TAXONOMY OF THE ASPIDIPHORUS UENOI SPECIES GROUP (COLEOPTERA:

SPHINDIDAE)

by

JUANITA ANN FORRESTER

(Under the Direction of Joseph V. McHugh)

ABSTRACT

Examination of more than 3,000 museum specimens yielded 102 new species of *Aspidiphorus*. Of those, thirteen are hypothesized to form a monophyletic group, here named the *Aspidiphorus uenoi* species group. A taxonomic treatment of this species group is provided, including a morphological study, new species descriptions, keys, illustrations, and notes on *Aspidiphorus* distribution and biology. Due to its astonishing biodiversity, the small island of Madagascar is globally significant in terms of species conservation. Ideally, the logical progression toward conservation begins with an assessment of species present on the island. As in many tropical regions, insects and beetles, in particular, form a conspicuous part of Madagascar's fauna. Of the Sphindidae, two of nine genera occur in Madagascar: *Sphindus* and *Aspidiphorus*. The *Aspidiphorus* of Madagascar are herein described and illustrated, and a taxonomic key to those species is included.

INDEX WORDS: Sphindidae, morphology, Aspidiphorus, phylogeny

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CHAPTER 1

INTRODUCTION

The first part of this work concerns a new species group within the coleopteran family Sphindidae. Sphindidae is a family of diminutive, cryptic, myxomycophagous (slime mold feeding) beetles. Found in all major biogeographic regions of the world, the family is composed of fifty-eight species divided among nine genera. *Aspidiphorus* Zeigler in DeJean (1821) is one of the two largest, with seventeen described species. Although the genus does not occur in the New World, representatives of *Aspidiphorus* have been found on all continents of the Old World, suggesting a relatively late origin for the genus (Sen Gupta & Crowson 1977).

Despite records indicating that *Aspidiphorus* has been around for over a century, very little is known about the biology of these curious beetles. Presumably, all are myxomycophagous although specimens have been collected from various other habitats including rotting wood and puffballs (Bennet 1889; Blatch 1889; Bennet 1897; Joy 1903). However, many species of slime molds fruit on rotting wood and others very closely resemble puffballs, such as species of *Lycogala* L. As Burakowski and Ślipiński (1987) point out, adults in the field have been observed to lie dormant in woody clefts and leaf litter; however, larvae have never been seen anywhere except slime molds.

Over 3000 individual specimens of *Aspidiphorus* were borrowed from museums around the world, yielding approximately 102 new species. Of those, thirteen seem to form a monophyletic group, the *Aspidiphorus uenoi* species group. The genus, despite

being minute (1.5 - 2.0 mm), exhibits a wealth of morphological diversity, including characters that may be phylogenetically significant. One of these characters is the structure of the pygidium. The dorsal surface of the pygidium has several forms within Sphindidae. Some genera have a dorsal pygidial surface free of depressions or grooves (e.g., Eurysphindus Le Conte, Genisphindus McHugh) while in other genera (e.g., Carinisphindus McHugh, Notosphindus McHugh & Wheeler) there is a weakly demarked median longitudinal depression. In Aspidiphorus and Sphindiphorus Sen Gupta & Crowson, the median depression is very sharply demarked along its lateral edges. Within Aspidiphorus, the median longitudinal groove has two different forms, a parallel-sided form and an apically flared form. Because the median longitudinal depression (or groove) is parallel-sided in other sphindids, the divergent form of the groove observed in some Aspidiphorus species is interpreted here to be the derived condition and a synapomorphy supporting the A. uenoi species group clade. Further support for the monophyly of this group is found in the presence of a protuberance on an abdominal ventrite in adult males. Protuberances on abdominal sternites are not observed elsewhere in the family. This second apparent synapomorphy for the species group, however, is problematic. The ventrite protuberance, though only occurring in those species that also have a flared pygidial groove, violates the principles of position and composition for homology assessment because it occurs on three different ventrites among the species. Therefore, it cannot be considered an unambiguous synapomorphy at this time, although the congruence of its distribution with the fluted pygidial groove does lend support to the hypothesis of monophyly for this group of species.

Another unique morphological aspect of the *A. ueoni* species group involves the tarsal characteristics. Cucujoid beetles typically have dimorphic tarsal formulae: 5-5-5 in the female and 5-5-4 in the male, and simple tarsal claws. All sphindids were thought to have typical cucujoid tarsi (Sen Gupta & Crowson 1977). Some male members of the *A. uenoi* group, however, have a 5-5-5 tarsal formula and serrated tarsal claws. These unique features for Sphindidae are presumed synapomorphies for a small group within the *A. uenoi* species group and are unknown in any other sphindid species.

The second part of this work is a faunal study. Generally, studies of this nature are not recommended for systematics; however, due to Madagascar's small size and geographic isolation, studies of its inhabitants can be useful. Such investigation lays the groundwork for other studies, in particular those concerning evolutionary patterns, migration and dispersal, and niche partitioning. Such inquiries also have the benefit of allowing an enhanced understanding of Madagascar's biodiversity so that it might be compared with floral and faunal variety elsewhere. Due to its isolation, the insects of Madagascar remain understudied at best. The coleopteran family Sphindidae, or slime mold beetles, contains two Malagasy genera: *Sphindus* Chevrolat and *Aspidiphorus* Zeigler in DeJean (McHugh, 1993).

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CHAPTER 2

LITERATURE REVIEW

I. Taxonomic history and classification of Aspidiphorus

Sphindidae is a family of diminutive, cryptic, myxomycophagous (slime mold feeding) beetles. Found in all major biogeographic regions of the world, the family is composed of fifty-eight species divided among nine genera. *Aspidiphorus* Zeigler in DeJean (1821) is one of the two largest, with seventeen described species. Although the genus does not occur in the New World, representatives of *Aspidiphorus* have been found on all continents of the Old World, suggesting a relatively late origin for the genus (Sen Gupta & Crowson 1977).

The nomenclatural history of *Aspidiphorus* is, at best, a morass. DeJean (1821) first published the generic name as "*Arpidiphorus* Zeigler", which contained the nominal species *Nitidula orbiculata* Gyllenhal (1808). Sturm (1826) also referred to *N. orbiculata*, but placed it in the genus *Aspidiphorus* rather than *Arpidiphorus*; however, Zeigler was still credited as having authored the genus. Latrielle (1829) referenced *N. orbiculata* and included it in *Aspidiphorus*, with authorship attributed to Zeigler in DeJean. DeJean's (1837) subsequent catalog referred to *Aspidiphorus*. Seemingly, *Arpidiphorus* was a misspelling. As McHugh (1995) points out, etymological considerations advocate that a misspelling did indeed occur. In classical languages, the stem 'arpid-' is meaningless. However, 'aspid-' is from the Greek word meaning

"shield". When joined with 'phorus' (=bearer), especially given the shape of these beetles, *Aspidiphorus* is appropriate.

Thomson (1859) was the first to recognize *Aspidiphorus* and *Sphindus* Megerle in DeJean (1821) as being confamilial. He erected the genus *Coniporus*, and added the single species *Aspidiphorus orbiculatus* Gyllenhal (1808). He then placed *Coniporus* (a junior synonym of *Aspidiphorus*) into a new tribe, the 'Coniporina' and *Sphindus* into the tribe Cioina, and both tribes in the family Cioidae.

Three years later Jacquelin du Val (1861) transferred the two genera to the new 'Familie des Sphindides'. In 1863, Thomson raised the tribe 'Coniporina' to family level as Coniporidae, which contained *C. orbiculatus* Gyllenhal. He kept the family name Sphindidae for *Sphindus*. Keisenwetter (1877) later proposed the family Aspidiphoridae to include only *Aspidiphorus*, with Coniporidae and *Coniporus* listed as synonyms. Despite Jacquelin du Val's unification of *Sphindus* and *Aspidiphorus* in Sphindidae, many authors continued to recognize Aspidiphoridae Keisenwetter as the family name for *Aspidiphorus* (e.g., Houlbert 1922; Schenkling 1931; Horion 1960). Subsequent works continued to include *Aspidiphorus* within the family Sphindidae (Sen Gupta & Pal 1982; McHugh 1993). As McHugh (1995) notes, Aspidiphoridae has priority over Sphindidae because of Thomson's (1859) creation of the tribe Coniporina. However, it was decided that due to the nearly universal usage of 'Sphindidae' to refer to the family containing both *Sphindus* and *Aspidiphorus*, 'Sphindidae' should be placed on the Official List of Family-Group Names in Zoology (ICZN 1997). A summary of Sphindid morphology is provided by Sen Gupta and Crowson (1977). The family is thought to occupy a basal position within the Cucujoidea, and the position of *Aspidiphorus* within Sphindidae is relatively clear based on phylogenetic studies by McHugh (1993) and Chiao and McHugh (2000). *Aspidiphorus* is the sister group to the clade (*Eurysphindus* LeConte + *Genisphindus* McHugh) and is distinguishable from closely related genera by the greatly broadened intercoxal process.

II. Aspidiphorus biology

Myxomycophagy occurs in a number of families of Polyphaga, most notably Leiodidae, but also Rhysodidae, Staphylinidae, Clambidae, Eucinetidae, Cerylonidae, and Lathridiidae. Sphindidae, however, is unique among families in being myxomycophagous in all species as both larvae and adults (Lawrence & Newton 1980; Crowson 1981). Aspidiphorus has been collected from various slime mold species, including Stemonitis fusca Roth (Keys 1914), Reticularia lycoperdon Bulliard, and Fuligo septica L. (Lawrence & Newton 1980). Several collectors report finding the obscure genus in "a powdery fungus" either under bark or in rotting wood (Bennet 1889; Blatch 1889; Champion 1893; Bennet 1897). Additionally, at least one author claims to have found Aspidiphorus in an unknown species of puffball (Joy 1903) although several species of slime molds, e.g., *Lycogala* L., closely resemble puffballs. Individual adult specimens may be found in alternative habitats; however, there are no records for Aspidiphorus larvae anywhere other than slime mold spore masses. Burakowski and Slipiński (1987) note that adults in the field hibernate under loose bark, in crevices of wood, or leaf litter, so perhaps those specimens not found in myxomycetes were in fact

overwintering elsewhere. In addition to notes pertaining to the habitat of *Aspidiphorus*, Burakowski and Ślipiński (1987) provide the only detailed life history of an *Aspidiphorus* species (*Aspidiphorus orbiculatus* Gyllenhal).

III. New contributions to the study of Sphindidae

With estimates of undescribed coleopteran species ranging anywhere from 5 to 30 million (Erwin, 1988), it is apparent that taxonomists have but scratched the surface of Earth's biodiversity. Despite their small size (1.5-2.0 mm), there is a wealth of morphological diversity found within *Aspidiphorus*. Specimens borrowed from museums around the world yielded 102 new species, which, when described, will triple the current size of the genus. Of those undesecribed species, thirteen seem to form a monophyletic group. This group, here named the *Aspidiphorus uenoi* species group, is the focus of this study. The purpose of this investigation is to establish the new species group by providing a morphological study, descriptions of new species, an identification key, and summaries of biological and distributional information.

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CHAPTER 3

THE ASPIDIPHORUS UENOI SPECIES GROUP (COLEOPTERA: SPHINDIDAE)¹

¹ Forester, Juanita A. and J. V. McHugh. To be submitted to *Annales Zoologici*.

Abstract. Examination of more than 3,000 museum specimens yielded 102 new species of *Aspidiphorus*. Of those, thirteen are hypothesized to form a monophyletic group, here named the *Aspidiphorus uenoi* species group. A taxonomic treatment of this species group is provided, including a morphological study, new species descriptions, keys, illustrations, and notes on *Aspidiphorus* distribution and biology.

Species included: A. annabelleae sp.n., Japan; A. bidentatus sp.n., Kenya; A. bilineaus sp.n., South Africa, Congo; A. bipennis sp.n., Congo, Nigeria; A. crowsoni sp.n., South Africa; A. geminuspunctatus sp.n., South Africa; A. japonicus Reitter, Japan; A. lacunamagnus sp.n., Congo; A. latuscanalis sp.n., Sumatra; A. palascutellus sp.n., Congo; A. planuscrus sp.n., Congo, Ghana, Kenya; A. rotundiclaviger sp.n., Madagascar; A. uenoi sp.n., Japan.

INTRODUCTION

Sphindidae is a small family of cryptic, myxomycophagous (slime mold feeding) beetles. Comprised of nine genera and fifty-eight species, the family is a prominent part of the fauna associated with slime molds. One of the larger genera of sphindids, *Aspidiphorus* Zeigler in DeJean (1821) includes seventeen known species and is found exclusively in the Old World.

Aspidiphorus enjoys a convoluted nomenclatural history. The genus was first described as "*Arpidiphorus* Zeigler" (DeJean 1861), and contained a single species, *Nitidula orbiculata* Gyllenhal (1808). Subsequently, several authors (e.g., Sturm 1826, Latrielle 1829), including DeJean (1837) referred to the genus as *Aspidiphorus* with credit given to Zeigler as the author. *Arpidiphorus* was an apparent misspelling of *Aspidiphorus* in DeJean's 1821 work. As McHugh (1995) observes, etymological considerations also support *Aspidiphorus*: in classical languages, the stem 'arpid-' means nothing, while 'aspid-' is the Greek word for "shield". When 'aspid-' is combined with 'phorus' (=bearer), the name *Aspidiphorus* is very appropriate given the appearance of the beetles.

Thomson (1859) was the first to recognize the confamilial relationship of *Aspidiphorus* and *Sphindus* Megerle in DeJean (1821). He placed them both in the family Cioidae, but assigned *Aspidiphorus orbiculatus* Gyllenhal (1808) to the new genus *Coniporus* (a junior synonym of *Aspidiphorus*). Additionally, he erected two new tribes, Coniporina and Cioina, which contained *Aspidiphorus* and *Sphindus*, respectively.

In 1861, Jacquelin du Val created the 'Familie des Sphindides', which, like Cioidae, included both *Aspidiphorus* and *Sphindus*. Later, Thomson (1863) elevated Coniporina to family level as Coniporidae (which included *C. orbiculatus* Gyllenhal) while keeping the family name Sphindidae for *Sphindus*. Keisenwetter (1877) then published the family name Aspidiphoridae, which contained only *Aspidiphorus*, and listed Coniporidae and *Coniporus* as synonyms. In spite of Jacquelin du Val's unification of *Sphindus* and *Aspidiphorus* in Sphindidae, some later authors continued to refer to the family containing *Aspidiphorus* as Aspidiphoridae Keisenwetter (e.g., Houlbert 1922; Schenkling 1931; Horion 1960). Because Thomson (1859) established the tribe Coniporina based on a junior synonym of *Aspidiphorus*, Aspidiphoridae has priority over Sphindidae (McHugh, 1995). However, the ICZN (1997) ruled that Sphindidae should be placed on the Official List of Family-Group Names in Zoology, due to the nearly universal usage of Sphindidae in reference to the family containing both *Aspidiphorus*

Although *Aspidiphorus* has been recognized for over a century, very little is known about the biology of these curious beetles. Presumably, all are myxomycophagous although specimens have been collected from various other habitats including rotting wood and puffballs (Bennet 1889; Blatch 1889; Bennet 1897; Joy 1903). However, many species of slime molds fruit on rotting wood and others very closely resemble puffballs, such as species of *Lycogala* L. As Burakowski and Ślipiński (1987) point out, adults in the field have been observed to lie dormant in woody clefts and leaf litter; however, larvae have never been seen anywhere except slime molds.

Over 3000 individual specimens of *Aspidiphorus* were borrowed from museums, yielding 102 new species. Of those, thirteen are hypothesized to form a monophyletic group, the *Aspidiphorus uenoi* species group, which is the subject of this report.

MATERIALS AND METHODS

Specimens were sorted initially and examined using a Leica Wild Type MZ8 stereoscopic microscope. For further study, dried, point-mounted specimens were carefully removed from their paper points by immersion in distilled water or 75% ethanol, depending upon the type of glue used to secure them. Specimens were further prepared for dissection by immersion in a weak potassium hydroxide solution. Beetles were dissected in 75% ethanol then slide mounted in glycerol for ease of movement. Illustrations were made using a Leica Leitz DMRB compound microscope fitted with a camera lucida.

The following museums and individuals have graciously loaned material for this study and will hereafter be referred to by the following abbreviations:

ANIC - Australian National Insect Collection, Canberra, Australia

BPBM – Bishop Museum, Honolulu, Hawaii, USA

CASC - California Academy of Sciences, San Francisco, California, USA

CMNC - Canadian Museum of Nature, Ottawa, Ontario, Canada

CMNH - Carnegie Museum, Pittsburgh, Pennsylvania, USA

HNHM – Hungarian Natural History Museum, Budapest, Hungary

MCZ - Museum of Comparative Zoology, Harvard University, Cambridge,

Massachusetts, USA

MHNG - Museum d'Historie Naturelle, Geneva, Switzerland

MRAC – Musee Royal de L'Afrique Centrale, Tervuren, Belgium

- TMSA Transvaal Museum, Pretoria, South Africa
- UENO Teruhisha Ueno, personal collection, Japan
- USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
- ZMHB Museum Fur Naturkunde, Berlin, Germany

ASPIDIPHORUS ZEIGLER IN DEJEAN (1821)

Description. Length 1.5 – 2.0 mm. Body shape ovate, sometimes elongate oval; laterally convex and hemispherical to somewhat dorsoventrally compressed (Fig. 2.1). Color uniformly brown to reddish black, occasionally with antennal club and pronotum darker than overall body color. Head deflexed, only partially visible from above (Fig. 2.1).

Head with posterior margin deeply sinuate, with none to several basal rows of deep, enlarged punctures (Figs. 2.2, 2.27, 2.29), basal punctures sometimes elongate, sometimes uniformly rounded with discrete margins; other dorsal head punctures usually distinctly smaller, shallower (Figs. 2.2, 2.27, 2.29); clypeus slightly emarginate laterally, apex straight to feebly arcuate, frontoclypeal suture arcuate (Figs. 2.2, 2.27 - 2.29); eye black, moderately coarsely facetted, prominent but not bulging (Figs. 2.1, 2.2, 2.27 –

2.29); 1 antennal groove reaching from antennal origin over dorsal eye margin to lateral edge of head (Figs. 2.2, 2.27 - 2.29); ventral surface with inwardly curving, somewhat shallow antennal grooves (Fig. 2.3); antennae ten-segmented; antennomere I large, asymmetrical, elongate, curved; II subglobose, asymmetrical, shorter than I; III cylindrical, elongate; IV elongate to submoniliform; V-VII submoniliform, gradually increasing in width; VIII-X enlarged to form a densely pubescent club; VIII trapezoidal, almost always widest apically, usually longer than wide, IX typically about as wide as long, X frequently longer than wide (Figs. 2.4, 2.32, 2.33), occasionally about as long as wide (Figs. 2.30, 2.31), apex rounded (Figs. 2.30, 2.31) to acutely pointed (Figs. 2.4, 2.32, 2.33); labrum small, almost completely covered by clypeus, apex straight to weakly bilobed (Figs. 2.5, 2.6), mandible with deep cavity opening partially covered by prominent tubercle, tubercle appearing slightly flattened, dorsal mandibular surface with depressed area extending from midpoint of tubercle to lateral mandibular margin, gradually widening apically, with well developed mola, 1 apical tooth and 1 subapical denticle (Fig. 2.36), or 1 apical tooth and 2 (Fig. 2.35), 3 (Fig. 2.34), or 4 smaller serrations (Figs. 2.7); lacinia elongate, with laterally projecting, stout spine, galea slender, with setose apex, maxillary palp 4-segmented, with palpomere I slender, II robust, III somewhat elongate, and IV lengthened and cylindrical (Fig. 2.8); labium trapezoidal with deep, round punctures, palpi 3 segmented, with basal segment small, middle segment inflated, and distal segment slender and cylindrical (Fig. 2.9).

Pronotum convex, narrowest anteriorly, punctation evenly scattered and generally similar to that of dorsal head, anterior margin straight or nearly so, posterior margin markedly sinuate, emarginate opposite scutellum, slightly compressed laterally, lateral

margins smooth (Fig. 2.12); prosternum very narrow ventrally, prosternal process narrowest basally, widest posteriorly, with several large punctures (Fig. 2.13), procoxal cavities widely opened exteriorly.

Mesosternum with sinuate anterior edge abruptly cleft opposite apex of prosternal process; posterior edge with rectangular indention for reception of prosternal process. Metasternum inflated, most often with impunctate area adjacent to posterior margin bearing indented, rectangular ledge to receive intercoxal process (Fig. 2.14). Legs fairly long, slender. Procoxa rounded (Fig. 2.11), mesocoxa slightly transverse (Fig. 2.14), metacoxa elongate (Fig. 2.17). Femur widest medially, moderately setose, often grooved ventrally to receive tibia, rounded to squared distally (Figs. 2.11, 214, 2.17). Tibia longer, narrowest basally, gradually to dramatically flared apically, with an inverted vshaped apical groove (Fig. 2.38) or with weak depression between two longitudinal carinae (Fig. 2.39) for tarsal reception, apex ringed with short, stout setae (Figs. 2.11, 2.14, 2.17, 2.38, 2.39). Tarsi 5-5-5 female, 5-5-5 or 5-5-4 male, tarsomeres simple, apical tarsomere as long as others combined, all tarsomeres moderately setose ventrally (Figs. 2.11, 2.14, 2.17), claws simple except for tooth-like serrations in 5-5-5 males (Fig. 2.18). Scutellum of moderately large size, normally wider than long (Fig. 2.10), occasionally elongate medially (Fig. 2.37), apex somewhat rounded to acute (Figs. 2.10, 2.37). Elytron covering entire abdomen, convex with prominent, impunctate humeral callus; dorsal surface with 11 long rows of punctures, punctures arranged singly to geminate (Figs. 2.1, 2.16, 2.40) with somewhat convex, pubescent strial interspace with 1-2 rows of posteriorly directed, pale, suberect setae (Fig. 2.1); membranous wing with 2 anal veins, jugal lobe absent (Fig. 2.15).

Abdomen with 5 visible ventrites, I uniformly punctate and about twice as long as others, II – V approximately equal in length with a basal row of moderately large depressions, sternites overlapping slightly, males and some females with a single raised, square protuberance on sternite II (Fig. 2.41), III (Fig. 2.42), IV, or V (Figs. 2.19, 2.20, 2.24). Intercoxal process wide, about as broad as long (Figs. 2.19, 2.24, 2.41, 2.42). Pygidium with relatively large depressions over dorsal surface, widest basally, with toothed apical ledge, truncate to broadly rounded apex, bearing medial longitudinal groove; groove parallel sided basally, distal portion of groove sometimes flared, relatively large depressions over dorsal surface, groove with 1-2 rows of punctures (Figs. 2.21, 2.25, 2.43-2.47).

Biology. All species apparently feed on myxomycetes.

Distribution. Exclusively Old World.

Remarks. This genus superficially resembles *Eurysphindus* and *Genisphindus* in that it has 10-segmented antennae, an impunctate area on the metasternum, widely open procoxal cavities, and a convex, oval body shape. It is distinguishable from *Eurysphindus* by having one to several rows of enlarged punctures along the posterior head margin and differs from both *Eurysphindus* and *Genisphindus* in having a somewhat flattened mandibular tubercle with indented area dorsally, a lacinial spine, a well defined pronotal emargination opposite the scutellum, no jugal lobe on the membranous wing, a greatly broadened intercoxal process, and a discrete pygidial slot.

Species included: A. annabelleae sp.n., Japan; A. bidentatus sp.n., Kenya; A. bilineaus sp.n., South Africa, Congo; A. bipennis sp.n., Congo, Nigeria; A. crowsoni sp.n., South Africa; A. geminuspunctatus sp.n., South Africa; A. japonicus Reitter, Japan;

A. lacunamagnus sp.n., Congo; *A. latuscanalis* sp.n., Sumatra; *A. palascutellus* sp.n.,
Congo; *A. planuscrus* sp.n., Congo, Ghana, Kenya; *A. rotundiclaviger* sp.n., Madagascar; *A. uenoi* sp.n., Japan.

KEY TO THE ASPIDIPHORUS UENOI SPECIES GROUP

1.	Protibia cylindrical, with distal, inverted v-shaped, longitudinal tarsal groove
	(Fig. 2.38)
-	Protibia flattened with shallow tibial groove demarked by two longitudinal
	carinae (Fig. 2.39)4
2.(1)	Basal region of dorsal head surface with multiple rows of enlarged punctures or
	depressions (Fig. 2.27)
-	Basal region of dorsal head surface with a single row of enlarged punctures or
	depressions (Figs. 2.2, 2.28)
3.(2)	Elytral punctures arranged in single rows (Figs. 2.1, 2.16)A. lacunamagnus
-	Elytral punctures arranged in geminate rows (Fig. 2.40)
4.(1)	Mandible with multiple subapical serrations (Figs. 2.7, 2.34, 2.35)
-	Mandible with one subapical denticle (Fig. 2.36)
5.(4)	Mandible with four subapical serrations (Fig. 2.7)
-	Mandible with less than four subapical serrations (Figs. 2.34, 2.35)7
6.(5)	Protrusion on abdominal ventrite V (Figs. 2.19, 2.20, 2.24)
-	Protrusion on abdominal ventrite III (Fig. 2.42)
7.(5)	Pygidial apex truncate (Figs. 2.21, 2.43-2.45)
-	Pygidial apex rounded (Figs. 2.46, 2.47)

8.(7)	Pygidial groove flare wide, greater than or equal to 5 puncture
	diameters
-	Pygidial groove flare narrow, less than 5 puncture diameters11
9.(7)	Antennal club segments broad, appearing rounded. (Figs. 2.30, 2.31,
	2.33)
-	Antennal club segments elongate, subcylindrical. (Figs. 2.4, 2.32)10
10.(9)	Scutellum broadly rounded apically (Fig. 2.10)
-	Scutellum elongate medially, spade-shaped (Fig. 2.37)A. palascutellus
11.(8)	Mandibles with three subapical serrations.(Fig. 2.34)12
-	Mandibles with two subapical serrations (Fig. 2.35)
12.(11)	Basal region of dorsal head surface with three discrete rows of enlarged
	punctures, remaining surface impunctate
-	Basal region of dorsal head surface with two rows of enlarged puctures,
	remaining surface with widely spaced punctures (Fig. 2.29)

TAXONOMY

Aspidiphorus annabelleae sp. n. (Figs. 2.34, 2.38, 2.48, 2.49)

Description. Dorsal surface of head with single row of partially fused, enlarged punctures along posterior margin, other punctures smaller; clypeal apex rounded, frontoclypeal suture acute; 1 dorsal antennal groove, extending from antennal base to lateral margin of head; antennomere IV elongate, cylindrical, similar in size and shape to III, club elongate, apex acute; mandible with 1 apical tooth and 3 serrations, serrations increasing in size toward apex (Fig. 2.34).

Tibia flattened laterally, widest apically, with inverted longitudinal v-shaped groove extending 2/3 the length of tibia for reception of tarsus (Fig. 2.38). Scutellum wider than long, apex broadly rounded. Elytral punctures arranged in single, straight rows, punctures small; interstices wide, width of 1 puncture.

Pygidial apex truncate; groove with single longitudinal row of punctures, flared apex 3 punctures wide at widest point, groove edge reaching posterior margin of pygidium.

Male. Small protrusion on abdominal ventrite V. Dorsal apex of parameres sinuate (Fig. 2.48), with two rectangular, setose protuberances ventrally (Fig. 2.49).

Holotype, *(*), JAPAN: label data: "RYUKYU IS.", "Ishigaki I.", "Mt. Omoto, 200m", "17-20.XI.1963, "U.S.-Japan", "Coop. Sci.", "Program", G.A. Samuelson", "Malaise trap", "BISHOP".

Additional material, "Mt. Omoto", "Is. Ishigaki", "11 iv 1986", "S. Nomura leg", "JAPAN: RYUKYUS", "*Aspidiphorus*", "sp.1", "det. T. Ueno, 1997" 4 ♂♂, 1 ♀, UENO); "Takeda", "17 March 1989", "T. Ueno leg", "Is. Ishigake", "Okinawa Pref.", "Ryukyus", "*Aspidiphorus*", "sp.1", "det. T. Ueno, 1997" (1 ♂, UENO); "Tokyo, Japan", "V-17-31", "L. Grassitt", "Collector", "L. Grassitt", "Collection" (1 ♂, CASC); "Ishigaki I.", "Mt. Omoto, 200m", "17-20.XI.1963, "U.S.-Japan", "Coop. Sci.", "Program", G.A. Samuelson", "Malaise trap", "BISHOP" (1 ♂, BPBM); "RYUKYU IS.", "Ishigaki I.", "XI-XII 1952", "G.Z. Bohart" (1 gender undet., BPBM).

Etymology. Named in honor of my daughter, Annabelle.

Remarks. This species is similar to *A. japonicus* and *A. lacunamagnus* in that it has a single row of enlarged punctures on the basal region of the dorsal head surface, but is distinguishable by the cylindrical, longitudinally grooved tibia.

Aspidiphorus bidentatus sp. n. (Figs. 2.41, 2.52, 2.53)

Description. Body hemispherical, color dark, orange-brown, shiny, legs and antennomeres I-VII lighter.

Head with dorsal surface bearing single row of basal punctures, other punctures on dorsal surface small, shallow. Antennomere IV submoniliform, similar in size and shape to V-VII, VIII longer than wide, IX wider than long, X with pointed apex; mandible with 1 fairly large subapical denticle.

Metasternum with impunctate region slightly reduced, punctures scattered about in normally impunctate area. Tibia with wide, shallow, bicarinate groove for reception of tarsus. Elytron moderately elongate, with punctures mostly arranged in single rows, some geminate pairs, interstices wide.

Pygidium with rounded apex, median longitudinal groove 2 punctures wide, apical flare slight, only 3 punctures wide distally, groove margins not reaching pygidial apex.

Male. Tarsal formula 5-5-5. Protrusion on abdominal sternite II very small, much more reduced than in other forms (Fig. 2.41). Fused tip of parameres with straight dorsal margin (Fig. 2.52), ventrally with single, tear-shaped protrusion (Fig. 2.53).

Holotype, gender undet., label data: "Kenya, 23.XI.74", "Shimba. Hills", "Aladabaza Pumping", "Station. Malruert" (MHNG).

Additional material, "Chypre", "Maumonia", "C. Besuchet" (1 \Diamond , MHNG).

Etymology. Latin, meaning "two teeth" in reference to the bidentate mandibles.

Remarks. This species is similar to *A. uenoi* in that both have a single row of depressions along the posterior head margin, submoniliform antennomere IV, flattened protibiae, and males with 5-5-5 tarsi, but *A. bidentatus* has one subapical mandibular denticle as compared to 4 subapical serrations in *A. uenoi* and the abdominal protuberance is located on ventrite II, not V as in *A. uenoi*.

Aspidiphorus bilineaus sp. n. (Figs. 2.29, 2.43)

Description. Head with double row of enlarged punctures along posterior margin, several large punctures scattered about over remaining dorsal surface (Fig. 2.29); clypeal apex straight or nearly so, frontoclypeal suture arcuate and acutely pointed; antennomere IV submoniliform, similar to V-VII, club elongate, apex acute; mandible with 1 apical tooth and 3 serrations, third serration small.

Mesothorax with notched anterior margin; metathorax with impunctate region along posterior margin, region extending slightly upward at midline to form an arch. Tibia flattened, flared, and grooved apically for tarsal reception, groove fairly shallow. Scutellum wider than long, almost trapezoidal, with small, shallow, round punctules. Elytral punctures small, arranged in single, mostly straight rows, interstices wide.

Pygidium with large punctures over entire surface, apex truncate; groove with single row of punctures, flared apex four punctures wide at widest point, groove edges reaching posterior pygidial margin (Fig. 2.43).

Male. Protuberance on abdominal ventrite V, fused tip of parameres weakly bilobed apically with no ventral protrusion.

Holotype, ♂, "S. Afr. Zululand", "Mtubetube-Dukuduku", "28.22 S-32.19E", "7.4.1974; E-Y; 335", "indig. Forest litter", "leg. Endrody-Younga" (TMSA).

Additional material, same label data as holotype, (3 & 3, 2 & 9, 10 gender undet.)TMSA); "Congo-Belge: P.N.A.", "11-12-v-1955", "P. Vanschuytbroeck", "13.071-74", "Secteur Nord", "riv. Meya", "affl. Ikono, 840 m." (1 ♀, 1 gender undet., MRAC); " RSA:E. Transvaal", "Kruger Park, Pretoriuskop", "13.XII.85, S.&J. Peck", "Ficus sycamorus fruit", "litter Berlese, thorn scrub", (1 Å, CMNC); "Kenya 3.XI.74", "am N de Kisumu", "1400m.abahmert" (2 33, MHNG); "Africa or.", "Katona 905", "Pangani", "1905.V.10" (2 gender undet., HNHM); "Mus. Roy. Afr. Centr.", "Brazzaville; Foret Pattes", "d'Ole, IX-1960", "J.P. Adam" (1 gender undet., MRAC), "Congo Belge P.N.G.", "Miss H. DeSaeger", "PpK. 9/g/9, 10-ix-52", "H. DeSaeger. 4044" (1 3), MRAC); "GHANA: Western region", "Pretsea", "30m, N 4 55 - W 1 52", "Dr. S. Endrody-Younga", "Nr. 339", "singling", "23.IV.1969" (1 ♂, 1 ♀, MRAC); "Coll. Mus. Congo", "Bambesa", "VII-1937", J. Vrydagh" (1 \bigcirc , 1 \bigcirc , 1 gender undet.); "Congo Belge P.N.G.", "Miss H. DeSaeger", "II/fd/17, 11-VI-1951", "Rec. H. DeSaeger. 1899" (1 3), MRAC); "Congo Belge P.N.G.", "Miss H. DeSaeger", "II/ke/9, 12-X-1951", "Rec. H. DeSaeger. 2602" (1 Q, MRAC); "Congo Belge P.N.G.", "Miss H. DeSaeger", "II/id/8, 31-X-1951", "Rec. H. DeSaeger. 2708" (1 ♀, MRAC); "Congo Belge P.N.G.", "Miss H. DeSaeger", "11/fd/17, 6-VIII-1951", "Rec. H. DeSaeger. 2224" (1 ♀, MRAC); "GHANA: Asbanti region", "Ofinso", "259 m, N 6 54- W 1 39", "Dr. S. Endrody -Younga", "Nr. 65", "singling", "4.IX.1965" (1 ♀, HNHM); "Musee du Congo",

"Bambesa", "L-X-1937", "J. Vrydagh" (1 ♀, MRAC); "KENYA, Kakamega Forrest",
"Reserve, submontane", "rainforest, 1800m", "beneath stones", "& logs, 30.1.1992",
"No. 520, O. Merkl" (4 gender undetermined, HNHM); "Congo Belge P.N.G.", "Miss H.
DeSaeger", "II/fd/5, 25.X.1951", "Rec. H. De Saeger. 2678" (1 gender undet., MRAC);
"Musee du Congo", "Congo da Lemba", "V-1912", "R. Mayne" (1 gender undet.,
MRAC); "Musee du Congo", "Bambesa", "2.X.1937", "J. Vrydagh" (1 gender undet.,

Etymology. Latin, meaning "two lines", referring to the double row of enlarged punctures along the posterior head margin.

Remarks. This species is similar to *A. annabelleae*, *A. japonicus*, *A. planuscrus*, and *A. palascutellus* in that all have three subapical mandibular serrations, but differs from all in the two rows of enlarged punctures along the posterior margin of the dorsal head surface.

Aspidiphorus bipennis sp. n. (Figs. 2.33, 2.35)

Description. Body oval, convex, head deflexed. Color uniformly dark brown; antennomeres I-VII and legs lighter brown.

Head with narrow, depressed line along posterior margin, punctures not discrete, punctures on dorsal surface evenly distributed, small and shallow; frontoclypeal suture arcuate, but not acutely so; one antennal groove extending from antennal insertion over dorsal margin of eye to lateral margin of head; antennal segment IV elongate, nearly half as long as III, VIII as wide as long, X short, almost as wide as long, with rounded appearance, (Fig. 2.33); mandible with 1 apical tooth and 2 serrations (Fig. 2.35).

Metasternum with posterior impunctate region forming a "bell curve" shape, punctures in straight line along posterior edge. Femur widely grooved for reception of tibia. Tibia short, only as long as femur, laterally flattened, apically flared, with darkened carinae demarking shallow groove for reception of tarsus. Elytron with double to confused rows of punctures, interstice wide, greater than one puncture width.

Pygidium with rounded apex, groove with single row of punctures, flare 3 punctures wide at apex, groove margin short, not reaching posterior edge of pygidium.

Male. Small, knob-like protuberance on abdominal ventrite II.

Holotype, ♀, CONGO: label data: "Congo Belge P.N.G.", "Miss H. DeSaeger", "II/fd/17, 3-IV-1952", "H. DeSaeger. 3279", "Aspidiphoridae" (MRAC).

Additional material, "Congo Belge P.N.A.", "5-VIII-1954", "P. Vanschuytbroeck &", "H. Synave 9816-21", "Massif Ruwenzori", "Mont Ngulingo", "pres de Nyamgaleke", "2500m, ex P.N.A." (1 \Diamond , MRAC); "Nigeria: Zugurama", "NW State 15 Sep. 1974", " J.T. Medler Coll." (2 $\Diamond \Diamond$, USNM); "Musee du Congo", "Kisantu", "-1932", "R.P. Vanderyst", "Aspidophorus", "Det. By R. Leschen" (1 \Diamond , MRAC); "Nigeria: Ile-Ife", W. State, Oct. 1973", "J.T. Medler Coll."(1 \heartsuit , MHNG); "Congo-Belge, P.N.G.", "Miss H. DeSaeger", "II/gd/11, 11-III-1952", "H. DeSaeger, 3183" (4 $\image \diamondsuit$, MRAC); "Musee Du Congo", "Congo da Lemba", "II-III-1913", "R. Mayne" (1 gender undet., MRAC); "Congo Belge P.N.A.", "5-VIII-1954", "P. Vanschuytbroeck &", "H. Synave 9816-21", "Massif Ruwenzori", "Mont Ngulingo", "pres de Nyamgaleke", "2500m, ex P.N.A." (1 gender undet., MRAC).

Etymology. Latin meaning, "double edge", in reference to the bicarinate tibiae.

Remarks. This species resembles *A. planuscrus*, but has small punctures on the dorsal head surface, not large ones like *A. planuscrus*. *A. bipennis* also differs from *A. planuscrus* in having 2 subapical mandibular serrations as opposed to 3, and the rounded pygidial apex instead of a truncate apex like *A. planuscrus*.

Aspidiphorus crowsoni sp. n. (Figs. 2.42, 2.44, 2.50, 2.51)

Description. Body form ovate, laterally convex. Color deep red-black, pronotum slightly darker.

Head with single depressed line along sinuate posterior margin, punctures in basal row not discrete, remainder of dorsal surface with large, somewhat scattered punctures, greater than one puncture width between; one pair of antennal grooves, from antennal insertion to lateral head margin; clypeal apex straight; frontoclypeal suture arcuate, but not acutely pointed; antennomere IV submoniliform, more similar to V-VII than to III, VIII narrow basally, widest apically, almost trapezoidal in form, IX wider than long, X elongate, apex acute; mandible with 1 apical tooth and 4 small serrations; labrum feebly sinuate apically.

Metasternum with impunctate area slightly reduced, punctures present along midline. Tibia widest apically, bicarinate to form a wide, shallow groove for tarsal reception. Scutellum wider than long, widest apically, apex straight or nearly so. Elytron with medium sized punctures arranged in single rows, some with geminate pairs, interstices about 1 puncture diameter wide. Pygidium with groove extending 2/3 of pygidial length, flare is present, but only slightly depressed, groove 2 punctures wide at narrowest point, 6 punctures wide at widest point, pygidial apex truncate (Fig. 2.44).

Male. Protrusion present on abdominal ventrite III (Fig. 2.42). Fused tip of parameres with dorsal apex slightly rounded (Fig. 2.50), ventrally with single, bilobed protrusion (Fig. 2.51).

Holotype, ♀, label data: "REP. S. AFRICA: Cape", "Prov. Stormsrivier", "Goesabos 5-30 Dec.", "1981 81-142 podocarp", "forest, malaise", "trough, S. & J. Peck" (ANIC).

Paratypes, same label data as holotype, (1 \Diamond , 3 \bigcirc \Diamond , ANIC).

Etymology. Named in honor of the great coleopterist, Roy A. Crowson.

Remarks. This species is easily recognized among congeners by the incomplete pygidial groove.

Aspidiphorus geminuspunctatus sp. n.

Description. Head with a single row of enlarged depressions along sinuate posterior margin, other punctures on dorsal surface smaller; clypeal apex straight or nearly so, frontoclypeal suture acute; 1 antennal groove reaching from antennal insertion to lateral margin of head; antennomere IV submoniliform, similar in size and shape to V-VII, club segments elongate, apex acute; labrum with straight apical margin, mandible with 1 apical tooth and 2 serrations, with the most distal serration very small.
Tibia widest apically, with bicarinate, shallow groove for reception of tarsus. Scutellum wider than long, scattered with small punctures. Elytral punctures larger, arranged in double rows, interstices approximately 1 puncture diameter wide.

Pygidial apex truncate, groove 2 punctures wide, flared apex 4 punctures wide at widest point, groove edges not reaching posterior margin of pygidium.

Male. Tarsi 5-5-5. Raised protrusion on abdominal sternite V. Fused tip of parameres with sinuate dorsal margin and two setose lobes on either side of midline; ventrally with broad, slightly bilobed protrusion.

Holotype, ♂, label data: "RSA: E. Transvaal, 11km SE", "Pilgrim's Rest, 1400m", "11-31.XIII.85. S.& J. Peck", "relicnativeforest", "flightintercepttraps" (CMNC).

Additional material, "RSA: E. Transvaal", "21kmW Trichardtsdal", "23-30.XII.85, S.& J. Peck", "Malta, riverineforest", "intercepttrap, 940m", (1 ♂, CMNC). "RSA: E. Transvaal, 11km SE", "Pilgrim's Rest, 1400m", "11-31.XIII.85. S.& J. Peck", "relicnativeforest", "flightintercepttraps" (1 ♂, CMNC); "S. AFRICA. Tvl. 20km", "Kruger N. Pk. Skukuza", "12-14.XII.1985", H & A Howden" (1 ♂, CMNC); "RSA: E. Transvaal", "Kruger Park, Satara", "15-18.XII.85, S.& J. Peck", "streamsidethornscrub", "malaise-FIT" (1 ♀, CMNC); "RSA: E. Transvaal", "Kruger Park, Skukuza", "12-15.XII.85, S. & J. Peck", "thornscrubforest", "malaise-FIT" (2 ♀♀, CMNC).

Etymology. Latin for "double, paired punctures" in reference to the paired rows of elytral punctures.

Remarks. This species is similar to *A. uenoi* with the single row of fused depressions on the posterior head margin and 5-5-5 male tarsal formula, but can be differentiated by the 2 mandibular serrations and geminate elytra.

Aspidiphorus japonicus Reitter (Figs. 2.27, 2.40, 2.45, 2.54)

Description. Body hemispherical, convex. Head, pronotum, scutellum, elytra, and antennal clubs dark brown; antennomeres I-VII and legs lighter brown. Setation of fairly dense, suberect to erect, pale golden setae.

Head with 3 rows of enlarged punctures, dorsal surface with punctures evenly distributed, smaller, and shallower than posterior row; 1 antennal groove extending from antennal insertion over dorsal margin of eye to lateral margin of head (Fig. 2.27); antennomere IV elongate, cylindrical, more similar to III than to V-VII; mandible with 1 apical tooth and 3 small serrations.

Pronotum narrow anteriorly, wider posteriorly, curved at sides, slightly flattened laterally with smooth edges, basal margin sinuate with scutellary arch, dorsal surface uniformly covered with small, shallow punctures. Mesosternum with sinuate, notched and darkened anterior carina. Metasternum inflated, with fairly large, moderately dense punctures, impunctate posteriorly with single row of punctures along basal edge; excavated, rectangular depression for reception of intercoxal process present. Femur slightly inflated medially, with slightly darkened dorsal and ventral edges. Tibia laterally flattened, widest apically, with bicarinate, inverted v-shaped groove extending more than half the length of tibia, surface moderately setose, setae becoming denser apically, terminating in a crown of short, stout spurs. Tarsi 5-5-4 male, 5-5-5 female, tarsomeres

simple, cylindrical, with apical tarsomere about as long as preceding ones together, claws simple. Scutellum wider than long, apex broad, almost straight, surface covered with distinct, small punctures, sparsely setose. Elytron broad, almost hemispherical, elytral surface with large, fairly deep punctures; punctures arranged in 11 double rows, interstices 2 punctures wide, finely punctate and setose, weakly convex (Fig. 2.40).

Pygidium uniformly punctate; pygidial groove widely flared posteriorly, with a single row of punctures; punctures increasing in density toward groove flare; flared apex 4 punctures wide at widest point, groove margins not reaching posterior edge of pygidium; pygidial apex truncate (Fig. 2.45).

Male. Abdominal ventrite V with raised, square protuberance.

Female. Coxites widely separated (Fig. 2.54).

Holotype, ♂, label data: "Japonicus m", "Japan", "Hiller", "HOLOTYPUS 1879",

"Aspidiphorus", "japonicus", "Reitter", "Coll. Reitter" (HNHM).

Paratype, 1 \mathcal{E} , label data same as that of holotype.

Additional material, "JAPON TOYAMA", "Kaminikawa 19C-", "Arimine, 1150m", "Lobl, 29.7.1980" (1 ♂, MHNG); "JPN: HOKKAIDO", "Oketo-cho", "Shikanoko dam", "4-18.viii.1994", "S. Hori leg." (1 ♂, 3 ♀♀, UENO); "JAPAN: Hokkaido", "Sapporo, Tozankei" "360m VIII.89", "F. Maetet, M. Sharkey", (1 ♂, CMNC); "JAPAN: Shikoku", "Ishizuchi Mtn. NP", "Tsuchigoya, 1400m", "11-18-1980", "Malaise trap", "trough, Faqus-", "Abies forest", "S.+ J. Peck" (2 ♀♀, 1 gender undet., MCZN); "Mt. Takao, Japan", "XII.29.31", "L. Gresritt, Coll." (1 ♀, CASC); "Mt. Jyoyama", "Munakata C.", "Fukuoka P.", "8.iii.1986", "S. Nomura leg." (1 ♂, UENO); "JAPAN: Nara", "Mt. Wasamati", "22-vii-1992", "T. Ueno leg." (1 ♂, UENO); "JAPAN: Fukui", "Mt. Aoba-san", "14-viii-1992", "T. Ueno leg." (1 ♂, UENO); "Mt. Tachibana", "Fukuoka P.", "25.vii.1984", "S. Nomura leg." (1 ♂, UENO); "Nakatsuya vall.", "Yoshiwa-mura", "Hiroshima P.", "8.vi.1987", "S. Nomura leg." (1 ♂, UENO).

Remarks. This species is very similar to *A. uenoi*, but can be distinguished by the 3 mandibular serrations, the cylindrical protibia, the 5-5-4 male tarsal formula, and the broadly oval elytra.

Aspidiphorus lacunamagnus sp. n. (Fig. 2.36)

Description. Overall body color dark orange-bronze with pale setation.

Head with 2 rows of enlarged basal punctures along posterior margin, remainder of dorsal head surface with large, widely spaced punctures; 1 antennal groove extending from antennal insertion to lateral margin of head, antennomere IV elongate, cylindrical, more similar to III than to V-VII, club elongate, apex acute. Mandible with 1 apical tooth and 1 subapical denticle (Fig. 2.36).

Femur shallowly grooved for tibial reception. Tibia with inverted v-shaped groove for reception of tarsus. Scutellum widest posteriorly, sparsely punctate, posterior edge narrows medially to form a slightly pointed apex. Elytral punctures large, arranged in single to slightly geminate rows.

Pygidial apex truncate, groove widens slightly apically, flare 4 punctures wide at widest point.

Male. Raised protuberance on abdominal ventrite V.

Holotype, ♂, label data: "Congo Belge: P.N.A.", "7-15-vii-1955", "P.

Vanschuytbroeck", "13274-309", "Mont Hoyo", "1.280m", "sur plantes basses" (MRAC);

Additional material, "Congo-Belge P.N.A.", "28-vii-11-viii-1955", "P. Vanschuytbroeck", "13.703-07", "Mont Hoyo", "entrée grotte Matata", "1.160m, (terreau)" (1 Å, MRAC); "Soil-Zoological Exp.", "Congo-Brazzaville", "Foret Classee 30km", "W from Brazzaville", "26.12.1963, #520", "sifted litter", "leg. Endrody – Younga" (1 Å, HNHM); "D.O. Afrika", "Amani 20.III.05", "Vosseler S.C." (2 ÅÅ, 1 gender undet., ZMHB); "Coll. Mus. Congo", "Mongbwalu", "VII-1938", "Mme. Scheitz" (1 gender undet., MRAC); "Coll. Mus. Congo", "Yangambi", "VI-1948", P. L. G. Benoit" (1 gender undet., MRAC); "Mus. Roy. Afr. Centr.", "Brazzaville: Foret Pattes", "d'Ole: X.1960", "J.P. Adam" (1 gender undet., MRAC).

Etymology. Latin for "large pit", referring to the large punctures on the dorsal head surface of this beetle.

Remarks. The large punctures on the head of this beetle are reminiscent of *A*. *planuscrus*, but this one can be distinguished by the double row of depressions along the posterior head margin and the bidentate mandibles.

Aspidiphorus latuscanalis sp. n. (Figs. 2.32, 2.46)

Description. Body broadly oval, laterally inflated.

Head with single depressed line of fused, emarginate punctures along posterior margin, punctures on dorsal surface evenly distributed, small; clypeal apex straight or nearly so, frontoclypeal suture arcuate, but not pointed; 1 antennal groove extending from

antennal insertion over dorsal margin of eye to lateral margin of head; antennal segment IV elongate, comparable to and nearly half as long as III, VIII longer than wide, almost parallel sided, club elongate with rounded apex (Fig. 2.32); mandible with 1 apical tooth and 2 subapical serrations, second serration very small.

Metasternum with impunctate "arch" posteriorly, punctures occurring along midline and posterior margin. Femur grooved for tibial reception. Tibia flattened, flared apically, and bicarinate for reception of tarsus. Elytron with punctures arranged in single, straight rows, interstices narrow, less than 1 puncture width.

Pygidial apex curved; groove 3 punctures wide, flare exceptionally wide, 8 punctures at apex, edges of groove complete to posterior pygidial edge (Fig. 2.46).

Holotype, gender undet., SUMATRA: label data: "ACEH", "-SELATAN 7-8-

83", "Babahroth 100m", "J. Klapperich" (MHNG).

Paratypes, $1 \stackrel{\bigcirc}{\downarrow}$, 4 gender undet., same data as holotype.

Etymology. Latin meaning "wide groove", referring to the extremely wide apex of the pygidial slot.

Remarks. This species is similar to *A. bidentatus* and *A. bipennis* in having a rounded pygidial apex, but is easily separated from all congeners by the particularly wide apex of the pygidial groove.

Aspidiphorus palascutellus sp. n. (Figs. 2.37, 2.39, 2.47)

Description. Color deep reddish brown, elytral punctures darker. Setation moderately dense, suberect, golden.

Head with single row of enlarged, fused punctures posteriorly, punctures on dorsal surface of variable size, with larger ones scattered among the smaller, shallower ones; frontoclypeal suture arcuate, but obtuse; 1 antennal groove extending from antennal insertion over dorsal margin of eye to lateral margin of head; antennal segment IV submoniliform, similar in size and shape to V-VII; VIII longer than wide; apex acutely pointed. Mandible with 1 apical tooth and 3 serrations.

Metasternum with impunctate "arch", punctures occurring along midline and posterior margin. Femur grooved for tibial reception. Tibia widely flaring apically, bicarinate for reception of tarsus (Fig. 2.39). Scutellum longer than wide, spade-shaped with small, shallow punctures, apex arcuate (Fig. 2.37). Elytral punctures larger, deeper, darker in color than remainder of body, arranged in nonparallel rows of 2, interstices narrow, about 1 puncture width.

Pygidial groove with small punctures, 3 puncture diameters wide at narrowest point, 10 wide at apex of groove flare, groove margin reaches posterior edge of rounded pygidial apex (Fig. 2.47).

Holotype, ♀, CONGO: label data: "Congo Belge, P.N.A.", "1-VI-1955, 13.429-32", "Secteur Nord, Mutsora 1.200m", "terreau riv. Talya, P. Vanschuytbroeck & V. Hendrickx, 5151-66" (MRAC);

Additional material, CONGO: "Congo Belge, P.N.A.", "17-18-VIII-1953", "P. Vanschuytbroeck &", "V. Hendrickx 5151-66", "Massif Ruwenzori", "Mont Ngulingo", "pres Nyamgaleke", "2.500m, ex P.N.A." (1 ♀, MRAC); "Congo Belge, P.N.A.", "7-9-IV-1955", "P. Vanschuytbroeck", "12.743-58", "Secteur Nord", "riv. Mukandwe", "affl. Talya, 1.200m" (1 ♀, MRAC), "Congo Belge: P.N.A.", "1-vi-1955", "P. Vanschuytbroeck", "13.429-32", "Secteur Nord", "Mutsora. 1.200 m", "terreau, riv. Talya" (1 gender undet., MRAC); "Recolte dans", "l'humus", "I.R.S.A.C.-mus Congo", "Kivu: Terr. Fizi", "Itombwe Nord, 900m", "IV-1951", "N. Leleup" (1 gender undet., MRAC).

Etymology. From the Latin "pala", meaning "spade", in reference to the elongate, spade shaped scutellum of this beetle.

Remarks. This species is unique in the *A. uenoi* species group in having an elongate, spade- shaped scutellum as opposed to having a scutellum that is clearly wider than long with a relatively straight apex.

Aspidiphorus planuscrus sp. n. (Figs. 2.28, 2.30)

Description. Body ovate, head partially visible dorsally. Head, pronotum, scutellum, elytra, and antennal clubs fuscus; antennomeres I-VII and legs lighter with darkened carinae. Setation of fairly dense, suberect to erect, pale golden setae.

Head with single row of fused depressions along posterior margin, large, widely spaced punctures covering remainder of dorsal head surface; clypeal apex straight or nearly so, frontoclypeal suture obtuse; 1 antennal groove extending from antennal insertion over dorsal margin of eye to lateral margin of head (Fig. 2.28); antennomere IV cylindrical, about half as long as III, antennal segment VIII about as long as wide, IX wider than long, club appearing more rounded than elongate, apex obtuse (Fig. 2.30); mandible with 1 apical tooth and 3 serrations.

Pronotum slightly narrowed anteriorly, wider posteriorly, lateral margins slightly compressed, but not completely flattened; metasternum with impunctate region reduced

to narrow band just anterior to basal margin. Elytron with mostly geminate, small punctures and wide interstices.

Pygidial apex truncate; groove with double row of punctures, flared apex 5 punctures wide, margin of groove not reaching posterior margin of pygidium.

Male. Small, knob-like protuberance on abdominal sternite III; dorsal margin of parameres straight or nearly so, with single protrusion ventrally (Fig. 2.46).

Holotype, &, CONGO: label data: "Congo Belge: P.N.A.", "5-VIII-1954", "P. Vanschuytbroeck &", "H. Synave 9816-21", "Massif Ruwenzori", "Mont Ngulingo pres", "de Nyamgaleke", "2.500m, ex P.N.A." (MRAC) "Congo Belge: P.N.A.", "1-VI-1955", "P. Vanschuytbroeck", "13.429-32", "Secteur Nord", "Mutsora, 1.200 m", "terreau, riv. Talya" (MRAC).

Additional material, CONGO: "Congo Belge: P.N.A.", "1-VI-1955", "P. Vanschuytbroeck", "13.429-32", "Secteur Nord", "Mutsora, 1.200 m", "terreau, riv. Talya" (1 ♂, MRAC), "Congo Belge: P.N.A.", "5-VIII-1954", "P. Vanschuytbroeck &", "H. Synave 9816-21", "Massif Ruwenzori", "Mont Ngulingo pres", "de Nyamgaleke", "2.500m, ex P.N.A." (1 ♀, MRAC); "Congo Belge: P.N.A.", "6-IV-1955", "P. Vanschuytbroeck", "12.759-63", "Secteur Nord", "riv. Rahekavitiri", "affl. Mukandwe", "1.200 m, ex P.N.A." (1 ♀, MRAC); "Soil-Zoological Exp.", Congo-Brazzaville", "Sibiti", "IRHO", "25.11.1963. No244", "by lamplight", "leg. Endrody-Younga" (1 ♀, HNHM); KENYA: "Kenya 9-XI-74", "au N de Kisumu", "1400m Wahmert" (1 ♀, MHNG); GHANA: "Ghana: Northern region", "Nakpandure", "430m, N 10 38-W O 32", "Dr. S. Endrody-Younga", "Nr. 252", "beating", "8.VIII.1967" (1 ♀, HNHM). *Etymology*. Latin for "flat leg", in reference to the flattened, dramatically flared protibia.

Remarks. This species is comparable to *A. bipennis*, but differs in the larger punctures on the head, obtuse antennal apex, 3 subapical mandibular serrations, wider pygidial groove, and truncate pygidial apex.

Aspidiphorus rotundiclaviger sp. n. (Fig. 2.31)

Description. Body egg-shaped, convex, shiny dark brown with lighter brown legs and antennomeres I-VII; body moderately pubescent overall. Head partially visible from above.

Posterior head margin with 3 rows of enlarged punctures, other puctures on dorsal surface small, shallow; clypeal apex straight or nearly so, frontoclypeal suture arcuate, but not pointed; 1 antennal groove extending from antennal insertion, over dorsal margin of eye, to lateral margin of head; antennomere IV submoniliform, appearing very much like V-VII, VIII almost as wide as long, IX wider than long, X almost as wide as long, apex acute; overall club appearance short, rounded (Fig. 2.31); mandible with 1 apical tooth and 3 serrations, serration III very small.

Venter of pterothorax uniformly punctate except for a narrow line along posterior margin forming a slight arch along midline of metasternum. Femur grooved ventrally for reception of tibia. Tibia flattened, flared apically, bicarinate for tarsal reception; groove wide, flat. Scutellum wider than long, apex obtuse, punctules small, shallow, round. Elytral punctures arranged in single, predominantly straight rows, punctures medium sized, interstices wide.

Pygidium with truncate apex, groove with single row of punctures basally, flared apex 2 punctures wide at widest point, groove margin complete to posterior pygidial apex.

Male. Knob-like protrusion present on abdominal ventrite III. Dorsal apex of parameres sinuate, ventral protrusion arched and wide.

Holotype, gender undet., label data: "MADAGASCAR: Manangotry", "N. of Ft. Dauphin. 80m.", "[Tolanaro]. 16-18 Nov.", "1994. 24.46'S, 46.52'E", "M.A. Ivie. D. A. Pollock", MTEC.

Additional material, $1 \circlearrowleft, 4$ gender undet., same label data as holotype.

Etymology. Latin, meaning "round club", in reference to the rotund appearance of the antennal club.

Remarks. This species is similar to *A. planuscrus*, but can be distinguished by the 3 rows of enlarged punctures on the posterior head margin, lack of enlarged punctures on the dorsal head surface, the submoniliform antennomere IV, the acute apex of antennomere X, and the single rows of elytral punctures.

Aspidiphorus uenoi sp. n. (Figs. 2.1-2.26)

Description. Body broadly oval, laterally convex, head projecting downward. Head, antennal club, pronotum, and elytra dark bronze, with lighter bronze antennomeres I-VII, legs and humeral calli. Body uniformly covered with lightly colored, moderately dense, posteriorly directed setae (Fig. 2.1).

Head wider than long, posterior margin sinuate with 1 row of enlarged punctures along posterior margin, dorsal punctures varied in size, mostly moderately large and at least 1 puncture width apart; clypeus slightly rounded apically, frontoclypeal suture arcuate, but not acutely pointed; 1 antennal groove extending straight from antennal insertion over dorsal margin of eye to lateral margin of head (Figs. 2.1, 2.2); antennomere I large, crescent-shaped, II subglobose, asymmetrical, III elongate, cylindrical, IV submomiliform, more similar in size and shape to V-VIII than to III, V-VII moniliform; antennal club elongate, densely pubescent, VIII longer than wide, widest basally, IX slightly longer than wide, X elongate, apex acute (Fig. 2.4); labrum small, slightly bilobed apically (Figs. 2.5, 2.6); mandible with 1 apical tooth and 4 serrations, decreasing in size distally; tubercle slightly flattened dorsally, rounded apical margin extending slightly over kidney-shaped cavity; dorsal surface with excavate region narrow over tubercle and flaring dramatically to lateral margin of mandible (Fig. 2.7).

Pronotum narrow anteriorly, wider posteriorly, curved at sides, slightly flattened laterally with smooth edges, basal margin sinuate with a scutellary arch, dorsal surface uniformly covered with small, shallow punctures (Fig. 2.12), prosternum very narrow, procoxal cavities widely open (Fig. 2.13); prosternal process elevated, trapezoidal, and pitted (Fig. 2.13). Mesosternum with sinuate, notched and darkened anterior edge. Metasternum inflated, with fairly large, moderately dense punctures, bell-shaped impunctate region posteriorly with single row of punctures along basal edge; excavated, rectangular depression for reception of intercoxal process present (Fig. 2.14). Legs fairly long, procoxa and mesocoxa rounded (Figs. 2.11, 2.14), metacoxa elongate, transverse (Fig. 2.17). Trochanter rounded laterally, longer than wide. Femur slightly inflated medially, with slightly darkened dorsal and ventral edges. Protibia widest apically, flattened anterolaterally for reception of tarsi (Fig. 2.11); groove somewhat shallow with

double carina, meso- and metatibiae with inverted v-shaped groove for reception of tarsi, all tibiae with an apical crown of short, stout setae (Figs. 2.11, 2.14, 2.17). Tarsi 5-5-5 male, 5-5-5 female, tarsomeres cylindrical, with apical tarsomere about as long as preceding tarsomeres together (Figs. 2.11, 2.14, 2.17), claws simple, metatarsal claw with a row of teeth along each margin (Figs. 2.17, 2.18). Scutellum wider than long, with small, shallow punctures, moderately pubescent, apex straight or nearly so (Fig. 2.10). Elytron slightly elongate, entirely covering abdomen, with 11 single rows of fairly large punctures, rows becoming confused posteriorly, interstices narrow, less than 1 puncture diameter, finely punctate and setose, feebly convex; humeral callus moderately prominent, impunctate (Fig. 2.16).

Abdomen with 5 visible sternites, I about twice as long as II, uniformly punctate with large, fairly dense punctures, II-V equal in length and with a row of moderately deep, U-shaped basal depressions, sternites overlapping. Intercoxal process as wide as long (Fig. 2.19). Pygidium with large, deep depressions uniformly covering dorsal surface, groove 2 punctures wide at narrowest, 5 punctures wide at flared apex, groove reaches posterior pygidial margin, apex truncate with sinuate, toothed carina just posterior to groove periphery (Fig. 2.21).

Male. Raised, square protuberance on fifth abdominal ventrite (Figs. 2.19, 2.20). Fused tip of parameres with dorsal margin sinuate (Fig. 2.22), ventrally with bilobed, setose protrusion extending beyond dorsal edge (Figs. 2.23).

Female. Very small protrusion on abdominal ventrite V (Fig. 2.24). Apical margin of pygidium sinuate, apex somewhat pointed (Fig. 2.25); coxites widely separated (Fig. 2.26).

Holotype, ♂, JAPAN: label data: "Ohdaigahara", "21/22-vii-1992", "T. Ueno leg." (UENO).

Paratypes, "JAPAN: KYUSHU", "Kagoshima P.", "Mt. Kurinodake", "6.viii.1994", "T. Ueno leg." (1 \Diamond , 1 \Diamond , UENO); "JAPAN: KYUSHU", "Mt. Kotakatsuka", "Is. Yakushima", "alt. ca. 1500m", "9.viii.1994", "T. Ueno leg." (1 \Diamond , 2 $\Diamond \Diamond$, UENO); "JAPAN: KYUSHU", "Ohita Prefecture", "Mt. Kurodake", 20.viii.1995", "T. Ueno leg." (8 $\Diamond \Diamond$, 14 $\Diamond \Diamond$, 2 gender undet., UENO); "MALAWI: Chitipa District", "Jembya Reserve, 18km. SSE", "Chisenga. 10-08S; 33-27E", "1,870m., 21-31 Dec. 1988", "J. Rawlins, S. Thompson", "Sphindidae" (2 $\Diamond \Diamond$, 2 $\Diamond \Diamond$, 2 $\Diamond \Diamond$, CMNH); "JAPON, NARA", "Nara Park", "8.8.1980", "Lobl" (1 \Diamond , MHNG).

Additional material, "Mt. Ariake", "Is. Tsushima", "Nagasaki Pref.", "8-vii-1992", "T. Ueno leg." ($3 \circ \circ , 2 \circ \circ , 1 \in N$, UENO); "JAPAN: Nara", "Ohdaigahara", "21/22vii-1992", "T. Ueno leg." ($1 \circ , 1 \in N$, UENO); "Mt. Shiratake", "Is. Tsushima", "Nagasake Pref.", "5-vii-1992", "T. Ueno leg." ($4 \circ \circ , 6 \circ \circ , 1 \in N$, UENO); "Mt. Hiko", "Fukuoka Pref.", "21.v.1986", "S. Nomura leg." ($1 \circ , 1 \in N$, UENO); "JAPAN: KYUSHU", "Fukuoka Pref.", "Mt. Tachibana", "(alt. 367m)", "18.vi.1997", "T. Ueno leg." ($3 \circ \circ , 2 \circ \circ , 1 \in N$, "JAPAN: KYUSHU", "Kagoshima P.", "Mt. Kurinodake", "6.viii.1994", "T. Ueno leg." ($1 \circ , 1 \circ , 1 \circ , 1 \in N$, UENO); "Japani P.", "Mt. Kurinodake", "6.viii.1994", "T. Ueno leg." ($1 \circ , 1 \circ , 1 \circ , 1 \in N$, UENO); "Japani P.", "Hokkaido", "9.vii.1986", "S. Nomura leg." ($1 \circ , 1 \circ$ "4.x.1986, T. Ueno" (1 ♀, UENO); "JAPON: EHIME", "via Mt. Ishizuchi", "1000m",
"Lobl, 14.8.1980" (1 ♀, MHNG); "JAPON: EHIME", "via Mt. Ishizuchi", "1350m",
"Lobl, 13.8.1980" (1 ♀, MHNG); "JAPON: EHIME", "Ishizuchi N. Park", "Omogo,
900m", "Lobl, 12.8.1980" (1 ♀, MHNG); "JAPON: GUNMA", "4 km SW Tsumagoi",
"1050m", "Lobl, 18.7.1980" (1 ♀, MHNG).

Etymology. Named in honor of the collector of this beetle, Teruhisha Ueno, who has been helpful to the authors in this and other projects.

Remarks. This species is similar to *A. japonicus*, but differs in that there is only one row of enlarged punctures along the posterior head margin, the punctures on the dorsal surface of the head are larger, the tarsal claws are toothed, and the elytra are more elongate.

DISCUSSION

Aspidiphorus beetles, despite being minute (1.5 - 2.0 mm), exhibit a wealth of morphological diversity, including characters with presumed phylogenetic significance. The pygidium has a diverse array of forms within Sphindidae. A few genera lack any conspicuous depressions or grooves on the pygidium (e.g., *Eurysphindus, Genisphindus*), while in other genera (e.g., *Carinisphindus* McHugh, *Notosphindus* McHugh & Wheeler) there is a weakly demarked median longitudinal depression on the dorsal surface. In *Aspidiphorus* and *Sphindiphorus* Sen Gupta & Crowson, the median depression is very sharply demarked along its lateral edges. Within *Aspidiphorus*, the median longitudinal groove has two different forms, a parallel-sided form and an apically flared form (Figs. 2.21, 2.25, 2.43 – 2.47). Because the median longitudinal depression (or groove) is

parallel-sided in other sphindids, the divergent form of the groove observed in some *Aspidiphorus* species is interpreted here to be the derived condition and a synapomorphy supporting the *A. uenoi* species group clade.

Additional support for the monophyly of this group is found in the appearance of a protuberance on an abdominal ventrite in adult males (Figs. 2.19, 2.23). Such protuberances on abdominal ventrites are unknown elsewhere in the family. This second apparent synapomorphy for the species group, however, is problematic. Although the ventrite protuberance appears only in the *Aspidiphorus* species that also have a fluted pygidial groove, it appears on three different ventrites among the species, violating the principles of position and composition for homology assessment. Without a more involved analysis of the underlying causes for the protuberance, it cannot be considered to be an unambiguous synapomorphy at this time, although the congruence of its distribution with the fluted pygidial groove does lend support to the hypothesis of monophyly for this group of species.

Another unique morphological aspect of the *A. ueoni* species group involves the tarsal morphology. Cucujoid beetles typically have dimorphic tarsal formulae: 5-5-5 in the female and 5-5-4 in the male, and simple tarsal claws. All sphindids were thought to have typical cucujoid tarsi (Sen Gupta & Crowson 1977). Some male members of the *A. uenoi* group, however, have a 5-5-5 tarsal formula (Fig. 2.14, 2.17) and serrated tarsal claws (Fig. 2.18). These unique features for Sphindidae are presumed synapomorphies for a small group within the *A. uenoi* species group and are unknown in any other sphindid species. These characteristics make the *Aspidiphorus uenoi* species group noteworthy.

The protuberance on the abdominal venter is curious because it occurs on different ventrites in different species. Six of the 13 beetles in the *A. uenoi* group have this protrusion on ventrite V (Fig. 2.19, 2.20): *A. annabelleae*, *A. bilineaus*, *A. geminuspunctatus*, *A. japonicus*, *A. lacunamagnus*, and *A. uenoi*. *Aspidiphorus bidentatus* and *A. bipennis* have the protrusion on ventrite II (Fig. 2.41), while *A. crowsoni*, *A. planuscrus*, and *A. rotundiclaviger* have it on ventrite III (Fig. 2.42).

These protrusions on different ventrites cannot be assumed to be homologues because they violate the principles of position and composition, but it is interesting that they are completely congruent with two other presumed synapomorphies for this group. The function of these structures remains unknown. They may be used during copulation or may represent some internal morphological modification. Perhaps when more is known about their function, one could make a case that this character is, indeed, a synapomorphy.

Perhaps the most extraordinary morphological features of the *A. uenoi* group involve the tarsal morphology. Males of *A. bidentatus*, *A. geminuspunctatus*, and *A. uenoi* have 5-5-5 tarsi (Figs. 2.14, 2.17) and serrated metathoracic tarsal claws (Fig. 2.18). These unusual features require modification of the current family description for Sphindidae.

There are no obvious biogeographic patterns observed in the distributions of the species in the *A. uenoi* group. Sphindid beetles are sampled relatively infrequently by general collecting methods and may be easily overlooked. In the future it is likely that the distributions of the species treated here will expand as new material becomes available. It is also likely that more new species will be found in addition to the

remaining 89 undescribed *Aspidiphorus* species that were observed, but not treated, in the course of this study.

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FIGURE LEGENDS

- 2.1. Aspidiphorus uenoi, male, habitus, dorsal view.
- 2.2. A. uenoi, male, head capsule, dorsal view.
- 2.3. A. uenoi, male, head capsule, ventral view.
- 2.4. A. uenoi, male, left antenna, dorsal view.
- 2.5. A. uenoi, male, labrum, dorsal view.
- 2.6. A. uenoi, male, labrum, ventral view.
- 2.7. A. uenoi, male, right mandible, dorsal view.
- 2.8. A. uenoi, male, right maxilla, dorsal view.
- 2.9. A. uenoi, male, labium, ventral view.
- 2.10. A. uenoi, male, scutellum, dorsal view.
- 2.11. A. uenoi, male, left prothoracic leg, ventrolateral view.
- 2.12. A. uenoi, male, pronotum, dorsal view.
- 2.13. A. uenoi, male, pronotum, ventral view.
- 2.14. A. uenoi, male, pterothorax, ventral view.
- 2.15. A. uenoi, male, right membranous wing, dorsal view.
- 2.16. A. uenoi, male, right elytron, dorsal view (setae omitted for clarification).
- 2.17. A. uenoi, male, left metathoracic leg, ventrolateral view
- 2.18. A. uenoi, male, left metatarsal claw, ventral view.
- 2.19. A. uenoi, male, abdomen, ventral view.
- 2.20. A. uenoi, male, abdominal segments IV and V, ventral view.
- 2.21. A. uenoi, male, pygidium, dorsal view.
- 2.22. A. uenoi, male, fused tip of parameres, dorsal view.

- 2.23. A. uenoi, male, fused tip of parameres, ventral view.
- 2.24. A. uenoi, female, abdomen, ventral view.
- 2.25. A. uenoi, female, pygidium, dorsal view.
- 2.26. A. uenoi, female, genitalia, dorsal view.
- 2.27. A. japonicus, male, head, dorsal view.
- 2.28. A. planuscrus, male, head, dorsal view.
- 2.29. A. bilineaus, male, head, dorsal view.
- 2.30. A. planuscrus, male, right antenna, dorsal view.
- 2.31. A. rotundiclaviger, male, right antenna, dorsal view.
- 2.32. A. latuscanalis, female, right antenna, dorsal view.
- 2.33. A. bipennis, male, right antenna, dorsal view.
- 2.34. A. annabelleae, male, right mandible, dorsal view.
- 2.35. A. bipennis, male, right mandible, dorsal view.
- 2.36. A. lacunamagnus, female, right mandible, dorsal view.
- 2.37. A. palascutellus, female, scutellum, dorsal view.
- 2.38. A. annabelleae, male, prothoracic tibia and tarsi, lateral view.
- 2.39. A. palascutellus, female, prothoracic tibia and tarsi, dorsolateral view.
- 2.40. A. japonicus, male, right elytron, dorsal view (setae omitted for clarification).
- 2.41. A. bidentatus, male, abdomen, ventral view.
- 2.42. A. crowsoni, male, abdomen, ventral view.
- 2.43. A. bilineaus, male, pygidium, dorsal view.
- 2.44. A. crowsoni, male, pygidium, dorsal view.
- 2.45. A. japonicus, male, pygidium, dorsal view.

2.46. A. latuscanalis, female, pygidium, dorsal view.

- 2.47. A. palascutellus, female, pygidium, dorsal view.
- 2.48. A. annabelleae, male, fused tip of parameres, dorsal view.
- 2.49. A. annabelleae, male, fused tip of parameres, ventral view.
- 2.50. A. crowsoni, male, fused tip of parameres, dorsal view.
- 2.51. A. crowsoni, male, fused tip of parameres, ventral view.
- 2.52. A. bidentatus, male, fused tip of parameres, dorsal view.
- 2.53. A. bidentatus, male, fused tip of parameres, ventral view.
- 2.54. A. japonicus, female, genitalia, dorsal view.
- 2.55. Distribution of the A. uenoi species group.

























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CHAPTER 4

THE ASPIDIPHORUS OF MADAGASCAR (COLEOPTERA: SPHINDIDAE)

¹ Forester, Juanita A. and J. V. McHugh. To be submitted to *Annales Zoologici*.

Abstract. Due to its astonishing biodiversity, the small island of Madagascar is globally significant in terms of species conservation. Ideally, the logical progression toward conservation begins with an assessment of species present on the island. The *Aspidiphorus* of Madagascar are herein described and illustrated, and a taxonomic key to those species is included.

Species included: A. bisulcus sp.n., A. densquadratus sp.n., A. perplexus, sp.n., A. rotundiclaviger Forrester and McHugh.

INTRODUCTION

The laws of biology are written in the language of diversity.

- E. O. Wilson, 1989

Anyone wishing to experience the vast biodiversity of Earth needs look no further than the Texas-sized island of Madagascar. As a result of having been separated from Greater India about 88 million years ago, Madagascar's fauna shows high levels of endemism (Gillespie and Roderick, 2002). While unparalleled in its megadiversity, Madagascar does have commonality with other ecologically rich regions: habitats and the species they harbor are disappearing at an alarming rate (Brooks, et al., 2002). Thus, it is imperative for those species to be assessed before further damage is done. Such investigation lays the groundwork for other studies, in particular those concerning evolutionary patterns, migration and dispersal, and niche partitioning. Such inquiries also have the benefit of allowing an enhanced understanding of Madagascar's biodiversity so that it might be compared with floral and faunal variety elsewhere. Due to its isolation, the insects of Madagascar remain understudied. The coleopteran family Sphindidae, or slime mold beetles, contains two Malagasy genera: *Sphindus* Chevrolat and *Aspidiphorus* Zeigler in DeJean (McHugh, 1993).

Aspidiphorus, with seventeen described species, is one of the larger genera within the Sphindidae. Known only from the Old World, there are no described species of *Aspidiphorus* known from Madagascar; however, there are records of *Aspidiphorus* being present on the island

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(McHugh, 1993). Inspection of 3000 museum specimens yielded 102 undescribed species, four of which occur in Madagascar: *A. bisulcus*, sp.n.; *A. densquadratus*, sp.n.; *A. perplexus*, sp.n.; and *A. rotundiclaviger* Forrester and McHugh (Forrester and McHugh, in prep).

MATERIALS AND METHODS

Preliminary assessment of specimens was facilitated using a Leica Wild Type MZ8 stereoscopic microscope. When permitted, dried, point-mounted specimens were removed from their mounts by immersion in either 75% ethanol or distilled water. The beetles were then prepared for dissection by submersion in a heated solution of potassium hydroxide and distilled water. After clearing, excess KOH was rinsed off with distilled water. All dissections were performed in 75% ethanol and slide-mounted in glycerol. Illustrations were completed using a camera lucida attached to a Leica Leitz DMRB compound microscope.

The following museums loaned specimens for this endeavor and will be referred to with the following codens:

FMNH – Field Museum of Natural History, Chicago, Illinois, USA
USNM – National Museum of Natural History, Smithsonian Institution,
Washington, D.C., USA

KEY TO THE ASPIDIPHORUS OF MADAGASCAR

1.	Head with 2 antennal grooves (Fig. 3.2), protibia with inverted, v-shaped
	longitudinal groove2
-	Head with 1 antennal groove (Fig. 3.11, 3.14), protibia more flattened, with broad,
	shallow, depressed area demarked by 2 longitudinal carinae
2(1).	Body shape somewhat hemispherical, clypeus small (Fig. 3.2), elytral punctures
	arranged in single, parallel rows, pygidial apex rounded (Fig.3.9)
-	Body shape slightly elongate, clypeus large, convex, elytral punctures confused (Fig.
	3.1), pygidial apex truncate
3(1).	Basal region of head with three rows of enlarged punctures (Fig. 3.14), antennal club
	appearing more rounded with antennomere IX wider than long, X almost as wide as long
	appearing more rounded with antennomere IX wider than long, X almost as wide as long (Fig. 3.15), mandible with 3 subapical serrations (Fig. 3.16) <i>A. rotundiclaviger</i>
_	appearing more rounded with antennomere IX wider than long, X almost as wide as long (Fig. 3.15), mandible with 3 subapical serrations (Fig. 3.16) <i>A. rotundiclaviger</i> Basal region of head with two rows of enlarged punctures (Fig. 3.11), antennal club
-	appearing more rounded with antennomere IX wider than long, X almost as wide as long (Fig. 3.15), mandible with 3 subapical serrations (Fig. 3.16) <i>A. rotundiclaviger</i> Basal region of head with two rows of enlarged punctures (Fig. 3.11), antennal club elongate (Fig. 3.12), mandible with 2 blunt subapical serrations (Fig. 3.13)

THE ASPIDIPHORUS OF MADAGASCAR

Aspidiphorus bisulcus sp. n. (Figs. 3.2-3.10)

Description. Body form broadly oval, convex. Color dark orange-brown with paler, suberect setae.

Head (Fig. 3.2) with dorsal posterior margin only slightly sinuate, with single row of elongate depressions along posterior margin, remainder of dorsal surface with small, shallow punctules; clypeus small, frontoclypeal suture arcuate; 2 pairs of anteriorly confluent antennal grooves, separated by a 45 degree angle; antennomere IV elongate, cylindrical, more similar in size and shape to antennomere III than to V-VII, club elongate, apex acute (Fig. 3.3); labrum small, almost completely concealed by clypeus, weakly bilobed apically (Fig. 3.4); mandible with narrow, reduced dorsal furrow, mandible with 1 apical tooth and 4 subapical serrations (Fig. 3.5); labium somewhat rectangular, margins weakly crenulate, palpi three segmented; palpomere I elongate, II inflated, III cylindrical (Fig. 3.6).

Scutellum shield shaped, apex arcuate, with small, shallow punctures (Fig. 3.7). Venter of mesosternum and metasternum laterally inflated with large punctures ventrally, metasternum with impunctate "arch" present, with impunctate patches in anterior region along midline. Tibia not particularly flattened, but with bicarinate, longitudinal groove for reception of tarsus (Fig. 3.8). Elytron with darkly colored punctures arranged in single, parallel rows, interstices approximately one puncture wide. Pygidium triangular with rounded apex, dorsal surface with large punctures interspersed with smaller, shallower ones; median longitudinal slot parallel sided, entire to posterior pygidial edge, slot 1 puncture wide (Fig. 3.9).

Male. Fused tip of parameres uniformly curved dorsally, ventral protrusion evenly rounded, not truncate or bilobed (Fig. 3.10).

Holotype, M, label data: "MADAGASCAR: Prov.", "Fianarantsoa, 7 km", "W.

Ranomafana, 900m", "1-9 February 1990", "W. E. Steiner", "flight intercept", "yellow pan trap in", "Malaise trap in", "small clearing,", "montane rainforest" (USNM).

Paratypes, $1 \Diamond, 3 \heartsuit \heartsuit$, same label data as holotype.

Etymology. Latin, meaning "two furrows", referring to the 2 pairs of antennal grooves.

Distribution. Known only from the type locality.

Remarks. This species is distinguishable from all congeners by the narrow, S-shaped furrow extending longitudinally over the dorsal mandibular surface.

Aspidiphorus densquadratus sp. n. (Figs. 3.11 – 3.14)

Description. Body form broadly oval, color dark brown-black with lighter brown, suberect, moderately dense setae.

Head (Fig. 3.11) with a double row of enlarged punctures along posterior margin, remainder of punctures on dorsal surface small, shallow; clypeal apex weakly bilobed; frontoclypeal suture broadly rounded; 1 dorsal antennal groove extending from antennal insertion to lateral head margin; antennomere IV submoniliform, similar in size and shape to V- VII, club elongate, apex acute (Fig. 3.12); mandible with 2 serrations just posterior to large apical tooth, serrations large and square (Fig. 3.13).

Scutellum wider than long, with small, shallow punctules. Metasternum with large punctures, impunctate "arch" present, with additional impunctate patches anteriorly. Tibia widest apically, with shallow, bicarinate groove for tarsal reception. Elytron with single rows of punctures, interstices somewhat convex, approximately 1 puncture diameter wide.

Pygidium wider than long, apex truncate, median longitudinal slot parallel sided, with single to geminate punctures.

Holotype, ♀, label data: "MADAGASCAR: Prov.", "Fianarantsoa, 7 km", "W. Ranomafana, 900m", "22-31 October 1988", "W. E. Steiner", "flight intercept", "yellow pan trap in", "Malaise trap in", "small clearing,", "montane rainforest" (USNM).

Additonal material, $2 \sqrt[3]{3}$, same label data as holotype; "MADAGASCAR: Prov.", "Fianarantsoa, 7 km", "W. Ranomafana, 900m", "20-31 January 1990", "W. E. Steiner", "flight intercept", "yellow pan trap in", "Malaise trap in", "small clearing,", "montane rainforest" (1 $\sqrt[3]{3}$, 1 \bigcirc , USNM); "MADAGASCAR: Prov.", "Fianarantsoa, 7 km", "W. Ranomafana, 900m", "1-7 November 1988", "W. E. Steiner", "flight intercept", "yellow pan trap in", "Malaise trap in", "small clearing,", "montane rainforest" (1 \bigcirc , USNM); "MADAGASCAR: Prov.", "Fianarantsoa, 7 km", "W. Ranomafana, 900m", "23-28 February 1990", "W. E. Steiner", "flight intercept", "yellow pan trap in", "Malaise trap in", "small clearing,", "montane rainforest" (3 \bigcirc Q, USNM).

Etymology. Latin, meaning "square tooth", in reference to the peculiar square-shaped serrations present on the mandibles of this animal.

Distribution. Known only from the type locality.

Remarks. This species is easily differentiated from congeners by the broad, square mandibular teeth.

Aspidiphorus perplexus sp. n. (Fig. 3.1)

Description. Body form somewhat elongate, but not quite parallel sided, laterally inflated with humpbacked appearance black with pale setation (Fig. 3.1).

Head with 2 antennal grooves, confluent anteriorly, diverging at approximately forty-five degree angle; clypeus rather large and convex; frontoclypeal suture arcuate, but not acutely pointed; antennomere IV elongate, cylindrical, subequal to III, club elongate with acute apex.

Scutellum shield shaped, with small, round punctules over dorsal surface. Metasternum with impunctate region slightly reduced, punctures occurring along midline. Leg moderately long, slender; tibia cylindrical, but with bicarinate, longitudinal groove for reception of tarsus. Elytron slightly elongate, punctures medium sized, confused.

Pygidium with parallel sided groove, slot with single row of punctures, margins of slot entire, reaching posterior pygidial edge.

Holotype, ♀, label data: "MADAGASCAR: Befin-", "-gotra (11.0km W SW)", "Res. Anjanharibe-Sud", "14.45'S, 49.27'E", "1565m, montane rain-", "-forest, 16.XI.1994", "FMHD #94-58, Winkler", "extraction of sifted litter", "(leaf mold, rotten wood)", "B.L. Fisher #1232 (1-50)" (FMNH).

Etymology. Latin, "confused", in reference to the lack of arrangement of elytral punctures.

Distribution. Known only from the type locality.

Remarks. This species is easily distinguishable from congeners by the particularly large, convex clypeus and the confused elytral punctuation.

DISCUSSION

The genus *Aspidiphorus* is a taxonomic nightmare. Current research by Forrester and McHugh (2003, in prep) increases the number of known species in the genus from 17 to 30. Still, 89 species remain undescribed. The minute size of the beetles combined with the plasticity of many of their morphological characters renders a robust phylogenetic analysis based on morphology virtually impossible. Only one species group, the *Aspidiphorus uenoi* group, has been hypothesized as monophyletic based on morphology. Of the Malagasy species, *A. rotundiclaviger* is a member of this group (Forrester and McHugh, in prep). The other three species from Madagascar, *A. bisulcus, A. densquadratus*, and *A. perplexus*, are not part of any monophyletic subgroup of *Aspidiphorus*. However, it is appropriate to treat the geographically delineated assemblage due to other factors, such as biodiversity studies and conservation of Madagascar's fauna.

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FIGURE LEGENDS

- 3.1. Aspidiphorus perplexus, habitus, lateral view.
- 3.2. Aspidiphorus bisulcus, head, dorsal view.
- 3.3. A. bisulcus, right antenna, dorsal view.
- 3.4. A. bisulcus, labrum, dorsal view.
- 3.5. A. bisulcus, left mandible, dorsal view.
- 3.6. A. bisulcus, labium, ventral view.
- 3.7. A. bisulcus, scutellum, dorsal view.
- 3.8. A. bisulcus, right prothoracic leg, lateral view.
- 3.9. A. bisulcus, pygidium dorsal view.
- 3.10. A. bisulcus, fused tip of parameres, dorsal view.
- 3.11.A. densquadratus, head, dorsal view.
- 3.12. A. densquadratus, right antenna, dorsal view.
- 3.13. A. densquadratus, left mandible, dorsal view.
- 3.14. A. rotundiclaviger, head, dorsal view.
- 3.15. A. rotundiclaviger, right antenna, dorsal view.
- 3.16. A. rotundiclaviger, left mandible, dorsal view.



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CHAPTER 4

CONCLUSIONS

There are few systematists clamoring to study Sphindidae, much less the rather cryptic genus *Aspidiphorus*. These beetles are exceedingly small, and the lack of abundance of taxonomic features renders their identification difficult at best. The conspicuous lack of cladistic analysis for *Aspidiphorus* is due to the absence of good morphological characters. Those characters that are present appear to be quite plastic, making a robust phylogenetic analysis nearly impossible at the species level.

Nevertheless, one species group, the *Aspidiphorus uenoi* group, seems to be monophyletic based on the presence of an apically flared pygidial groove. The appearance of a protuberance on one of the abdominal sternites lends support to this hypothesis. This character cannot be considered a true homology at this time, though, because is violates the principles of position and composition for homology assessment. However, its concordance with the fluted pygidial groove supports the monophyly of the species group. The occurrence of 5-5-5 tarsi in some males of the group implies that a smaller monophyletic group may exist within the *A. uenoi* group.

Due to the lack of apparent morphological synapomorphies within *Aspidiphorus*, other characters, such as geography, must be considered when attempting to peel away taxonomically relevant layers of the genus. Unfortunately, no insight can be gained based on the distribution of *Aspidiphorus* in the Old World. However, it is appropriate to

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describe species from Madagascar due to the isolation and high level of endemism on the island.

The task of undertaking a thorough taxonomic revision of *Aspidiphorus* may discourage even the most energetic systematist. However, without alpha taxonomic work, molecular and evolutionary studies may lack explanation or soundness. With this preliminary inquiry into the taxonomy of *Aspidiphorus*, the scope of knowledge regarding the taxonomy of this obscure genus is greatly increased.