scutEx2	0	0	3	0	0	0	0	0	0	0
sp.5Panama	0	4	3	1	0	1	0	0	0	0
sp.6Mexico	0	3	{12}	0	0	0	0	0	0	0
sp.7Mexico	0	1	{12}	0	0	1	0	0	0	0
sp.8GUAT	2	0	3	0	1	1	0	0	0	0
sp.9GUAT	2	0	{23}	0	2	0	0	0	0	0
sp.10GUAT	2	1	{23}	0	2	0	0	0	0	0

Character #	**181**	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**
ecliptEx1	1	1	0	0	0	0	0	2	0	0
ecliptEx2	1	1	0	0	0	0	0	2	1	0
ecliptEx3	1	1	0	0	0	0	0	2	1	0
ecliptEx4	1	1	0	0	0	0	0	1	1	0
ecliptEx5	1	1	0	0	0	0	0	2	0	0
erotylus	0	1	0	0	0	0	0	2	1	1
magd	0	1	1	0	0	1	0	2	1	1
margEx1	0	1	0	0	0	0	0	2	1	1
margEx2	0	1	0	0	0	0	0	2	1	1
refugicornis	0	1	0	0	0	0	0	2	1	1
tet4lam	0	1	0	0	0	0	0	2	1	1
tet5lamAM	1	1	0	0	0	0	0	2	1	1
tet5lamBOL	0	1	0	0	0	0	0	2	1	1
sp.1COL	1	1	0	0	0	0	0	2	1	1
sp.2VEN	0	1	1	0	0	0	0	2	1	1
gibbEx1	1	1	0	0	0	0	0	2	1	1
gibbEx4	1	1	0	0	0	0	0	2	1	1
gibbEx3	1	1	0	0	0	0	0	2	1	1
gibbEx6	1	1	0	0	0	0	0	2	1	1
gibbEx2	1	1	0	0	0	0	0	2	1	1
gibbEx5	1	1	0	0	0	0	0	2	1	1
gibbEx7	1	1	0	0	0	0	0	2	1	1
gibbEx8	1	1	0	0	0	0	0	2	1	1
sp.3BOL	0	1	0	0	0	0	0	1	1	1
sp.4VENEx1	1	1	0	{01}	0	0	0	2	1	1
sp.4VENEx2	1	1	0	1	0	0	0	2	1	1
haagi	1	1	0	0	0	0	0	2	1	{01}
haagiint	1	1	0	0	0	0	0	2	1	0
hirsutus	1	1	0	0	0	0	0	2	1	1

kling	1	1	0	0	0	0	0	2	0	1
lenzi	1	1	0	0	0	0	0	1	1	1
mysticus	1	1	0	0	0	0	0	2	1	1
punct	1	1	0	0	0	0	0	2	1	1
scutEx1	1	1	0	0	0	0	0	2	1	1
scutEx2	1	1	0	0	0	1	0	2	1	?
sp.5Panama	1	1	0	0	1	0	0	2	0	0
sp.6Mexico	1	1	0	1	0	0	0	2	1	0
sp.7Mexico	0	1	0	0	0	1	0	2	1	1
sp.8GUAT	1	1	0	0	0	0	0	2	1	0
sp.9GUAT	1	1	0	0	0	0	0	2	1	1
sp.10GUAT	1	1	0	0	0	0	0	{12}	0	1

Character #	**191**	**192**	**193**	**194**	**195**	**196**	**197**	**198**	**199**	**200**
ecliptEx1	1	0	0	0	3	1	0	0	4	4
ecliptEx2	1	1	0	1	3	1	0	0	4	3
ecliptEx3	1	0	0	1	3	{01}	{12}	2	4	4
ecliptEx4	0	0	0	0	3	2	1	1	4	2
ecliptEx5	1	0	0	1	3	{01}	1	2	4	3
erotylus	1	0	0	0	3	1	1	2	3	2
magd	0	1	0	0	3	2	2	1	1	1
margEx1	1	0	0	0	3	1	0	0	4	2
margEx2	1	1	0	0	3	1	0	0	4	2
refugicornis	1	1	1	0	3	0	1	2	4	2
tet4lam	1	1	0	1	3	2	2	2	1	0
tet5lamAM	1	{01}	0	1	3	1	2	2	{13}	{01}
tet5lamBOL	1	0	0	1	3	1	1	2	4	1
sp.1COL	1	0	0	1	3	1	1	2	4	3
sp.2VEN	1	1	1	0	3	1	1	1	3	1
gibbEx1	1	0	1	0	3	{12}	1	1	3	1
gibbEx4	1	{01}	1	0	3	1	1	1	1	0
gibbEx3	1	1	0	0	3	1	1	1	1	0
gibbEx6	1	1	0	0	3	1	1	2	1	0
gibbEx2	1	1	1	0	3	1	1	1	4	3
gibbEx5	1	0	1	0	3	2	2	1	1	1
gibbEx7	1	0	1	0	3	1	1	1	3	2
gibbEx8	1	0	1	0	3	1	1	1	3	1
sp.3BOL	1	1	0	0	3	0	0	1	3	2
sp.4VENEx1	1	0	0	0	3	2	2	2	4	2
sp.4VENEx2	1	1	0	0	3	2	2	2	4	2
haagi	1	1	0	1	3	1	0	1	1	0
haagiint	1	1	0	1	3	1	1	0	1	0
hirsutus	1	1	0	0	3	1	2	2	3	1

kling	1	2	0	1	2	1	1	1	1	1
lenzi	1	1	0	1	2	1	2	1	3	0
mysticus	1	1	0	1	1	1	2	1	1	1
punct	1	1	0	1	2	1	2	1	3	0
scutEx1	1	1	0	1	3	2	2	1	3	1
scutEx2	1	1	0	1	3	1	2	1	4	2
sp.5Panama	1	1	0	1	1	{01}	{23}	1	0	0
sp.6Mexico	1	1	0	0	2	2	3	1	4	3
sp.7Mexico	1	2	0	1	3	0	1	1	1	0
sp.8GUAT	1	1	0	1	3	1	1	1	3	2
sp.9GUAT	1	1	0	1	3	1	1	1	3	1
sp.10GUAT	1	1	0	1	3	0	0	1	3	0

Character #	**201**	**202**	**203**	**204**	**205**	**206**	**207**	**208**	**209**	**210**
ecliptEx1	2	3	1	2	1	0	1	1	1	1
ecliptEx2	1	2	0	1	1	0	1	1	1	1
ecliptEx3	1	3	0	2	1	{01}	1	1	1	0
ecliptEx4	1	3	0	2	1	?	1	1	1	1
ecliptEx5	2	{23}	0	2	1	{01}	1	1	1	0
erotylus	1	1	0	{01}	1	0	1	0	1	0
magd	1	1	0	1	1	0	1	1	1	1
margEx1	1	1	0	0	1	0	1	0	1	0
margEx2	1	1	0	0	1	0	1	0	1	0
refugicornis	1	1	0	1	1	0	1	1	1	1
tet4lam	1	1	0	1	1	0	1	0	1	0
tet5lamAM	2	{12}	0	{01}	1	0	1	{01}	1	{01}
tet5lamBOL	1	1	0	2	1	0	1	0	1	0
sp.1COL	1	1	0	1	1	0	1	1	1	0
sp.2VEN	1	1	0	0	1	0	?	1	1	1
gibbEx1	1	{01}	0	1	1	0	1	1	1	1
gibbEx4	1	1	0	0	1	0	1	{01}	1	1
gibbEx3	1	{01}	0	0	1	0	1	0	1	1
gibbEx6	1	1	0	0	1	?	1	1	1	1
gibbEx2	1	0	0	0	1	0	1	1	1	1
gibbEx5	1	0	0	0	1	0	1	1	1	1
gibbEx7	1	1	0	0	1	0	1	1	1	1
gibbEx8	1	0	0	0	1	0	1	0	1	1
sp.3BOL	2	0	1	0	1	0	1	1	1	1
sp.4VENEx1	1	0	{01}	0	1	0	1	1	1	{12}
sp.4VENEx2	1	0	1	0	1	?	1	1	1	1
haagi	5	1	0	2	1	0	1	1	1	0
haagiint	5	1	0	2	1	0	1	1	1	0
hirsutus	5	1	0	2	1	0	1	0	1	1

kling	1	1	0	1	1	0	1	1	1	0
lenzi	5	1	0	{12}	1	0	1	1	1	0
mysticus	1	1	0	2	1	0	1	0	1	0
punct	5	1	0	{12}	1	0	1	1	1	0
scutEx1	1	1	0	0	1	0	1	0	1	0
scutEx2	2	1	0	0	1	0	1	0	1	0
sp.5Panama	5	1	0	1	1	1	1	1	{01}	0
sp.6Mexico	5	1	0	{01}	1	0	1	1	1	1
sp.7Mexico	1	{23}	{01}	2	1	0	1	0	1	1
sp.8GUAT	0	1	0	1	1	0	1	1	1	{01}
sp.9GUAT	0	1	0	2	1	0	1	1	1	0
sp.10GUAT	3	2	0	2	1	0	1	1	1	0

Character #	211	212	213	214	215	216	217	218	219	220
ecliptEx1	0	2	1	0	2	3	2	1	0	1
ecliptEx2	0	1	2	0	2	4	2	1	0	1
ecliptEx3	0	2	2	{01}	2	{23}	2	1	0	1
ecliptEx4	0	2	0	0	?	?	?	?	?	?
ecliptEx5	0	2	1	{01}	2	4	2	1	0	1
erotylus	0	{01}	1	0	1	3	2	2	0	0
magd	0	2	1	0	2	2	2	2	0	0
margEx1	0	0	1	0	1	2	2	2	0	0
margEx2	0	2	1	0	?	?	?	?	?	?
refugicornis	0	1	1	0	?	?	?	?	?	?
tet4lam	0	{12}	1	0	2	1	2	2	0	0
tet5lamAM	0	1	1	0	2	0	2	2	0	0
tet5lamBOL	0	2	0	?	?	?	?	?	?	?
sp.1COL	0	1	1	0	{12}	{23}	2	2	0	0
sp.2VEN	0	0	1	0	?	?	?	?	?	?
gibbEx1	0	{12}	{01}	0	{12}	2	2	2	0	0
gibbEx4	0	1	0	0	1	2	2	2	0	0
gibbEx3	0	1	{01}	0	1	2	2	2	0	0
gibbEx6	0	0	1	0	2	4	2	2	0	0
gibbEx2	0	0	0	0	1	2	2	2	0	0
gibbEx5	0	0	0	0	?	?	?	?	?	?
gibbEx7	0	1	0	?	2	4	2	2	0	0
gibbEx8	0	0	0	0	1	0	2	2	0	0
sp.3BOL	0	0	0	0	1	0	2	2	0	0
sp.4VENEx1	0	{01}	0	0	2	2	2	2	0	0
sp.4VENEx2	0	0	0	0	2	1	2	2	0	0
haagi	0	2	1	0	0	1	2	2	0	0
haagiint	0	2	1	1	2	1	2	2	0	0
hirsutus	0	2	1	0	2	4	2	2	0	0

kling	1	2	{12}	0	2	1	2	2	0	0
lenzi	0	2	1	0	2	0	2	2	0	0
mysticus	0	2	1	0	2	1	2	2	0	0
punct	0	2	1	0	2	3	2	2	0	0
scutEx1	1	1	1	0	?	?	?	?	?	?
scutEx2	1	1	1	0	2	1	2	2	0	0
sp.5Panama	0	2	{01}	1	2	4	2	2	0	0
sp.6Mexico	1	1	0	0	1	3	0	2	0	0
sp.7Mexico	0	2	1	0	1	1	2	2	0	1
sp.8GUAT	1	{12}	0	0	2	1	2	2	0	0
sp.9GUAT	1	2	1	{01}	?	?	?	?	?	?
sp.10GUAT	1	2	1	0	2	1	1	2	0	0

Character #	**221**	**222**	**223**	**224**	**225**	**226**	**227**	**228**	**229**	**230**
ecliptEx1	1	0	1	2	0	2	0	1	0	0
ecliptEx2	1	0	1	0	0	2	0	1	0	0
ecliptEx3	1	0	1	0	0	1	{01}	0	1	0
ecliptEx4	?	?	?	?	?	?	?	?	?	?
ecliptEx5	1	0	1	2	0	1	{01}	0	1	2
erotylus	0	1	2	2	0	0	1	0	1	0
magd	0	0	2	0	0	0	1	0	1	0
margEx1	0	1	2	2	0	0	0	0	0	0
margEx2	?	?	?	?	?	?	?	?	?	?
refugicornis	?	?	?	?	?	?	?	?	?	?
tet4lam	1	1	2	0	0	0	1	0	0	0
tet5lamAM	0	1	2	0	0	0	0	0	0	0
tet5lamBOL	?	?	?	?	?	?	?	?	?	?
sp.1COL	0	1	2	2	0	0	1	0	1	0
sp.2VEN	?	?	?	?	?	?	?	?	?	?
gibbEx1	{01}	1	2	1	0	1	1	0	1	0
gibbEx4	1	1	{02}	1	0	1	0	0	0	0
gibbEx3	1	1	2	1	0	1	1	0	0	0
gibbEx6	1	1	0	0	0	1	0	0	1	0
gibbEx2	1	1	2	2	0	1	1	0	0	0
gibbEx5	?	?	?	?	?	?	?	?	?	?
gibbEx7	0	1	2	0	0	0	0	0	1	0
gibbEx8	0	1	2	1	0	1	1	0	1	0
sp.3BOL	0	1	2	1	0	1	1	0	1	0
sp.4VENEx1	1	0	2	0	0	2	0	0	0	0
sp.4VENEx2	1	1	2	1	0	1	0	0	0	0
haagi	1	0	1	1	0	0	1	0	1	2
haagiint	1	1	0	0	0	0	1	0	1	2
hirsutus	1	0	1	0	0	1	1	0	1	0

kling	1	1	1	0	0	1	1	0	1	0
lenzi	1	0	1	0	0	1	1	0	1	0
mysticus	1	1	1	0	0	1	1	1	0	0
punct	1	0	1	0	0	1	0	{01}	1	0
scutEx1	?	?	?	?	?	?	?	?	?	?
scutEx2	1	1	1	0	0	1	1	0	1	1
sp.5Panama	1	0	0	1	0	1	1	0	0	0
sp.6Mexico	1	1	0	0	0	1	1	0	1	2
sp.7Mexico	1	1	1	2	0	1	1	0	1	0
sp.8GUAT	1	1	0	1	0	1	1	1	1	0
sp.9GUAT	?	?	?	?	?	?	?	?	?	?
sp.10GUAT	1	1	1	2	0	1	0	0	0	0

Character #	**231**	**232**
ecliptEx1	1	0
ecliptEx2	1	0
ecliptEx3	1	0
ecliptEx4	?	?
ecliptEx5	1	0
erotylus	2	{34}
magd	2	2
margEx1	2	2
margEx2	?	?
refugicornis	?	?
tet4lam	2	2
tet5lamAM	2	2
tet5lamBOL	?	?
sp.1COL	2	2
sp.2VEN	?	?
gibbEx1	2	3
gibbEx4	2	3
gibbEx3	2	4
gibbEx6	2	{34}
gibbEx2	2	2
gibbEx5	?	?
gibbEx7	2	3
gibbEx8	2	4
sp.3BOL	2	2
sp.4VENEx1	2	3
sp.4VENEx2	2	{23}
haagi	2	4
haagiint	2	4
hirsutus	2	{34}

kling	2	3
lenzi	2	2
mysticus	2	{34}
punct	2	3
scutEx1	?	?
scutEx2	2	2
sp.5Panama	2	3
sp.6Mexico	2	3
sp.7Mexico	2	2
sp.8GUAT	2	3
sp.9GUAT	?	?
sp.10GUAT	2	2

VITA

Alan Roy Gillogly was born in Pasadena, California and graduated from Verdugo Hills High School in Tujunga, California. After two years of study at Glendale City College, he transferred to the University of California, Riverside where he was awarded a B.S. (1965) and M.S. (1967) in entomology, with an emphasis on the systematics of Coleoptera. While on a one year leave of absence from the University of California, Riverside and attending San Jose State College, in San Jose, California to take courses in entomology that were not offered by the University of California, Riverside, his education was interrupted by the Vietnam War.

Alan was granted a commission in the U.S. Army and served just short of 25 years as a medical entomologist, with considerable time spent overseas. During that period he had the immense privilege of sharing life with his son, (now Dr.) Thomas E.T. Gillogly.

After retiring from the U.S. Army, Alan applied and was accepted into graduate school at Texas A&M University, and had the immense pleasure of participating in an active, stimulating and highly competent group of systematic entomologists, both faculty, staff and students.

In the midst of his PhD program Alan had the great good fortune to marry his soul mate, Patricia O. Gillogly….and is now living happily ever after!

His permanent address is 1821 Nueces Drive, College Station, Texas 77840.