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THE MORPHOLOGY OF THE HIND WING
ARTICULATION AND WING BASE OF THE
SCARABAEOIDEA (COLEOPTERA) WITH SOME
PHYLOGENETIC IMPLICATIONS

by

D. J. BROWNE & C. H. SCHOLTZ

BONNER ZOOLOGISCHE MONOGRAPHIEN, Nr. 40
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ABSTRACT

Two character suites, the hind wing articulation, comprised of the first, second and third axillaries and the median plate, and the hind wing base, comprised of the first and second basal plates, are described for Glaresidae, Passalidae, Diphylostomatidae, Lucanidae, Glaphyridae, Trogidae, Bolboceratidae, Pleocomidae, Geotrupidae, Hybosoridae, Ochodaecidae, Ceratocanthidae and Scarabaeidae (Aphodiinae, Aegialiinae, Aulonocneminae, Orphninae, Melolonthinae, *Acoma*, Oncerinae, Chasmatopterinae, Hopliinae, Rutelinae, Dynastinae, Cetoniinae, Trichiinae and Valginae). Due to the magnitude of this study, large number of characters and high degree of variability of the structures, it was not possible, at this early stage, to adequately analyse the phylogenetic content of the various character states. However, some notes concerning genealogical relationships among the major taxa are given.

INTRODUCTION

The Scarabaeoidea are one of the largest and most variable superfamilies of Coleoptera. Members of the superfamily vary tremendously in size, facies and habits but are united by several unique characters (Lawrence & Britton 1991). Most adults are robust, short-legged beetles with a typically lamellate antennal club, highly modified prothorax with large coxae, usually dentate tibiae, strong intrinsic wing-folding mechanism, the second abdominal sternite represented only by a lateral portion, the eighth tergite forming a true pygidium and four Malpighian tubules. Hind coxal plates are absent. Larvae are grub-like and usually C-shaped, with well-developed antennae and legs. They are without urogomphi. Scarabaeoids feed on a wide range of plant and animal matter and dung. This varies from detritus and most types of dung through lower plants to virtually all higher plant tissues and carrion to predation on other insects. Their habits range from free-living through fairly sophisticated forms of brood care to sub-social behaviour.

The Scarabaeoidea are morphologically one of the best-studied beetle groups. There have been many broadly based comparative studies covering most major structures. These include: antennae (Iablokoff-Khnzorian 1977), antennal sensilla (Meinecke 1975), eye (Caveney 1986), mouthparts (Nel & Scholtz 1990), prothorax (Hlavac 1975), coxae (Ritcher 1969c; Hlavac 1975), spiracles (Richer 1969a,b), wing venation (Crowson 1967; Iablokoff-Khnzorian 1977), alimentary canal (unpublished), metendosternite (Crowson 1938; Iablokoff-Khnzorian 1977), male genitalia (d'Hotman & Scholtz 1990a,b), female genitalia (Tanner 1927; Holloway 1972; Lawrence & Newton 1982; unpublished), ovarioles (Ritcher & Baker 1974), karyotype (Smith & Virkki 1978; Yadav & Pillai 1979), central nervous system (Iablokoff-Khnzorian 1977; unpublished), spermatozoan number (Virkki 1969), malpighian tubules (Caveney 1986) and larvae (Areekull 1957; Ritcher 1966; Hinton 1967; Costa et al. 1988) to name a few. These character suites were recently reviewed and phylogenetically assessed by Scholtz (1990).

The current project is one of a series by members of our research team in which various morphological structures of the major groups of Scarabaeoidea are being studied to

determine phylogenetic trends in them as an indication of possible relationships between the groups (d'Hotman & Scholtz 1990a,b; Nel & Scholtz 1990; Scholtz 1990; Browne et al. 1993; Browne & Scholtz 1994, 1995; Scholtz & Browne in press; Scholtz et al. 1994, submitted). These studies are complementary to the ones undertaken by various authors over the past 20 years (see above). However, because of the magnitude of this project and because of the lack of published data on comparative morphology of scarabaeoid hind wing articulation and wing base and the difficulty of interpreting phylogenetic trends, it was decided to separate the comparison of the morphological structures from the analysis of phylogenetic trends in hind wing articulation and wing base structure. The former is reported here and the latter will be dealt with in a separate communication to be published later.

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MATERIAL AND METHODS

In this contribution we present the database of a major report of the cladistic relationships of the families of Scarabaeoidea based on characters of the hind wing articulation and hind wing base (Browne 1993). More than 250 genera, representing all of the major scarabaeoid taxa from most geographical regions, were examined.

Specimen preparation and examination

All material examined was either dried museum specimens or prepared slides. Besides material from our own collection, dried museum material was also obtained from Prof. J.

Doyen (University of California, Berkeley); Prof. E. Holm (University of Pretoria); Mr. M. Kerley (The Natural History Museum, London); Mrs. J. McNamara (Biosystematics Research Centre, Ottawa); and Dr. O. Merkl (Hungarian Museum of Natural History, Budapest). Prepared slides were obtained from Dr. A. Hardy (Department of Food and Agriculture, California) and Dr. D. Carlson (Orangeville, California).

In order to relax the specimens, they were boiled for approximately five minutes in distilled water. The specimens were then pinned to a styrofoam platform and further prepared in one of two methods. The first consisted of using fine forceps to remove the wings at the tergum, keeping the wing articulation intact. The right wing was placed on a clean slide with several drops of absolute alcohol. The wing was spread, and held until the alcohol had evaporated. No mounting medium was used, but in many instances putty was used to fix the wing in an outstretched position (especially large wings). The first, second and third axillaries, of the left wing, were dissected and mounted on paper points. The second method involved pinning the just-boiled specimen to a spreading board, securing the right elytron by either excising it or pinning it away from the anterior margin of the wing, and securing the wing in an outstretched position for drying. Softening and clearing the wings in either hot or cold KOH did not prove to be useful and was attempted only a few times before this method was abandoned.

High contrast photographs which clearly indicated veins and degree of sclerotization were produced by placing the wing and slide into a Durst 609 enlarging camera and exposing directly onto Ilford Ilfospeed Multigrade II photographic paper. Exposure times varied from 2 seconds for poorly sclerotized, small wings, to 60 seconds for well sclerotized, large wings. The exposed paper was developed using Ilford PQ Universal developer and Amfix high speed developer. Developing times were gauged by eye and feature contrast. The wing articulation, wing base and fine veinal features, such as the radial cell and hinges, were poorly reproduced using this method. For these a Hitachi Model S-450 scanning electron microscope was used for both viewing and photographing.

Illustrations of the hind wing articulation, wing base and wing venation were completed using a Zeiss dissecting binocular microscope and a Zeiss 1,8 Camera Lucida. Finer features, from small species, were drawn directly from SE micrographs. Correction of drawings was completed with a Zeiss compound microscope. Photographing directly through a Zeiss dissecting microscope produced poor photographs, with uneven glare due to strong wing fluting and poor resolution.

Taxa studied

Hind wings of the following genera were examined during the course of this study. Family and subfamily concepts are from Scholtz (1990), Browne (1993), and Scholtz & Browne (Bolboceratidae, in press).

Superfamily Scarabaeoidea

Glareidae: *Glareis*

Passalidae: *Aceraius*, *Aulacocyclus*, *Ceracupes*, *Didimus*, *Odontotaenius*, *Oileus*, *Passalus*, *Proculejus*, *Verres*, *Veturius*

Diphyllostomatidae: *Diphyllostoma*

Lucanidae: *Aegus*, *Aesalus*, *Ceruchus*, *Chiasognathus*, *Dorcus*, *Figulus*, *Lamprima*, *Neolucanus*, *Nicagus*, *Nigidius*, *Penichrolucanus*, *Platycerus*, *Prosopocoilus*, *Sinodendron*, *Syndesus*

Glaphyridae: *Amphicoma*, *Lichnanthe*

Trogidae: *Trox*, *Omorgus*, *Polynoncus*

Bolboceratidae: *Athyreus*, *Australobolbus*, *Blackbolbus*, *Blackburnium*, *Bolbaineus*, *Bolbapium*, *Bolboceras*, *Bolbocerastes*, *Bolbocerosoma*, *bolbocerosum*, *Bolbochromus*, *Bolbogonium*, *Bolbohamatum*, *Bolbelasinus*, *Bolboleus*, *Bolborhachium*, *Bolborhinum*, *Bolborhombus*, *Bradycinetulus*, *Elephastomus*, *Eucanthus*, *Gilletinus*, *Neothyreus*, *Pereirabolbus*, *Stenaspidius*

Pleocomidae: *Pleocoma*

Geotrupidae: *Anoplotrupes*, *Ceratophyus*, *Ceratotrupes*, *Chromogeotrupes*, *Cnemotrupes*, *Enoplotrupes*, *Epigeotrupes*, *Frickius*, *Geohowdenius*, *Geotrupes*, *Haplogeotrupes*, *Megatrupes*, *Mycotrupes*, *Odontotrupes*, *Onthotrupes*, *Phelotrupes*, *Sericotrupes*, *Thorectes*, *Typhoeus*

Hybosoridae: *Anaides*, *Araeotanopus*, *Brenskea*, *Chaetodus*, *Dalmothoracodes*, *Hapalonychus*, *Hybochaetodus*, *Hybosorus*, *Liparochrus*, *Microphaeochroops*, *Phaeochridius*, *Phaeochroops*, *Phaeochrous*, *Trichops*

Ceratocanthidae: *Astaenomoechus*, *Ceratocanthus*, *Cloeotus*, *Cyphopisthes*, *Eubrittoniella*, *Eusphaeropeltis*, *Madrasostes*, *Perignamptus*, *Philharmostes*, *Pterorthochaetes*, *Synarmostes*

Ochodaëidae: *Chaetocanthus*, *Ochodaeus*, *Pseudochodaeus*, *Synochodaeus*

Scarabaeidae: *Acognatha*, *Acoma*, *Aegialia*, *Agamopus*, *Alaberoides*, *Allokotarsa*, *Amphimallon*, *Anachalcos*, *Anatochilus*, *Anisonyx*, *Anomala*, *Anomaluera*, *Aphodius*, *Aphonides*, *Apogonia*, *Archophileurus*, *Asthenopholis*, *Ataenius*, *Aulonocnemis*, *Bolax*, *Brachymacroma*, *Callirhinus*, *Camenta*, *Camentoserica*, *Campilipus*, *Campsiura*, *Catharsius*, *Canthidium*, *Canthon*, *Cartwrightia*, *Chironitis*, *Chlorocala*, *Chnaunanthus*, *Circellium*, *Coenochilus*, *Colobopterus*, *Comythovalgus*, *Copris*, *Coprophanaeus*, *Coptorhiua*, *Cotinus*, *Cyclocephala*, *Cyclomera*, *Cymophorus*, *Cyphonistes*, *Cyptochirus*, *Cyrioperta*, *Deltochilum*, *Deltorrhium*, *Diasticus*, *Dichelonyx*, *Dichelus*, *Dichotomius*, *Dinacoma*, *Diplognatha*, *Diplotaxis*, *Drepanocanthus*, *Drepanocerus*, *Drepanopodus*, *Dynastes*, *Dyscinetus*, *Eriesthis*, *Euoniticellus*, *Euparia*, *Eurysternus*, *Eutheola*, *Garetta*, *Geniates*, *Genuchus*, *Gnorimella*, *Golofa*, *Gymnoloma*, *Gymnopleurus*, *Heliocopris*, *Heteronychus*, *Hoplia*, *Hybaloides*, *Hybalus*, *Hyboscherna*, *Hypselogenia*, *Kheper*, *Larupea*, *Lepidota*, *Lepithrix*, *Leptohoplia*, *Leucothyreus*, *Liatongus*, *Macroductylus*, *Melinsthes*, *Milichus*, *Neoserica*, *Nyassinus*, *Olbaberoides*, *Oncerus*, *Oniticellus*, *Onitis*, *Onthophagus*, *Oplostomus*, *Orizabus*, *Orphnidus*, *Orphnus*, *Osmoderma*, *Oxygrylius*, *Oxysternon*, *Pachycnema*, *Paracotalpa*, *Parathyce*, *Pedaria*, *Pedaridium*, *Pelidnota*, *Peritrichia*, *Phacosoma*, *Phallogogonia*, *Phalops*, *Phanaeus*, *Phileurus*, *Philoscaptus*, *Phobetus*, *Phyllopertha*, *Phyllophaga*, *Popillia*, *Proagoderus*, *Pseudachloa*, *Pseudataenius*, *Pseudorphnus*, *Pycnoschema*, *Raceloma*, *Rhinocoeta*, *Rhyssemus*, *Sarophorus*, *Scarabaeus*, *Scatimus*, *Sceliages*, *Scelophysa*, *Schizonycha*

Serica, Sisyphus, Sparmannia, Spilophorina, Stethpseudincta, Strategus, Strigodermella, Sulcophanaeus, Syrichthodontus, Tephraea, Tragiscus, Trichiorhyssemus, Trochalus, Trogodes, Uroxyys, Valgus, Xinidium, Xyloryctes

The figures occur together at the end of this book. The abbreviations used in the descriptions and figures are given in the Appendix.

THE MORPHOLOGY AND TERMINOLOGY OF THE HIND WING ARTICULATION AND WING BASE OF SCARABAEOIDEA (COLEOPTERA)

General structure of the wing

The wing is divided into three main sections: (1) the wing articulation; (2) the wing base, and (3) the membranous wing and veins. The wing articulation and wing base are separated by a hinge line (Kukalová-Peck 1983) (Figs.1, 2b). Muscles attached to the wing articulation mobilize the sclerites, while the wing base conveys the movement of the wing articulation to the wing blade.

We are in agreement with Kukalová-Peck (1983) that there were eight veinal pairs in the ancestral protowing (Fig.1). From leading edge to trailing edge, the primary veins are as follows (abbreviations to be used in the text are in brackets): Precosta (PC), Costa (C), Subcosta (Sc), Radius (R), Media (M), Cubitus (Cu), Anal (A) and Jugal (J). Each primary vein was primitively composed of two fluted sectors, a convex anterior (A+) and a concave posterior (P-). Thus, ScA denotes the anterior subcostal sector while CuP denotes the posterior cubital sector. Branching of veins was primitively even (=dichotomous). For example, MP branched into MP1+2 and MP3+4 then branched again into MP1, MP2, MP3, and MP4. Each primary veinal sector branched about three times in the primitive condition.

The ancestral articulation was a simple, broad band extending between the wing and the tergum and continuing ventrally under the wing. Dorsally, the band was fissured into eight rows of four sclerites, aligned with eight veinal pairs, giving 32 sclerites (Fig.1). The articular sclerites serve as channels which keep the blood passages between the wing veins and the body cavity open.

The nomenclature of the articular band is based on the articulation of Palaeodictyoptera: Homiopteridae. Abbreviations given in brackets will be used in the remainder of the text. The basivenalia (B) are the most distal column of sclerites and are the sclerites which are continuous with or hinged to the veinal pair. They are followed proximally by fulcalaria (F) which primitively have musculature and provide the hinges for wings of the Pterygota, axalaria (AX), and proxalaria (P) which are the most varied in shape, length and width. Each row of sclerites is named by using the primary vein with which it is aligned as an adjective. For example, PCu denotes the cubital proxalare while BJ denotes the jugal basivenale.

The primitively separated proxalaria, axalaria and fulcalaria are, in Neoptera, fused together to form several typical clusters (= strongest neopterous synapomorphy; Kukalová-Peck 1983, 1991): the humeral plate (HP), the first axillary (1Ax), the second axillary (2Ax), the median plate (MED), the third axillary (3Ax), and sometimes the fourth axillary (4Ax) (not illustrated) (Figs.2a-b, 3) (for additional details see Snodgrass 1935 and Kukalová-Peck 1983, 1991). In the Coleoptera the basivenalia have fused together to form the *first basal plate (1BP)* and the *second basal plate (2BP)* (Fig.3) (Browne & Scholtz 1994).

The Wing Articulation

First Axillary (1Ax).

The first axillary is composed of four fused sclerites (Figs.2b, 4): subcostal fulcalare, subcostal axalare, radial axalare and medial proxalare (FSc + AXSc + AXR + PRM). Recent evidence from Neuroptera clearly shows that the head is composed of only one sclerite (FSc), the neck by two sclerites (AXSc and AXR) and the tail by a single sclerite (PRM) (J.Kukalová-Peck, personal communication 1993; the interpretation proposed by Kukalová-Peck & Lawrence (1993:203) that the head is composed of FSc + AXSc, the neck by AXM and the tail by PRM should be replaced by this new interpretation). Proximally 1Ax articulates with the subcostal proxalare (PRSc) and the radial proxalare (PRR), which are fused together (Fig.2b), anteriorly with the anterior subcostal basivenale (BScA) (Figs.2b, 3) and distally with the second axillary (2Ax) (Figs.2a, 3).

Dorsal view (Figs.2a-b, 3, 4): 1Ax, as mentioned above, articulates with PRSc + PRR proximally (Fig.2b), BScA anteriorly (Figs.2b, 3) and 2Ax distally (Figs.2a, 3). The distal margin of the neck articulates with 2Ax (Figs.2a, 3). In all Polyphaga this articulation takes the form of a concavity, termed the *distal embayment* (Fig.4).

The deltoid-shaped tail is divided into two main sections the *proximal arch* and the *distal arch* (Fig.4). In Coleoptera PRR is enlarged posteriorly. The proximal arch of 1Ax is recurved along the entire length (Fig.4) and articulates just below the distal margin of the more proximal PRR (which is fused to the tergum - Fig.2b). This junction is termed the *PRR articulation*. The distal arch articulates with 2Ax (Figs.2a, 3). Both articulations are mediated by tough membranes.

Ventral view (Fig.5): Ventrally, the distal margin of the neck folds proximad to form a very broad, crescent-shaped ridge, termed the *distal neck ridge*. The proximal margins of the head and neck are curved ventrad to form a second, slender ridge, termed the *proximal neck ridge*. Medially the head and neck are deeply concave.

The proximal and distal arches of the tail are each often margined by a ridge extending along the entire length of each arch. Often these ridges extend posteriad and fuse to a third ridge which extends along the posterior margin of the tail, forming a triangle with an open top. These ridges are termed the *proximal tail ridge*, *posterior tail ridge* and *distal tail ridge* and are of variable width and length. The ridges and the concavities accommodate the proximal ridge and lobe of 2Ax.

Anterior view (Fig.6): The head is armed with one or two teeth and a long concave projection which surrounds the postero-proximal corner of BScA. The ventral tooth is referred to as *FSc1* and the dorsal as *FSc2*. The teeth are usually separated by a *ventral projection* and an *embayment*.

FSc1 is formed as a convex tooth which extends along the ventral margin of the ventral projection. *FSc1* articulates in a groove formed between two large convexities on the proximal margin of BScA and is prevented from pivoting anteriorly by the dorsal margin of BScA.

The ventral projection, a slender, concave structure, articulates with the inner surface of the posterior convexity on the proximal margin of BScA. A concavity, which is of variable length, runs the length of the ventral projection. The embayment separates *FSc1*/ventral projection from *FSc2*, and surrounds the most posterior convexity on the proximal margin of BScA. *FSc2* is formed as a slender, convex tooth. It articulates in a deep concavity formed along the posterior margin of BScA.

Second Axillary (2Ax).

The second axillary is composed of the medial axillare and radial fulcalare (AXM + FR) (Figs.2b, 3b, 7a). The bulk of 2Ax is formed by AXM (Fig.7a).

Dorsal view (Figs.2b, 3, 7): FR, the arm, connects with the posterior radial basivenale (BRP) (Figs.2b, 3) anteriorly and AXM posteriorly (Figs.2b, 3, 16). FR may be very large and strongly sclerotized (Figs.2b, 3, 16), slender (Fig.7a) or absent.

AXM is a bi-lobed structure (Fig.7). It is composed of a *dorso-proximal lobe* (*d-pl*), a *dorso-distal lobe* (*d-dl*), a *dorso-proximal ridge* (*d-pr*) and a *dorso-distal ridge* (*d-dr*) (Fig.7b). The ridges and lobes are collectively termed the arm and body respectively. Each lobe is generally either deltoid- or harp-shaped. The ridges extend between and separate the lobes. Anteriorly and posteriorly, one ridge may conceal another. Medially the ridges are often separated by a *medial groove* (*mg*) (Fig.7c) which articulates with the 1Ax distal embayment and arch. Anteriorly the ridges may be very long or short, strongly or weakly elevated, but they always articulate with the 1Ax distal embayment and arch. Posteriorly the ridges are broadly separated from their ventral components to form a concavity to accommodate a tendon (see below). The proximal lobe and ridge are concealed under 1Ax in intact specimens leaving only the distal ridge and lobe visible (compare Fig.3, an intact wing articulation, with Fig.7, a dissected 2Ax). The proximal lobe articulates with the 1Ax ridges. Distally, the distal lobe is broadly fused to the medial plate (MED) (Fig.3b). The distal ridge and lobe articulate with FR (Fig.7a).

Ventral view (Fig.8): Both lobes and ridges have ventral components. For convenience the prefix ventro- is added. It is composed of a *ventro-proximal lobe* (*v-pl*), a *ventro-distal lobe* (*v-dl*), a *ventro-proximal ridge* (*v-pr*) and a *ventro-distal ridge* (*v-dr*).

The proximal lobe is equipped with a convexity. This convexity is termed the *posterior wing process junction* (*PWP*) and articulates with the posterior wing process by a short section of tough membrane.

The ventro-distal ridge terminus, here termed the *subalare tendon attachment point (STAP)* is generally spatulate and broadly separated from its dorsal components. This section forms a very large attachment point for a long section of very stiff membrane or tendon which is connected to PRA+PRJ. It is the latter which is joined to the subalare and finally the M79 muscle.

Median Plate (MED).

The median plate is composed of FM1 proximally and FM2 distally (Fig.3). Anteriorly, FM1 is fused to the proximal margin of the anterior medial basivenale (BMA), while FM2 is fused to the proximal margin of the posterior medial basivenale (BMP). The proximal margin of FM1 is fused to 2Ax, the postero-proximal margin is loosely associated with 1Ax distal arch terminus and the postero-distal margin is fused to the third axillary (3Ax). Therefore, the junction between 1Ax+2Ax and 3Ax is mediated by FM1. FM1 and FM2 may be separated, or partially or fully fused. FM1 is generally very large. Although FM1 can be greatly reduced, a small remnant always remains to mediate the junction between 1Ax+2Ax and 3Ax.

Third Axillary (3Ax).

The third axillary is composed of the cubital, anal and jugal axalaria and fulcalaria (AXCu + AXA + AXJ + FCu + FA + FJ) (Fig.9).

The head of 3Ax is composed of AXCu proximally, FCu medially and FA distally. The neck is composed of AXCu proximally and FA distally. The prong lies at the proximal margin of the neck and articulates with the detached AXCu fragment. The prong is often extended posteriorly and proximally to form a ridge. In some scarabaeoids FA and/or AXCu is greatly enlarged, forming a distinct arm.

The tail is composed of AXA proximally and FJ distally. These two sclerites are often separated by a medial weakening which is termed the window. The detached AXCu fragment is a small, separated piece of 3Ax, specifically AXCu (Figs.3b, 9). The M71 muscle inserts into this fragment, which, when contracted, pulls it down causing the proximal part of 3Ax to sink down and the distal part to lift and slightly rotate. This allows 3Ax to fold upon itself. The folding is mediated by the detached AXCu fragment and the 3Ax neck prong.

The Wing Base

First Basal Plate (1BP).

The first basal plate is composed of the precostal and costal fulcalaria and basivenalia (FPC + BPC + FC + BC collectively known as the humeral plate (HP)), the anterior subcostal basivenale (BScA), the posterior subcostal basivenale (BScP hidden beneath BScA), the subcosta anterior vein base (ScA bulge) and the radial basivenale (BR) (Figs.3, 10). 1BP is articulated to 1Ax, 2Ax and MED (Fig.3).

Dorsal view (Figs.3, 10-11, 17): HP distally is continuous with PC and C and folds posteriorly along its whole length (Figs.3b, 10-11). The membranous gap between HP and BScA + ScA can be of varying width (compare Fig.10 with Fig.11).

BScA is usually deltoid and separated into a *proximal section* and a *distal section* (Figs.10-11). The postero-proximal and posterior margins of BScA articulate with the 1Ax head via deep grooves and convexities mediated by tough membranous strips (Fig.3). Two convexities separated by a narrow groove are located proximally and a very deep concavity extends along the posterior margin of BScA.

The ScA bulge lies distal to BScA and is partially separated from the latter by a concavity of varying width and depth (compare Fig.3b with Fig.11). Posteriorly, the ScA bulge is adjacent to, and may be fused with, the anterior margin of BR. In some taxa a small convexity, an extension of the postero-proximal margin of the ScA bulge, overlaps the antero-distal margin of BR. This is termed the *ScA-BRP brace* (found only in Geotrupidae).

BRP is an arch-shaped structure curving anteriorly (Figs.3, 10, 13). The proximal and distal sections are termed the *proximal arch* and *distal arch* (Fig.13). Medially BRP forms a membranous embayment (Fig.13). If the embayment is wider anteriorly than posteriorly, then BRP is termed *closed* (Fig.13b). If not then BRP is termed *open* (Fig.13a). The proximal arch is usually secondarily divided into a large main arch and a small, proximal sub-arch termed *brp* (Fig.13a). The posterior margins of both *brp* and the proximal arch articulate with FR (Fig.3). Anteriorly, *brp* gives rise to a long extension which fuses with the posterior margin of BScA, forming part of the concavity which articulates with FSc2 (Fig.3b). This extension is termed the *brp projection* (Fig.13a). Distally, the distal arch gives rise to, and is fused with, RP (Figs.3b, 13).

Anterior view (Fig.12): HP is a slender structure which is usually clavate proximally and slender apically. The apex is continuous with PC and C (Fig.3b). The proximal section of HP folds dorsally and ventrally.

Ventral view (Fig.15): HP forms an eyelet which surrounds the small, proximal section of the basalare (see Fig.72 in Kukalová-Peck & Lawrence 1993:245). This junction is strengthened by a short section of tough membrane.

BScP (Fig.15) is a polished, smooth, usually deltoid structure which articulates with the distal section of the basalare when the wing is extended. No membrane mediates this junction. Distally BScP is continuous with ScP.

Second Basal Plate (2BP).

The second basal plate is a large central plate composed of the anterior and posterior medial basivenale, the anterior and posterior cubital basivenale and the base of the cubitus anterior vein (BMA + BMP + BCuA + BCuP + CuA) (Figs.3b, 13). 2BP is articulated to MED and 3Ax (Fig.3).

BMA has a similar shape to BR, an arch-shaped structure curving posteriorly (Fig.13a). It too is separated into a *proximal arch* and a *distal arch* (Fig.13b). The posterior margins of the BRP arches meet, but do not fuse with, the anterior margins of the BMA arches (Fig.13b). The BMA proximal arch is often extended ventrad below the BRP proximal

arch terminus (Fig.17). Posteriorly BMA is fused with BMP. This fusion may be incomplete (Figs.13a, 18) or complete (Fig.13b). Distally BMA is primitively continuous with MA.

BMP is a rectangular sclerite, which narrows proximally and broadens distally (Fig.13a). It is composed of a postero-proximal section, which lies posterior of BMA, and a distal section, which lies distal to BMA. The distal margin is continuous with MP and gives rise to one, or rarely two, tube-like braces, depending on the taxon concerned. These braces extend from BMP and fuse with either the base of BCuA or with CuA. They are termed the *BMP-BCuA brace* (Figs.3b, 13a, 19) and the *BMP-CuA brace* (Fig.13b) respectively. Browne (1991b:223) incorrectly termed these braces the *bma1+bmp1-BCuA brace* and the *bma1+bmp1-CuA brace* having erroneously concluded that BMA also shared in the formation of the brace with BMP. BCuA is either adjacent to or fused with BCuP (Figs.3b, 13b). The fusion can be deep and broad or secondarily reduced as a distal concavity, termed the *distal embayment* (Fig.13b).

Basalare (BAS).

The basalare is composed of a *head*, *neck*, and *tail*. It is not strictly part of the dorsal wing articulation but it serves an important function in the depression and elevation of the wing.

The head is clavate and bi-lobed, and articulates with HP and BScP. The proximal lobe articulates with the eyelet formed by HP ventrally and is termed the *HP lobe* (Fig.14). When the wing is closed, the distal lobe fits in an eyelet between the postero-ventral margin of HP and the antero-ventral margin of BScA. When the wing is extended the distal lobe articulates with BScP and is termed the *BScP lobe* (Fig.14).

Anteriorly the neck separates the two lobes and posteriorly it extends ventrad as a long tube-like structure which terminates at the tail. The tail is embedded in the proximal margin of the tergum, anterior of the posterior wing process (see Fig.72 in Kukalová-Peck & Lawrence 1993:245). It is broad and scaphoid.

Additional Structures.

The subcostal and radial proxalaria (PRSc + PRR) are fused together (Fig.2b). Their proximal margins are fused to the tergum while their distal margins are stiffly hinged to the proximal margin of 1Ax.

The cubital, anal and jugal proxalaria (PRCu, PRA, PRJ) are also fused to the tergum (Fig.2b). PRCu medially extends distad as a projection termed the medial extension. It can be of variable length and is associated with the proximal margin of the detached AXCu fragment of 3Ax.

PRA and PRJ are fused together and the antero-distal margin articulates weakly with the proximal margin of the 3Ax tail (Fig.2b). The ventral side of the postero-distal margin is stiffly connected to 2Ax by a very strong strip of membrane. Ventrally it is connected to the subalare which is attached to the M79 muscle. Posteriorly the subalare is connected to the lateral process of the epimeron by the short M70 muscle.

The anal basivenalia (BAA + BAP) are of variable size and degree of sclerotization (Fig.2b). Distally they are continuous with AA and AP respectively. The anterior margin of BAA is often closely associated with, or fused to, BCuP. The jugal basivenalia (BJA + BJP) are very small to absent (Fig.2b). Distally they are continuous with JA and JP respectively.

RESULTS AND DISCUSSION

Description format

Descriptions of scarabaeoid families and scarab subfamilies, and most other taxa of uncertain phylogenetic status were constructed based on a broad examination of many scarabaeoid taxa. To avoid undue repetition a hierarchical system of italic and plain font styles are employed. An hypothetical example of a 2Ax description format is as follows:

“Body - Dorsal View: Proximal lobe deltoid; long; arises medially from arm. *Base* very broad. *Apex* narrowly rounded; weakly curved anteriorly. Antero-proximal margin with a concavity. Distal lobe deltoid ...”

This indicates that the structure being described is 2Ax body (one dash) in the dorsal view (full colon). More specifically, the description details the dorsal view of the proximal lobe including observations about its base and apex (italics). An additional note concerning the antero-proximal margin of the apex is also given. A description of the distal lobe follows and the hierarchical system is repeated.

The descriptions which follow are groundplans. Therefore, any modification of those states can be considered as derived.

Glaresidae

Introduction

Glaresidae are a small (about 50 species), virtually cosmopolitan monotypic family (Scholtz 1990) accommodating the genus *Glaresis* Erichson. It has wide geographical distribution which includes Africa, southern and eastern Europe, and North- and South America. It is absent from Australia. Approximately 50 species are included in the genus. Glaresidae biology and phylogeny were dealt with by Scholtz et al. (1987).

Glaresis was originally placed in the Trogidae based on a few generalized characters. The lack of any demonstrable apomorphies led Scholtz et al. (1987) to propose the family Glaresidae. Based on the non-chiasmatic Xyp sex chromosome, Smith & Virkki (1978) concluded that *Glaresis* is the most archaic living scarabaeoid genus. This view was reiterated by Scholtz et al. (1994) in a review of all characters suites, including those of the hind wing articulation and wing base.

Hind Wing Articulation Description

First Axillary (Fig.20)

Head - Dorsal surface normal size. *Antero-dorsal margin* oriented weakly postero-distad; normal width; planate. *Antero-proximal margin* strongly enlarged ventrally. *Postero-proximal margin* weakly and narrowly enlarged proximally. *FSc2* base normal width. *Apex* oriented postero-distad; rounded. Anterior surface broad; very long; not waisted medially. *FSc1* absent. *Ventral projection* short but of normal width; tapers from base to apex; oriented disto-ventrad and curved posteriad; deeply concave. Apex narrow. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented dorsad. *FSc2* oriented distad and weakly dorsad; deltoid; extremely short and broad. Dorsal surface not enlarged. Head and neck dorsal surface weakly curved proximad.

Neck normal width and length; weakly oriented antero-distad; broadly articulated with 2Ax; discontinuous with tail. Proximal margin entire; curved ventrad; convex. Distal margin concave. *Distal embayment* weakly concave; shallow but broad.

Tail - Dorsal view: Proximal arch normal size; weakly concave. *Antero-proximal margin* concave. *Postero-proximal margin* convex. Articulation with PRR very weak. Posterior margin moderately concave. Distal arch normal size. *Apex* weakly curved ventrad and posteriad; acuminate. *Distal margin* straight. - Ventral view: Proximal, distal and posterior margins with very weak ridges.

Second Axillary (Figs.16, 21)

Radial Fulcalare strikingly broadly ovoid and extremely large; very strongly sclerotized; fused to the entire anterior margin of 2Ax distal lobe and ridge; almost indistinct from 2Ax. Ridge - Dorsal view: Proximal ridge only very weakly differentiated from the body. *Apex to postero-median section* absent. *Postero-median to terminus* extremely narrow along the entire length; straight; very short; weakly distinct from lobe; strongly depressed below the distal ridge; weakly extended past the posterior margin of lobe; straight; oriented posteriad. Distal ridge only very weakly differentiated from the body. *Apex* oriented ventro-proximad; convex and broadly falcate; extremely short. *Anterior section* arises from the anterior margin of the distal lobe; extremely short; very broad; curves proximad. *Anterior to terminus* absent. Articulation with 1Ax weak; anteriorly 1Ax distal arch articulates below the proximal margin of the distal lobe; posteriorly 1Ax distal arch articulates between the proximal ridge and distal lobe. - Ventral view: Proximal and distal ridges are only weakly differentiated from each other; proximal ridge completely conceals the distal ridge. *Apex* broadly truncate. *Anterior to antero-median section* stout; curved distad. *Median to posterior section* not visible; obscured by the distal lobe. *Subalare tendon attachment point* moderately long and narrow; extends posteriad from the median; visible dorsally along the postero-proximal and postero-distal margins of the body; the postero-dorsal section of the proximal ridge is extended past the terminus of the subalare tendon attachment point. Terminus narrowly rounded; not curved ventrad; oriented posteriad.

Body - Dorsal view: about as long as broad. Proximal lobe oriented proximad; arises ventrally from the postero-medial section of the distal lobe and ridge; short; clavate;

strongly sclerotized; convex. *Base* narrow. *Apex* very broadly rounded; straight. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe large; deltoid; much larger than proximal lobe; strongly sclerotized; planate; not sloped ventrad. *Anterior margin* normal length; straight; oriented postero-distad. *Base* extremely broad; extends from the apex to the terminus of the ridge. *Apex* very broadly rounded. *Posterior margin* straight; not reduced. - Ventral view: Proximal lobe short; convex. *Posterior wing process junction* ovoid; occupies the posterior margin of the lobe. Distal lobe extremely large; continuous with ridge; weakly concave.

Median Plate (Fig.3)

FM1 oriented posteriad. *Anterior to posterior section* extremely broad. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* very broadly and strongly fused to 3Ax. FM2 moderately long; oriented posteriad; very broadly acerose; separated from FM1 by a short, extremely narrow section of membrane.

Third Axillary (Fig.22)

Head weakly convex; normal length. Proximal margin weakly convex. Anterior margin weakly convex; not enlarged ventrally. *Antero-proximal and antero-distal margins* not extended anteriorly. AXCu present as a very slender, anterior extension along the proximal margin of head. FCu normal size; occupies most of the head; weakly ovoid to deltoid. FA moderately narrow; occupies the distal margin of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck very weakly elevated proximally but not distally. FCu section of neck absent. AXCu forms entire neck; extremely long. Proximal margin elevated as a weakly distinct ridge. *Ridge* does not curve distad; very long. Dorsal surface of ridge is weakly curved proximad. Posterior section absent. Prong armed with a single extremely narrow and short tooth; oriented postero-proximad. Detached AXCu fragment slenderly ovoid; moderately sclerotized.

Tail long; narrow; convex. Dorsal surface oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section very weakly concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. AXA straight. FJ+AXJ and AXA equally narrow. Suture line between FJ and AXJ present. Suture line between FA+AXJ and AXA present. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.10)

Humeral Plate extremely narrow; long. Anterior margin convex; lies very distant from BScA and ScA. Apex very weakly deltoid; extremely narrow; not curved ventrad. Dorsal margin sinuate. Proximal margin convex; very weakly curved ventrad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC present. *FC+BC* present as a very long and narrow sclerite posterior to FPC+BPC.

Anterior Subcostal Basivenale oriented antero-distad; slenderly ovoid; convex; weakly elevated dorsad. Proximal section indistinct from the distal section. *Distal margin* discontinuous from the ScA bulge; separated by a shallow concavity. Apex broadly rounded. – Subcosta Anterior moderately convex. Bulge very broad.

Radial Basivenale extremely broadly open; broadly convex but extremely narrow; continuous with radial stem; angled antero-proximad. Proximal arch slenderly deltoid; continuous with the anterior margin of BR; extensions absent; angled postero-proximad. *Posterior margin* rounded. *Anterior margin* strongly elevated above the posterior margin of the ScA bulge; very broad; straight; angled antero-proximad. Embayment broad but extremely shallow; broadly deltoid. Distal arch absent. *br* absent. *br projection* narrow; convex; fused to the postero-distal margin of BSca.

Second Basal Plate (Figs.23, 17-19)

MA-BMA Junction present. – MP-BMP Junction: MP broadly continuous with BMP along all margins and surfaces. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present: very strong but slender; extends posteriad; distinct from BMP; much more strongly convex than BMP. Posterior fused within a deep concavity on the antero-proximal margin of BCuA.

Medial Basivenalia massive; BMA and BMP incompletely fused. BMA extremely broad and very long; scaphoid; lies anterior of BMP. *Postero-medial section* gives rise to FM2. *Proximal, medial and distal surfaces* very strongly convex. *Anterior margin* broadly concave. *Proximal arch* planate and straight; extremely long; extremely broad; oriented antero-proximad. Apex terminates below BR proximal arch apex. Postero-proximal section gives rise to FM1. *Distal arch* Dorsal view: weakly differentiated from the posterior section of BMA but distinct; weakly extended distad. – Ventral view: strongly extended distad and continuous with BMA remnant. BMP *proximal and distal sections* undifferentiated; broadly fused to both IBP and BCu. *Anterior section* weakly rectangular; convex; curves anterior; incompletely fused to BMA, separated by a very deep groove; discontinuous with the posterior section of BMP. *Posterior section* present; broadly deltoid; flat; strongly depressed below BMA and BMP anterior section; weakly sclerotized; fused to BMA. *Distal section* distinct from the BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia narrowly fused. Posterior margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA deltoid; small; convex; oriented postero-distad; strongly sclerotized; lies posteriad of BMP and anterior of the CuA base. *Anterior margin* with a moderately broad but shallow concavity. *Posterior margin* continuous with CuA. BCuP very large; ovoid; convex; oriented postero-distad; moderately sclerotized. Distal embayment absent. – Cubitus Anterior fused to BCuA. Junction marked by a distinct suture.

Basalare

Head - HP lobe very small; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects dorsad.

Dorsal surface ovoid; weakly convex; polished; not depressed from neck. *Ventral surface* polished. – Posterior Subcostal Basivenale deltoid, polished.

Discussion

Glaresidae exhibit the generalized scarabaeoid state of all characters, including those of the wing articulation and wing base which leaves no doubt that Glaresidae are the most archaic family in the Scarabaeoidea, quite likely very close in structure to the ancestral scarabaeoid (Scholtz et al. 1994), and the sister group of all other scarabaeoids (Browne & Scholtz 1995). This family does not display any autapomorphic characters of the hind wing articulation or wing base (Browne 1991a, 1993; Scholtz et al. 1994; Browne & Scholtz 1995).

Passalidae

Introduction

The Passalidae are a virtually cosmopolitan family with approximately 40 genera and 500 species which are most abundant in tropical regions (Reyes-Castillo 1970).

The Passalidae are a well-defined family whose monophyly is supported by numerous derived characters and there is little doubt that it is one of the more archaic scarabaeoid families (Reyes-Castillo 1970). The numerous and unusual derived features exhibited by Passalidae have led some workers to suggest that they be excluded completely from the Scarabaeoidea (Reyes-Castillo pers. comm. 1990). This family is comprised of two subfamilies, Aulacocyclinae and Passalinae (Reyes-Castillo 1970).

Hind Wing Articulation Description

First Axillary (Fig.24)

Head - Dorsal surface normal size. *Antero-dorsal margin* normal width; weakly deplanate; oriented weakly postero-distad. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* base normal width. Apex rounded; oriented postero-distad. Anterior surface broad; very long; not waisted medially. *FSc1* very weak. *Ventral projection* tapers from the base to apex; short but of average width; deeply concave; oriented disto-ventrad and curved posteriad. Apex narrow. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented dorsad. *FSc2* deltoid; broad; very convex; oriented distad and weakly dorsad. *Dorsal margin* not enlarged. Head and neck dorsal surface weakly curved proximad.

Neck normal width and length; weakly oriented antero-distad; broadly articulated with 2Ax. Proximal margin straight. Distal margin weakly concave. *Distal embayment* concave; moderately narrow.

Tail - Dorsal view: Proximal arch strongly reduced along all margins. *Antero-proximal margin* concave. *Dorsal surface* weakly concave. *Postero-proximal margin* weakly convex; weakly recurved. Articulation with PRR strong. Posterior margin concave. Distal arch

strongly expanded anteriorly and distally. *Distal margin* very weakly convex. *Apex* very weakly curved ventrad and posteriad; acuminate. - Ventral view: Proximal arch margined by a broad ridge. Posterior margin with a long ridge; entire but weak. Distal margin with a broad ridge.

Second Axillary (Fig.25)

Radial Fulcalare moderately broad. Terminus fused to the 2Ax ridge-body junction. *Point of fusion* moderately broad; weakly extended along the anterior margin of 2Ax.

Ridges - Dorsal view: Proximal ridge entire; weakly distinct from lobe. *Apex* narrow. *Anterior section* partially concealed by the distal ridge. *Antero-median to postero-median section* extremely narrow; partially enlarged above the distal ridge. *Posterior section* strikingly enlarged above the distal ridge; oriented posteriad. *Apex* narrow. Distal ridge very weakly distinct from lobe. *Apex* narrow but broadly falcate; convex; moderately short; oriented ventro-proximad; not fused to the proximal ridge apex. *Anterior section* moderately short; moderately narrow; strongly curved proximad. *Median to posterior section* slender; oriented posteriad. - Ventral view: Proximal ridge moderately narrow; distinct from lobe. *Anterior to median section* conceals the proximal section of the distal ridge; curved proximad. *Postero-median to posterior section* partially obscured by the distal ridge; visible proximally as a slender, concave piece. Distal ridge moderately broad; very long. *Postero-median to posterior section* rectangular; moderately broad. *Proximal and posterior sections* arise from the posterior margin of the distal lobe. *Subalare tendon attachment point* extends posteriad from the median; strikingly lengthened; slender.

Body - Dorsal view: about as long as broad. Proximal lobe small; deltoid; arises antero-medially from ridge but depressed below the ridge; strongly sclerotized; convex; oriented proximad. *Base* very narrow. *Apex* truncate; weakly curved anteriorly. *Anterior margin* deeply concave. *Posterior margin* weakly concave; weakly enlarged. Distal lobe strikingly reduced posteriorly and apically; longer and broader than the proximal lobe; strongly sclerotized; weakly concave; arises from the extreme anterior section of the ridge. *Proximal half* very thick; strongly sclerotized. *Distal half* thin; strongly sclerotized; weakly concave. *Anterior margin* strongly sclerotized; weakly sinuate; normal length. *Base* broad. *Apex* reduced; rounded. *Posterior margin* concave; reduced. - Ventral view: Proximal lobe partially concealed by the distal ridge; slender; cylindrical; convex; distinct from proximal ridge; oriented weakly antero-proximad. *Posterior wing process junction* weakly ovoid; occupies the posterior margin of the lobe. *Base* narrow. *Apex* round. Distal lobe deltoid; flat; small; distinct from distal ridge.

Median Plate (Fig.26)

FM1 large. *Anterior section* very narrow. *Antero-median section* abruptly broad. *Antero-distal margin* fused with FM2; a small membranous gap separates the two anteriorly. *Proximal margin* broadly fused with 2Ax from a point just posterior of the apex to the terminus. *Distal margin* broadly fused to 3Ax along the antero-proximal margin to the median. FM2 weakly distinct from FM1; short; deltoid.

Third Axillary (Fig.27)

Head moderately broad; normal length; weakly convex. Proximal margin straight. Anterior margin straight; not enlarged ventrally. AXCu absent. FCu normal size; weakly convex to concave. FA large; long; rectangular; extends far ventrad along the entire length of the head and dorsally occupies about one fourth of the head. Suture line between FCu and AXCu present. Suture line between FCu and FA present. Suture line between FA and AXCu present.

Neck not elevated dorsad; oriented postero-proximad. FCu section of neck absent. Neck comprised of AXCu proximally and medially, and FA distally. AXCu weakly elevated; broad; extended proximally and posteriorly. *Proximal embayment* oriented postero-proximad; extremely broad; deeply concave. *Distal margin* extended ventrad; large. Prong very broad. Ridge enlarged dorsally relative to AXA. *Apex* armed with two very weak teeth; extremely broad. Apices broadly rounded. Detached AXCu fragment deltoid; very large; slender. *Proximal margin* broadly but weakly concave. *Distal margin* convex; aciculate.

Tail long and narrow; weakly convex; very weakly sclerotized; oriented posteriad; lies ventrad to the head+neck. *Dorsal surface* oriented laterad. AXA and AXJ indistinct; slender and very weakly sclerotized; straight. *Suture line* absent. FJ deltoid; moderately sclerotized. *Posterior* separates AXJ from AXA. *Apex* recurved to form a "stem" connecting the more dorsal FA with the tail. Anterior margin of the tail extends anteriorly below the head+neck. Proximal and distal margins straight.

Hind Wing Base Description

First Basal Plate (Fig.28)

Humeral Plate extremely narrow and very long; distant from BScA. Anterior margin not curved posteriad. Dorsal and ventral margins nearly straight. *Apex* weakly curved ventrad. Suture lines between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale broadly deltoid; weakly bi-lobed; weakly convex; oriented distad. Proximal margin with two embayments separated by a long ridge. *Embayments and ridge* oriented proximad. Posterior embayment margined posteriorly by a small ridge. Proximal and distal sections indistinct from each other. BScA ventrally deeply concave. BR, br and the br projection broadly fused to BScA. *Suture lines* absent. – Subcosta Anterior weakly convex. Bulge not prominent.

Radial Basivenale open; long; convex; slenderly deltoid; oriented proximad. Proximal arch extremely broad; very long; rectangular; continuous with the anterior margin of BR; oriented posteriad. *Postero-distal section* rounded. Anterior margin convex; moderately narrow. Embayment normal size. Distal arch absent. br very broad; strongly sclerotized. *br projection* extremely broad; fused to the distal and posterior margins of BScA.

Second Basal Plate (Fig.29)

MA-BMA Junction absent. – MP-BMP Junction entire; MP continuous with BMP. – Crimp Patterns absent. – BMP-CuA Brace – slender; convex; adjacent to, but more convex and

distinct from, the distal margin of 2BP; intervening membrane sclerotized. Anterior section continuous with MP. Posterior section continuous with CuA. – BMP-BCuA Brace absent.

Medial Basivenalia massive; strongly sclerotized. BMA broadly scaphoid; very large; angled postero-proximad; flat but elevated above and separated from BMP by a deep groove; lies anteriorly, but not proximad, of BMP; fully fused to BMP. *Anterior margin* concave. *Proximal arch* planate; straight; broad; enlarged antero-proximally. *Distal arch* extremely long; allantoid; extends far distad. BMP planate; large; broadly fused to 1BP and BCuA; very weakly separated into anterior and posterior sections; discontinuous with brace. *Anterior margin* concave; fused to 1BP. *Proximal margin* deeply concave. *Posterior margin* fused to BCuA and CuA; indistinct. *Distal margin* discontinuous with brace.

Cubital Basivenalia large; ovoid or weakly deltoid; narrowly fused. Postero-distal margin of BCuA fused to antero-proximal margin of BCuP. *Suture line* very weak but present. BCuA about the same size as BCuP; oriented postero-distad. Distal margin with a very deep embayment. *Embayment* strongly sclerotized. BCuP oriented antero-distad. – Cubitus Anterior basally connected to BCuA along the postero-proximal margin. Anterior interrupted by the BMP-CuA Brace.

Basalare (Fig.30)

Head - HP lobe short; broad; weakly elevated. *Dorsal surface* truncate; weakly polished. BScP lobe large; broad; oriented disto-ventrad; laterally ovoid. *Dorsal surface* broadly ovoid; polished. *Ventral surface* polished. – Posterior Subcostal Basivenale ovoid; long; polished; oriented proximo-ventrad.

Discussion

As with other morphological characters (see Scholtz 1990), passalids exhibit numerous autapomorphic wing articulation and wing base character states. Monophyly of the Passalidae is supported by the fact that all of the taxa in this family share the following 13 apomorphic character states of the wing articulation and wing base:

1. 1Ax: the proximal arch is very strongly reduced along all margins.
2. the distal arch strongly expanded anteriorly and distally;
3. 2Ax: the distal lobe is strikingly reduced posteriorly and apically.
4. arises from the extreme anterior section of the ridge;
5. 3Ax: the tail is very weakly sclerotized.
6. the demarcation between sclerites absent.
7. the tail extends anteriorly below the posterior margin of the neck,
8. is separated from the head+neck by a tube-shaped stem;
9. 1BP: the proximal margin of BScA is interrupted by a deep and broad groove, giving it a bi-lobed appearance which provides additional support for the 1Ax head teeth,
10. the proximal and distal sections of BScA are indistinct from each other,
11. the proximal arch of BR is extremely broad, very long and rectangular.
- 12/13. BR, br and the br projection apices are fused to, and indistinguishable from BScA.

Passalidae share six apomorphic character states of the wing articulation and wing base with Diphylostomatidae, Lucanidae, Glaphyridae, Trogidae, Bolboceratidae and Pleocomidae (Browne & Scholtz 1995).

Diphylostomatidae

Introduction

The Diphylostomatidae are a monotypical family with three species endemic to the western USA. Males and females are dimorphic. Males are smaller and long-winged and females are larger, with reduced wings, eyes and antennae. Nothing is known about their biology and the larvae are unknown.

Diphylostoma was described as a member of Aesalinae (Lucanidae) but since it apparently has little in common with Lucanidae, Holloway (1972) elevated *Diphylostoma* to family status. She based this on the presence of exposed protrochantin, exposed second abdominal segment, reduced female genitalia in *Diphylostoma* and differences in wing venation, male genitalia and leg structure between *Diphylostoma* and Lucanidae. This system is currently accepted by other workers in the field (Scholtz 1990).

Holloway (1972) suggested that Diphylostomatidae are closely related to Geotrupidae. Recently, Caveney (1986) suggested, based on synapomorphic ommatidium structure, that Diphylostomatidae are probably more closely related to Lucanidae. This relationship is supported by wing articulation and wing base characters (Browne & Scholtz 1995).

Hind Wing Articulation Description

First Axillary (Fig.31)

Head - Dorsal surface normal size. *Antero-dorsal margin* normal width; weakly deplanate; oriented weakly postero-distad. *Postero-proximal margin* weakly enlarged proximally. *Proximal margin* strongly enlarged ventrally. *FSc2* base normal width. Apex rounded; oriented postero-distad. Anterior surface broad; very long; not waisted medially. *FSc1* very weak. *Ventral projection* tapers from base to apex; short but of normal width; deeply concave; oriented disto-ventrad and curved posteriad. Apex narrow; rounded. Concavity located in the preapical area; surrounded by three unequally strong ridges of unequal length. *Distal embayment* oriented dorsad. *FSc2* deltoid; broad; very convex; oriented distad and weakly dorsad; not enlarged dorsally. Head and neck dorsal surface weakly curved proximad.

Neck normal width and length; strongly curved proximad; weakly oriented antero-distad. Proximal margin moderately convex. Distal margin deeply but narrowly concave; broadly articulated with 2Ax. *Distal embayment* concave.

Tail - Dorsal view: Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* concave. *Postero-proximal margin* convex; weakly recurved. Articulation with PRR strong but short. Distal arch normal size; slightly longer than the proximal arch; weakly oriented postero-proximad. *Apex* aciculate; weakly curved ventrad and posteriad. *Distal margin* straight. - Ventral view: Proximal arch margined by very weak ridges.

Posterior margin with a long ridge; entire but very weak. Distal arch with a very broad, but weakly elevated ridge.

Second Axillary (Fig.32)

Radial Fulcalare very narrow; virgate; poorly sclerotized. Terminus fuses to the 2Ax ridge. *Point of fusion* very narrow; restricted to the medial section of the 2Ax ridge; absent from body.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Anterior to antero-medial section* concealed distally by distal ridge. *Antero-medial to posterior section* moderately broad; partially elevated above the distal ridge. *Posterior section* acerose; strikingly enlarged above the distal ridge; oriented posteriad. Distal ridge distinct from lobe. *Apex* narrowly falcate; moderately short; convex; curved; oriented ventro-proximad. *Anterior section* slender; moderately short; curved proximad. Fuses with the anterior margin of the distal lobe. *Median section* curved distad. *Posterior section* obscured by the proximal ridge. - Ventral view: Proximal ridge broad; indistinct from the proximal lobe. *Apex* aciculate. *Anterior section* broadly acerose; weakly curved proximad; conceals the distal ridge proximally. *Median to posterior section* concealed by the distal ridge. Distal ridge moderately broad. *Median and posterior sections* arise from the proximal and posterior margins of the distal lobe; indistinct from lobe. *Median section* convex. *Subalare tendon attachment point* moderately long and narrow; extends posteriad from the median; not curved ventrad. Posterior margin rounded. Distal separated from the dorsal surface of the ventro-distal lobe.

Body - Dorsal view: Proximal lobe narrow but long; deltoid; arises postero-medially from ridge; moderately sclerotized; flat; depressed below the ridge; oriented proximad. *Base* enlarged anteriorly and posteriorly. *Anterior and posterior margins* greatly enlarged; concave. *Median to apex* reduced. *Apex* narrowly rounded. Distal lobe roundly deltoid; small; reduced distally; shorter but broader than proximal lobe; weakly sclerotized; weakly concave. *Anterior margin* normal length; weakly concave. *Posterior margin* weakly concave. - Ventral view: Proximal lobe distally concealed by the distal ridge; slender; weakly convex. *Posterior wing process junction* ovoid; occupies the posterior margin of the lobe. Distal lobe weakly concave; continuous with ridge.

Median Plate (Fig.33)

FM1 and FM2 fused as a single plate; weakly sclerotized. *Anterior, median and posterior margins* about equally broad. *Proximal margin* broadly fused to 2Ax. *Distal margin* broadly fused to 3Ax.

Third Axillary (Fig.34)

Head narrow; normal length; weakly convex. Proximal margin straight. Anterior margin narrow; not enlarged ventrally; weakly convex. FCu normal size. *Distal margin* reduced by FA. FA broad; weakly sclerotized; only visible laterally. AXCu large; occupies the proximal margin of the head. *Anterior margin* weakly enlarged anteriad. Suture line

between FCu and FA present. Suture line between FCu and AXCu present. Suture line between AXCu and FA present. Suture line between FA and FJ present.

Neck weakly elevated dorsad. FCu section of neck absent. Neck comprised of AXCu. *Proximal embayment* oriented proximad; small; shallowly concave. Ridge posterior section present. Prong armed with a single tooth. *Tooth* short; deltoid. Apex weakly rounded. Detached AXCu fragment very small; slender; weakly sclerotized.

Tail long; moderately broad. Dorsal surface oriented laterad. Anterior section only weakly concave. Median and posterior section very weakly convex to planate. *Window* absent. FJ and AXJ equally broad; moderately sclerotized. *Suture line* present. FJ occupies an equal amount of the tail as FJ+AXJ. AXA moderately long; straight. Suture line between FJ+AXJ and AXA present. Suture line between AXA and AXCu strong.

Hind Wing Base Description

First Basal Plate (Fig.35)

Humeral Plate slender. Anterior margin convex sinuate. Apex curved ventrad. Dorsal margin weakly sinuate; slender; distant from BScA. Ventral margin weakly sinuate. Suture lines between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale broadly deltoid; weakly convex; oriented distad. Proximal section separated from the distal section by a prominent suture; as large as the distal section. Antero-median section oriented anteriad; weakly convex; terminus adjacent to HP. Apex broadly rounded; oriented distad. – Subcosta Anterior convex. Bulge not prominent; narrow; separated from BScA by a weak concavity.

Radial Basivenale strongly open; straight; slender; oriented proximad; continuous with radial stem. Proximal arch slenderly deltoid; oriented posteriad. *Anterior section* present. *Postero-distal margin* rounded. Anterior margin weakly convex to straight; narrow. Embayment normal size. Distal arch absent. *br* weak. *br projection* moderately narrow; strongly convex; extends anteriad from the antero-proximal margin of *br*; distinct from BScA.

Second Basal Plate (Fig.36)

MA-BMA Junction absent. – MP-BMP Junction not entire. Anterior margin continuous with BMP. – Crimp Patterns absent. – BMP-CuA Brace slender; convex; entire; adjacent to, but distinct from, the distal margin of 2BP. Anterior section continuous with MP. Point of fusion discontinuous. Posterior section continuous with CuA. – BMP-BCuA Brace absent.

Medial Basivenalia very large; rectangular. Anterior and posterior margins weakly convex. Anterior margin separated from BR by membrane. Posterior margin separated from BCuA by a sclerotized, concave groove. BMA broadly scaphoid; weakly convex; separated from BMP by a broad, shallow groove; lies anteriad, but not proximad of BMP; fully fused to BMP. *Proximal arch* planate; straight; enlarged antero-proximally; slightly shorter than the distal arch. *Distal arch* distinct; oriented antero-distad. BMP rectangular; convex; discontinuous with brace; distinct from 1BP and BCu. *Anterior section* rectangular; weakly

convex; separated from the posterior section by a weak impression. *Posterior section* present; weakly convex; depressed below the anterior section.

Cubital Basivenalia large; ovoid to deltoid; broadly fused. Posterior margin of BCuA fused with anterior margin of BCuP. *Suture line* weak. BCuA about the same size as BCuP; deltoid; convex; oriented weakly postero-distad; strongly sclerotized; an extension enters CuA along the anterior margin, just proximal of the brace-vein junction; curved anteriorly. BCuP large; oriented distad; weakly sclerotized. *Proximal margin* forms a convex ridge. Embayment shallow. – Cubitus Anterior fused to BCuA; only partially separated by a weak sclerotized groove. Anterior section interrupted by the BMP-CuA Brace.

Basalare (Fig.37)

Head - HP lobe digitate; very thin; small. *Apex* clavate; weakly curved ventrad. *Base* adjacent to, but separated from, BScP lobe. BScP lobe claviform; convex; bulbous; obscures neck: much larger than HP lobe. *Dorsal surface* moderately polished. *Ventral surface* rough. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Monophyly of the Diphyllostomatidae is supported by the fact that all of the taxa in this family share the following five apomorphic character states of the wing articulation and wing base:

1. 1Ax: the distal margin of the neck is deeply, but narrowly concave;
2. 2Ax: the dorso-proximal lobe base is greatly enlarged anteriorly and posteriorly,
3. but medially to apically reduced,
4. the distal margin of the subalare tendon attachment point is strongly separated from the dorsal surface of the ventro-distal lobe, the latter extends posteriorly beneath the former;
5. 2BP: BCuA curves anteriorly.

Analysis of wing articulation and wing base characters indicates that Diphyllostomatidae are a distinctive family warranting familial status and the sister group of Lucanidae (Browne & Scholtz 1995). Diphyllostomatidae share six apomorphic character states of the wing articulation and wing base with Passalidae, Lucanidae, Glaphyridae, Trogidae, Bolboceratidae and Pleocomidae (Browne & Scholtz 1995).

Lucanidae

Introduction

The Lucanidae are a large family with five large subfamilies and several small ones which include approximately 100 genera and 750 species with virtually world-wide distribution. Lucanidae are a well defined family whose monophyly is supported by many derived characters (Crowson 1967, 1981; Howden 1982; Scholtz 1990). Caveney (1986) suggested, based on synapomorphic ommatidium structure, that Lucanidae are probably more closely related to Diphyllostomatidae. This relationship was reiterated by Scholtz (1990) and is supported by wing articulation and wing base characters (Browne & Scholtz 1995).

Hind Wing Articulation Description

First Axillary (Fig.38)

Head - Dorsal surface normal size. *Antero-dorsal margin* normal width; weakly deplanate; oriented weakly postero-distad. *Postero-proximal margin* weakly enlarged proximally. *Proximal margin* strongly enlarged ventrally. *FSc2* base normal width. Apex rounded; oriented postero-distad. Anterior surface broad; very long; not waisted medially. *FSc1* very weak. *Ventral projection* tapers from base to apex; short but of normal width; deeply concave; oriented disto-ventrad and curved posteriad. Apex narrow. Concavity located in the preapical area; surrounded by three unequally strong ridges of unequal length. *Distal embayment* oriented dorsad. *FSc2* deltoid; broad; very convex; oriented distad and weakly dorsad; not enlarged dorsally. Head and neck dorsal surface weakly curved proximad.

Neck normal width and length; weakly oriented antero-distad; recurved relative to tail. Proximal margin convex. Distal margin weakly concave; broadly articulated with 2Ax. *Distal embayment* shallow; broad.

Tail - Dorsal view: weakly concave. Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* concave. *Postero-proximal margin* weakly convex. Articulation with PRR strong but short. Posterior margin weakly concave. Distal arch normal size; slightly larger than the proximal arch; weakly oriented postero-proximad. *Apex* aciculate; weakly curved ventrad and posteriad. *Distal margin* very weakly concave. - Ventral view: Proximal and distal arches with ridges. Posterior margin with a prominent ridge.

Second Axillary (Fig.39)

Radial Fulcalare present as re-enforced membrane.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* lengthened anteriorly, beyond the ventro-distal ridge apex. *Anterior to antero-median section* partially concealed distally by distal ridge; strongly curved ventro-distad beneath the distal ridge; separated from the distal ridge by a broad gap which extends to the mid-line of 2Ax. *Antero-median to posterior section* moderately broad; elevated above the distal ridge. *Posterior section* acerose; strikingly enlarged above the distal ridge; oriented posteriad. Distal ridge distinct from lobe. *Apex* narrowly falcate; moderately short; convex; very strongly curved distad; reduced distally and anteriorly, revealing the distal and apical sections of the dorso-proximal ridge. *Anterior section* slender; moderately short; shorter than the proximal ridge; strongly curved proximad; recurved, but curves abruptly ventrad towards the apex. Fuses with the anterior margin of the distal lobe. *Subapical to antero-median section* strongly oriented postero-distad. *Median to posterior section* strongly depressed ventrad, curving beneath the antero-median section of the dorso-proximal ridge, giving the appearance that the dorso-distal ridge and lobe twists around the dorso-proximal ridge and lobe. - Ventral view: Proximal ridge moderately broad; indistinct from the proximal lobe. *Apex* aciculate. *Anterior section* broadly acerose; weakly curved proximad; conceals the distal ridge proximally. *Median to posterior section* concealed by the distal ridge. Distal ridge moderately broad. *Median and posterior sections* arise from the proximal and posterior

margins of the distal lobe; indistinct from lobe: short; narrow. *Median section* convex. *Subalare tendon attachment point* moderately long and narrow; extends posteriad from the median; not curved ventrad; weakly visible dorsally. Posterior margin rounded.

Body - Dorsal view: Proximal lobe short; narrow; deltoid; arises postero-medially from ridge; moderately sclerotized; flat; depressed below the ridge; oriented proximad. *Base* weakly enlarged. *Anterior and posterior margins* greatly enlarged; concave. *Apex* narrowly rounded; curved anteriad. Distal lobe large and broad; roundly deltoid; not reduced distally; much larger than proximal lobe; weakly sclerotized; convex; slopes strongly ventrad from the ridge giving the appearance that the distal ridge and lobe are curving and twisting around the proximal ridge and lobe. *Base* very broad. *Apex* broadly rounded. *Anterior margin* normal length; weakly concave. *Posterior margin* weakly concave. - Ventral view: Proximal lobe narrow and long; weakly convex. *Posterior wing process junction* ovoid; occupies the posterior margin of the lobe. Distal lobe weakly concave; continuous with ridge; planate.

Median Plate (Fig.40)

FM1 oriented proximad anteriorly and postero-proximad medially and posteriorly; rectangular. *Anterior, median and posterior sections* extremely broad. *Proximal margin* straight. Articulation with 2Ax extends from apical angle of the distal lobe over the posterior section of the ventral ridge. *Distal margin* broadly fused to 3Ax. FM2 oriented proximad and weakly posteriad; rectangular; separated from FM1 by a moderately wide section of membrane; very small; acerose.

Third Axillary (Fig.41)

Head narrow; normal length; weakly convex. Proximal margin straight. Anterior margin narrow; not enlarged ventrally; weakly convex. FCu normal size. *Distal margin* strongly reduced by FA and AXCu. FA broad; weakly sclerotized; only visible laterally. AXCu large; occupies half of the head. *Anterior margin* enlarged anteriad. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between AXCu and FA present. Suture line between FA and FJ present.

Neck very weakly elevated dorsad. FCu section of neck absent. Neck comprised of AXCu. *Proximal embayment* oriented proximad; small; shallowly concave. Ridge posterior section present. Prong armed with a single tooth. *Tooth* short; weakly deltoid. Apex moderately broadly rounded. Detached AXCu fragment very small; slender; weakly sclerotized.

Tail long; aciculate; convex. Dorsal surface oriented laterad. Anterior only weakly convex. Median and posterior very weakly convex to planate. *Window* absent. FJ and AXJ equally broad; moderately strongly sclerotized. *Suture line* present. FJ occupies an equal amount of the tail as FJ+AXJ. AXA moderately long; straight. Suture line between FJ+AXJ and AXA present. Suture line between AXA and AXCu strong.

Hind Wing Base Description

First Basal Plate (Fig.42)

Humeral Plate moderately long. Anterior margin weakly sinuate. Apex deltoid; curved ventrad. Dorsal margin weakly sinuate; distant from BScA. Ventral margin weakly sinuate. Suture lines between FPC+BPC and FC+BC present.

Anterior Subcostal Basivenale broadly deltoid; weakly convex; oriented distad. Proximal section long; separated from the distal section by a prominent suture; as large as the distal section. Antero-median oriented arteriad; weakly convex; terminus distant from HP. Apex broadly rounded; oriented distad. – Subcosta Anterior weakly convex. Bulge narrow.

Radial Basivenale convex; strongly open; slender; oriented antero-proximad; continuous with radial stem. Proximal arch narrow; short; oriented postero-proximad. *Anterior section* present. *Postero-distal margin* rounded. Anterior margin elevated above BScA; narrow. Embayment normal size. Distal arch absent. *br* moderately sclerotized; large; discontinuous with BR. *br projection* apically broad; distinct from BSc.

Second Basal Plate (Fig.43)

MA-BMA Junction absent. – MP-BMP Junction entire. MP almost continuous with BMP; enters below the distal plate. – Crimp Patterns absent. – BMP-CuA Brace moderately broad; convex; entire; adjacent to, but distinct from, the distal margin of 2BP. Anterior continuous with MP. Point of fusion discontinuous. Posterior continuous with CuA. – BMP-BCuA Brace absent.

Medial Basivenalia very large; rectangular. Anterior and posterior margins concave. Anterior margin separated from BR by membrane. Posterior margin separated from BCuA by a sclerotized, concave groove. BMA broadly scaphoid; weakly convex; separated from BMP by a broad, shallow groove; lies anteriad, but not proximad of BMP; fully fused to BMP. *Proximal arch* allantoid; long; weakly convex; straight; enlarged antero-proximally. *Distal arch* distinct; oriented distad. BMP rectangular; convex; discontinuous with brace; distinct from 1BP and BCu. *Anterior section* rectangular; weakly convex; separated from the posterior section by a weak impression. *Posterior section* present; weakly convex; depressed below the anterior section.

Cubital Basivenalia broadly fused. Posterior margin of BCuA fused with anterior margin of BCuP. *Suture line* weak. BCuA about the same size as BCuP; deltoid; strongly convex; oriented weakly distad. BCuP deltoid; weakly convex; oriented postero-distad; weakly sclerotized. *Proximal margin* forms a convex ridge. Embayment very shallow. – Cubitus Anterior fused to BCuA. Anterior interrupted by the BMP-CuA Brace.

Basalare (Fig.44)

Head - HP lobe weakly claviform; convex; dorsally elevated from neck; continuous with neck. *Apex* curved ventrad. *Dorsal surface* polished. *Ventral surface* rough. BScP lobe claviform; weakly concave; not elevated from neck. *Dorsal surface* lenticular; polished; lies below the ventral margin of the HP lobe. *Ventral surface* rough. – Posterior Subcostal Basivenale weakly deltoid to ovoid; polished.

Discussion

Monophyly of the Lucanidae is supported by the fact that all of the taxa in this family share the following six apomorphic character states of the wing articulation, all confined to 2Ax:

1. the apex of the dorso-distal ridge is very strongly curved distad,
2. reduced distally and anteriorly,
3. revealing the distal and apical sections of the dorso-proximal ridge, the anterior section of the dorso-distal ridge is recurved with the apex assuming a ventral orientation (in addition to the distal curvature discussed above),
4. the subapical to antero-median section of the dorso-distal ridge is strongly oriented postero-distad,
5. the median to posterior section of the dorso-distal ridge and lobe is strongly depressed ventrad, curving beneath the antero-median section of the dorso-proximal ridge, giving the appearance that the dorso-distal ridge and lobe twists around the dorso-proximal ridge and lobe,
6. the dorso-proximal ridge apex is lengthened anteriorly, beyond the ventro-distal ridge apex.

Lucanidae share six apomorphic character states of the wing articulation and wing base with Passalidae, Diphylostomatidae, Glaphyridae, Trogidae, Bolboceratidae and Pleocomidae (Browne & Scholtz 1995).

Howden (1982) considered lucanids to be most closely related to Passalidae. Caveney (1986) suggested, based on synapomorphic acone ommatidium structure between all diphylostomatids and many lucanids, that Lucanidae are probably more closely related to Diphylostomatidae, a view which is supported here (Browne & Scholtz 1995).

The Lucanidae do not exhibit any wing articulation and wing base character states which support Howden's (1982) proposal that it branched off early from other members of the Scarabaeoidea and subsequently followed a separate evolutionary pathway, as do Passalidae.

Glaphyridae

Introduction

Glaphyridae are represented in the Holarctic Region by Glaphyrinae (with *Amphicoma* and *Lichnanthe* the largest genera) and in South America by Lichniinae (*Lichnia* and *Cratoscelis*). Adults are long-legged, hairy and brightly coloured.

The males of *Amphicoma* spp. are pollen feeders and visit flowers (Crowson 1967), whereas, according to Ritcher (1958), adults of *Lichnanthe* never feed. Ritcher (1958) noted that larvae of *Lichnanthe vulpina* (Hertz) feed on cranberry roots and those of *L. rathvoni* Le Conte on decaying leaves and other plant debris. The length of the life cycle is 3-4 years (Ritcher 1966).

Hind Wing Articulation Description

First Axillary (Fig.45)

Head - Dorsal surface normal size. *Antero-dorsal margin* normal width; weakly deplanate; oriented weakly postero-distad. *Antero-proximal margin* extended anteriorly as a large convexity. *Postero-proximal margin* weakly enlarged proximally. *Proximal margin* strongly enlarged ventrally; convex. *FSc2* base normal width. Apex rounded; oriented postero-distad. Anterior surface broad; very long; not waisted medially. *FSc1* very weak. *Ventral projection* tapers from base to apex; short but of normal width; shorter than *FSc2*; deeply concave; oriented disto-ventrad and curved posteriad. Apex narrow. Dorsal surface concave. - Ventral surface flattened. Concavity located in the preapical area; surrounded by three unequally strong ridges of unequal length. *Distal embayment* oriented dorsad. *FSc2* deltoid; broad; very convex; oriented distad and weakly dorsad; not enlarged dorsally. Proximal margin broadly fused to the ventrad projection. Dorsal surface convex. Ventral surface concave. Head and neck dorsal surface weakly curved proximad.

Neck normal width and length; narrower than head; recurved relative to tail; weakly oriented antero-distad. Proximal margin straight. Distal margin concave; broadly articulated with *2Ax*. *Distal embayment* concave; moderately deep; broad.

Tail - Dorsal view: concave. Proximal arch normal size; extended postero-proximad and weakly so postero-distad. *Dorsal surface* weakly concave. *Antero-proximal margin* convex. *Postero-proximal margin* convex. Articulation with *PRR* strong but short. Posterior margin weakly concave. Distal arch normal size; weakly curved ventrad; extended postero-distad. *Apex* aciculate; strongly curved ventrad and posteriad. *Distal margin* very weakly concave. - Ventral view: Proximal arch with a broad ridge. Posterior margin with a narrow but prominent ridge. Distal arch with a very small ridge.

Second Axillary (Fig.46)

Radial Fulcalare not sclerotized; present only as re-enforced membrane.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Anterior to antero-median section* concealed by the distal ridge. *Antero-median to posterior section* moderately broad; strongly elevated above the distal ridge; extends adjacent to the distal ridge. *Posterior section* acerose; strikingly enlarged above the distal ridge; oriented posteriad. Distal ridge distinct from lobe; extends anteriorly and curves very weakly proximally from the dorso-distal lobe base. *Apex* extremely broad; falcate; moderately short; convex; oriented weakly ventro-proximad. *Anterior section* broad; moderately short; curved proximad. *Median section* abruptly curved ventrad. *Posterior section* extends adjacent to, but lies below, the proximal ridge. - Ventral view: Proximal ridge very broad; indistinct from lobe. *Apex* very broadly rounded; curved distad. *Anterior section* very broad; sinuate; conceals the distal ridge proximally. *Median to posterior section* concealed by the distal ridge. Distal ridge extremely broad. *Anterior to median section* concealed by the proximal ridge. *Median and posterior sections* arise from the proximal, posterior and postero-distal margins of the distal lobe; indistinct from lobe; short; extremely broad. *Median section* convex. *Postero-median section* waisted. *Subalare tendon attachment point* moderately long and narrow; extends posteriad from the median; not curved ventrad; spatulate; moderately visible dorsally.

Body - Dorsal view: Proximal lobe short; broad; arises ventrally and postero-medially from the ridge; moderately sclerotized; flat; oriented proximad. *Base* strongly enlarged anteriorly and posteriorly; broad. *Anterior and posterior margins* greatly enlarged; concave. *Apex* broadly rounded; curved anteriorly. Distal lobe small and broad; roundly deltoid; reduced distally; broader but shorter than the proximal lobe; moderately sclerotized; convex. *Base* very broad. *Apex* broadly rounded. *Anterior margin* normal length; weakly concave. *Posterior margin* weakly concave. - Ventral view: Proximal lobe extremely small; weakly convex; nearly completely obscured by the distal ridge. *Posterior wing process junction* small; ovoid; occupies the posterior margin of the lobe. Distal lobe weakly concave; continuous with ridge; small.

Median Plate (Fig.47)

FM1 oriented proximad anteriorly and postero-proximad medially and posteriorly; rectangular. *Anterior section* narrow. *Median and posterior section* extremely broad. *Proximal margin* straight. Articulation with 2Ax extends from apical angle of the distal lobe over the posterior section of the ventral ridge. *Distal margin* moderately narrowly fused to 3Ax. FM2 oriented proximad and weakly posteriorly; rectangular; separated from FM1 by a moderately wide section of membrane; very small; acerose.

Third Axillary (Fig.48)

Head strikingly convex; moderately broad; normal length. Anterior margin narrow; not enlarged ventrally; weakly convex. FCu normal size; occupies the anterior to antero-medial section of head. *Posterior and proximal margins* reduced by a greatly enlarged AXCu. *Distal margin* strongly reduced by FA and AXCu. FA broad; convex; extended distad along its entire length. AXCu large; occupies about half of the head. *Anterior margin* extended anteriorly. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between AXCu and FA present. Suture line between FA and FJ present. Neck elevated dorsad. FCu section of neck absent. Neck comprised by AXCu. *Proximal embayment* oriented proximad; small; shallowly concave. Ridge posterior section present. Prong armed with a single tooth. *Tooth* very broad; long; deltoid. Apex broadly rounded. Detached AXCu fragment large; broad; moderately sclerotized.

Tail long; aciculate; dorsal surface is recurved. Dorsal surface oriented laterad. Anterior section only weakly convex. Median and posterior section very weakly convex to flat. *Window* absent. Distal margin straight. FJ and AXJ equally broad; moderately strongly sclerotized. *Suture line* present. AXA occupies an equal amount of the tail as FJ+AXJ; straight. Suture line between FJ+AXJ and AXA present. Suture line between AXA and AXCu strong.

Hind Wing Base Description

First Basal Plate (Fig.49)

Humeral Plate moderately broad and short. Anterior margin sinuate. Apex broadly rounded; curved ventrad. Dorsal margin convex; distant from BScA. Distal margin reduced. Ventral

margin concave. Suture line between FPC+BPC and FC+BC present. FPC+BPC small; rectangular; much shorter than FC+BC; distinct.

Anterior Subcostal Basivenale broadly deltoid; weakly convex; oriented distad. Proximal section extended as a short, narrow rectangle; separated from the distal section by a prominent suture; as large as the distal section. Distal section continuous with the ScA bulge. Apex broadly rounded; oriented distad. – Subcosta Anterior weakly convex. Bulge narrow.

Radial Basivenale convex; open; slender; oriented antero-proximad; continuous with the radial stem. Proximal arch moderately narrow; short; directed strongly postero-proximad. *Anterior section* present. *Posterior margin* extended proximad. Postero-distal margin rounded. Anterior margin elevated above BScA; narrow. Embayment of normal size; very strongly deltoid; surrounding margins are straight. Distal arch extremely weak; oriented posteriad. *br* moderately sclerotized; very small; discontinuous with BR. *br projection* dove-tail shaped; apically broad; arises from the antero-proximal margin of BR; distinct from BScA.

Second Basal Plate (Fig.50)

MA-BMA Junction absent. – MP-BMP Junction entire. MP continuous with BMP. – Crimp Patterns absent. – BMP-CuA Brace moderately broad and convex; adjacent to, but distinct from, the distal margin of 2BP. Anterior margin slightly reduced; appears to arise from below MP; oriented postero-distad. Point of fusion discontinuous with MP. Posterior margin continuous with CuA; curved postero-distad. – BMP-BCuA Brace absent. – False BMP-BCuA Brace present as a very strongly convex tube; formed from the median section of BMP. Posterior margin distant from CuA and BCuA.

Medial Basivenalia very large. Anterior and posterior margins concave. Anterior margin adjacent to BR. Posterior margin separated from BCuA by a sclerotized concave groove and membrane. BMA broadly scaphoid; completely fused with but distinct from BMP. *Anterior margin* concave. *Median* convex. *Posterior margin* reduced. *Proximal arch* allantoid; planate; straight; enlarged antero-proximally. *Distal arch* distinct; oriented antero-distad; very small. BMP extremely narrow and short; discontinuous with the BMP-CuA brace; indistinct from the False BMP-BCuA brace; distinct from 1BP and BCu. *Proximal section* extremely small; weakly convex. *Medial section* distinct; tube-shaped; separated from the proximal and distal sections by deep grooves. *Distal section* slender; more weakly convex than the medial section. Antero-distal section separated from the posterior section by a weak impression. Postero-distal section present; very weakly depressed below the anterior section. *Distal margin* strongly elevated from the surrounding membrane.

Cubital Basivenalia fused. Postero-proximal margin of BCuA fused with the antero-distal margin of BCuP. *Suture line* present. BCuA slightly smaller than BCuP; deltoid; convex; oriented distad; strongly sclerotized. BCuP weakly ovoid and convex; oriented posteriad; weakly sclerotized. Embayment shallow. – Cubitus Anterior adjacent to, but not fused with BCuA. Junction formed as a deep groove.

Basalare (Fig.51)

Head - HP lobe convex; dorsally elevated from neck; continuous with neck. *Apex* not curved. *Dorsal and ventral surfaces* rough. BScP lobe claviform; convex; weakly elevated from neck. *Dorsal surface* lenticular; slender; polished; lies below the ventral margin of the HP lobe. *Ventral surface* polished. - Posterior Subcostal Basivenale weakly square-shaped; polished.

Discussion

Monophyly of the Glaphyridae is supported by the fact that all of the taxa in this family share the following five apomorphic character states of the wing articulation and wing base:

1. 1Ax: the distal arch apex of the tail is strongly curved ventrad;
2. 2Ax: the apex of the dorso-distal ridge is extremely broad along its entire length, extends anteriorly, and curves very weakly proximally from the dorso-distal lobe base,
3. the subalare tendon attachment point is very short, very broad, and apically shallowly and narrowly concave;
4. 1BP: the BR embayment is of normal size, but is more strongly deltoid, with all margins straight;
5. 2BP: the medial section of BMP is distinct from the remainder of BMP as an elevated tube-shaped structure.

The phylogenetic position of Glaphyridae within the Scarabaeoidea has been an issue of some debate. This family was once accorded superfamily status due to its unusual distinctiveness, but Hinton (1967) more realistically accorded family status. Based on male and female genitalia, Zunino (1988) claimed that glaphyrids occupy an intermediate position between Melolonthinae and Scarabaeidae. Holloway (1972) noted that, according to Crowson's (1967) key, glaphyrids occupy a position close to Diphylostomatidae. d'Hotman & Scholtz (1990a,b) and Scholtz (1990) presented convincing evidence, from numerous adult and larval characters, which suggests that glaphyrids are archaic. More importantly, they found that the basal piece of the male genitalia is very similar to some lucanid genera.

Analysis of wing articulation and wing base characters indicates that Glaphyridae are the sister group of Trogidae + Bolboceratidae + Pleocomidae, with whom they share a single derived state of the hind wing base (Browne & Scholtz 1995).

Trogidae

Introduction

The Trogidae are a monophyletic, cosmopolitan family, consisting of three genera and about 300 species. Trogids have wide distribution, but occur mainly on the southern continents in sandy arid regions (Scholtz 1986). *Trox* Fabricius occurs naturally in Europe, North America and Africa. *Omorgus* Erichson occurs in South and North America,

Australia and Africa, whereas *Polynoncus* Burmeister occurs only in South America. Adults and larvae are keratin-feeders.

The Trogidae are a well-defined family whose monophyly is supported by numerous derived characters (Scholtz 1986; Scholtz 1990; Scholtz & Peck 1990; Browne et al. 1993). Their phylogenetic position within the Scarabaeoidea as one of the most archaic families has been proposed by Crowson (1967, 1981) and Scholtz (1986). Howden (1982) concluded that trogids are highly apomorphic and probably closely related to the Hybosoridae. The wings of Trogidae have previously been well-studied (Browne et al. 1993).

Hind Wing Articulation Description

First Axillary (Fig.52)

Head - Dorsal surface normal size weakly convex; moderately broad. *Antero-dorsal margin* normal width; weakly deplanate; oriented postero-distad. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* base normal width. Apex rounded; oriented postero-distad. Anterior surface broad; very long; not waisted medially. *FSc1* very weak. *Ventral projection* tapers from base to apex; short but of normal width; deeply concave; oriented disto-ventrad and curved posteriad. Apex narrow. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* moderately broad; oriented dorsad. *FSc2* deltoid; broad; very convex; oriented distad and weakly dorsad. Dorsal surface concave. Ventral surface convex. Apex blunt. *Dorsal margin* not enlarged. Head and neck dorsal surface weakly curved proximad.

Neck moderately broad; moderately long; oriented weakly antero-distad; broadly articulated with 2Ax. Proximal margin weakly convex. Distal margin concave. *Distal embayment* moderately concave. Embayment re-enforcement moderately strong.

Tail - Dorsal view: Proximal arch normal size; weakly concave. *Postero-proximal margin* convex. Articulation with PRR strong. Posterior margin weakly concave. Distal arch normal size. *Apex* weakly curved postero-ventrad; acuminate. -Ventral view: Proximal arch with a slender ridge. Posterior margin with a prominent ridge. Distal margin with a slender ridge.

Second Axillary (Fig.53)

Radial Fulcalare slender; weakly sclerotized.

Ridges - Dorsal view: Proximal ridge distinct from lobe; entire. *Anterior to antero-median section* partially concealed by the distal ridge. *Antero-median to posterior section* strongly enlarged above the distal ridge; demarcated from body by an impression. *Posterior section* incorporated into lobe; distinct from lobe but only weakly extended past the posterior margin of lobe; moderately enlarged above the distal ridge; extends posteriad. Distal ridge weakly distinct from lobe. *Apex* oriented ventro-proximad; convex and broadly falcate; moderately short. *Anterior section* slender; moderately short; curved proximad and weakly ventrad. *Median to posterior section* extends below the proximal ridge; very weakly

demarcated from body by an impression. *Posterior section* strongly acerose; extends far past the posterior margin of lobe. - Ventral view: Proximal ridge moderately broad; long; curved distad; distinct from lobe. *Apex* aciculate. *Anterior to antero-median section* digitate; slender; obscures distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge broad but short. *Anterior to median section* concealed by the proximal ridge. *Median and posterior sections* arise from the proximal and posterior margins of the distal lobe; weakly distinct from lobe; broad but short. *Median section* convex. *Postero-median section* waisted. *Subalare tendon attachment point* very long and narrow; apically not curved ventrad; posterior margin rounded; extends posteriad from the median; weakly visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe oriented proximad; long; moderately small; weakly deltoid; arises from the postero-medial section of ridge; strongly sclerotized; convex. *Base* broad. *Posterior margin* weakly enlarged; concave. *Apex* weakly curved antero-proximad; narrowly truncate. Distal lobe large and broad; roundly deltoid; much larger than proximal lobe; moderately sclerotized; planate. *Base* moderately broad. *Apex* broadly rounded. *Anterior margin* normal length; straight. *Posterior margin* very weakly concave; very weakly reduced. - Ventral view: Proximal lobe narrow and long; convex. *Posterior wing process junction* formed as an ovoid convexity which extends antero-proximally from the postero-distal corner of the lobe; long. Distal lobe discontinuous with ridge; planate.

Median Plate (Fig.54)

FM1 narrow; oriented proximad anteriorly and postero-proximad medially and posteriorly. *Anterior section* broad narrow. *Median and posterior section* extremely broad. *Proximal margin* convex. Articulation with 2Ax extends along the posterior third of the distal lobe over the posterior section of the ventral ridge. *Distal margin* weakly and narrowly fused to 3Ax. FM2 very long; oriented posteriad; acerose. *Apex* separated from FM1; separated by a membranous gap.

Third Axillary (Fig.55)

Head broad and truncate; strikingly convex; normal length. Proximal margin straight. Anterior margin weakly convex; not enlarged ventrally. FCu normal size; occupies two-thirds of the head; weakly ovoid. FA moderately large; occupies the distal third of head, broadening posteriorly; narrowly deltoid. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck moderately elevated dorsad. FCu forms the anterior portion of neck. FA forms the distal portion of neck. AXCu section of neck extremely narrow; moderately elevated. Prong armed with two teeth. *Anterior tooth* very small; fastigate. *Apex* rounded. *Posterior tooth* moderately short; fastigate. *Apex* rounded. Ridge enlarged dorsally relative to AXA. Detached AXCu fragment pectinate; thin. *Apex* aciculate; armed with one long posterior tooth, and two short anterior teeth.

Tail narrow, long and convex; acerose. Dorsal surface oriented mesad. Anterior section concave. Median section concave. Posterior section convex. *Window* absent. FJ antero-

distal margin strongly curved ventrad. FJ+AXJ slender; weakly concave. AXA strongly sclerotized; occupies about two-thirds of the tail area; straight. Suture line between FJ and AXJ absent. Suture line between FJ+AXJ and AXA present. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.56)

Humeral Plate slender; lies distant from BScA. Anterior margin weakly sinuate; moderately sclerotized. *Apex* weakly curved ventrad. Dorsal margin weakly sinuate. *Apex* concave. Ventral margin weakly sinuate. Suture line between FPC+BPC and FC+BC present.

Anterior Subcostal Basivenale deltoid; convex; oriented distad. Proximal and distal sections separated by a distinct suture. *Proximal section* as large as the distal section. *Apex* broadly rounded. Postero-proximal margin with an embayment. Distal margin separated from ScA bulge by a deep concavity. – Subcosta Anterior weakly convex. Bulge very broad.

Radial Basivenale very weakly convex; broadly open; oriented antero-proximad; continuous with radial stem. Proximal arch slenderly deltoid; small; straight; continuous with the anterior section of BR; directed posteriad. *Postero-distal section* rounded. Anterior margin straight; very narrow; only medially weakly elevated dorsad. Embayment normal size. Distal arch absent. *br* weak but present; very slender; moderately sclerotized; continuous with BR. *br projection* apically broad; distinct from BSc.

Second Basal Plate (Fig.57)

MA-BMA Junction absent. – MP-BMP Junction entire. MP almost continuous with BMP; arises from below the distal plate. – Crimp Patterns weak to moderately strong; found on MP and the antero-distal section of 2BP. Crimps are weakly convex; margined by impressions; dense proximally, sparse distally. – BMP-CuA Brace present; moderately thin; convex; distant from distal margin of 2BP; extends postero-proximad from 2BP. Anterior entire; fused to the postero-proximal corner of MP and the antero-distal corner of BMP. Point of fusion continuous. Posterior discontinuous with CuA; fused to the antero-proximal angle of CuA. *Point of fusion* marked by a suture line. – BMP-BCuA Brace absent. – False BMP-BCuA Brace present as a moderately broad and strongly convex tube extending along the distal margin of 2BP. Anterior margin with overlapping plates. Posterior margin terminates adjacent to, but not touching or fused with, BCuA.

Medial Basivenalia - General habitus: very large; broad and long. Anterior and posterior margins distally weakly concave. BMA broadly scaphoid; completely fused to BMP. *Proximal and medial surfaces* flat. *Distal surface* convex. *Anterior margin* weakly concave. *Proximal arch* weakly convex and straight; enlarged antero-proximally; deltoid to weakly allantoid. *Distal arch* weakly distinct. BMP rectangular; convex; distinct from brace; separated from both 1BP and BCu. *Proximal section* weakly convex; separated from BMA by a shallow concavity. *Postero-median section* concave. *Antero-distal section* formed as a large, rectangular convexity; distinct from the postero-distal section. Distal

margin forms the anterior half of the BMP-BCuA brace; elevated from surrounding membrane. Antero-distal margin aquiline; with many overlapping plates. *Postero-distal section* forms the posterior half of the BMP-BCuA brace; as equally elevated as the antero-distal section.

Cubital Basivenalia broadly fused. Posterior margin of BCuA fused with anterior margin of BCuP. *Suture line* present. BCuA slightly smaller than BCuP; deltoid; strongly convex; oriented distad; strongly sclerotized; lies proximal to the base of CuA. BCuP weakly rectangular; less convex than BCuA; oriented distad; moderately sclerotized. Distal embayment weak. – Cubitus Anterior arises from within a toroid concavity in BCuA.

Basalare (Fig.58)

Head - HP lobe weakly claviform; convex; elevated from neck; continuous with neck. *Dorsal surface* polished. BScP lobe moderately claviform; concave; weakly elevated from neck. *Dorsal surface* lenticular; polished. *Ventral surface* rough. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Monophyly of the Trogidae is supported by the fact that all of the taxa in this family share the following four apomorphic character states of the wing articulation and wing base (Browne et al. 1993 only recorded three, autapomorphy no. 1 is new):

1. 2Ax: the subalare tendon attachment point is short, narrow and apically rounded;
2. 2BP: with transverse crimps on the medial vein, mesal of the medial bridge and distal of 2BP.
3. the BMP-CuA brace is either reduced or modified (both are autapomorphic) depending on the genus;
4. RP3+4 is lost.

Trogidae share six apomorphic character states of the wing articulation and wing base with Passalidae, Diphylostomatidae, Lucanidae, Glaphyridae, Bolboceratidae and Pleocomidae (Browne & Scholtz 1995). Analysis of wing articulation and wing base characters indicates that Trogidae occupy an intermediate position between Glaphyridae and Bolboceratidae + Pleocomidae, more closely related to the latter (Browne & Scholtz 1995).

Bolboceratidae

Introduction

The Bolboceratidae are a large, well-defined family whose monophyly is supported by numerous derived characters (Scholtz 1990; Browne 1991a,b; Scholtz & Browne, in press).

Bolboceratidae, previously classified as one of four subfamilies of Geotrupidae, have recently been elevated to family status since there is little evidence for the traditional view that Geotrupidae constitute a monophyletic assemblage (Ritcher 1969a,b; Scholtz 1990;

Browne 1991a; Scholtz & Browne, in press). Bolboceratid wings are well known (Browne 1991a,b; Browne & Scholtz 1995). The following is a summary of those findings.

Hind Wing Articulation Description

First Axillary (Fig.66)

Head - Dorsal surface normal size; convex. *Antero-dorsal margin* normal width; weakly deplanate; very strongly oriented ventro-distad. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* convex. Base normal width. Apex rounded; oriented postero-distad. Anterior surface broad; very long; not waisted medially. *FSc1* very weak; small; slender; fused to the proximal margin of the ventrad projection. Dorsal and ventral surfaces convex. *Apex* acute. *Ventral projection* weakly tapered from the base to apex; short but of average width; deeply concave; oriented disto-ventrad and curved posteriad. Apex narrower than the base; rounded. Concavity located in the preapical area; surrounded by three unequally strong ridges. Dorso-medial surface concave. Ventral surface convex. *Distal embayment* oriented dorsad. *FSc2* weakly deltoid to digitate; moderately broad; oriented distad and weakly dorsad. Dorsal surface very convex; not enlarged. Ventral surface convex. Apex truncate. Head and neck dorsal surface weakly curved proximad. Ventral re-enforcing ridge prominent.

Neck normal width but extremely short; weakly oriented antero-distad; broadly articulated with 2Ax; discontinuous with tail. Proximal margin curved ventrad. Distal margin concave. *Distal embayment* concave; with an extremely strong secondary embayment supported posteriorly by a sclerotized plate; extremely deep but very narrow.

Tail - Dorsal view: Proximal arch strongly but narrowly expanded postero-distally; falcate; strongly curved postero-distad. *Antero-proximal margin* deeply concave. *Dorsal surface* weakly concave. *Postero-proximal margin* extremely convex; strikingly recurved; strongly enlarged proximad. Articulation with PRR posteriorly extremely strong; very weak anteriorly; markedly enlarged posteriorly and distally; with a broad and strong connection along the medial groove and recurved arch. Posterior margin moderately concave. Distal arch normal size. Apex very weakly curved ventrad and posteriad; aciculate. Distal margin straight. - Ventral view: Proximal arch with a slender ridge. Posterior margin with a prominent ridge. Distal arch with an extremely slender ridge.

Second Axillary (Fig.67)

Radial Fulcalare extremely slender; moderately sclerotized; articulation with 2Ax ridge extremely narrow.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* not spatulate. *Anterior to antero-median section* partially concealed by the distal ridge. *Antero-median to postero-median section* strongly elevated above the distal ridge; demarcated from body by an impression. *Posterior section* moderately enlarged above the dorso-distal ridge; slender; incorporated into lobe; distinct from lobe but only weakly extended past the posterior margin of lobe; extends posteriad from the median. Distal ridge weakly distinct from lobe. *Apex* oriented ventro-proximad; convex and broadly falcate; moderately short.

Anterior section moderately short; curved proximad and very weakly ventrad. *Median to posterior section* extends adjacent but below the proximal ridge; very weakly demarcated from body by an impression. *Posterior section* acerose; very weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge slender; long; curved distad; distinct from lobe. *Apex* aciculate. *Anterior to antero-median section* digitate; slender; conceals the distal margin of the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge slender; long. *Anterior to median section* partially concealed by the proximal ridge; curves proximad. *Median and posterior sections* arise from the posterior margin of the distal lobe; distinct from lobe; broad and moderately long. *Median section* convex. *Postero-median section* not waisted. *Subalare tendon attachment point* moderately long and narrow; apically not curved ventrad; posterior margin rounded; extends posteriad from the median reversal; broadly visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe oriented proximad; arises from the postero-medial section of the ridge, depressed below the ridge; short and small; deltoid; strongly sclerotized; concave. *Posterior margin* weakly enlarged; concave. *Base* moderately broad. *Apex* narrowly rounded; weakly curved anteriorly. Distal lobe moderately large and broad; deltoid; much larger than proximal lobe; moderately sclerotized; very strongly convex. *Anterior margin* normal length; concave. *Apex* narrowly rounded. *Posterior margin* straight; weakly reduced. - Ventral view: Proximal lobe extremely small; convex. *Posterior wing process junction* nearly completely conceals the proximal lobe; formed as a prominent ovoid convexity which extends anteriorly from the posterior margin of the distal ridge. Distal lobe moderately large and broad; discontinuous with ridge; weakly concave.

Median Plate (Fig.68)

FM1 oriented strongly postero-distad. *Anterior section* very narrow. *Median section* narrow. *Postero-median to posterior section* very broad; convex. *Proximal margin* convex. Articulation with 2Ax extends from the postero-medial margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* very weakly and narrowly fused to 3Ax. FM2 very short; oriented posteriad; acerose; separated from FM1 by a long, broad section of membrane.

Third Axillary (Fig.69)

Head planate; moderately broad; normal length. Proximal margin straight. Anterior margin weakly convex; not enlarged ventrally; from the proximal angle it slopes sharply postero-distad. *Antero-proximal margin* extended anteriorly; very broadly rounded. *Antero-distal margin* extended ventrad; broadly but shallowly concave. Posterior section enlarged dorsally to form an arm; proximally continuous with the neck. FCu normal size; distinct; occupies most of the head; broadly deltoid. FA extremely small. *Anterior margin* strongly reduced by a much enlarged FCu. AXCu reduced proximally; very narrowly margins the postero-proximal margin of FCu. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck proximally moderately elevated; distally weakly elevated as an arm. FCu section of neck absent. AXCu forms entire neck. Proximal margin elevated as a very narrow ridge. *Ridge* extends to antero-median of the proximal margin of tail; moderately short; enlarged dorsally relative to AXA. Dorsal surface of ridge is curved distad. Medial and distal margins weakly convex; formed by FCu anteriorly and FA posteriorly. Prong armed with a single short tooth; oriented proximo-dorsad; narrow. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail narrowly deltoid; long; planate. *Dorsal surface* oriented mesad. Anterior and median section weakly calceolate. Posterior section planate. *Window* present; weak; occupies most of the tail. FJ+AXJ very slender; occupies distal fifth of tail; moderately sclerotized. Suture line between FJ and AXJ present. Suture line between FA+AXJ and AXA present. AXA more weakly sclerotized than FA+AXJ; the former occupies less than a fifth of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.70)

Humeral Plate moderately broad and short. Anterior margin sinuate; strongly sclerotized; lies distant from BScA. Apex very narrow; weakly curved ventrad. Dorsal margin strongly sinuate; distant from BScA. Proximal margin weakly sinuate; curved proximo-ventrad. Ventral margin strongly sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; broadly deltoid; weakly convex. Proximal and distal sections separated by a prominent suture. *Proximal section* about the same size as the distal section. Apex broadly rounded. Proximal margin extended as a long, narrow rectangle curving postero-ventrad. Distal section continuous with ScA bulge; separated by a weak concavity. – Subcosta Anterior moderately convex. Bulge moderately broad.

Radial Basivenale convex; open; very weakly discontinuous with radial stem; angled antero-proximad; rectangular. Proximal arch slenderly deltoid; moderately long; angled posteriad; continuous with the anterior margin of BR. *Postero-distal section* rounded. Anterior margin not elevated above the posterior margin of ScA bulge; broad; straight; angled antero-proximad. Embayment normal size. Distal arch very weakly discontinuous with radial stem; oriented posteriad. br strongly sclerotized; occupies more than half of the proximal arch; discontinuous with BR. *br projection* small.

Second Basal Plate (Fig.71)

MA-BMA Junction absent. – MP-BMP Junction: MP discontinuous with BMP; arises from below the distal plate. – Crimp Patterns absent. – BMP-CuA Brace present; slender; convex; extends postero-distad from 2BP. Anterior section reduced; fused to the postero-distal corner of 2BP; not fused with BMP or the MP-BMP junction. Posterior section continuous with CuA; fused to the antero-proximal angle of CuA. – BMP-BCuA Brace absent.

Medial Basivenalia moderately reduced on all margins; narrow and long; rectangular but narrowing proximally. Anterior and posterior margins concave. BMA narrow; completely fused to BMP. *Proximal and medial surfaces* flat. *Distal surface* convex. *Anterior margin* concave. *Proximal arch* broadly deltoid; planate; enlarged antero-proximally. *Distal arch* distinct; very long; slender; convex. BMP junction with BMA discontinuous and very broad; rectangular; very weakly separated from BMA by a shallow concavity; flat; distinct from brace; separated from 1BP and BCu. *Postero-median, antero-distal and postero-distal sections* indistinguishable from each other. Distal margin strongly elevated above the surrounding membrane.

Cubital Basivenalia narrowly fused; slender and long. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA very narrow and long; convex; oriented postero-distad; strongly sclerotized; lies proximal of CuA. BCuP very narrow and long; convex; oriented postero-distad; weakly sclerotized. Distal embayment narrow but deep. – Cubitus Anterior adjacent to, but discontinuous with, BCuA. Junction separated by a concavity. Base strongly shifted distad.

Basalare (Fig.72)

Head - HP lobe small; continuous with neck. *Apex* broadly rounded. *Dorsal surface* elevated from neck; not polished. BScP lobe claviform; projects posteriad from neck. *Dorsal surface* ovoid; weakly convex; polished; not elevated from neck. *Ventral surface* polished. – Posterior Subcostal Basivenale broadly deltoid; polished.

Discussion

Monophyly of the Bolboceratidae is supported by the fact that all of the taxa in this family share the following 12 apomorphic character states of the wing articulation and wing base:

1. 1Ax: the ventral surface of the head has a prominent ridge,
2. the dorsal surface of the head is very strongly oriented ventro-distad,
3. the neck is extremely short,
4. the distal embayment is secondarily extremely deep, but very narrow,
5. posteriorly strengthened by a sclerotized plate;
6. 2Ax: the anterior margin of the dorso-distal lobe is concave,
7. the dorsal surface of this lobe is very strongly convex,
8. the subalare tendon attachment point is very short, very broad, and apically shallowly and narrowly concave;
9. 3Ax: the posterior section of the head is enlarged dorsally to form an arm, which is proximally continuous with the neck;
10. 2BP: the postero-distal section of BMP is continuous with the BMP-CuA brace,
11. the latter is very strongly convex, broad and oriented more strongly distad than posteriad,
12. the base of CuA is shifted distad.

Bolboceratidae share six apomorphic character states of the wing articulation and wing base with Passalidae, Diphyllotomatidae, Lucanidae, Glaphyridae, Trogidae and Pleocomidae (Browne & Scholtz 1995). Analysis of wing articulation and wing base characters

indicates that Bolboceratidae are the sister group of Pleocomidae (Browne & Scholtz 1995).

Pleocomidae

Introduction

The Pleocomidae are a monotypic family. The genus *Pleocomia* Le Conte consists of 33 described species and three subspecies (Hovore 1977). *Pleocomia* has a very restricted distribution, occurring in the western USA., especially Oregon, California and Utah. Crowson (1981), Virkki (1967) and Ritcher (1966) treated Pleocomidae as a family and it is regarded as such in this study. Males are winged and females flightless.

Hind Wing Articulation Description

First Axillary (Fig.59)

Head - Dorsal surface large; convex; enlarged posteriorly; convex. *Antero-dorsal margin* normal width; weakly deplanate; oriented weakly postero-distad. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* convex. Base normal width. Apex rounded; oriented postero-distad. Anterior surface broad; very long; not waisted medially. *FSc1* very weak; very small and narrow; fused to the ventral projection. Dorsal surface convex. Ventral surface planate. *Ventral projection* weakly tapered from the base to apex; short but of average width; deeply concave; oriented disto-ventrad and curved posteriad. Apex narrower than the base but truncate. Concavity located in the preapical area; surrounded by three unequally strong ridges. Dorso-medial surface concave. Ventral surface convex. *Distal embayment* oriented dorsad. *FSc2* weakly deltoid to digitate; moderately broad; oriented distad and weakly dorsad. Dorsal surface very convex; not enlarged. Ventral surface weakly concave. Apex acute. Head and neck dorsal surface weakly curved proximad.

Neck normal width and length; weakly oriented antero-distad; broadly articulated with 2Ax. Proximal margin weakly convex; curved ventrad. Distal margin concave. *Distal embayment* shallow and broad.

Tail - Dorsal view: Proximal arch strongly but narrowly expanded postero-distally; falcate; strongly curved postero-distad. *Antero-proximal margin* concave. *Dorsal surface* weakly concave. *Postero-proximal margin* convex; strikingly recurved. Articulation with PRR posteriorly extremely strong; very weak anteriorly; markedly enlarged posteriorly and distally. Posterior margin straight. Distal arch normal size. Apex very weakly curved ventrad and posteriad; aciculate. -Ventral view: Proximal arch with a narrow but prominent ridge. Posterior margin with a narrow but prominent ridge. Distal arch with an extremely slender but long ridge.

Second Axillary (Fig.60)

Radial Fulcalare moderately broad; articulation with 2Ax ridge moderately broad.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Anterior to antero-median section* partially concealed by the distal ridge. *Antero-median to postero-median section* strongly elevated above the distal ridge; demarcated from body by an impression. *Posterior section* moderately enlarged above the dorso-distal ridge; extremely long; not incorporated into lobe; distinct from lobe and extremely strongly extended past the posterior margin of lobe; extends posteriad from the median. Distal ridge weakly distinct from lobe. *Apex* oriented ventro-proximad; convex and broadly falcate; moderately short. *Anterior section* moderately short; curved proximad. *Median to posterior section* extends below the proximal ridge; very weakly demarcated from body by an impression. *Posterior section* strongly acerose; weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge broad; moderately long; straight; distinct from lobe. *Apex* acuminate. *Anterior to antero-median section* digitate; broad; obscures distal ridge except the apex. *Median to posterior section* obscured by the distal ridge. Distal ridge broad but short. *Apex* narrow. *Anterior to median section* concealed by the proximal ridge. *Median and posterior sections* arise from the proximal and posterior margins of the distal lobe; distinct from lobe; slender. *Median section* concave. *Postero-median section* convex and waisted. *Subalare tendon attachment point* extremely long and slender; apically not curved ventrad; posterior margin rounded; extends posteriad from the median; strongly visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe oriented proximad; arises from the postero-medial section of the ridge, depressed below the ridge; strikingly small; deltoid; strongly sclerotized; convex. *Posterior margin* weakly enlarged; concave. *Base* extremely narrow. *Apex* narrowly rounded; very weakly curved anteriorly. Distal lobe moderately long and broad; roundly deltoid; larger than proximal lobe; moderately sclerotized; markedly convex. *Anterior margin* normal length; straight. *Apex* narrowly rounded. *Posterior margin* very weakly concave; reduced. - Ventral view: Proximal lobe extremely small; only the apex is visible; convex. *Posterior wing process junction* obscures most of the proximal lobe; formed as a prominent ovoid convexity which extends anteriorly from the posterior margin of the distal ridge. *Base* ridge-like; convex. *Apex* small; ovoid. Distal lobe discontinuous with ridge; weakly concave.

Median Plate (Fig.61)

FM1 oriented strongly postero-distad. *Anterior to posterior section* very broad. *Proximal margin* convex. Articulation with 2Ax extends along the entire margin of the distal lobe over the posterior section of the ventral ridge. *Distal margin* fused to the proximal margin of 3Ax from the antero-distal corner to just anterior to the neck of 3Ax. FM2 very short; oriented posteriad; acerose; separated from FM1 by a long slender section of membrane.

Third Axillary (Fig.62)

Head strikingly convex; moderately broad; normal length. Proximal margin straight. Anterior margin weakly convex; not enlarged ventrally. Antero-proximal margin rounded; very weakly cleft. Antero-distal margin rounded. FCu normal size; distinct; ovoid. FA narrow; short; displaced anteriorly by FCu. AXCu does not form part of the head. Suture

line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck moderately elevated proximally; distally very weakly so. FCu section of neck absent. AXCu forms entire neck. Proximal margin elevated as a weak ridge; extends to mid-line of proximal margin of tail; short. Prong armed with a single slender tooth. Ridge enlarged dorsally relative to AXA. Detached AXCu fragment deltoid; moderately sclerotized.

Tail broadly deltoid; long; planate. *Dorsal surface* oriented mesad. Anterior section broad; concave; weakly calceolate. Posterior section concave to flat. *Window* weak. FJ+AXJ slender; occupies distal third of tail; strongly sclerotized. Suture line between FJ and AXJ present. Suture line between FA+AXJ and AXA present. AXA more weakly sclerotized than FA+AXJ; occupies more than half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.63)

Humeral Plate slender; apically weakly clavate. Anterior margin sinuate; strongly sclerotized. Apex very broad; clavate; curved ventrad. Dorsal margin slender; distant from BScA; strongly sinuate. Proximal margin J-shaped; curved proximo-ventrad. Ventral margin strongly sinuate. Distal section narrow. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; very broadly deltoid; very weakly convex. Proximal and distal sections separated by a prominent suture. *Proximal section* about the same size as the distal section. Apex broadly rounded. *Distal section* extremely broad; separated from ScA by a shallow concavity. – Subcosta Anterior weakly convex. Bulge extremely broad.

Radial Basivenale very small; convex; narrowly open; weakly angled antero-proximad; continuous with radial stem. Proximal arch slenderly deltoid; long; curved postero-proximad; continuous with the anterior margin of BR. *Postero-distal section* rounded. Anterior margin convex; moderately narrow; weakly elevated dorsad. Embayment normal size. Distal arch extremely weak; oriented posteriad. br strongly sclerotized; occupies the antero-proximal corner of BR; weakly discontinuous with BR. *br projection* apically broad; medially concave; indistinct from BSc.

Second Basal Plate (Fig.64)

MA-BMA Junction absent. – MP-BMP Junction: MP discontinuous with BMP; arises from below the distal margin. – Crimp Patterns absent. – BMP-CuA Brace present; slender; strongly convex; entire; distant from the distal margin of 2BP; extends postero-proximad. Anterior section reduced; not fused with BMP or the MP-BMP junction; arises from below the antero-distal margin of 2BP; more strongly convex than BMP. Posterior section continuous with CuA; fused to the antero-proximal angle of CuA. Point of fusion not marked by a suture line. – BMP-BCuA Brace absent.

Medial Basivenalia moderately reduced on all margins. Anterior and posterior margins isolated from surrounding sclerites. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* flat. *Distal surface* convex. *Anterior margin* concave. *Proximal arch* short; broad; straight; planate; enlarged antero-proximally. *Distal arch* distinct; slender; strongly convex. BMP junction with BMA discontinuous and very broad; extremely small; rectangular; strongly convex to flat; distinct from brace; separated from 1BP and BCu. *Proximal section* extremely small; flat to weakly convex; very weakly distinguishable from BMA. Antero-distal and postero-distal margins sharply aquiline. *Median section* deeply concave. *Distal section* formed as a very large, rectangular convexity; strongly convex; prominent. Distal margin deeply concave; very strongly elevated above the surrounding membrane. Antero-distal and postero-distal sections continuous and equally elevated.

Cubital Basivenalia partially fused. Postero-proximal margin of BCuA fused with antero-proximal margin of BCuP. *Suture line* present. BCuA larger than BCuP; ovoid to weakly deltoid; strongly convex; oriented postero-distad; strongly sclerotized; lies proximal of CuA. *Median section* concave. BCuP C-shaped; smaller than BCuA; moderately convex proximally; weakly so distally; oriented postero-distad; weakly sclerotized especially distally. Distal embayment very deep. – Cubitus Anterior continuous with BCuA.

Basalare (Fig.65)

Head - HP lobe broad; continuous with neck; smaller than BScP lobe; very thin in cross-section. *Apex* broadly rounded. *Dorsal surface* weakly curved posteriad; elevated from neck; not polished. BScP lobe claviform; projects posteriad from neck. *Dorsal surface* ovoid; convex; polished; equally elevated as the HP lobe. *Ventral surface* polished. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Monophyly of the Pleocomidae is supported by the fact that all of the taxa in this family share the following three apomorphic character states of the wing articulation and wing base:

1. 2Ax: the dorso-proximal lobe is strikingly small and basally extremely narrow,
2. the subalare tendon attachment point is extremely long and narrow;
3. 2BP: BMP is very strongly convex and extremely small.

Pleocomidae share six apomorphic character states of the wing articulation and wing base with Passalidae, Diphylostomatidae, Lucanidae, Glaphyridae, Trogidae and Bolboceratidae (Browne & Scholtz 1995; Scholtz et al., submitted).

Pleocomidae have long been considered the sister group of Geotrupidae (Bolboceratini-Athyreini-Lethrini, Howden 1982) based on doubtful synapomorphies (Scholtz 1990). However, it has been suggested that this family may be related to Melolonthinae due to the highly modified club with 4-7 annuli (Howden has subsequently favoured the latter relationship over the former, pers. comm. 1991). Browne's analyses (1991a, 1993), based on synapomorphic wing structure and a subsequent analysis examining all character suites (Scholtz et al., submitted), supported Howden (1982). Pleocomidae and Geotrupidae have similar spiracle (Ritcher 1969a,b) and eye structure (Caveney 1986). Some genitalic and

mouthpart character states are similar to those of Diphyllostomatidae, but Pleocomidae share more derived character states with Geotrupidae (d'Hotman & Scholtz 1990b; Nel & Scholtz 1990; Scholtz 1990). Analysis of hind wing articulation and wing base characters indicates that Pleocomidae are the sister group of Bolboceratidae (Browne & Scholtz 1995).

Geotrupidae

Introduction

The Geotrupidae are a large widespread family which comprises three subfamilies: Geotrupinae, Lethrinae and Taurocerastinae (*Frickius* and *Taurocerastes*). The wingless Lethrinae were not examined here.

Hind Wing Articulation Description

First Axillary (Fig.73)

Head - Dorsal surface normal size; convex. *Antero-dorsal margin* oriented moderately postero-distad; normal width; weakly deplanate. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* base normal width. Apex oriented postero-distad; moderately narrow. Anterior surface broad; very long; not waisted medially. *FSc1* very weak; slender; fused to the proximal margin of the ventrad projection. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* tapers from base to apex; short but of average width; deeply concave; oriented disto-ventrad and curved posteriad. Dorsal surface concave. Ventral surface convex. Apex narrow but truncate. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented dorsad; narrow. *FSc2* oriented strongly dorsad and weakly distad; deltoid; very convex; broad. Dorsal surface convex. Ventral surface convex. Apex narrowly truncate. *Dorsal margin* not enlarged. Head and neck dorsal surface strongly curved proximad.

Neck normal width and length; weakly oriented antero-distad; broadly articulated with 2Ax; continuous with tail. Proximal margin moderately curved ventrad. Distal margin sinuate. *Distal embayment* very weakly concave; narrow.

Tail - Dorsal view: Proximal arch normal size; not extended posteriad and only very weakly so proximad; straight. *Dorsal surface* weakly concave. *Antero-proximal margin* convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; strong; long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface weakly concave. Posterior margin straight. Distal arch normal size; weakly extended posteriad. *Apex* very weakly curved ventrad and posteriad; acuminate. *Distal margin* straight. - Ventral view: Proximal arch with a broad ridge. Posterior margin with a prominent but narrow ridge. Distal arch with a slender ridge.

Second Axillary (Fig.74)

Radial Fulcalare weakly sclerotized; slender.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* narrow. *Anterior section* distally obscured by the distal ridge. *Anterior to antero-median section* depressed below the distal ridge. *Antero-median to postero-median section* strongly enlarged above the distal ridge. *Posterior section* moderately enlarged above the distal ridge; oriented posteriad; slender; very long; incorporated into lobe; distinct from lobe and strongly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* not fused to the proximal ridge apex; oriented ventrad; broadly spatulate; slender. *Anterior section* extremely short; curved proximad. *Median to posterior section* extends adjacent to, but lies below, the proximal ridge; very weakly demarcated from body by an impression. *Posterior section* acerose; very weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge slender; curved distad; distinct from lobe. *Apex* acuminate. *Anterior to antero-median section* digitate; slender; conceals the proximal margin of the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge slender. *Anterior to median section* partially concealed by the proximal ridge; straight. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; very broad but short. *Median section* convex. *Postero-median section* waisted. *Subalare tendon attachment point* short and broad; apically not curved ventrad; posterior margin rounded; extends posteriad from the median; spatulate; visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe short and moderately small; deltoid; arises medially from ridge, but depressed below the ridge; strongly sclerotized; convex; oriented proximad. *Base* moderately broad. *Apex* broadly rounded. *Anterior margin* very weakly concave. *Posterior margin* very weakly enlarged; very weakly concave. Distal lobe large and broad; deltoid; much larger than proximal lobe; moderately sclerotized; convex. *Apex* acute. *Anterior margin* straight. *Posterior margin* straight; weakly reduced. - Ventral view: Proximal lobe small; convex. *Posterior wing process junction* formed as a large ovoid convexity which conceals the base of the proximal lobe; extends anteriorly from the posterior corner of the lobe base. *Base* moderately narrow. *Apex* round. Distal lobe deltoid; moderately large and broad; discontinuous with ridge; weakly concave.

Median Plate (Fig.75)

FM1 oriented strongly postero-distad. *Anterior section* moderately narrow. *Median to posterior section* very broad. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section of the ventral ridge. *Distal margin* very broadly and strongly fused to 3Ax. FM2 very short; oriented posteriad; acerose; separated from FM1 by a long, broad section of membrane.

Third Axillary (Fig.76)

Head very broad; dorso-ventrally flattened; dorsal surface moderately and extensively concave. Proximal margin convex. Anterior margin dorsally weakly convex; anteriorly weakly concave; not enlarged ventrally; from the proximal angle it slopes abruptly antero-distad. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* not extended

ventrad; narrow; straight. FCu reduced distally; large; broadly ovoid; weakly convex. FA small. *Anterior margin* entire; not reduced by FCu. AXCu absent. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally; depressed distally. FCu section of neck absent. AXCu forms entire neck. Proximal margin elevated as a broad ridge. *Ridge* extends to postero-median of the proximal margin of tail; moderately long; enlarged dorsally relative to tail. Dorsal surface of the ridge curves distad. Prong armed with a single short tooth; oriented proximo-dorsad; narrow. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail deltoid; very broad; short; planate. *Dorsal surface* oriented mesad. *Window* absent. FJ+AXJ narrow; occupies the distal half of the tail; moderately sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA equally sclerotized as FA+AXJ; the former occupies the postero-proximal half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.77)

Humeral Plate moderately broad and long. Anterior margin convex; strongly sclerotized; distant from BScA. Apex moderately narrow; curved ventrad. Dorsal margin concave. Proximal margin weakly concave; curved proximo-ventrad. Ventral margin strongly sinuate. Suture line between FPC+BPC and FC+BC present.

Anterior Subcostal Basivenale broadly deltoid; strongly convex. Proximal and distal sections separated by a prominent suture. *Proximal section* extends postero-ventrad as a broad convexity; about as large as the distal section. *Distal section* continuous with ScA bulge; separated by a weak concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior strongly convex. Bulge broad. *Postero-proximal margin* with a distinct ScA-BR Brace.

Radial Basivenale convex; closed; continuous with radial stem; angled proximad; extremely broadly rectangular. Proximal arch strikingly broad; deltoid; continuous with the anterior margin of BR; angled posteriad. *Postero-distal section* rounded. Anterior margin strongly depressed below the posterior margin of ScA bulge; not visible dorsally; weakly convex; angled proximad. Embayment normal sized. Distal arch very weak; continuous with radial stem; oriented posteriad. br strongly sclerotized; occupies less than half of the proximal arch; discontinuous with BR. *br projection* weakly distinct from BSc as a long, dove-tail shaped extension.

Second Basal Plate (Fig.78)

MA-BMA Junction absent. – MP-BMP Junction: MP only very weakly continuous with the anterior margin of BMP; arises from below the distal plate. – Crimp Patterns absent. – BMP-CuA Brace absent.

BMP-BCuA Brace partially reduced; weakly distinct; short; moderately narrow; formed as a tube-like convexity from the distal margin of 2BP; extends posteriad from 2BP antero-distal section; equally broad along the entire length. Anterior to postero-median section partially reduced. Posterior section continuous with BCuA. Terminus not prominent; weakly fused to the anterior section of BCuA, just mesad of the distal margin.

Medial Basivenalia - General habitus: broad and moderately long; rectangular. Anterior and posterior margins straight. Distal margin deeply concave; strongly elevated from surrounding membrane. BMA broadly scaphoid; short; completely fused to BMP. *Proximal surface* weakly convex. *Medial and distal surfaces* strongly convex. *Anterior margin* straight. *Proximal arch* weakly distinct; planate and straight; enlarged antero-proximally; extremely small; slender; acerose. *Distal arch* weakly distinct; extremely broad but short; strongly convex. BMP rectangular; markedly convex; very weakly separated from BMA by a shallow concavity; brace fused to BMP; separated from both 1BP and BCu by membrane. *Proximal section* weakly separated from BMA; convex; slopes ventro-distad. *Antero-distal section* long; narrow; rectangular; strongly convex; discontinuous from the postero-distal section. *Postero-distal section* similar to the latter, but less convex.

Cubital Basivenalia moderately narrowly fused. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA narrow; moderately long; convex; oriented distad; strongly sclerotized. *Anterior margin* with a moderately broad, but shallow, concavity. *Distal margin* strongly extended posteriad as a slender convexity; weakly sinuate. BCuP broad; convex; oriented posteriad; moderately sclerotized. Distal embayment broad but moderately shallow. – Cubitus Anterior continuous with BCuA. Junction marked by a narrow concave groove.

Basalare (Fig.79)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* very strongly elevated from neck; not polished. BScP lobe claviform; short; projects posteriad from neck. *Dorsal surface* ovoid; weakly convex; polished; elevated from neck but not as strongly as the HP lobe. *Ventral surface* not polished. – Posterior Subcostal Basivenale broadly deltoid; polished.

Discussion

Monophyly of the Geotrupidae is supported by the fact that all of the taxa in this group share the following three apomorphic character states of the wing articulation and wing base:

1. 2Ax: the dorso-distal ridge apex is long and curved
2. the anterior section is strikingly elongate
3. 1BP: ScA-BR brace present.

Geotrupidae share 12 apomorphic character states of the wing articulation and wing base with Hybosoridae, Ochodaeidae and Ceratocanthidae (Browne & Scholtz 1995). Analysis of wing articulation and wing base characters indicates that Geotrupidae are the sister group of Hybosoridae + Ochodaeidae + Ceratocanthidae (Browne & Scholtz 1995).

Hybosoridae

Introduction

The Hybosoridae are a large variable cosmopolitan family which is best represented in the tropics (Scholtz 1990). This family contains 28 genera and 275 species (Allsop 1984; Kuijten 1986).

Hind Wing Articulation Description

First Axillary (Fig.80)

Head - Dorsal surface normal size; convex; clavate. *Antero-dorsal margin* oriented moderately postero-distad; normal width; weakly deplanate. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* base normal width; long. Apex oriented anteriorly; moderately narrow. Anterior surface broad; very long; not waisted medially. *FSc1* very weak; very small; slender; fused to the proximal margin of the ventrad projection. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* tapers from base to apex; short but of average width; deeply concave; oriented disto-ventrad and curved posteriad. Dorsal surface concave. Ventral surface convex. Apex narrow and broadly truncate. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented dorsad; narrow; concave. *FSc2* oriented strongly dorsad and weakly distad; deltoid; very convex; broad. Dorsal surface convex. Ventral surface convex. Apex aciculate. Dorsal margin not enlarged. Head and neck dorsal surface strongly curved dorsad.

Neck normal width and length; weakly oriented antero-distad; broadly articulated with 2Ax; continuous with tail. Proximal margin moderately curved ventrad. Distal margin concave. *Distal embayment* concave; moderately broad.

Tail - Dorsal view: Proximal arch normal size; weakly extended posteriad and proximad; weakly convex. *Apex* very weakly curved ventrad. *Dorsal surface* weakly concave. *Antero-proximal margin* concave. *Postero-proximal margin* convex. Articulation with PRR extends along the entire length of the proximal arch; strong; long and moderately broad; moderately recurved. Antero-dorsal and postero-dorsal surfaces concave. Posterior margin concave. Distal arch normal size. *Apex* very weakly curved ventrad and posteriad; aciculate. *Distal margin* straight. - Ventral view: Proximal arch with a weak ridge. Distal arch with a very small ridge. Posterior margin with a prominent but slender ridge.

Second Axillary (Fig.81)

Radial Fulcra weakly sclerotized; slender.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* narrow. *Anterior to median section* obscured by the distal ridge. *Median to posterior section* strongly enlarged above the distal ridge. *Posterior section* moderately enlarged above the distal ridge; oriented posteriad; slender; moderately long; distinct from lobe and moderately extended past the posterior margin of lobe. Distal ridge distinct from lobe. *Apex* not fused to the proximal ridge apex; oriented ventrad; convex; spatulate; moderately short. *Anterior*

section moderately short; curved antero-ventrad, basally abruptly, and strongly, curved distad. *Median to posterior section* extends adjacent to, but lies below, the proximal ridge; very weakly demarcated from the body by an impression. *Posterior section* acerose; very weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge slender; short; curved distad; distinct from lobe. *Apex* aciculate. *Anterior to antero-median section* digitate; slender; conceals the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge slender; short. *Anterior to median section* concealed by the proximal ridge. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; broad but short. *Median section* convex. *Postero-median section* waisted. *Subalare tendon attachment point* short and broad; apically not curved ventrad; posterior margin rounded, but truncate; extends posteriad from the median; spatulate; weakly visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe moderately long and broad; deltoid; arises medially from the ridge, but depressed below the ridge; strongly sclerotized; convex; oriented proximad. *Base* moderately broad. *Apex* broadly rounded; weakly curved anteriad. *Anterior margin* very weakly concave. *Posterior margin* very weakly enlarged; very weakly concave. Distal lobe moderately small and broad; deltoid; shorter but broader than the proximal lobe; moderately sclerotized; concave. *Anterior margin* convex. *Apex* aciculate; oriented proximad. *Posterior margin* straight; very weakly reduced. - Ventral view: Proximal lobe moderately large; convex. *Posterior wing process junction* formed as a large, slenderly ovoid convexity which conceals the posterior section of the proximal lobe from the base to the apex; occupies the posterior section of the lobe. Distal lobe large and broad; discontinuous with ridge; deeply concave.

Median Plate (Fig.82)

FM1 oriented strongly postero-distad. *Anterior section* narrow. *Median to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section, over the posterior section of the ventral ridge. *Distal margin* narrowly and weakly fused to 3Ax. FM2 moderately long and slender; oriented postero-distad; acerose. *Anterior to postero-median section* separated from FM1 by a long, narrow section of membrane. *Postero-median to posterior section* fused to FM1.

Third Axillary (Fig.83)

Head very broad; dorso-ventrally flattened. Dorsal surface deeply and extensively concave. Proximal margin convex. Anterior margin dorsally weakly convex; not enlarged ventrally; from proximal angle it is oriented antero-distad. *Antero-proximal margin* not extended anteriad. *Antero-distal margin* not extended ventrad; narrow. *Posterior margin* with a weak concavity which extends to the tail. FCu strongly reduced distally; moderately large; distinct; occupies about half of the head; broadly ovoid. FA moderately large; occupies about half of the head; smaller than FCu. *Anterior margin* entire; not reduced by FCu. AXCu absent. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally; depressed distally. FCu section of neck absent. AXCu forms the entire neck. Proximal margin elevated as a broad ridge. Ridge extends to postero-median of the proximal margin of the tail; moderately long; enlarged dorsally relative to tail. Dorsal surface of the ridge is curved distad. *Embayment* deep; extends to the medial margin of the tail. Prong armed with a single tooth; oriented proximo-dorsad. Detached AXCu fragment slender; deltoid; moderately sclerotized.

Tail deltoid; broad; short; planate. *Dorsal surface* oriented mesad. *Window* absent. FJ+AXJ narrow; occupies the distal half of the tail; weakly sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA as equally sclerotized as FA+AXJ; the former occupies the postero-proximal half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.84)

Humeral Plate slender. Anterior margin convex; lies distant from BScA. Apex slender; ovoid; oriented proximad. Dorsal margin convex. Proximal margin convex; curved proximo-ventrad. Ventral margin concave. Suture line between FPC+BPC and FC+BC present. FPC+BPC formed as a moderately large sclerite below the ventro-proximal margin of FC+BC.

Anterior Subcostal Basivenale broadly deltoid; convex; moderately elevated. Proximal and distal sections separated by a prominent suture. Proximal section extended postero-ventrad as a very broad convexity; about as large as the distal section. Distal section discontinuous with the ScA bulge; separated by a narrow but deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior convex. Bulge moderately broad; distinct.

Radial Basivenale large; strongly convex; open; discontinuous with the radial stem; angled proximad; very strongly recurved; moderately broadly rectangular. Arises from the radial stem and curves very strongly dorsad away from both ScA and BScA. Proximal arch strikingly broad; angled posteriad; deltoid; posteriorly strongly extended proximad and distad; continuous with the anterior margin of BR. *Postero-distal section* rounded. *Posterior margin* extremely broad; deeply concave; surrounds the terminus of BMA proximal arch. Anterior margin strongly elevated above the posterior margin of the ScA bulge and BScA; narrow; convex; angled antero-distad; continuous with the distal arch. Embayment normal size. Distal arch very weak; discontinuous with the radial stem; very narrow; strongly recurved; oriented posteriad. *br* strongly sclerotized; large; rectangular; occupies one-half of the proximal arch; discontinuous with BR; posteriorly extended postero-proximad. *br projection* distinct from BSc as a slender extension; oriented antero-ventrad.

Second Basal Plate (Fig.85)

MA-BMA Junction absent. – MP-BMP Junction: MP only very weakly continuous with the anterior margin of BMP; arises from below the distal plate. – Crimp Patterns absent. – BMP-CuA Brace absent.

BMP-BCuA Brace partially reduced; weakly distinct; moderately narrow; formed as a secondary tube-like convexity from the postero-distal margin of 2BP; curves postero-proximad from 2BP postero-distal section; equally broad along the entire length. Anterior section weakly reduced. Posterior section continuous with BCuA. Terminus fused to the anterior section of BCuA, just mesad of the distal margin.

Medial Basivenalia broad and moderately long; rectangular. Anterior and posterior margins straight. Distal margin concave; strongly elevated from the surrounding membrane. BMA broadly scaphoid; moderately short but broad; completely fused to BMP. *Proximal surface* weakly convex. *Medial and distal surfaces* concave. *Anterior margin* moderately concave. *Proximal arch* moderately long; planate and falcate; moderately broad; enlarged antero-proximally. *Distal arch* weakly distinct; moderately broad; extremely short; convex. BMP rectangular; convex; separated from BMA by a shallow concavity; brace fused to BMP. *Proximal section* moderately broad; rectangular; very weakly separated from BMA; deeply concave. *Distal section* very weakly separated into anterior and posterior sections; indistinct from MP; rectangular; broad; strongly convex. Postero-distal section less convex than the antero-distal section.

Cubital Basivenalia moderately narrowly fused; moderately broad and short. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA moderately broad and short; convex; oriented distad; moderately sclerotized. *Anterior margin* with a moderately broad, but shallow, concavity. *Distal margin* extended posteriad as a moderately strong, broad convexity. BCuP slender; very weakly convex; oriented posteriad; very weakly sclerotized. Distal embayment broad but moderately shallow. – Cubitus Anterior continuous with BCuA. Junction marked by a shallow groove.

Basalare (Fig.86)

Head - HP lobe moderately long and very narrow; continuous with neck. *Apex* narrowly rounded. *Dorsal surface* elevated from BScP lobe; not polished. BScP lobe claviform; moderately broad; reduced; projects dorsally from neck. *Dorsal surface* ovoid; convex; polished; elevated from neck. *Ventral surface* polished. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

This family displays the following two autapomorphic character states of the wing articulation:

1. 1Ax: FSc2 is falcate
2. and broad.

Hybosorids are thought to occupy an intermediate position between Ochodaeidae and Ceratocanthidae (d'Hotman & Scholtz 1990b; Nel & Scholtz 1990; Scholtz 1990). Analysis of wing articulation and wing base characters supports this position (Browne & Scholtz 1995). Howden & Gill (1988) placed hybosorids between Trogidae and Ceratocanthidae. Analysis of wing articulation and wing base characters does not support such a relationship. Ceratocanthidae are generally considered to be the sister group of

Hybosoridae (Howden & Gill 1988; d'Hotman & Scholtz 1990b; Nel & Scholtz 1990; Scholtz 1990). Analysis of wing articulation and wing base characters supports such a relationship (Browne & Scholtz 1995).

Hybosoridae share 12 apomorphic character states of the wing articulation and wing base with Geotrupidae, Ochodaeidae and Ceratocanthidae (Browne & Scholtz 1995).

Ceratocanthidae

Introduction

The Ceratocanthidae are a small family with pantropical distribution. Species occur mainly in forests in Asia (three genera; 58 species), Africa (11 genera, 41 species) and America (three genera; unknown number of species. Paulian 1977a; 1978), as well as on various islands. The southern African and Australian ceratocanthids were recently revised by Paulian (1977a,b, 1978).

Hind Wing Articulation Description

First Axillary (Fig.87)

Head - Dorsal surface normal size; convex. *Antero-dorsal margin* oriented moderately postero-distad; normal width; weakly deplanate. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* base normal width; long. Apex oriented anteriad; moderately narrow. Anterior surface broad; very long; not waisted medially. *FSc1* very weak; very small; slender; fused to the proximal margin of the ventral projection. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* tapers from base to apex; short but of average width; deeply concave; oriented disto-ventrad and curved posteriad. Dorsal surface concave. Ventral surface convex. Apex narrow and broadly truncate. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented dorsad; narrow; concave. *FSc2* oriented strongly dorsad and weakly distad; falcate; very convex; narrow. Dorsal surface convex. Ventral surface convex. Apex aciculate. Dorsal margin not enlarged. Head and neck dorsal surface strongly curved dorsad. *Apex* aciculate.

Neck normal width and length; weakly oriented antero-distad; broadly articulated with 2Ax; continuous with tail. Proximal margin moderately curved ventrad. Distal margin concave. *Distal embayment* moderately concave; broad.

Tail - Dorsal view: Proximal arch normal size; extended posteriad and proximad; convex. *Apex* very weakly curved ventrad. *Dorsal surface* weakly concave. *Antero-proximal margin* concave. *Postero-proximal margin* convex. Articulation with PRR extends along the entire length of the proximal arch; strong; long and moderately broad; moderately recurved. Antero-dorsal and postero-dorsal surfaces concave. Posterior margin concave. Distal arch normal size. *Apex* very weakly curved ventrad and posteriad; aciculate. *Distal margin* straight. - Ventral view: Proximal arch with a small ridge. Posterior margin with a prominent ridge. Distal margin with a very small ridge.

Second Axillary (Fig.88)

Radial Fulcalare weakly sclerotized; slender.

Ridges - Dorsal view: Proximal ridge entire; distinct from the lobe. *Apex* narrow. *Anterior to median section* obscured by the distal ridge. *Median to posterior section* strongly enlarged above the distal ridge. *Posterior section* moderately enlarged above the distal ridge; oriented posteriad; slender; moderately long; distinct from lobe and moderately extended past the posterior margin of lobe. Distal ridge distinct from lobe. *Apex* not fused to the proximal ridge apex; oriented ventrad; convex; spatulate; moderately short. *Anterior section* moderately short; curved antero-ventrad, basally abruptly, but weakly, curved distad. *Median to posterior section* extends adjacent to, but lies below, the proximal ridge; very weakly demarcated from the body by an impression. *Posterior section* acerose; very weakly extended past the posterior margin of the lobe. - Ventral view: Proximal ridge slender; short; curved proximad; distinct from lobe. *Apex* acuminate. *Anterior to antero-median section* digitate; slender; conceals the distal ridge. *Median to posterior section* digitate; slender; conceals the distal ridge. Distal ridge slender; short. *Anterior to median section* concealed by the proximal ridge. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from the lobe; broad but short. *Median section* convex. *Postero-median section* waisted. *Subalare tendon attachment point* short and broad; apically not curved ventrad; posterior margin rounded, but truncate; extends posteriad from the median; spatulate; weakly visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe moderately long and broad; deltoid; arises medially from the ridge, but depressed below the ridge; strongly sclerotized; convex. *Base* broad. *Apex* broadly rounded; straight. *Anterior margin* very weakly concave. *Posterior margin* very weakly enlarged; very weakly concave. Distal lobe moderately large and broad; deltoid; shorter but broader than the proximal lobe; moderately sclerotized; concave. *Anterior margin* convex. *Apex* broadly rounded. *Posterior margin* convex; very weakly reduced. - Ventral view: Proximal lobe large; convex. *Posterior wing process junction* formed as a large, slenderly ovoid convexity; arises from the postero-distal margin of the lobe and extends antero-proximad to the lobe mid-line. Distal lobe moderately large and broad; discontinuous with ridge; deeply concave.

Median Plate (Fig.89)

FM1 oriented strongly postero-distad. *Anterior section* very narrow. *Median to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section, over the posterior section of the ventral ridge. *Distal margin* narrowly and weakly fused to 3Ax. FM2 moderately long and slender; oriented postero-distad; acerose. *Anterior to posterior section* separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.90)

Head very broad and convex; dorso-ventrally flattened. Dorsal surface deeply and extensively concave. Anterior margin dorsally weakly convex; not enlarged ventrally; from proximal angle it is oriented antero-distad. *Antero-proximal margin* not extended anteriad.

Antero-distal margin not extended ventrad; narrow. *Posterior margin* with a narrow concavity which extends to the tail. FCu strongly reduced distally; large; distinct; occupies most of the head; broadly ovoid. FA small. *Anterior margin* entire; not reduced by FCu. AXCu present; moderately narrow; extends to the antero-proximal margin. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally; depressed distally. FCu section of neck absent. AXCu forms the entire neck. Proximal margin elevated as a broad ridge. Ridge extends to postero-medial of the proximal margin of tail; moderately long; enlarged dorsally relative to tail. Dorsal surface of ridge is curved distad. *Embayment* very deep; extends past the medial margin of tail. Prong armed with a single very long and broad tooth; oriented proximo-dorsad. Detached AXCu fragment slender; ovoid; moderately sclerotized.

Tail deltoid; broad; short; planate. *Dorsal surface* oriented mesad. *Window* absent. FJ+AXJ narrow; occupies the distal half of the tail; weakly sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA as equally sclerotized as FA+AXJ; the former occupies the postero-proximal half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.91)

Humeral Plate moderately broad and long. Anterior margin weakly sinuate; lies distant from BScA. Apex moderately broad; deltoid; oriented proximad. Dorsal margin convex. Proximal margin convex; oriented proximad; straight. Ventral margin concave. Suture line between FPC+BPC and FC+BC present. FPC+BPC formed as a small sclerite below the ventro-proximal margin of FC+BC.

Anterior Subcostal Basivenale broadly deltoid; convex; moderately elevated. Proximal and distal sections separated by a prominent suture. *Proximal section* extended postero-ventrad as a very broad convexity; about as large as the distal section. *Distal section* discontinuous with the ScA bulge; separated by a very broad and extremely deep concavity. Apex broadly rounded; oriented distad.

Subcosta Anterior strongly convex. Bulge moderately broad; distinct. *Median section* deeply concave; all other margins strongly convex.

Radial Basivenale large; strongly convex; open; discontinuous with the radial stem; angled antero-proximad; very strongly recurved; moderately broadly rectangular. Arises from the radial stem and curves very strongly antero-proximad and dorsad away from both ScA and BScA. Proximal arch strikingly broad; angled posteriad; deltoid; posteriorly strongly extended proximad and distad; continuous with the anterior margin of BR. *Postero-distal section* rounded. *Posterior margin* extremely broad; deeply concave; surrounds the terminus of BMA proximal arch. Anterior margin strongly elevated above the posterior margin of the ScA bulge and BScA; moderately broad; convex; angled antero-distad; continuous with the distal arch. *Embayment* normal size. Distal arch very weak; discontinuous with the radial stem; very broad; strongly recurved; oriented posteriad. br

strongly sclerotized; extremely large; deltoid; occupies one-half of the proximal arch; discontinuous with BR; posteriorly strongly extended proximad and posteriad as a broad sclerite. *br projection* distinct from BSc as an long and slender extension; oriented antero-ventrad.

Second Basal Plate (Fig.92)

MA-BMA Junction absent. – MP-BMP Junction: MP continuous with BMP along all margins. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace partially reduced; weakly distinct; moderately narrow; formed as a secondary tube-like convexity from the posterior margin of 2BP; extends posteriad from 2BP postero-distal section; oriented posteriad; equally broad along the entire length. Anterior section weakly reduced. Posterior section continuous with BCuA; fused to the antero-distal angle of BCuA. Terminus fused to the anterior section of BCuA, just mesad of the distal margin.

Medial Basivenalia broad and moderately long; rectangular. Anterior and posterior margins straight. Distal margin extremely deeply concave; strongly elevated from the surrounding membrane. BMA broadly scaphoid; short but broad; completely fused to BMP. *Proximal surface* weakly convex. *Medial and distal surfaces* flat. *Anterior margin* deeply concave. *Proximal arch* moderately long; planate and falcate; moderately broad; enlarged antero-proximally. *Distal arch* weakly distinct; moderately broad; extremely short; convex. BMP separated from BMA by a shallow concavity; brace fused to BMP. *Proximal section* extremely narrow; almost absent; rectangular; very weakly separated from BMA; convex. *Distal section* very weakly separated into anterior and posterior sections; indistinct from MP; formed as a reversed C-shape; slender; strongly convex. Postero-distal section less convex than the antero-distal section.

Cubital Basivenalia broadly fused. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA moderately broad and short; convex; oriented distad; strongly sclerotized. *Anterior margin* with a moderately broad, but shallow, concavity. *Distal margin* extended posteriad as a moderately strong, broad convexity. BCuP stout; weakly convex; oriented posteriad; weakly sclerotized especially posteriorly. Distal embayment broad but moderately shallow. – Cubitus Anterior continuous with BCuA. Junction marked by a shallow groove.

Basalare (Fig.93)

Head - HP lobe long; discontinuous with neck; appears to arise from the anterior margin of a greatly enlarged BScP lobe; curves posteriad. *Apex* rounded. *Dorsal surface* very weakly elevated above the BScP lobe; not polished. BScP lobe claviform; broad and extended distad and anteriorly; projects posteriad and strongly distad from neck. *Dorsal surface* ovoid; strongly convex; polished; elevated from neck. *Ventral surface* polished. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Monophyly of the Ceratocanthidae is supported by the fact that all of the taxa in this family share the following two apomorphic character states of the wing articulation:

1. 1Ax: FSc2 strongly oriented anteriorly
2. strikingly long and narrow.

Ceratocanthidae share 12 apomorphic character states of the wing articulation and wing base with Geotrupidae, Ochodaecidae and Hybosoridae (Browne & Scholtz 1995). Ceratocanthids are closely related to Ochodaecidae and Hybosoridae. Hybosoridae are generally considered to be the sister group of Ceratocanthidae (Howden & Gill 1988; d'Hotman & Scholtz 1990b; Nel & Scholtz 1990; Scholtz 1990). Analysis of wing articulation and wing base characters supports such a relationship (Browne & Scholtz 1995).

Ochodaecidae

Introduction

The Ochodaecidae consist of two subfamilies, eight genera and approximately 80 species. The family has a virtually cosmopolitan distribution, with the genus *Ochodaecus* Serville occurring in Africa, North and South America, Madagascar, Europe, the Orient and on Oriental and Palearctic Islands. *Pseudochodaecus* Carlson & Ritcher occurs in the western USA, *Namibiotalpa* Scholtz & Evans is restricted to sandy areas of the Namib Desert, *Codocera* Eschscholtz is widespread in eastern Europe and *Enodognathus* Benderitter occurs on Madagascar. The latter four genera are monotypic. *Chaetocanthus* Pringuey and *Synochodaecus* Kolbe are endemic to southern Africa, as is *Odontochodaecus* Paulian to Madagascar (Scholtz et al. 1988). Other important works on the Ochodaecidae are those of Carlson (1975) and Carlson & Ritcher (1974).

Hind Wing Articulation Description

First Axillary (Fig.94)

Head - Dorsal surface normal size; convex. *Antero-dorsal margin* oriented moderately postero-distad; normal width; weakly deplanate. *Antero-proximal margin* very strongly enlarged ventrally. *Postero-proximal margin* weakly enlarged proximally. *FSc2* base normal width. Apex oriented anteriorly; moderately narrow. Anterior surface broad; very long; not waisted medially. *FSc1* very weak; very small; slender; fused to the proximal margin of the ventrad projection. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* tapers from base to apex; short but of average width; deeply concave; oriented disto-ventrad and curved posteriorly. Dorsal surface concave. Ventral surface convex. Apex narrow and rounded. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented dorsad; narrow; concave. *FSc2* oriented strongly dorsad and weakly distad; falcate; very convex; extremely narrow. Dorsal surface very convex; not enlarged. Ventral surface convex. Apex aciculate. Head and neck dorsal surface strongly curved dorsad.

Neck normal width and length; weakly oriented antero-distad; broadly articulated with 2Ax; continuous with tail. Proximal margin moderately curved ventrad. Distal margin concave. *Distal embayment* moderately concave; broad.

Tail - Dorsal view: Proximal arch normal size; not extended posteriad and only very weakly so proximad; weakly convex. *Apex* very weakly curved ventrad. *Dorsal surface* weakly concave. *Antero-proximal margin* concave. *Postero-proximal margin* weakly convex. Articulation with PRR extends along the entire length of the proximal arch; strong; long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface weakly concave. Posterior margin very weakly concave. Distal arch normal size. *Apex* very weakly curved ventrad and posteriad; acuminate. *Distal margin* straight. - Ventral view: Proximal arch with a tapering ridge. Distal arch with an extremely small ridge. Posterior margin with a prominent ridge.

Second Axillary (Fig.95)

Radial Fulcra very weakly sclerotized; very slender.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* narrow. *Anterior to median section* obscured by the distal ridge. *Median to posterior section* strongly enlarged above the distal ridge. *Posterior section* moderately enlarged above the distal ridge; oriented posteriad; slender; moderately long; distinct from lobe and moderately extended past the posterior margin of lobe. Distal ridge very weakly distinct from lobe. *Apex* not fused to the proximal ridge apex; oriented ventrad; convex; narrowly spatulate; moderately short. *Anterior section* moderately short; straight; curved antero-ventrad, basally abruptly curved distad. *Median to posterior section* extends adjacent to, but lies below, the proximal ridge; very weakly demarcated from body by an impression. *Posterior section* acrose; very weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge slender; short; curved distad; distinct from lobe. *Apex* acuminate. *Anterior to antero-median section* digitate; slender; very weakly conceals the proximal margin of the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge slender; short. *Anterior to median section* partially concealed by the proximal ridge; curved proximad. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; broad but short. *Median section* convex. *Postero-median section* waisted. *Subalare tendon attachment point* short and broad; apically not curved ventrad; posterior margin weakly rounded; extends posteriad from the median; spatulate; weakly visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe long and broad; deltoid; arises medially from ridge, but depressed below the ridge; strongly sclerotized; convex; oriented proximad. *Base* broad. *Apex* broadly rounded to truncate; weakly curved anteriorly. *Anterior margin* very weakly concave. *Posterior margin* very weakly enlarged; very weakly concave. Distal lobe weakly reduced; large and broad; deltoid; much larger than the proximal lobe; weakly sclerotized; concave. *Anterior margin* straight. *Apex* acute. *Posterior margin* straight; very weakly reduced. - Ventral view: Proximal lobe extremely small; convex. *Posterior wing process junction* formed as a large ovoid convexity which conceals the posterior section of the proximal lobe from the base to the apex; occupies the posterior section of the lobe. Distal lobe large and broad; discontinuous with ridge; flat.

Median Plate (Fig.96)

FM1 oriented strongly postero-distad. *Anterior section* narrow. *Median to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section, over the posterior section of the ventral ridge. *Distal margin* narrowly and weakly fused to 3Ax. FM2 moderately long and slender; oriented postero-distad; acerose. *Anterior to postero-median section* separated from FM1 by a long, narrow section of membrane. *Postero-median to posterior section* fused to FM1.

Third Axillary (Fig.97)

Head large; dorso-ventrally flattened. Dorsal surface moderately and extensively concave. Proximal margin convex. Anterior margin dorsally weakly convex; not enlarged ventrally; from the proximal angle it is oriented distad. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* not extended ventrad; narrow. *Posterior margin* with a narrow concavity which extends to the tail. FCu reduced distally; distinct; broadly ovoid. FA large. *Anterior margin* entire; not reduced by FCu. AXCu absent. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally; depressed distally. FCu section of neck absent. AXCu forms entire neck. Proximal margin elevated as a broad ridge. Ridge large; moderately long; extends to postero-median of the proximal margin of tail; enlarged dorsally relative to tail. Dorsal surface of ridge is curved distad; concavity absent. *Embayment* very deep; extends past the medial margin of tail. Prong armed with a single short tooth; oriented proximo-dorsad; narrow. Detached AXCu fragment slender; rectangular; weakly sclerotized.

Tail deltoid; very broad; short; planate. *Dorsal surface* oriented mesad. *Window* absent. FJ+AXJ narrow; occupies distal half; weakly sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA as equally sclerotized as FA+AXJ; the former occupies the postero-proximal half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description**First Basal Plate (Fig.98)**

Humeral Plate slender. Anterior margin moderately convex; weakly sclerotized; lies distant from BScA. Apex narrow; curved ventrad. Dorsal margin convex. Proximal margin convex; curved proximo-ventrad. Ventral margin concave. Suture line between FPC+BPC and FC+BC present. FPC+BPC formed as a small sclerite below the ventro-proximal margin of FC+BC.

Anterior Subcostal Basivenale broadly deltoid; convex. Proximal and distal sections separated by a prominent suture. *Proximal section* extended postero-ventrad as a moderately broad convexity; about as large as the distal section. *Distal section* continuous with the ScA bulge; separated by a weak concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior weakly convex. Bulge broad.

Radial Basivenale large; convex; broadly open; discontinuous with the radial stem; angled antero-proximad; broadly rectangular. Proximal arch strikingly broad; angled postero-proximad; deltoid; posteriorly weakly extended proximad and distad; continuous with the anterior margin of BR. *Postero-distal section* rounded. *Posterior margin* concave; surrounds the terminus of BMA proximal arch. Anterior margin elevated above the posterior margin of ScA bulge; extremely narrow; convex; angled antero-proximad; continuous with the distal arch. Embayment normal size. Distal arch very weak; discontinuous with the radial stem; extremely narrow; recurved; oriented posteriad. br strongly sclerotized; extremely large; deltoid; occupies over three-quarters of the proximal arch; discontinuous with BR; posteriorly strongly extended proximad and posteriad as a broad sclerite. *br projection* distinct from BSc as a slender, deltoid extension; oriented antero-ventrad.

Second Basal Plate (Fig.99)

MA-BMA Junction absent. – MP-BMP Junction: MP only very weakly continuous with the anterior margin of BMP; arises from below the distal plate. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace partially reduced; weakly distinct; moderately narrow; formed as a secondary tube-like convexity from the distal margin of 2BP; extends posteriad from 2BP antero-distal section; equally broad along the entire length. Anterior section weakly reduced. Posterior section continuous with BCuA. Terminus prominent; fused to the anterior section of BCuA, just mesad of the distal margin.

Medial Basivenalia broad and moderately long; rectangular. Anterior and posterior margins straight. Distal margin deeply concave; strongly elevated from the surrounding membrane. BMA broadly scaphoid; very short but broad; completely fused to BMP. *Proximal surface* weakly convex. *Medial and distal surfaces* flat. *Anterior margin* concave. *Proximal arch* long; planate and falcate; very narrow; enlarged antero-proximally. *Distal arch* weakly distinct; moderately broad; extremely short; strongly convex. BMP rectangular; convex; separated from BMA by a shallow concavity; brace fused to BMP; separated from both 1BP and BCu by membrane. *Proximal section* narrow; deltoid; weakly separated from BMA; convex. *Antero-distal section* long; narrow; rectangular; strongly convex; discontinuous from the postero-distal section. *Postero-distal section* similar to the latter but less convex.

Cubital Basivenalia completely fused. Posterior margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA very narrow and long; convex; oriented distad; strongly sclerotized. *Anterior margin* with a moderately broad, but shallow, concavity. *Distal margin* strongly extended posteriad as a moderately strong, slender convexity. BCuP very broad; ovoid; convex; oriented posteriad; moderately sclerotized. Distal embayment absent. – Cubitus Anterior continuous with BCuA. Junction marked by a narrow concave groove.

Basalare (Fig.100)

Head - HP lobe moderately small; continuous with neck. *Apex* narrowly truncate. *Dorsal surface* very strongly elevated from neck; not polished. BScP lobe claviform; stout;

projects posteriad from neck. *Dorsal surface* ovoid; strongly convex; polished; elevated from neck, but lies below the HP lobe. *Ventral surface* not polished. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Ochodaeidae do not display any autapomorphic character states of the wing articulation or wing base (Browne & Scholtz 1995). They share 12 apomorphic character states of the wing articulation and wing base with Geotrupidae, Hybosoridae and Ceratocanthidae (Browne & Scholtz 1995).

Carlson & Ritcher (1974) implied that close relationship exists between Ochodaeidae and Hybosoridae, Iablokoff-Khinzorian (1977) suggested that Aclopidae are more closely related to Ochodaeidae, Crowson (1981) implied relationship between Ochodaeidae, Hybosoridae and Geotrupidae, and Lawrence & Newton (1982) concluded that Ochodaeidae, Hybosoridae and Ceratocanthidae appear to be closely related. Scholtz et al. (1988) corroborated Lawrence & Newton (1982) and proposed that ochodaeids are the sister group of Hybosoridae-Ceratocanthidae, a view confirmed by Browne (1993) and reiterated here.

Scarabaeidae

The Scarabaeidae are a large family consisting of the following taxa: Aphodiinae, Aegialiinae, Aulonocneminae, Orphninae, Melolonthinae, *Acoma*, Oncerinae, Chasmatopterinae, Hopliinae, Rutelinae, Dynastinae, Cetoniinae, Trichiinae and Valginae (Browne 1993). The family is characterized by the loss of functional spiracles, membranization of pregenital segments, the loss of one of the free anal veins in the wing, and by larvae with 4-jointed antennae and the absence of stridulatory organs on the legs (Lawrence & Newton 1982).

All scarabaeids share the following 23 apomorphic character states of the wing articulation:

1. 1Ax: head proximal margin reduced,
2. dorsal surface posteriorly reduced,
3. anterior surface narrow,
4. ventral projection long and narrow,
5. embayment mesad,
6. neck long;
7. 2Ax: dorso-proximal and dorso-distal margins of dorso-proximal enlarged proximally and distally,
- 8./9. antero-median to posterior sections of the dorso-proximal ridge enlarged laterad over dorso-distal ridge,
10. anterior section of dorso-distal ridge basally curved distad,
11. posterior wing process ridge-shaped, enlarged to occupy both the anterior margin of the ventro-proximal lobe to the postero-proximal corner of subalare tendon attachment point,

12. subalare tendon attachment point very short, very broad, and apically deeply and broadly concave
13. with the base arising from the distal section of 2Ax and extends postero-proximad;
14. 3Ax: distorted, moderately long to very short,
- 15./16. tail curved, very short and very broad;
17. 1BP: anterior section of proximal arch of BR reduced by a greatly enlarged br.
18. distal arch of BR large and convex.
19. HP curves postero-dorsad close to, or even over, BScA;
20. 2BP: strongly reduced proximally.
21. proximal arch of BMA strongly oriented antero-proximad and ventrad,
22. BMP convex and very narrow.
23. the BMP-BCuA brace greatly enlarged, very broad and very convex.

Aphodiinae

Introduction

The Aphodiinae are a large subfamily with some 1 200 species representing numerous genera in five tribes. Their distribution is world wide. Adults are characterized by 8/9-jointed antennae and tarsi with distinct claws (Arnett 1968). The mouthparts are usually concealed by the clypeus. Seven pairs of spiracles are present, all situated in the pleural membrane and the pygidium is covered (in dorsal view).

The adults of most species are dung feeders, although some have been found feeding on decaying fungi, in decaying organic matter, or in the soil (Ritcher 1966). A few species are associated with ants. Larvae live on dung, organic matter, or may be root feeders (Ritcher 1966).

Hind Wing Articulation Description

First Axillary (Fig.101)

Head - Dorsal surface strikingly reduced posteriorly; convex; all margins are equally extremely narrow and very long. *Antero-dorsal margin* oriented weakly postero-distad; reduced in width; planate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement reduced and absent. *FSc2* base normal width. Apex oriented postero-distad; rounded. Anterior surface strikingly narrow; strikingly short; not waisted medially. *FSc1* distinct; short but broad. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* long and narrow; enlarged mesally; deeply concave; strongly oriented postero-distad, weakly ventrad and not curved posteriad. Dorsal surface concave. Ventral surface convex. Apex narrow; rounded. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented mesad. *FSc2* fused to the distal margin of the ventral projection; oriented distad and weakly dorsad; reduced; small; round; planate; broad. Dorsal surface not enlarged; convex. Ventral surface convex. Apex rounded. Head and neck dorsal surface extended antieriad.

Neck strikingly narrow; strikingly long; strongly oriented distad and ventrad; articulation with 2Ax narrow, reduced anteriorly; continuous with tail. Proximal margin not curved ventrad. Distal margin straight. *Distal embayment* very weakly concave; narrow.

Tail - Dorsal view: Proximal arch strikingly reduced anteriorly and posteriorly; expanded proximally; strongly convex. *Dorsal surface* weakly concave. *Antero-proximal margin* concavity absent. *Postero-proximal margin* strongly convex. Articulation with PRR strong along the entire length of the proximal arch; long and broad; strongly recurved. Antero-dorsal surface concave. Postero-dorsal surface weakly concave. Posterior margin deeply concave. Distal arch markedly reduced anteriorly and posteriorly; strikingly elongated distally; curved ventrad along its entire length. *Apex* strongly curved ventrad and posteriad; aciculate. *Distal margin* weakly convex; appears twisted. - Ventral view: Proximal arch with a very broad ridge. Distal arch with a small ridge. Posterior margin with a broad ridge; medially narrow.

Second Axillary (Fig.102)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; indistinct from lobe; strongly sinuate. *Anterior section* completely concealed by the distal ridge. *Antero-median to postero-median section* strikingly enlarged above and laterad over the distal ridge; extremely slender; curves abruptly postero-proximad from the antero-median to postero-median. *Postero-median section* moderately broad and long; moderately extended past the posterior margin of the lobe; curves abruptly postero-distad and ventrad over, and conceals, the distal ridge posterior. *Posterior section* weakly enlarged above the distal ridge; oriented posteriad. Distal ridge weakly distinct from lobe. *Apex* enlarged; strongly curved ventro-proximad; convex; strikingly narrowly falcate; short. *Anterior section* moderately short; extended antero-proximad; strongly recurved. *Anterior to median section* extends adjacent to, but lies below, the proximal ridge. *Posterior section* concealed by the proximal ridge. - Ventral view: Proximal ridge stout; curved distad; distinct from lobe. *Apex* broad and truncate. *Anterior to antero-median section* broadly digitate; lies adjacent to the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge broad; short. *Anterior to median section* moderately broad; curved proximad. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; narrow and short. *Median section* strongly convex. *Postero-median section* not waisted. *Subalare tendon attachment point* weakly spatulate; moderately long and narrow; apically strongly curved ventrad around the dorso-proximal ridge terminus; posterior margin rounded; extends weakly postero-distad from the median; strongly recurved; visible dorsally.

Body - Dorsal view: extremely short. Proximal lobe very long and narrow; lingulate; oriented postero-proximad; arises posteriorly from the ridge; enlarged to the same dorsal plane as the ridge; weakly sclerotized; concave. *Base* narrow. *Apex* narrowly rounded; weakly curved anteriad. *Anterior margin* concave. *Posterior margin* strikingly enlarged; broadly convex. Distal lobe very long and narrow; lingulate; longer than the proximal lobe; arises anteriorly from the ridge; weakly sclerotized; planate. *Apex* rounded. *Anterior margin* normal length; weakly concave. *Posterior margin* straight; reduced. - Ventral view:

Proximal lobe moderately large; convex. *Posterior wing process junction* formed as an extremely long, ridge-like convexity; shifted posteriad to occupy the extreme postero-proximal corner of the subalare tendon attachment point. Distal lobe moderately long and narrow; discontinuous with ridge; planate.

Median Plate (Fig.103)

FM1 oriented strongly postero-distad. *Anterior section* narrow. *Median to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section, over the posterior section of the ventral ridge. *Distal margin* broadly but and weakly fused to 3Ax. FM2 absent.

Third Axillary (Fig.104)

Head weakly convex; strikingly reduced posteriorly. Proximal margin shallowly concave. Anterior margin weakly concave; broad; enlarged ventrally. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* extended distad. FCu normal size; distinct; occupies two-thirds of the head; ovoid. *Proximal margin* not reduced by AXCu. *Posterior margin* weakly reduced by an enlarged AXCu. *Distal margin* reduced by an enlarged FA. FA moderately small; extended proximad. *Anterior margin* entire. AXCu weakly extended anteriorly onto head. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck elevated proximally; distally depressed. FCu section of neck absent. AXCu forms entire neck. Proximal margin very strongly and extensively elevated as a narrow ridge. *Ridge* extends close to the postero-proximal margin of the tail; very long. Dorsal surface of ridge is weakly curved distad; enlarged dorsally relative to AXA. *Embayment* moderately deep. Prong armed with a single short tooth; oriented proximo-dorsad; narrow. Detached AXCu fragment slender; rectangular; weakly sclerotized.

Tail reduced; moderately deltoid; short. *Dorsal surface* oriented mesad. Anterior to posterior section concave. *Window* absent. FJ+AXJ narrow; occupies the distal half of the tail; weakly sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA as equally sclerotized as FA+AXJ; the former occupies the postero-proximal half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.105)

Humeral Plate broad. Anterior margin weakly sinuate; weakly sclerotized; lies adjacent to BScA. Apex moderately narrow; curved ventrad. Dorsal margin sinuate. Proximal margin convex; curved proximo-ventrad. Ventral margin weakly concave. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; slenderly ovoid; convex; strongly elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended as a very narrow convexity; about as large as the distal section. *Distal section* continuous with ScA bulge; separated by a deep concavity. Apex broadly spatulate;

strongly curved ventrad beneath the postero-proximal margin of the ScA bulge. – Subcosta Anterior weakly convex. Bulge narrow.

Radial Basivenale extremely broad but very short; convex; narrowly open; discontinuous with the radial stem; angled proximad; slenderly ovoid. Proximal arch strikingly broad; with proximal and distal extensions; angled posteriad; broadly deltoid. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Median section* narrow. *Posterior section* extremely broad; moderately extended proximad and very strongly extended distad. Posterior margin concave; surrounds the terminus of the BMA proximal arch. *Postero-distal margin* rounded. Anterior margin elevated above the posterior margin of the ScA bulge; extremely narrow; convex; angled proximad; continuous with the distal arch. Embayment extremely narrow. Distal arch present; convex; broadly curved proximad; discontinuous with the radial stem; recurved. br strongly sclerotized; large; occupies one-half of the proximal arch; discontinuous with BR; posteriorly extended proximad. *br projection* distinct from BSc as a very short extension; oriented antero-ventrad.

Second Basal Plate (Fig.106)

MA-BMA Junction absent. – MP-BMP Junction: MP continuous with BMP on all margins. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; broadly continuous with BMP; entire but only moderately strong; strongly shifted distad; slender; equally broad along the entire length; convex; arises and extends postero-distad from the MP-BMP junction. Terminus appears fused with the base of BCuA but actually fuses with the distal margin of BCuA. *Point of fusion* continuous.

Medial Basivenalia very strongly reduced on all margins; extremely narrow and long; tube-shaped. BMA very narrowly scaphoid; long; strongly convex along all margins; completely fused to BMP. *Anterior margin* moderately concave. *Proximal arch* planate; straight but strongly curved ventrad; long; moderately broad. Apex spatulate; curved antero-ventrad beneath the BR proximal arch. *Distal arch* indistinct; continuous with the anterior margins of both BMP and the BMP-BCuA brace. BMP junction with BMA continuous and narrowly tubular; fused to the BMP-BCuA brace to form a narrow, looping tube; separated from both IBP and BCu by membrane; anterior margin strongly convex; extremely narrow; strongly elevated dorsad. *Postero-distal section* absent.

Cubital Basivenalia moderately narrowly fused; small and ovoid. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA small and ovoid; convex; oriented antero-distad; strongly shifted anteriorly to occupy the postero-distal section of 2BP; moderately sclerotized. *Distal margin* anteriorly of the antero-proximal margin of CuA. BCuP moderately small; ovoid; long; convex; oriented postero-distad; weakly sclerotized. Distal embayment narrow but deep. – Cubitus Anterior discontinuous with BCuA.

Basalare (Fig.107)

Head - HP lobe slender; continuous with neck. *Apex* narrowly rounded. *Dorsal surface* strongly elevated from neck; not polished. BScP lobe broad; claviform; projects posteriad

from the neck. *Dorsal surface* ovoid; strongly convex; polished; elevated from the neck but not as strongly as the HP lobe. *Ventral surface* not polished. – Posterior Subcostal Basivenale broadly deltoid; polished.

Discussion

Although aphodiines do not exhibit any autapomorphic wing articulation and wing base characters, they do share seven derived states of the wing articulation and wing base with Aulonocneminae and Aegialiinae, which together form a monophyletic group (Browne 1993). It is likely that these three taxa together form Aphodiinae, as has been implied by other workers (Koshantschikov 1913; Scholtz 1990). Aphodiinae share 46 apomorphic character states of the wing articulation and wing base with Aegialiinae, Aulonocneminae and Scarabaeinae (Browne 1993).

Aegialiinae

Introduction

Aegialiines are usually small and resemble aphodiines. They have been reported from North America, Europe, India and Tasmania (Arnett 1968). The Aegialiinae was divided by Iablokoff-Khnzorian (1977) into three tribes, the Chironini, Aegialiini, Eremazini. Representatives of the latter two tribes will be discussed. Adults are thought to be saprophagous and larvae feed on decaying organic matter (Iablokoff-Khnzorian 1977).

Hind Wing Articulation Description

First Axillary (Fig.108)

Head - *Dorsal surface* strikingly reduced posteriorly; convex; all margins are equally extremely narrow and very long. *Antero-dorsal margin* oriented weakly postero-distad; reduced in width; planate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement reduced and absent. *FSc2* base normal width. Apex oriented postero-distad; rounded. Anterior surface strikingly narrow; strikingly short; not waisted medially. *FSc1* distinct; short but broad. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* long and narrow; enlarged mesally; deeply concave; strongly oriented postero-distad, weakly ventrad and not curved posteriad. Dorsal surface concave. Ventral surface convex. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented mesad. *FSc2* fused to the distal margin of the ventral projection; oriented distad and weakly dorsad; reduced; small; round; planate; broad. Dorsal surface not enlarged; convex. Ventral surface convex. Apex rounded. Head and neck dorsal surface extended anteriorly.

Neck strikingly narrow; strikingly long; strongly oriented distad and ventrad; articulation with 2Ax narrow, reduced anteriorly; continuous with tail. Proximal margin not curved ventrad. Distal margin straight. *Distal embayment* shallow.

Tail - Dorsal view: Proximal arch strikingly reduced anteriorly and posteriorly; expanded proximally; strongly convex. *Dorsal surface* weakly concave. *Antero-proximal margin*

concavity absent. *Postero-proximal margin* strongly convex. Articulation with PRR strong along the entire length of the proximal arch; long and broad; strongly recurved. Antero-dorsal surface concave. Postero-dorsal surface weakly concave. Posterior margin deeply concave. Distal arch markedly reduced anteriorly and posteriorly; strikingly elongated distally; curved ventrad along its entire length. *Apex* strongly curved ventrad and posteriad; aciculate. *Distal margin* weakly convex; appears twisted. - Ventral view: Proximal arch with a very broad ridge. Distal arch with a small ridge. Posterior margin with a broad ridge; medially narrow.

Second Axillary (Fig.109)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; indistinct from lobe; strongly sinuate. *Anterior section* completely concealed by the distal ridge. *Antero-median to postero-median section* strikingly enlarged above and laterad over the distal ridge; extremely slender; curves abruptly postero-proximad from the antero-median to postero-median. *Postero-median section* moderately broad and long; moderately extended past the posterior margin of the lobe; curves abruptly postero-distad and ventrad over, and conceals, the distal ridge posterior. *Posterior section* weakly enlarged above the distal ridge; oriented posteriad. Distal ridge weakly distinct from lobe. *Apex* enlarged; strongly curved ventro-proximad; convex; strikingly narrowly falcate; short. *Anterior section* moderately short; extended antero-proximad; strongly recurved. *Anterior to median section* extends adjacent to, but lies below, the proximal ridge. *Posterior section* concealed by the proximal ridge. - Ventral view: Proximal ridge stout; curved distad; distinct from lobe. *Apex* broad and truncate. *Anterior to antero-median section* broadly digitate; lies adjacent to the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge broad; short. *Anterior to median section* moderately broad; curved proximad. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; narrow and short. *Median section* strongly convex. *Postero-median section* not waisted. *Subalare tendon attachment point* weakly spatulate; moderately long and narrow; apically strongly curved ventrad around the dorso-proximal ridge terminus; posterior margin rounded; extends weakly postero-distad from the median; strongly recurved; visible dorsally.

Body - Dorsal view: extremely short. Proximal lobe very long and narrow; lingulate; oriented postero-proximad; arises posteriorly from the ridge; enlarged to the same dorsal plane as the ridge; weakly sclerotized; concave. *Base* narrow. *Apex* narrowly rounded; weakly curved anteriorly. *Anterior margin* concave. *Posterior margin* strikingly enlarged; broadly convex. Distal lobe very long and narrow; lingulate; longer than the proximal lobe; arises anteriorly from the ridge; weakly sclerotized; planate. *Apex* rounded. *Anterior margin* normal length; weakly concave. *Posterior margin* straight; reduced. - Ventral view: Proximal lobe moderately large; convex. *Posterior wing process junction* formed as an extremely long, ridge-like convexity; shifted posteriad to occupy the extreme postero-proximal corner of the subalare tendon attachment point. Distal lobe moderately long and narrow; discontinuous with ridge; planate.

Median Plate (Fig.110)

FM1 oriented strongly postero-distad. *Anterior section* narrow. *Median to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* broadly but weakly fused to 3Ax. FM2 absent.

Third Axillary (Fig.111)

Head weakly convex; strikingly reduced posteriorly. Proximal margin shallowly concave. Anterior margin weakly concave; broad; enlarged ventrally. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* extended distad. FCu normal size; distinct; occupies two-thirds of the head; ovoid. *Proximal margin* not reduced by AXCu. *Posterior margin* weakly reduced by an enlarged AXCu. *Distal margin* reduced by an enlarged FA. FA moderately small; extended proximad. *Anterior margin* entire. AXCu weakly extended anteriorly onto head. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck elevated proximally; distally depressed. FCu section of neck absent. AXCu forms entire neck. Proximal margin very strongly and extensively elevated as a narrow ridge. *Ridge* extends close to the postero-proximal margin of the tail; very long. Dorsal surface of ridge is weakly curved distad; enlarged dorsally relative to AXA. *Embayment* moderately deep. Prong armed with a single short tooth; oriented proximo-dorsad; narrow. Detached AXCu fragment slender; rectangular; weakly sclerotized.

Tail reduced; moderately deltoid; short. *Dorsal surface* oriented mesad. Anterior to posterior section concave. *Window* absent. FJ+AXJ narrow; occupies the distal half of the tail; weakly sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA as equally sclerotized as FA+AXJ; the former occupies the postero-proximal half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.112)

Humeral Plate extremely broad. Anterior margin convex; weakly sclerotized; lies adjacent to BScA. Apex broad; curved ventrad. Dorsal margin deeply concave. Proximal margin convex; curved proximo-ventrad; clavate. Ventral margin concave. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; slenderly ovoid; convex; strongly elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended as a moderately narrow convexity; about as large as the distal section. *Distal section* continuous with ScA bulge; separated by a deep concavity. Apex broadly spatulate; strongly curved ventrad beneath the postero-proximal margin of the ScA bulge. – Subcosta Anterior weakly convex. Bulge broad.

Radial Basivenale extremely broad but very short; convex; narrowly open; discontinuous with the radial stem; angled proximad; slenderly ovoid. Proximal arch strikingly broad;

with proximal and distal extensions; angled posteriad; broadly deltoid. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Median section* narrow. *Posterior section* extremely broad; moderately extended proximad and very strongly extended distad. Posterior margin concave; surrounds the terminus of the BMA proximal arch. *Postero-distal margin* rounded. Anterior margin elevated above the posterior margin of the ScA bulge; extremely narrow; convex; angled proximad; continuous with the distal arch. Embayment extremely narrow. Distal arch present; convex; broadly curved proximad; discontinuous with the radial stem; recurved. br strongly sclerotized; large; occupies one-half of the proximal arch; discontinuous with BR; posteriorly extended proximad. *br projection* distinct from BSc as a slender, dove-tail shaped extension; oriented antero-ventrad.

Second Basal Plate (Fig.113)

MA-BMA Junction absent. – MP-BMP Junction: MP continuous with BMP on all margins. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; broadly continuous with BMP; entire but only moderately strong; strongly shifted distad; slender; equally broad along the entire length; convex; arises and extends postero-distad from the MP-BMP junction. Terminus appears fused with the base of BCuA but actually fuses with the distal margin of BCuA. *Point of fusion* continuous.

Medial Basivenalia very strongly reduced on all margins; extremely narrow and long; tube-shaped. BMA very narrowly scaphoid; long; strongly convex along all margins; completely fused to BMP. *Anterior margin* moderately concave. *Proximal arch* planate; straight but strongly curved ventrad; long; moderately broad. Apex spatulate; curved antero-ventrad beneath the BR proximal arch. *Distal arch* indistinct; continuous with the anterior margins of both BMP and the BMP-BCuA brace. BMP junction with BMA continuous and narrowly tubular; fused to the BMP-BCuA brace to form a narrow, looping tube; separated from both IBP and BCu by membrane; anterior margin strongly convex; extremely narrow; strongly elevated dorsad. *Postero-distal section* very weakly sclerotized; nearly absent.

Cubital Basivenalia moderately narrowly fused; small and ovoid. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA small and ovoid; convex; oriented antero-distad; strongly shifted anteriorly to occupy the postero-distal section of 2BP; moderately sclerotized. *Distal margin* anteriorly of the antero-proximal margin of CuA. BCuP moderately small; ovoid; long; convex; oriented postero-distad; weakly sclerotized. Distal embayment very weak. – Cubitus Anterior continuous with BCuA.

Basalare (Fig.114)

Head - HP lobe slender; continuous with neck. *Apex* narrowly rounded. *Dorsal surface* strongly elevated from neck; not polished. BScP lobe narrow; claviform; projects dorsad from neck. *Dorsal surface* narrowly ovoid; strongly convex; polished; elevated from neck but not as elevated as the HP lobe. *Ventral surface* not polished. – Posterior Subcostal Basivenale broadly deltoid; polished.

Discussion

Although Aegialiinae do not exhibit any autapomorphic wing articulation and wing base characters, they do share seven derived character states of the wing articulation and wing base with Aulonocneminae and Aphodiinae, which together form a monophyletic group (Browne 1993). It is likely that these three taxa together form Aphodiinae, as has been implied by other workers (Koshantschikov 1913; Scholtz 1990).

Many workers have suggested that aegialiines are most closely related to Aphodiinae (Stebnicka 1985; Cambefort 1987; Nel & Scholtz 1990; d'Hotman & Scholtz 1990a). Many primitive morphological characters support this relationship, including those of the mouthparts (Nel & Scholtz 1990), male genitalia (d'Hotman & Scholtz 1990a), spiracles (Ritcher 1969a,b), and chromosomes (Virkki 1967). This view is reiterated here. Aegialiinae share 46 apomorphic character states of the wing articulation and wing base with Aphodiinae, Aulonocneminae and Scarabaeinae (Browne 1993).

Aulonocneminae

Introduction

This is a small subfamily comprising four genera and about 50 species, which occur mainly on Madagascar but also on other Indian Ocean Islands, and in southern Africa. An *Aulonocnemis* larva was described by Paulian & Lumaret (1974). Adult characters include those of mouthparts that are not covered by the labrum or clypeus, a covered pygidium, and eyes that are visible in ventral view. They are thought to be sapro-xylophagous (Cambefort 1987).

Hind Wing Articulation Description

First Axillary (Fig.115)

Head - Dorsal surface strikingly reduced posteriorly; convex; all margins are equally extremely narrow and very long. *Antero-dorsal margin* oriented weakly postero-distad; reduced in width; planate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement reduced and absent. *FSc2* base normal width. Apex oriented postero-distad; rounded. Anterior surface strikingly narrow; strikingly short; not waisted medially. *FSc1* distinct; short but broad. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* moderately short and narrow; enlarged mesally; deeply concave; strongly oriented postero-distad, weakly ventrad and not curved posteriad. Dorsal surface concave. Ventral surface convex. Apex narrow; truncate. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented mesad. *FSc2* fused to the distal margin of the ventral projection; oriented distad and weakly dorsad; reduced; small; round; planate. Dorsal surface not enlarged; convex. Ventral surface convex. Apex rounded. Head and neck dorsal surface extended anteriorly.

Neck strikingly narrow; strikingly long; strongly oriented distad and ventrad; articulation with 2Ax narrow, reduced anteriorly; continuous with tail. Proximal margin not curved ventrad. Distal margin straight. *Distal embayment* very weakly concave.

Tail - Dorsal view: Proximal arch strikingly reduced anteriorly and posteriorly; expanded proximally; strongly convex; strongly curved posteriad. *Dorsal surface* weakly concave. *Antero-proximal margin* concavity absent. *Postero-proximal margin* strongly convex. Articulation with PRR strong along the entire length of the proximal arch; long and broad; strongly recurved. Antero-dorsal surface concave. Postero-dorsal surface weakly concave. Posterior margin deeply concave. Distal arch markedly reduced anteriorly and posteriorly; strikingly elongated distally; extremely long; curved ventrad along its entire length. *Apex* strongly curved ventrad and posteriad; aciculate. *Distal margin* weakly convex; appears twisted. - Ventral view: Proximal arch with an extremely broad ridge. Distal arch with a small ridge. Posterior margin with a very broad ridge; medially narrow.

Second Axillary (Fig.116)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire: indistinct from lobe; strongly sinuate. *Anterior* completely concealed by the distal ridge. *Antero-median to postero-median* strikingly enlarged above and laterad over the distal ridge; extremely slender; curves abruptly postero-proximad from the antero-median to postero-median. *Postero-median* moderately broad and long; moderately extended past the posterior margin of the lobe; curves abruptly postero-distad and ventrad over, and conceals, the distal ridge posterior. *Posterior* weakly enlarged above the distal ridge; oriented posteriad. Distal ridge weakly distinct from lobe. *Apex* enlarged; strongly curved ventro-proximad; convex; strikingly narrowly falcate; short. *Anterior* moderately short; extended antero-proximad; strongly recurved. *Anterior to median* extends adjacent to, but lies below, the proximal ridge. *Posterior* concealed by the proximal ridge. - Ventral view: Proximal ridge stout; curved distad; distinct from lobe. *Apex* broad and truncate. *Anterior to antero-median* broadly digitate; lies adjacent to the distal ridge. *Median to posterior* obscured by the distal ridge. Distal ridge broad; short. *Anterior to median* moderately broad; curved proximad. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; narrow and short. *Median* strongly convex. *Postero-median* not waisted. *Subalare tendon attachment point* weakly spatulate; moderately long and narrow; apically strongly curved ventrad around the dorso-proximal ridge terminus; posterior margin rounded; extends weakly postero-distad from the median; strongly recurved; visible dorsally.

Body - Dorsal view: extremely short. Proximal lobe very long and narrow; lingulate; oriented postero-proximad; arises posteriorly from the ridge; enlarged to the same dorsal plane as the ridge; weakly sclerotized; concave. *Base* narrow. *Apex* narrowly rounded; curved anteriorly. *Anterior margin* concave. *Posterior margin* strikingly enlarged; broadly convex. Distal lobe moderately short and narrow; shorter than the proximal lobe; arises anteriorly from the ridge; weakly sclerotized; planate. *Apex* rounded. *Anterior margin* normal length; weakly concave. *Posterior margin* straight; entire. - Ventral view: Proximal lobe moderately large; convex. *Posterior wing process junction* formed as an extremely long, ridge-like convexity; shifted posteriad to occupy the extreme postero-proximal corner of the subalare tendon attachment point. Distal lobe small; discontinuous with ridge; planate.

Median Plate (Fig.117)

FM1 oriented strongly postero-distad. *Anterior* narrow. *Median to posterior* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* broadly but weakly fused to 3Ax. FM2 absent.

Third Axillary (Fig.118)

Head weakly convex; strikingly reduced posteriorly. Proximal margin shallowly concave. Anterior margin weakly concave; broad; enlarged ventrally. *Antero-proximal margin* not extended anteriorad. *Antero-distal margin* extended distad. FCu normal size; distinct; occupies two-thirds of the head; ovoid. *Proximal margin* not reduced by AXCu. *Posterior margin* weakly reduced by an enlarged AXCu. *Distal margin* reduced by an enlarged FA. FA moderately small; extended proximad. *Anterior margin* entire. AXCu weakly extended anteriorad onto head. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck elevated proximally; distally depressed. FCu section of neck absent. AXCu forms entire neck. Proximal margin very strongly and extensively elevated as a narrow ridge. *Ridge* extends close to the postero-proximal margin of the tail; very long. Dorsal surface of ridge is weakly curved distad; enlarged dorsally relative to AXA. *Embayment* moderately deep. Prong armed with a single short tooth; oriented proximo-dorsad; narrow. Detached AXCu fragment slender; rectangular; weakly sclerotized.

Tail reduced; moderately deltoid; short. *Dorsal surface* oriented mesad. Anterior to posterior concave. *Window* absent. FJ+AXJ narrow; occupies the distal half of the tail; weakly sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA as equally sclerotized as FA+AXJ; the former occupies the postero-proximal half of the tail; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.119)

Humeral Plate very broad. Anterior margin sinuate; weakly sclerotized; lies adjacent to BScA. Apex clavate; curved ventrad. Dorsal margin sinuate. Proximal margin convex; curved proximo-ventrad. Ventral margin weakly concave. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; slenderly ovoid; convex; strongly elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended as a very narrow convexity; about as large as the distal section. *Distal section* continuous with ScA bulge; separated by a deep concavity. Apex broadly spatulate; strongly curved ventrad beneath the postero-proximal margin of the ScA bulge. – Subcosta Anterior weakly convex. Bulge narrow.

Radial Basivenale extremely broad but very short; convex; narrowly open; discontinuous with the radial stem; angled proximad; slenderly ovoid. Proximal arch strikingly broad; with proximal and distal extensions; angled posteriorad; broadly deltoid. *Anterior* strikingly

reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Median* narrow. *Posterior* extremely broad; moderately extended proximad and very strongly extended distad. Posterior margin concave; surrounds the terminus of the BMA proximal arch. *Postero-distal margin* rounded. Anterior margin elevated above the posterior margin of the ScA bulge; extremely narrow; convex; angled proximad; continuous with the distal arch. Embayment extremely narrow. Distal arch present; convex; broadly curved proximad; discontinuous with the radial stem; recurved. br strongly sclerotized; large; occupies one-half of the proximal arch; discontinuous with BR; posteriorly extended proximad. *br projection* distinct from BSc as a small, deltoid extension; oriented antero-ventrad.

Second Basal Plate (Fig.120)

MA-BMA Junction absent. – MP-BMP Junction: MP continuous with BMP on all margins. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified: broadly continuous with BMP; entire but only moderately strong; strongly shifted distad; slender; equally broad along the entire length; convex; arises and extends postero-distad from the MP-BMP junction. Terminus appears fused with the base of BCuA but actually fuses with the distal margin of BCuA. *Point of fusion* continuous.

Medial Basivenalia very strongly reduced on all margins; extremely narrow and long; tube-shaped. BMA very narrowly scaphoid; long; strongly convex along all margins; completely fused to BMP. *Anterior margin* moderately concave. *Proximal arch* planate; straight but strongly curved ventrad; long; moderately broad. Apex spatulate; curved antero-ventrad beneath the BR proximal arch. *Distal arch* indistinct; continuous with the anterior margins of both BMP and the BMP-BCuA brace. BMP junction with BMA continuous and narrowly tubular; fused to the BMP-BCuA brace to form a narrow, looping tube; separated from both 1BP and BCu by membrane; anterior margin strongly convex; extremely narrow; strongly elevated dorsad. *Postero-distal section* absent.

Cubital Basivenalia moderately narrowly fused; small and ovoid. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA small and ovoid; convex; oriented antero-distad; strongly shifted anteriorly to occupy the postero-distal section of 2BP; moderately sclerotized. *Distal margin* anteriorly of the antero-proximal margin of CuA. BCuP moderately small; ovoid; long; convex; oriented postero-distad; weakly sclerotized. Distal embayment small. – Cubitus Anterior discontinuous with BCuA.

Basalare (Fig.121)

Head - HP lobe slender; continuous with neck. *Apex* narrowly rounded. *Dorsal surface* strongly elevated from neck; not polished. BScP lobe broad; claviform; projects posteriorly from neck. *Dorsal surface* ovoid; strongly convex; polished; elevated from neck but not as elevated as the HP lobe. *Ventral surface* not polished. – Posterior Subcostal Basivenale broadly deltoid; polished.

Discussion

Although Aulonocneminae do not exhibit any autapomorphic character states of the wing articulation and wing base, they do share seven derived character states of the wing

articulation and wing base with Aegialiinae and Aphodiinae, which together form a monophyletic group (Browne 1993). It is likely that these three taxa together form Aphodiinae, as has been implied by other workers (Koshantschikov 1913; Scholtz 1990). Aulonocneminae share 46 apomorphic character states of the wing articulation and wing base with Aphodiinae, Aegialiinae and Scarabaeinae (Browne 1993). This relationship has been suggested previously (Stebnicka 1985; Cambefort 1987; Nel & Scholtz 1990; d'Hotman & Scholtz 1990a). Many morphological characters support this relationship, including those of the mouthparts (Nel & Scholtz 1990), male genitalia (d'Hotman & Scholtz 1990a), and others from the head, thorax and abdomen (Stebnicka 1985). Only a single diagnostic character separates aulonocnemines from Aphodiinae (Stebnicka 1985).

Scarabaeinae

Introduction

The Scarabaeinae are a large subfamily of approximately 4500 species and 200 genera (Halffter & Edmonds 1982). Members of the subfamily are generally known as the true dung beetles. The Scarabaeinae include six tribes, Onthophagini, Coprini, Eurysternini, Oniticellini, Onitini and Scarabaeini.

The adults and larvae of most Scarabaeinae utilize subliquid and liquid contents of dung and decaying vegetation, described by Stebnicka (1985) as coprophagy or soft saprophagy. For further information on biology, the reader is referred to the recent work by Halffter & Matthews (1966) and Halffter & Edmonds (1982).

Hind Wing Articulation Description

First Axillary (Fig.122)

Head - Dorsal surface strikingly reduced posteriorly; convex; all margins are equally extremely narrow and very long. *Antero-dorsal margin* oriented weakly postero-distad; reduced in width; planate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement reduced and absent. *FSc2* base normal width. Apex oriented postero-distad; rounded. Anterior surface strikingly narrow; strikingly short; not waisted medially. *FSc1* distinct; long and broad; oriented antero-dorsad; very strongly elevated over the base of the ventrad projection. Dorsal and ventral surfaces convex. Apex acute. *Ventral projection* long and narrow; enlarged mesally; deeply concave; strongly oriented postero-distad, weakly ventrad and not curved posteriad. Dorsal surface concave. Ventral surface convex. Apex narrow; rounded; weakly recurved. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* moderately shallow; oriented mesad. *FSc2* fused to the distal margin of the ventral projection; oriented distad and weakly dorsad; reduced; small; round; completely planate; broad. Dorsal surface not enlarged; convex. Ventral surface convex. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck very narrow; strikingly long; strongly oriented distad and ventrad; articulation with 2Ax narrow, reduced anteriorly; medially convex; discontinuous with tail. Proximal margin

very weakly sinuate; weakly curved ventrad. Distal margin very weakly sinuate. *Distal embayment* very weakly concave; narrow.

Tail - Dorsal view: perpendicular to neck. Proximal arch strikingly reduced anteriorly and posteriorly; expanded proximally; extremely small; convex. *Dorsal surface* weakly concave. *Antero-proximal margin* concavity present. *Postero-proximal margin* strongly convex. Articulation with PRR strong along the entire length of the proximal arch; very short but broad; strongly recurved. Antero-dorsal surface concave. Postero-dorsal surface weakly concave. Posterior margin straight. Distal arch very strongly reduced anteriorly and posteriorly; very strikingly expanded and elongated distally; strongly curved ventrad along its entire length; oriented distad. *Apex* strongly curved ventrad and weakly so posteriad; aciculate. *Distal margin* straight. - Ventral view: Proximal and distal margins each with prominent ridges.

Second Axillary (Fig.123)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe; strongly sinuate. *Anterior section* completely concealed by the distal ridge. *Antero-median to postero-median section* strikingly enlarged above and laterad over the distal ridge; extremely slender; curves abruptly postero-proximad from the antero-median to postero-median. *Postero-median section* moderately broad and long; moderately extended past the posterior margin of the lobe; curves abruptly postero-distad and ventrad over, and conceals, the distal ridge posterior. *Posterior section* strongly reduced posteriorly; does not extend past the posterior margin of the lobe; strikingly enlarged laterad over the distal ridge; oriented posteriad; does not curve ventrad. Distal ridge weakly distinct from lobe. *Apex* enlarged; strongly curved ventro-proximad; convex; strikingly narrowly falcate; short. *Anterior section* moderately short; extended antero-proximad; not recurved. *Antero-median to posterior section* concealed by the proximal ridge. - Ventral view: Proximal ridge moderately long; broadly acerose; curved distad; distinct from the lobe. *Apex* narrow and rounded. *Anterior to antero-median section* broadly acerose; lies adjacent to the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge broad; short. *Apex* narrow and rounded. *Anterior to median section* moderately long; broadly acerose; curved proximad. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from the lobe; moderately narrow and very short. *Median section* strongly convex. *Postero-median section* waisted. *Subalare tendon attachment point* weakly spatulate; moderately long and narrow; apically strongly curved ventrad around the dorso-proximal ridge terminus; posterior margin rounded; extends weakly postero-distad from the median; extremely strongly recurved; visible dorsally.

Body - Dorsal view: extremely short. Proximal lobe very long and narrow; lingulate; oriented postero-proximad; arises posteriorly from the ridge; enlarged to the same dorsal plane as the ridge; strongly sclerotized; weakly concave. *Base* very broad. *Apex* rounded; straight. *Anterior margin* concave. *Posterior margin* strikingly enlarged; concave. Distal lobe moderately short but very broad; broadly deltoid; as long as the proximal lobe; arises posteriorly from the ridge; weakly sclerotized; planate. *Apex* aciculate. *Anterior margin*

normal length; concave. *Posterior margin* straight; reduced. - Ventral view: Proximal lobe moderately large; convex. *Posterior wing process junction* formed as an extremely long, ridge-like convexity; shifted posteriad to occupy the extreme postero-proximal corner of the subalare tendon attachment point. Distal lobe moderately small and broad; continuous with ridge; planate.

Median Plate (Fig.124)

FM1 oriented strongly postero-distad. *Anterior section* narrow. *Median to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section, over the posterior section of the ventral ridge. *Distal margin* broadly and strongly fused to 3Ax; suture line indistinct. FM2 slender; fused to the distal margin of FM1 along its entire length; separated by a very weak suture line. *Postero-distal section* forms a strongly sclerotized convexity which extends over a complimentary concavity on the antero-proximal extension of the 3Ax head; posteriorly deeply concave.

Third Axillary (Fig.125)

Head moderately broad; weakly convex; strikingly reduced posteriorly. Proximal margin shallowly concave. Anterior margin weakly concave; broad; enlarged ventrally as a broad plate with a deep concavity. *Antero-proximal margin* weakly extended proximad; very strongly sclerotized; forms a ball and socket joint with FM2. Anterior margin of extension convex; articulates within the FM2 concavity. Posterior margin of extension concave; articulates with the FM2 convexity. *Proximal margin* deeply concave; strongly fused with FM1. *Antero-distal margin* strongly extended distad. FCu normal size; distinct; occupies two-thirds of the head; deltoid. *Posterior margin* not reduced by AXCu. *Distal margin* reduced by an enlarged FA and AXCu. AXCu strongly extended anteriorly along the distal margin of FCu. *Distal section* almost extending to the antero-distal corner of the head; lies between FCu and FA. FA moderately large; extended proximad. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ present.

Neck elevated proximally and distally along most of its length. FCu section of neck absent. AXCu forms entire neck. Proximal margin very strongly and extensively elevated as a very broad ridge. *Ridge* extends close to the postero-proximal margin of the tail; very long. Dorsal surface of ridge is very strongly curved distad over the distal margin of the tail; enlarged dorsally relative to AXA. Antero-distal margin not elevated. *Embayment* moderately shallow. Prong armed with a single tooth; oriented proximo-dorsad; narrow. *Proximal margin* fused to AXCu. Detached AXCu fragment slender; deltoid; weakly sclerotized.

Tail reduced; broadly deltoid; short. *Dorsal surface* oriented mesad. Anterior to posterior section concave. *Window* absent. FJ+AXJ narrow; occupies the most of the tail area; moderately sclerotized. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA as equally sclerotized as FA+AXJ; the former occupies

the postero-proximal section of the tail; strongly reduced; extremely small; straight. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.126)

Humeral Plate very broad. Anterior margin weakly sinuate; weakly sclerotized; lies adjacent to BScA. Apex broad; curved ventrad. Dorsal margin sinuate. Proximal margin straight; strongly curved proximo-ventrad. Ventral margin weakly concave. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; slenderly ovoid; convex; strongly elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended as a very narrow convexity; about as large as the distal section. *Posterior margin* deeply concave. *Distal section* extremely narrow and long; continuous with ScA bulge; separated by a deep concavity. Antero-distal to medio-distal margin separated from ScA by a deep concavity. Apex broadly spatulate; deeply concave; strongly curved ventrad beneath the postero-proximal margin of the ScA bulge. – Subcosta Anterior very strongly convex. Bulge extremely broad.

Radial Basivenale extremely broad but very short; convex; open; discontinuous with the radial stem; angled proximad; slenderly ovoid. Proximal arch strikingly enlarged; with proximal and distal extensions; angled posteriad; broadly deltoid. Distal extension strikingly enlarged antero- to postero-distally. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Median section* narrow. *Posterior section* extremely broad; moderately extended proximad and very strongly extended distad. Posterior margin concave; surrounds the terminus of the BMA proximal arch. *Postero-distal margin* rounded. Anterior margin not elevated above the posterior margin of the ScA bulge; extremely narrow; convex; angled proximad; continuous with the distal arch. Embayment strikingly narrow and falcate. Distal arch present; convex; broadly curved proximad; discontinuous with the radial stem; recurved. br strongly sclerotized; large; occupies one-half of the proximal arch; discontinuous with BR; posteriorly extended proximad. *br projection* distinct from BSc as a slender, dove-tail shaped extension; oriented antero-ventrad.

Second Basal Plate (Fig.127)

MA-BMA Junction absent. – MP-BMP Junction: MP continuous with BMP on all margins. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; broadly continuous with BMP; entire but only moderately strong; shifted distad; slender; equally broad along the entire length; convex; arises and extends postero-distad from the MP-BMP junction. Terminus fused with the distal margin of BCuA. *Point of fusion* discontinuous.

Medial Basivenalia very strongly reduced on all margins; extremely short and narrow; tube-shaped. BMA very narrowly scaphoid; long; strongly convex along all margins; completely fused to BMP. *Anterior margin* moderately concave. *Proximal arch* planate; straight but strongly curved ventrad; long; moderately narrow. Apex narrowly spatulate;

curved antero-ventrad beneath the BR proximal arch. *Distal arch* reduced; indistinct; continuous with the anterior margins of both BMP and the BMP-BCuA brace. BMP junction with BMA continuous and narrowly tubular; fused to the BMP-BCuA brace to form a narrow, looping tube; separated from both IBP and BCu by membrane; anterior margin strongly convex; extremely narrow; strongly elevated dorsad. *Postero-distal section* reduced.

Cubital Basivenalia broadly fused. Posterior margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA very small and ovoid; convex; oriented antero-distad; moderately shifted anteriorly to occupy the postero-distal section of 2BP; weakly sclerotized. *Proximal margin* proximad of CuA antero-proximal margin. BCuP large; deltoid; moderately short; very weakly convex; oriented postero-distad; very weakly sclerotized. Distal embayment absent. – Cubitus Anterior continuous with BCuA.

Basalare (Fig.128)

Head - HP lobe slender; continuous with neck. *Apex* narrowly rounded. *Dorsal surface* strongly elevated from neck; polished. BScP lobe moderately broad; claviform; projects dorsad and posteriad from neck. *Dorsal surface* ovoid; convex; polished; elevated from neck but not as strongly as the HP lobe. *Ventral surface* not polished. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Monophyly of the Scarabaeinae is supported by the fact that all of the taxa in this subfamily share the following 12 apomorphic character states of the wing articulation and wing base:

1. 1Ax: FSc1 is very strongly elevated, long and oriented antero-dorsad over the base of the ventral projection.
2. FSc2 is completely planate.
3. the neck is medially convex.
4. the distal arch of the tail is strongly reduced anteriorly, strongly elongated distally.
5. strongly reduced posteriorly;
6. 2Ax: the posterior section of the dorso-proximal ridge is strikingly enlarged laterad;
7. FM1+FM2 – together with the proximal extension of the 3Ax head are highly modified to form a ball-and-socket joint;
8. 3Ax: the antero-proximal section of the head is narrowly enlarged proximally to form a long extension;
9. 1BP: the proximal arch of BR is strikingly enlarged.
10. the distal extension of the proximal arch is strikingly enlarged antero- to postero-distally.
11. the BR embayment is strikingly narrow and falcate;
12. 2BP: extremely short and narrow.

Many workers have suggested that scarabaeines occupy an intermediate position between Aphodiinae and Melolonthinae, most closely related to the former (Howden 1982; Scholtz 1990). Many larval and adult characters support this relationship (Howden 1982)

including those of the mouthparts (Nel & Scholtz 1990) and male genitalia (d'Hotman & Scholtz 1990a). Scarabaeinae share 46 apomorphic character states of the wing articulation and wing base with Aegialiinae, Aulonocneminae and Aphodiinae (Browne 1993).

Orphninae

Introduction.

The Orphninae are a small Old World group with a few genera. Most species are in *Orphnus* and *Hybalus*. Adults and larvae have been recorded feeding on potatoes and sugar cane (Paulian & Lumaret 1982). The larvae of two species of *Hybalus* were also described in that paper.

Adults are short and convex, with a broad clypeus (similar to the Coprinae). Mouthparts are seldom visible in dorsal view (exposed). Antennae are 10-jointed and seven pairs of spiracles are present, all situated in the pleural membrane. The pygidium is visible in dorsal view and wing venation resembles that of *Brenskea* (Hybosoridae) (Iablokoff-Khnzorian 1977). Little is known about their biology.

Hind Wing Articulation Description

First Axillary (Fig. 129)

Head Dorsal surface strongly reduced posteriorly; broad; clavate; convex. *Antero-dorsal margin* oriented weakly postero-distad; normal width; planate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement moderate and broad. *FSc2* base normal width; deeply concave. Apex oriented postero-distad; rounded but weakly truncate. Anterior surface narrow; long; not waisted medially. *FSc1* absent. *Ventral projection* long and narrow; deeply concave; oriented ventrad and weakly postero-distad. Dorsal surface base to median concave. Ventral surface convex. Concavity located in the preapical area; surrounded by three unequally strong ridges. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; weakly deltoid; convex; broad; moderately short. Dorsal surface enlarged dorsally; convex; appears twisted. Ventral surface convex. Base proximally with a convexity. Apex aciculate. Head and neck dorsal surface extended antieriad.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin reduced; sinuate; not curved ventrad. Distal margin concave. *Distal embayment* moderately concave; moderately shallow but broad.

Tail - Dorsal view: Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; long and broad; strongly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin weakly concave. Distal arch normal size; curved ventrad along its entire length. *Apex* weakly curved posteriad; aciculate. *Distal margin* weakly concave. - Ventral view: Proximal arch

with a weak ridge. Posterior margin with a prominent ridge. Distal arch with a very slender ridge.

Second Axillary (Fig.130)

Radial Fulcalare present; moderately sclerotized; slender.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* partially obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; long; distinct from lobe; extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; convex; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anteriorad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely conceals the distal ridge. *Apex* aciculate. *Anterior to antero-median section* moderately narrow and very long; curved distad. *Median to posterior section* obscured by the distal ridge. Distal ridge *median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; broad; moderately long. *Antero-median section* weakly waisted. *Median section* convex. *Postero-proximal angle* not reduced. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* short and moderately broad; apically not curved ventrad; posterior margin medially concave; extends posteriorad from the median; weakly visible dorsally.

Body - Dorsal view: about as long as broad. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* moderately broad. *Apex* rounded; weakly curved anteriorad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe moderately long and broad; deltoid; shorter than proximal lobe; moderately sclerotized; planate; very weakly sloped ventrad. *Anterior margin* weakly convex; oriented postero-distad; moderately reduced. *Apex* aciculate. *Posterior margin* straight; weakly reduced. - Ventral view: Proximal lobe short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and partially running along the anterior margin of the lobe. Distal lobe moderately large; discontinuous with ridge; weakly concave.

Median Plate (Fig.131)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately broad. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acerose; separated from FM1 by a short and narrow section of membrane.

Third Axillary (Fig.132)

Head weakly convex; normal length. Proximal margin shallowly concave. Anterior margin weakly concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* very weakly extended anteriorly. AXCu occupies the proximal one-fifth of head; convex. FCu normal size; distinct; occupies the central three-fifths of the head; deltoid. FA moderately narrow; occupies the distal one-fifth of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximally; enlarged dorsally relative to AXA. Prong armed with a single very broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; deltoid; short. *Dorsal surface* oriented laterad. Proximal margin weakly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section deeply concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.133)

Humeral Plate moderately broad and long. Anterior margin concave; strongly sclerotized; adjacent to BScA. Apex rounded; moderately broad; curved ventrad. Dorsal margin sinuate. Proximal margin weakly convex; curved ventrad. Ventral margin very strongly sinuate. Suture line between FPC+BPC and FC+BC present.

Anterior Subcostal Basivenale oriented distad; broadly ovoid; convex; moderately elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended postero-proximally as a very broad convexity; larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior moderately convex; moderately extended posteriorly. Bulge broad.

Radial Basivenale convex; open; discontinuous with radial stem; angled antero-proximally; broadly rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; does not surround the BMA arch apex. *Postero-distal*

margin rounded. Anterior margin depressed below the posterior margin of ScA bulge; extremely narrow; convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. *br* strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* slenderly deltoid; concave; distinct from BScA.

Second Basal Plate (Fig.134)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; slender; equally broad along the entire length; convex; distinct from BMP. Terminus fused to the disto-medial section of BCuA. *Point of fusion* continuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* flat. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented antero-proximad; strongly curved ventrad. Apex terminates below distal section of the BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both IBP and BCu by membrane. *Proximal section* moderately broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia broadly fused. Postero-proximal margin of BCuA fused with the medial margin of BCuP. *Suture line* present. BCuA moderately large; convex; oriented postero-distad; lies posteriad of BMP; moderately sclerotized. *Anterior margin* with a moderately broad, shallow concavity. *Distal margin* continuous with CuA. BCuP large; ovoid; convex; oriented postero-distad; very weakly sclerotized. Distal embayment small. – Cubitus Anterior fused to BCuA. Junction marked by a distinct groove.

Basalare (Fig.135)

Head - HP lobe slender; continuous with neck. *Apex* narrowly truncate. *Dorsal surface* weakly elevated from neck; ovoid not polished. BScP lobe claviform; projects posteriad from neck. *Dorsal surface* weakly deltoid; convex; polished; weakly elevated from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale weakly rectangular; polished.

Discussion

Orphninae do not display any apomorphic character states of the wing articulation and wing base but rather are characterized by a plethora of primitive character states of the wing articulation and wing base relative to other members of the orphnine line (Browne 1993).

Orphninae have been related to Hybosoridae (Iablokoff-Khnzorian 1977; Paulian 1984), Ochodaeidae (Blackwelder 1944; Paulian 1984) and Aphodiinae + Melolonthinae (Chalumeau & Gruner 1974). d'Hotman & Scholtz (1990a) proposed that orphnines lie phylogenetically near Scarabaeinae and Melolonthinae. They found that the aedeagus resembles those of Hopliinae and several Melolonthinae genera.

Orphninae share 22 apomorphic character states of the wing articulation and wing base with Melolonthinae, Rutelinae, Dynastinae, Cetoniinae, Oncerinae, Chasmatopterinae, *Acoma*, Hopliinae, Trichiinae and Valginae (Browne 1993).

Melolonthinae

Introduction

The Melolonthinae are a very large, diverse group with cosmopolitan distribution. According to Ritcher (1958), adults do not feed or they are strictly phytophagous, feeding on leaves, flowers or young fruits. Larvae feed on plant roots or humus.

Hind Wing Articulation Description

First Axillary (Fig.136)

Head - Dorsal surface strongly reduced posteriorly; broad; weakly clavate; convex. *Antero-dorsal margin* oriented weakly postero-distad; normal width; very convex. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement moderate and broad. *FSc2* base weakly enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; waisted medially. *FSc1* absent. *Ventral projection* long and narrow; enlarged mesally; deeply concave; oriented ventrad and weakly postero-distad. Dorsal surface base to median concave. Ventral surface convex. Apex wider than base; strongly flared; truncate. Concavity basad and moderately extended apicad from the base of the ventral projection; surrounded by three unequally strong ridges. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; square; convex; broad; moderately short. Dorsal surface enlarged dorsally; convex; appears twisted. Ventral surface convex. Base proximally with a large convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin reduced; sinuate; not curved ventrad. Distal margin concave. *Distal embayment* moderately concave; moderately shallow but broad.

Tail - Dorsal view: Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin weakly concave. Distal arch normal size. *Apex* weakly curved posteriorly and ventrad; aciculate. *Distal margin* weakly concave. - Ventral view: Proximal arch with a weak ridge. Distal arch with a very small ridge. Posterior margin with a prominent but slender ridge.

Second Axillary (Fig.137)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* nearly completely obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-medial to postero-medial section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; long; distinct from lobe; strongly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; convex; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anterior. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* very strongly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely conceals the distal ridge. *Apex* aciculate. *Anterior to antero-medial section* moderately narrow and very long; curved distad. *Median to posterior section* obscured by the distal ridge. Distal ridge *median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; moderately broad; moderately long. *Antero-medial section* weakly waisted. *Median section* convex. *Postero-proximal angle* weakly reduced. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* short and moderately broad; apically not curved ventrad; posterior margin medially concave; extends posterior from the median; the postero-dorsal section of the proximal ridge is moderately extended past the terminus of the subalare tendon attachment point; moderately visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* moderately broad. *Apex* rounded; weakly curved posterior. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe short and moderately broad; deltoid; shorter than proximal lobe; moderately sclerotized; planate; moderately sloped ventrad. *Anterior margin* weakly convex; oriented antero-distad; moderately reduced. *Apex* broadly rounded. *Posterior margin* straight; moderately reduced. -Ventral view: Proximal lobe short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe small; discontinuous with ridge; concave.

Median Plate (Fig.138)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section, over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acerose; separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.139)

Head weakly convex; normal length. Proximal margin shallowly concave. Anterior margin weakly concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* weakly extended anteriorly. AXCu occupies the proximal one-fifth of head; convex. FCu normal size; distinct; occupies the central three-fifths of the head; deltoid. FA moderately narrow; occupies the distal one-fifth of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximad; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; deltoid; short. *Dorsal surface* oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.140)

Humeral Plate moderately narrow; long. Anterior margin sinuate; strongly sclerotized; adjacent to BScA. Apex deltoid; moderately narrow; curved ventrad. Dorsal margin sinuate. Proximal margin straight; curved ventrad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; broadly ovoid; convex; moderately elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended anteriorly and postero-proximally as a very broad convexity; larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad.

Subcosta Anterior moderately convex; moderately extended posteriorly. Bulge moderately broad. – Radial Basivenale convex; open; discontinuous with radial stem; angled antero-proximad; broadly rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* weakly truncate; very weakly extended distad. Anterior margin depressed

below the posterior margin of ScA bulge; extremely narrow; convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. *br* strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* broad along its entire length; concave; distinct from BScA.

Second Basal Plate (Fig.141)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; moderately enlarged; equally broad along the entire length; convex; distinct from BMP. Terminus fused to the disto-medial section of BCuA. *Point of fusion* continuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both IBP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia narrowly fused; slender and long. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA moderately narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized. *Anterior margin* with a broad shallow concavity. *Distal margin* continuous with CuA. BCuP ovoid; convex; oriented posteriad; moderately sclerotized. Distal embayment very broad and deep. – Cubitus Anterior fused to BCuA. Junction marked by a distinct suture.

Basalare (Fig.142)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* rectangular; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale rectangular; polished.

Discussion

Although Melolonthinae, as it is currently recognized, do not display any autapomorphic character states of the wing articulation and wing base, they do share two apomorphic character states of the wing articulation and wing base with *Acoma*, Hopliinae, Oncerinae and Chasmatopterinae. It is likely that these taxa together form Melolonthinae (Browne 1993).

Melolonthinae have been associated with Glaphyridae and Oncerinae (Fowler 1912, in Yadav & Pillai 1979), Aphodiinae (Yadav 1973) and Dynastinae (Howden 1982). However, Melolonthinae are most commonly considered to be the sister group of Rutelinae or

Rutelinae + Dynastinae (Ritcher 1969a,b; Yadav & Pillai 1979; Meinecke 1975; Caveney 1986; Scholtz 1990; Lawrence & Britton 1991).

Melolonthinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Rutelinae, Dynastinae, Cetoniinae, Oncerinae, Chasmatopterinae, *Acoma*, Hopliinae, Trichiinae and Valginae (Browne 1993).

Acoma

Introduction

Acoma is a small genus which occurs in the western United States (Howden 1958; Ritcher 1969a,b). *Acoma* is a well defined genus of uncertain phylogenetic status (Ritcher 1969a,b). Both Arrow (1912, in Ritcher 1969a,b) and Leng (1920) placed *Acoma* in Pleocomidae. Davis (1924, in Howden 1958) thought *Acoma* belonged near *Podolasia* while Blackwelder (1944) listed it in the tribe Chasmatopterini of the subfamily Melolonthinae. Howden (1958) stated that the phylogenetic placement of the genus is likely to remain in doubt until the morphology of the female is known. Ritcher (1969a,b) has suggested that *Acoma* is related to one of the scarab subfamilies, but he does not elaborate.

Hind Wing Articulation Description

First Axillary (Fig.143)

Head - Dorsal surface strongly reduced posteriorly; broad; clavate; convex. *Antero-dorsal margin* oriented weakly postero-distad; normal width; very convex. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement moderate and broad. *FSc2* base weakly enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; waisted medially. *FSc1* absent. *Ventral projection* long and narrow; enlarged mesally; deeply concave; oriented ventrad and weakly postero-distad. Dorsal surface base to median concave. Ventral surface convex. Apex wider than base; strongly flared; truncate. Concavity basad and moderately extended apicad from the base of the ventral projection; surrounded by three unequally strong ridges. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; moderately short. Dorsal surface enlarged dorsally; convex; appears twisted. Ventral surface convex. Base proximally with a large convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin reduced; sinuate; not curved ventrad. Distal margin concave. *Distal embayment* moderately concave; moderately shallow but broad.

Tail - Dorsal view: Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin weakly

concave. Distal arch normal size. *Apex* weakly curved posteriad and ventrad; acuminate. *Distal margin* weakly concave. - Ventral view: Proximal arch with a prominent ridge. Distal arch with a narrow and short ridge. Posterior margin with a prominent ridge.

Second Axillary (Fig.144)

Radial Fulcrae absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* nearly completely obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-medial to postero-medial section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; long; distinct from lobe; strongly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; convex; strikingly elongate; acuminate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anterior. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* very strongly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely conceals the distal ridge. *Apex* acuminate. *Anterior to antero-medial section* moderately narrow and very long; curved distad. *Median to posterior section* obscured by the distal ridge. Distal ridge *median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; moderately broad; moderately long. *Antero-medial section* weakly waisted. *Median section* convex. *Postero-proximal angle* enlarged. *Postero-distal angle* reduced. *Subalare tendon attachment point* short and moderately broad; apically not curved ventrad; posterior margin medially concave; extends posteriad from the median; the postero-dorsal section of the proximal ridge is strongly extended past the terminus of the subalare tendon attachment point; moderately visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; concave. *Base* moderately broad. *Apex* rounded; weakly curved anterior. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe short and moderately broad; deltoid; shorter than proximal lobe; moderately sclerotized; planate; strongly sloped ventrad. *Anterior margin* weakly convex; oriented antero-distad; moderately reduced. *Apex* broadly rounded; moderately reduced. *Posterior margin* straight; moderately reduced. - Ventral view: Proximal lobe moderately short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe small; weakly discontinuous with ridge; concave.

Median Plate (Fig.145)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal*

margin extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acerose; separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.146)

Head weakly convex; normal length. Proximal margin shallowly concave. Anterior margin weakly concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* weakly extended anteriorly. AXCu occupies the proximal one-fifth of head; convex. FCu normal size; distinct; occupies the central three-fifths of the head; deltoid. FA moderately narrow; occupies the distal one-fifth of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximad; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; deltoid. *Dorsal surface* oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median concave. Antero-median to posterior convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.147)

Humeral Plate moderately broad and long. Anterior margin concave; strongly sclerotized; adjacent to BScA. Apex rounded; moderately broad; curved ventrad. Dorsal margin convex. Proximal margin convex; curved ventrad. Ventral margin concave. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; broadly ovoid; convex; strongly elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended anteriorly and postero-proximally as a moderately broad convexity; larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad.

Subcosta Anterior moderately convex; moderately extended posteriorly. Bulge moderately broad. – Radial Basivenale convex; open; discontinuous with radial stem; angled antero-proximad; broadly rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior

margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge; extremely narrow; convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. br strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* deltoid; slender; concave; distinct from BScA.

Second Basal Plate (Fig.148)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; moderately enlarged; equally broad along the entire length; convex; distinct from BMP. Terminus fused to the disto-medial section of BCuA. *Point of fusion* continuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both 1BP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia narrowly fused; slender and long. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA very narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized. *Anterior margin* with a broad shallow concavity. *Distal margin* continuous with CuA. BCuP weakly ovoid; convex; oriented postero-distad; moderately sclerotized. Distal embayment slender and moderately deep. – Cubitus Anterior fused to BCuA Junction marked by a distinct suture.

Basalare (Fig.149)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* ovoid; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Although *Acoma* does not display any autapomorphic character states of the wing articulation and wing base, it does share two apomorphic character states of the wing articulation and wing base with Melolonthinae, Hopliinae, Oncerinae and Chasmatopterinae. It is likely that these taxa together form Melolonthinae (Browne 1993).

Acoma shares 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Dynastinae, Cetoniinae, Oncerinae, Chasmatopterinae, Hopliinae, Trichiinae and Valginae (Browne 1993).

Chasmatopterinae

Introduction

Chasmatopterinae is a poorly defined subfamily but there is little doubt that it is one of the more transformed scarab subfamilies closely related to Melolonthinae (Horn 1867; Saylor 1937; d'Hotman & Scholtz 1990a,b). Chasmatopterines were removed from Melolonthinae and elevated to subfamily status based on the position of the adult abdominal spiracles of the 7th and 8th segments in the pleural membrane (Saylor 1938), but Ritcher (1969a,b) found that these spiracles are situated in the lower parts of the tergites. However, chasmatopterines are more commonly considered to belong to either Chasmatopterini (Leng 1920; d'Hotman & Scholtz 1990a) or Melolonthini (Nel & Scholtz 1990).

Hind Wing Articulation Description

First Axillary (Fig.150)

Head - Dorsal surface strongly reduced posteriorly; broad; weakly clavate; convex. *Antero-dorsal margin* oriented weakly postero-distad; normal width; very convex. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement moderate and broad. *FSc2* base weakly enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; waisted medially. *FSc1* absent. *Ventral projection* long and narrow; enlarged mesally; deeply concave; oriented ventrad and weakly postero-distad. Dorsal surface base to median concave. Ventral surface convex. Apex wider than base; strongly flared; truncate. Concavity basad and moderately extended apicad from the base of the ventral projection; surrounded by three unequally strong ridges. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; moderately short. Dorsal surface enlarged dorsally; convex; appears twisted. Ventral surface convex. Base proximally with a large convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin reduced; sinuate; not curved ventrad. Distal margin concave. *Distal embayment* moderately concave; moderately shallow but broad.

Tail - Dorsal view: Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin weakly concave. Distal arch normal size. *Apex* weakly curved posteriorly and ventrad; aciculate. *Distal margin* weakly concave. - Ventral view: Proximal arch with a weak and very slender

ridge. Posterior margin with a prominent but very slender ridge. Distal arch with a small ridge.

Second Axillary (Fig.151)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* nearly completely obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; long; distinct from lobe; strongly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; convex; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anteriorad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* very strongly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely conceals the distal ridge. *Apex* aciculate. *Anterior to antero-median section* moderately narrow and very long; curved distad. *Median to posterior section* obscured by the distal ridge. Distal ridge *median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; moderately broad; moderately long. *Antero-median section* not waisted. *Median section* convex. *Postero-proximal angle* not reduced. *Postero-distal angle* reduced. *Subalare tendon attachment point* short and moderately broad; apically not curved ventrad; posterior margin medially concave; extends posteriorad from the median; the postero-dorsal section of the proximal ridge is very moderately extended past the terminus of the subalare tendon attachment point; moderately visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* moderately broad. *Apex* rounded; curved anteriorad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe short and moderately broad; deltoid; longer than proximal lobe; moderately sclerotized; planate; weakly sloped ventrad. *Anterior margin* weakly convex; oriented antero-distad; moderately reduced. *Apex* broadly rounded. *Posterior margin* straight; moderately reduced. - Ventral view: Proximal lobe short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe small; weakly discontinuous with ridge; concave.

Median Plate (Fig.152)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acerose; separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.153)

Head weakly convex; normal length. Proximal margin shallowly concave. Anterior margin weakly concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended anteriad. *Antero-distal margin* weakly extended anteriad. AXCu occupies the proximal one-fifth of head; convex. FCu normal size; distinct; occupies the central three-fifths of the head; deltoid. FA moderately narrow; occupies the distal one-fifth of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximad; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; deltoid; short. *Dorsal surface* oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.154)

Humeral Plate moderately broad and long. Anterior margin convex; strongly sclerotized; adjacent to BScA. Apex rounded; moderately narrow; weakly curved ventrad. Dorsal margin concave. Proximal margin weakly convex; curved ventrad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; broadly ovoid; convex; moderately dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended anteriorly and postero-proximally as a moderately broad convexity; larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior moderately convex; moderately extended posteriorly. Bulge moderately broad.

Radial Basivenale convex; open; discontinuous with radial stem; angled antero-proximad; broadly rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge;

extremely narrow; convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. *br* strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* deltoid; slender; concave; distinct from BScA.

Second Basal Plate (Fig.155)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; moderately enlarged; equally broad along the entire length; convex; distinct from BMP. Terminus fused to the disto-medial section of BCuA. *Point of fusion* continuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both IBP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia broadly fused. Posterior margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA small; convex; very weakly oriented postero-distad; lies posteriad of BMP; weakly sclerotized. *Anterior margin* with a broad shallow concavity. *Distal margin* partially continuous with CuA. BCuP deltoid; small; convex; oriented postero-distad; weakly sclerotized. Distal embayment absent. – Cubitus Anterior partially fused to BCuA. Junction marked by a distinct suture.

Basalare (Fig.156)

Head - HP lobe slender; continuous with neck. *Apex* narrowly truncate. *Dorsal surface* elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* ovoid; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale deltoid; polished.

Discussion

Although Chasmatopterinae do not display any autapomorphic character states of the wing articulation and wing base, they do share two apomorphic character states of the wing articulation and wing base with Melolonthinae, Hopliinae, Oncerinae and *Acoma*. The evidence indicates that neither subfamilial nor tribal status is warranted, and it should be returned to Melolonthinae as *Chnaunanthus* (Browne 1993).

Chasmatopterinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Dynastinae, Cetoniinae, Oncerinae, *Acoma*, Hopliinae, Trichiinae and Valginae (Browne 1993).

Hopliinae

Introduction

The Hopliinae have wide distribution. Most adults feed on flowers, but they have also been recorded feeding on young leaves and fruit. Larvae develop in the ground and are either rhizophagous or saprophagous (Iablokoff-Khznorian 1977). This ill-defined subfamily of uncertain phylogenetic status contains two tribes, Hopliini and Pachynemini (d'Hotman & Scholtz 1990a,b).

Hind Wing Articulation Description

First Axillary (Fig.157)

Head - Dorsal surface strongly reduced posteriorly; broad; weakly clavate; convex. *Antero-dorsal margin* oriented weakly postero-distad; normal width; very convex. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement moderate and broad. *FSc2* base weakly enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; waisted medially. *FSc1* absent. *Ventral projection* long and narrow; enlarged mesally; deeply concave; oriented ventrad and weakly postero-distad. Dorsal surface base to median concave. Ventral surface convex. Apex wider than base; strongly flared; truncate. Concavity basad and moderately extended apicad from the base of the ventral projection; surrounded by three unequally strong ridges. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; moderately short. Dorsal surface enlarged dorsally; convex; appears twisted. Ventral surface convex. Base proximally with a large convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin reduced; sinuate; not curved ventrad. Distal margin concave. *Distal embayment* moderately concave; moderately shallow but broad.

Tail - Dorsal view: Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin concave. Distal arch normal size. *Apex* weakly curved posteriorly and ventrad; aciculate. *Distal margin* weakly concave. - Ventral view: Proximal arch with a prominent and broad ridge. Distal arch with a moderately broad, but short ridge. Posterior margin with a prominent ridge.

Second Axillary (Fig.158)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* nearly completely obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal

ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; long; distinct from lobe; strongly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; convex; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anteriorad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* very strongly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely conceals the distal ridge. *Apex* weakly aciculate. *Anterior to antero-medial section* moderately narrow and very long; curved distad. *Median to posterior section* obscured by the distal ridge. Distal ridge *median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; moderately broad; moderately long. *Antero-medial section* not waisted. *Median section* convex. *Postero-proximal angle* not reduced. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* short and moderately broad; apically not curved ventrad; posterior margin medially concave; extends posteriorad from the median; the postero-dorsal section of the proximal ridge is moderately extended past the terminus of the subalare tendon attachment point; strongly visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* moderately broad. *Apex* rounded; curved anteriorad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe short and moderately broad; deltoid; slightly shorter than proximal lobe; moderately sclerotized; planate; moderately sloped ventrad. *Anterior margin* weakly convex; oriented antero-distad; moderately reduced. *Apex* broadly rounded; strongly reduced. *Posterior margin* straight. - Ventral view: Proximal lobe moderately short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe moderately small; weakly discontinuous with ridge; concave.

Median Plate (Fig.159)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acerose; separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.160)

Head weakly convex; normal length; very weakly bi-lobed. Proximal margin shallowly concave. Anterior margin weakly concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended anteriorad. *Antero-distal margin* weakly extended anteriorad. AXCu occupies the proximal one-fifth of head; convex. FCu normal size; distinct; occupies the central three-fifths of the head;

deltoid. FA moderately narrow; occupies the distal one-fifth of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximad; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; deltoid; short. *Dorsal surface* oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.161)

Humeral Plate moderately broad and long. Anterior margin weakly sinuate; strongly sclerotized; adjacent to BScA. Apex very weakly deltoid; moderately narrow; curved ventro-proximad. Dorsal margin sinuate. Proximal margin weakly concave; curved ventrad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; broadly ovoid; convex; moderately dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* extended anteriorly and postero-proximally as a moderately broad convexity; larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior moderately convex; moderately extended posteriorly. Bulge narrow.

Radial Basivenale convex; open; discontinuous with radial stem; angled antero-proximad; rectangular. Proximal arch slenderly deltoid; oriented posteriad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge; extremely narrow; convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. br strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* very slender; concave; distinct from BScA.

Second Basal Plate (Fig.162)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; moderately enlarged; equally broad along the entire length; convex; distinct from BMP. Terminus fused to the disto-medial section of BCuA. *Point of fusion* continuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both IBP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia broadly fused. Posterior margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA very narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized; very weakly distinguishable from CuA. *Anterior margin* with a broad shallow concavity. *Distal margin* continuous with CuA. BCuP weakly deltoid; convex; oriented postero-distad; moderately sclerotized. Distal embayment absent. – Cubitus Anterior fused to BCuA. Junction very weakly distinct.

Basalare (Fig.163)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* rectangular; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale weakly rectangular; polished.

Discussion

Hopliinae is one of the more transformed scarab subfamilies closely related to Melolonthinae (d'Hotman & Scholtz 1990a,b). Hopliines are sometimes considered to be rutelines (Scholtz & Holm 1985), "oncerines" (Leng 1920) but are more often treated as a melolonthine tribe (Blackwelder 1944; Ritcher 1969ab; Howden & Hardy 1971; Hardy 1977). Caveney (1986) found that the structure of the eye is similar to that of *Macroductylus*.

Although Hopliinae do not display any autapomorphic character states of the wing articulation and wing base, they do share two apomorphic character states of the wing articulation and wing base with Melolonthinae, Hopliinae, Oncerinae, Chasmatopterinae and *Acoma*. The lack of autapomorphic character states of the wing articulation and wing base in hopliines does not warrant subfamilial status and it is more likely that it is a Melolonthinae tribe, Hopliini, as it was previously treated by Scholtz (1990).

Hopliinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Dynastinae, Cetoniinae, Oncerinae, Chasmatopterae, *Acoma*, Trichiinae and Valginae (Browne 1993).

Oncerinae

Introduction

Oncerines are generally quite small and their distribution is rather localized in Southern and Lower California (Saylor 1938). They are a very small, poorly defined subfamily but there is little doubt that it is one of the more transformed scarab subfamilies closely related to Melolonthinae (Horn, 1867; Saylor 1938). Oncerines have commonly been treated as a separate subfamily based on the non-melolonthine position of the abdominal spiracles (Horn, 1867). Leng (1920) placed oncerines in a separate subfamily with *Chnaunanthus* (currently Chasmatopterae) and many genera which are currently placed in Melolonthinae.

Hind Wing Articulation Description

First Axillary (Fig.164)

Head - Dorsal surface strongly reduced posteriorly; broad; weakly clavate; convex. *Antero-dorsal margin* oriented weakly postero-distad; normal width; very convex. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement moderate and broad. *FSc2* base weakly enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; waisted medially. *FSc1* absent. *Ventral projection* long and narrow; enlarged mesally; deeply concave; oriented ventrad and weakly postero-distad. Dorsal surface base to median concave. Ventral surface convex. Apex wider than base; strongly flared; truncate. Concavity basad and moderately extended apicad from the base of the ventral projection; surrounded by three unequally strong ridges. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; moderately short. Dorsal surface enlarged dorsally; convex; appears twisted. Ventral surface convex. Base proximally with a large convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin reduced; sinuate; not curved ventrad. Distal margin concave. *Distal embayment* moderately concave; moderately shallow but broad.

Tail - Dorsal view: Proximal arch normal size. *Dorsal surface* weakly concave. *Antero-proximal margin* weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin weakly concave. Distal arch normal size. *Apex* weakly curved posteriorly and ventrad; aciculate. *Distal margin* weakly concave. - Ventral view: Proximal arch with a weak ridge. Posterior margin with a prominent ridge. Distal arch with a slender ridge.

Second Axillary (Fig.165)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* nearly completely obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; long; distinct from lobe; strongly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; convex; strikingly elongate; acuminate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anteriorad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* very strongly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely conceals the distal ridge. *Apex* acuminate. *Anterior to antero-median section* moderately narrow and very long; curved distad. *Median to posterior section* obscured by the distal ridge. Distal ridge *median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; moderately broad; moderately long. *Antero-median section* not waisted. *Median section* convex. *Postero-proximal angle* not reduced. *Postero-distal angle* reduced. *Subalare tendon attachment point* short and moderately broad; apically not curved ventrad; posterior margin medially concave; extends posteriorad from the median; the postero-dorsal section of the proximal ridge is very moderately extended past the terminus of the subalare tendon attachment point; moderately visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* moderately broad. *Apex* rounded; weakly curved anteriorad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe short and moderately broad; deltoid; shorter than the proximal lobe; moderately sclerotized; planate; moderately sloped ventrad. *Anterior margin* weakly convex; oriented antero-distad; moderately reduced. *Apex* acuminate. *Posterior margin* straight; moderately reduced. - Ventral view: Proximal lobe short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe small; weakly discontinuous with ridge; concave.

Median Plate (Fig.166)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately narrow. *Proximal margin section* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acroscite; separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.167)

Head weakly convex; normal length. Proximal margin shallowly concave. Anterior margin weakly concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* weakly extended anteriorly. AXCu occupies the proximal one-fifth of head; convex. FCu normal size; distinct; occupies the central three-fifths of the head; deltoid. FA moderately narrow; occupies the distal one-fifth of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximally; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender: moderately sclerotized.

Tail reduced; deltoid; short. *Dorsal surface* oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.168)

Humeral Plate moderately broad; long. Anterior margin convex; strongly sclerotized; adjacent to BScA. Apex deltoid; moderately narrow; curved ventrad. Dorsal margin concave. Proximal margin weakly convex; curved ventrad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; broadly ovoid; convex; moderately dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* weakly extended anteriorly and postero-proximally as a moderately broad convexity; larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior moderately convex; moderately extended posteriorly. Bulge moderately broad.

Radial Basivenale convex; open; discontinuous with radial stem; angled antero-proximally; broadly rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge; extremely

narrow; convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. *br* strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* slenderly deltoid; concave; distinct from BScA.

Second Basal Plate (Fig.169)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; moderately enlarged; equally broad along the entire length; convex; distinct from BMP. Terminus fused to the disto-medial section of BCuA. *Point of fusion* continuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both 1BP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia narrowly fused; small. Postero-proximal margin of BCuA fused with the antero-proximal margin of BCuP. *Suture line* present. BCuA very small; convex; oriented postero-distad; lies posteriad of BMP; weakly sclerotized. *Anterior margin* with a broad shallow concavity. *Distal margin* continuous with CuA. BCuP narrowly ovoid; convex; oriented postero-distad; weakly sclerotized. Distal embayment narrow but deep. – Cubitus Anterior fused to BCuA. Junction marked by a distinct suture.

Basalare (Fig.170)

Head - HP lobe slender; continuous with neck. *Apex* narrowly truncate. *Dorsal surface* elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* ovoid; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale ovoid; polished.

Discussion

Although Oncerinae do not display any autapomorphic character states of the wing articulation and wing base, they do share two apomorphic character states of the wing articulation and wing base with Melolonthinae, Hopliinae, Chasmatopterinae and *Acoma*. The evidence indicates that neither subfamilial nor tribal status is warranted, and it should be placed in Melolonthinae as *Oncerus* (Browne 1993).

Oncerinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Dynastinae, Cetoniinae, Chasmatopterinae, *Acoma*, Hopliinae, Trichiinae and Valginae (Browne 1993).

Rutelinae

Introduction

The Rutelinae are a very large, diverse cosmopolitan group. Adults either do not feed or they feed on leaves, fruits and flowers (Ritcher 1958). Larvae feed on humus, plant litter or plant roots (Ritcher 1966).

Hind Wing Articulation Description

First Axillary (Fig.171)

Head - Dorsal surface strongly reduced posteriorly; broad; not clavate; convex. *Antero-dorsal margin* oriented strikingly postero-distad; very broad; weakly deplanate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement strong and very broad. *FSc2* base moderately enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; not waisted medially. *FSc1* absent. *Ventral projection* long and narrow; enlarged mesally; convex; strongly oriented ventrad and posteriad. Dorsal surface base to subapical area convex. Ventral surface convex. Apex concave; wider than base; strongly flared; truncate. Concavity strongly shifted mesad just past the base of the ventral projection onto the anterior surface of the head, and not extended apicad; surrounded by three equally strong ridges of equal length. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; short. Dorsal surface not enlarged dorsally; convex; not twisted. Ventral surface convex. Base proximally with a large convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin not reduced; convex; curved ventrad. Distal margin concave. *Distal embayment* concave; moderately deep and broad.

Tail - Dorsal view: Proximal arch moderately expanded posteriorly and proximally. *Dorsal surface* moderately concave. *Antero-proximal margin* very weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface moderately concave. Postero-dorsal surface moderately concave. Posterior margin weakly concave. Distal arch strikingly reduced anteriorly, distally and posteriorly. *Apex* weakly curved posteriad and ventrad; very broadly rounded. *Distal margin* straight. - Ventral view: Proximal and posterior margins with very prominent ridges. Distal arch with a very slender ridge.

Second Axillary (Fig.172)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior*

section weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; moderately long; distinct from lobe; weakly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; partially planate; slender; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and antieriad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely concealed by the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge *apex* aciculate. *Anterior section* moderately narrow and very long; curved distad. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; moderately broad; long. *Antero-median section* weakly waisted. *Median section* convex. *Postero-proximal angle* strongly extended postero-proximad. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* long and moderately broad; apically not curved ventrad; posterior margin narrowly rounded; postero-distal margin reduced; dorsally concave; surrounds the dorso-proximal ridge posterior within the concavity; extends postero-proximad from the median; postero-dorsal section of the proximal ridge is very weakly extended past the terminus of the subalare tendon attachment point; strongly visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* moderately broad. *Apex* rounded; weakly curved posteriad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe very short and moderately broad; deltoid; shorter than proximal lobe; moderately sclerotized; planate; very strongly sloped ventrad. *Anterior margin* weakly convex; oriented postero-distad; strikingly reduced. *Apex* broadly rounded; strongly reduced. *Posterior margin* straight; moderately reduced. - Ventral view: Proximal lobe moderately short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe extremely small; weakly discontinuous with ridge; concave.

Median Plate (Fig.173)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acerose; separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.174)

Head weakly convex; normal length; very weakly bi-lobed. Proximal margin shallowly concave. Anterior margin weakly concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended antieriad.

Antero-distal margin weakly extended anteriorly. AXCu occupies the proximal one-seventh of head; convex. FCu normal size; distinct; occupies the central three-sevenths of the head; deltoid. FA moderately broad; occupies the distal three-sevenths of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximally; enlarged dorsally relative to AXA. Prong armed with a single moderately broad and long tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; deltoid; short. *Dorsal surface* oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.175)

Humeral Plate broad. Anterior margin convex; strongly sclerotized; very broadly adjacent to, and almost fused with BScA. Apex clavate; broad; very weakly curved ventrad. Dorsal margin concave. Proximal margin weakly convex; curved ventrad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; very broadly ovoid; moderately convex; moderately curved anteriorly. Proximal and distal sections separated by a prominent suture. *Proximal section* strongly and extremely broadly extended anteriorly and postero-proximally as a moderately broad convexity; larger than the distal section. *Distal section* weakly discontinuous with the ScA bulge; separated by a very shallow concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior convex; extended posteriorly. Bulge moderately broad.

Radial Basivenale convex; moderately broadly open; discontinuous with radial stem; angled antero-proximally; rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge; narrow; convex; angled antero-proximally. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved

proximad; oriented postero-proximad. br strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* narrow along its entire length; concave; distinct from BScA.

Second Basal Plate (Fig.176)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; anteriorly enlarged; convex; distinct from BMP. Terminus fused to a deep concavity on the disto-medial section of BCuA. *Point of fusion* discontinuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both 1BP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia moderately broadly fused. Postero-proximal margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized. *Anterior margin* with a moderately broad extremely deep concavity. *Distal margin* continuous with CuA. BCuP deltoid; convex; oriented postero-distad; moderately sclerotized. Distal embayment moderately deep and broad. – Cubitus Anterior fused to BCuA. Junction marked by a distinct suture.

Basalare (Fig.177)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* weakly rectangular; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale weakly deltoid; polished.

Discussion

Although Rutelinae do not display any autapomorphic character states of the wing articulation and wing base, they do share 19 apomorphic character states of the wing articulation and wing base with Dynastinae, Cetoniinae, Trichiinae and Valginae, and four apomorphic character states of the wing articulation and wing base with Dynastinae, its sister group (Howden 1982; Scholtz 1990; Browne 1993).

Rutelinae have usually been associated with both Melolonthinae and Dynastinae (Ritcher 1969a,b; Howden 1982; d'Hotman & Scholtz 1990a; Nel & Scholtz 1990; Scholtz 1990).

However, Rutelinae are considered to be more closely related to Dynastinae, and Melolonthinae being the sister group of this lineage (Meinecke 1975; Howden 1982).

Rutelinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Dynastinae, Cetoniinae, Oncerinae, Chasmatopterinae, *Acoma*, Hopliinae, Trichiinae and Valginae (Browne 1993).

Dynastinae

Introduction

The Dynastinae are a large cosmopolitan group, which may or may not feed as adults (Ritcher 1958). Ritcher also mentioned that those that do feed probably feed on plant juices obtained from underground stems, shoots or roots. Larval feeding habits are very diverse, and vary from dung, humus and other organic matter, to plant roots.

Hind Wing Articulation Description

First Axillary (Fig.178)

Head - Dorsal surface strongly reduced posteriorly; broad; not clavate; convex. *Antero-dorsal margin* oriented strikingly postero-distad; very broad; weakly deplanate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement strong and very broad. *FSc2* base moderately enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; not waisted medially. *FSc1* absent. *Ventral projection* long and narrow; enlarged mesally; convex; strongly oriented ventrad and posteriad. Dorsal surface base to subapical area convex. Ventral surface convex. Apex concave; wider than base; strongly flared; truncate. Concavity strongly shifted mesad just past the base of the ventral projection onto the anterior surface of the head, and not extended apicad; surrounded by three equally strong ridges of equal length. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; short. Dorsal surface not enlarged dorsally; convex; not twisted. Ventral surface convex. Base proximally with a large convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck normal width; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin not reduced; convex; curved ventrad. Distal margin concave. *Distal embayment* concave; moderately deep and broad.

Tail - Dorsal view: Proximal arch moderately expanded posteriorly and proximally. *Dorsal surface* moderately concave. *Antero-proximal margin* very weakly convex. *Postero-proximal margin* straight. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface moderately concave. Postero-dorsal surface moderately concave. Posterior margin weakly concave. Distal arch strikingly reduced anteriorly, distally and posteriorly. *Apex* weakly curved posteriad and ventrad; very broadly rounded. *Distal margin* straight. - Ventral view: Proximal posterior and distal margins with slender ridges.

Second Axillary (Fig.179)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; distinct from lobe. *Apex* obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; slender; moderately long; distinct from lobe; weakly extended past the posterior margin of lobe. Distal ridge weakly distinct from lobe. *Apex* narrow; partially planate; slender; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anteriad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely concealed by the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge *apex* aciculate. *Anterior section* moderately narrow and very long; curved distad. *Median and posterior sections* arise from the posterior and proximal margins of the distal lobe; distinct from lobe; moderately broad; long. *Antero-median section* weakly waisted. *Median section* convex. *Postero-proximal angle* strongly extended postero-proximad. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* long and moderately broad; apically not curved ventrad; posterior margin narrowly rounded; postero-distal margin reduced; dorsally concave; surrounds the dorso-proximal ridge posterior within the concavity; extends postero-proximad from the median; postero-dorsal section of the proximal ridge is very weakly extended past the terminus of the subalare tendon attachment point; strongly visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* moderately broad. *Apex* rounded; weakly curved posteriad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe very short and moderately broad; deltoid; shorter than proximal lobe; moderately sclerotized; planate; very strongly sloped ventrad. *Anterior margin* weakly convex; oriented postero-distad; strikingly reduced. *Apex* broadly rounded; strongly reduced. *Posterior margin* straight; moderately reduced. - Ventral view: Proximal lobe moderately short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe extremely small; weakly discontinuous with ridge; concave.

Median Plate (Fig.180)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* moderately narrow. *Proximal margin* convex. Articulation with 2Ax extends from the antero-distal margin of the distal lobe to the posterior section over the posterior section of the ventral ridge. *Distal*

margin extremely narrowly and weakly fused to 3Ax. FM2 moderately short; oriented proximad; acerose; separated from FM1 by a long, narrow section of membrane.

Third Axillary (Fig.181)

Head weakly convex; normal length; very weakly bi-lobed. Proximal margin shallowly concave. Anterior margin weakly convex; broad; narrow, not enlarged ventrally; from the proximal angle it slopes antero-distad. *Antero-proximal margin* not extended anteriorly. *Antero-distal margin* weakly extended anteriorly. AXCu occupies the proximal one-seventh of head; convex. FCu normal size; distinct; occupies the central three-sevenths of the head; deltoid. FA moderately broad; occupies the distal three-sevenths of head. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is weakly curved proximad; enlarged dorsally relative to AXA. Prong armed with a single moderately broad and long tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; deltoid; short. *Dorsal surface* oriented laterad. Proximal margin strongly elevated dorsad to the dorsal plane of the neck; slopes distad along its entire length. Anterior to antero-median section concave. Antero-median to posterior section convex; oriented dorso-distad. *Window* absent. FJ+AXJ broad; extends close to the dorsal plane of the neck; occupies the anterior half of the tail; moderately sclerotized; curved distad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.182)

Humeral Plate moderately broad but short. Anterior margin convex; strongly sclerotized; very broadly adjacent to, and almost fused with BScA. Apex deltoid; moderately narrow; curved ventrad. Dorsal margin concave. Proximal margin weakly convex; curved ventrad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; very broadly ovoid; moderately convex; moderately curved anteriorly. Proximal and distal sections separated by a prominent suture. *Proximal section* strongly and extremely broadly extended anteriorly and postero-proximally as a moderately broad convexity; larger than the distal section. *Distal section* weakly discontinuous with the ScA bulge; separated by a very shallow concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior convex; extended posteriorly. Bulge moderately broad.

Radial Basivenale convex; moderately broadly open; discontinuous with radial stem; angled antero-proximad; rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge; narrow; convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. br strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* moderately narrow; concave; distinct from BScA.

Second Basal Plate (Fig.183)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; anteriorly enlarged; convex; distinct from BMP. Terminus fused to a deep concavity on the disto-medial section of BCuA. *Point of fusion* discontinuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* weakly concave. *Proximal arch* moderately long; planate and straight; oriented proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both 1BP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia moderately broadly fused. Postero-proximal margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized. *Anterior margin* with a moderately broad extremely deep concavity. *Distal margin* continuous with CuA. BCuP very weakly deltoid; convex; oriented postero-distad; moderately sclerotized. Distal embayment moderately broad and deep. – Cubitus Anterior fused to BCuA. Junction marked by a distinct suture.

Basalare (Fig.184)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* weakly rectangular; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale weakly deltoid; polished.

Discussion

Although Dynastinae do not display any autapomorphic character states of the wing articulation and wing base, they do share 19 apomorphic character states of the wing articulation and wing base with Rutelinae, Cetoniinae, Trichiinae and Valginae, and four apomorphic character states of the wing articulation and wing base with Rutelinae, their sister group (Howden 1982; Scholtz 1990; see Browne 1993).

Dynastinae have usually been associated with Rutelinae by the presence of unequal tarsal claws and similar abdominal spiracle pattern, mouthparts and male genitalia (Ritcher 1969a,b; Howden 1982; d'Hotman & Scholtz 1990a; Nel & Scholtz 1990; Scholtz 1990).

Dynastinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Cetoniinae, Oncerinae, Chasmatopterinae, *Acoma*, Hopliinae, Trichiinae and Valginae (Browne 1993).

Cetoniinae

Introduction

The Cetoniinae are a large and diverse cosmopolitan subfamily (Scholtz 1990) consisting of several ill-defined tribes (E. Holm pers. comm. 1993).

Hind Wing Articulation Description

First Axillary (Fig.185)

Head - Dorsal surface strongly reduced posteriorly; extremely broad; clavate; convex. *Antero-dorsal margin* oriented strikingly postero-distad; very broad; weakly deplanate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement strong but very narrow. *FSc2* base moderately enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; not waisted medially. *FSc1* absent. *Ventral projection* extremely long and narrow; enlarged mesally; base to terminus; straight to weakly curved anteriad. Dorsal surface base to terminus convex. - Ventral surface convex. Apex convex; wider than base; flare reduced; truncate. Concavity strongly shifted dorso-mesad past the base of the ventral projection far onto the anterior surface of the head, and not extended apicad; surrounded by three ridges of equal length; the apical ridge is strongly reduced. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; long. Dorsal surface not enlarged dorsally; convex; not twisted. Ventral surface convex. Base proximally with a convexity. Apex aciculate. Head and neck dorsal surface extended anteriad.

Neck strikingly broad; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin sinuate; curved ventrad. Distal margin concave. *Distal embayment* broadly but shallowly concave.

Tail - Dorsal view: Proximal arch strikingly expanded posteriorly and proximally. *Dorsal surface* deeply concave. *Antero-proximal margin* weakly concave. *Postero-proximal margin* convex. Articulation with PRR strong along the entire length of the proximal arch;

very long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin weakly concave; angled strongly antero-distad. Distal arch moderately reduced anteriorly, distally and posteriorly. *Apex* very weakly curved postero-distad. *Distal margin* straight. - Ventral view: Proximal, posterior and distal margins with very prominent, broad ridges.

Second Axillary (Fig.186)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; weakly distinct from lobe. *Apex* obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; extremely short; distinct from lobe; weakly extended past the posterior margin of lobe. Distal ridge distinct from lobe. *Apex* narrow; completely planate; slender; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anteriorad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely concealed by the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge *apex* broadly rounded. *Anterior section* very broad and short; curved distad. *Median and posterior sections* moderately broad; long. *Antero-median section* weakly waisted. *Median section* very strongly convex to form a ridge. *Postero-proximal angle* strongly extended postero-proximad. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* long and moderately broad; apically not curved ventrad; posterior margin narrowly rounded; postero-distal margin reduced; dorsally concave; surrounds the dorso-proximal ridge posterior within the concavity; extends postero-proximad from the median; postero-dorsal section of the proximal ridge is very weakly extended past the terminus of the subalare tendon attachment point; strongly visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe moderately long; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* broad. *Apex* rounded; curved anteriorad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe very short and moderately broad; deltoid; shorter than proximal lobe; moderately sclerotized; planate; very strongly sloped ventrad. *Anterior margin* weakly convex; oriented postero-distad; strikingly reduced. *Apex* broadly rounded; strongly reduced. *Posterior margin* straight; moderately reduced. - Ventral view: Proximal lobe short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe extremely small; weakly discontinuous with ridge; concave.

Median Plate (Fig.187)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* extremely narrow and very long. *Proximal margin* straight. Articulation with 2Ax extends along the distal margin of the distal ridge over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 absent.

Third Axillary (Fig.188)

Head weakly convex; normal length; strikingly bi-lobed, embayment strong. Proximal margin strikingly deeply concave. Anterior margin very deeply concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes very strongly antero-distad. *Embayment* curves postero-distad. *Antero-proximal margin* strongly extended proximad as a lobe. Proximal lobe weakly convex; long; moderately narrow. *Antero-distal margin* strongly extended anteriorly as a lobe. Distal lobe very strongly convex; moderately broad and long. AXCu occupies the proximal one-third of the proximal lobe; convex. FCu strikingly reduced distally; moderately large; distinct; occupies distal two-thirds of the proximal lobe and the proximal one-half of the distal lobe. FA moderately narrow; occupies the distal one-half of the distal lobe. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent. Head and neck junction strikingly reduced, extremely narrow.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is strongly curved distad over the distal margin of the tail and strongly curved ventrad reducing the width of the tail; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; extremely narrow; very short. *Dorsal surface* oriented laterad. *Window* absent. FJ+AXJ extremely narrow and short; occupies the anterior half of the tail; moderately sclerotized; curved ventrad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description**First Basal Plate (Fig.189)**

Humeral Plate very broad and moderately short. Anterior margin convex; strongly sclerotized; adjacent to BScA. Apex clavate; moderately broad; weakly curved ventrad. Dorsal margin convex. Proximal margin deeply concave; strongly curved ventro-proximad. Ventral margin concave. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; rectangular; convex; moderately elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section*

strongly and extremely broadly extended anteriorly and postero-proximally as a very broad convexity; much larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior moderately convex; moderately extended posteriad. Bulge moderately broad.

Radial Basivenale convex; open; discontinuous with radial stem; angled proximad; rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge; moderately broad; straight; angled proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. br strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* deltoid; short; concave; weakly distinct from BScA.

Second Basal Plate (Fig.190)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; posteriorly enlarged; convex; distinct from BMP. Terminus fused to a deep concavity on the disto-medial section of BCuA. *Point of fusion* discontinuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* concave. *Proximal arch* very short; planate and straight; oriented antero-proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both IBP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia completely fused. Posterior margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA very narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized. *Anterior margin* with an extremely broad extremely deep concavity. *Distal margin* continuous with CuA. BCuP large; weakly deltoid; convex; oriented posteriad; moderately sclerotized. Distal embayment absent. – Cubitus Anterior fused to BCuA. Junction indistinct.

Basalare (Fig.191)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* weakly rectangular; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale weakly deltoid; polished.

Discussion

Analysis of wing articulation and wing base characters indicates that this subfamily is paraphyletic since it does not display any autapomorphic wing articulation and wing base characters but does share two apomorphic character states of the wing articulation and wing base with Trichiinae (excluding *Osmoderma*) (Browne 1993). It is likely that these taxa together form Cetoniinae (Browne 1993).

Cetoniines were once placed in Rutelinae (Leng 1920) but are now most commonly considered to be the sister group of Rutelinae and/or Dynastinae (Ritcher 1969a,b; Meinecke 1975; Howden 1982; Caveney 1986; d'Hotman & Scholtz 1990a; Nel & Scholtz 1990; Scholtz 1990). Krikken (1984) considers Trichiinae + Valginae to be the sister group of Cetoniinae, and Rutelinae and/or Dynastinae the sister group of Trichiinae + Valginae + Cetoniinae.

Cetoniinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Dynastinae, Oncerinae, Chasmatopterinae, *Acoma*, Hopliinae, Trichiinae and Valginae (Browne 1993).

Trichiinae

Introduction

The Trichiinae are a medium-sized group with cosmopolitan distribution. Adults of several species have been collected on flowers while others feed on sap that flows from bark. Larvae feed on decaying plant material (Ritcher 1966).

Hind Wing Articulation Description

First Axillary (Fig.192)

Head - Dorsal surface strongly reduced posteriorly; extremely broad; clavate; convex. *Antero-dorsal margin* oriented strikingly postero-distad; very broad; weakly deplanate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement strong but very narrow. *FSc2* base moderately enlarged; deeply concave. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; not waisted medially. *FSc1* absent. *Ventral projection* extremely long and narrow; enlarged mesally; base to terminus; straight to weakly curved anteriorly. Dorsal surface base to terminus convex. - Ventral surface convex. Apex convex; wider than base; flare reduced; truncate. Concavity strongly shifted dorso-mesad past the base of the ventral projection onto the anterior surface of the head, and not extended apicad; surrounded by three ridges of equal length; the apical ridge is weakly reduced. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and weakly dorsad; deltoid; convex; broad; long. Dorsal surface not enlarged dorsally; convex; not twisted. Ventral surface convex. Base proximally with a convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck strikingly broad; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin sinuate; curved ventrad. Distal margin concave. *Distal embayment* broadly but shallowly concave.

Tail - Dorsal view: Proximal arch strikingly expanded posteriorly and proximally. *Dorsal surface* deeply concave. *Antero-proximal margin* weakly concave. *Postero-proximal margin* convex. Articulation with PRR strong along the entire length of the proximal arch; very long but narrow; weakly recurved. Antero-dorsal surface concave. Postero-dorsal surface concave. Posterior margin weakly concave; angled strongly antero-distad. Distal arch moderately reduced anteriorly, distally and posteriorly. *Apex* moderately narrowly digitate; weakly curved postero-distad. *Distal margin* straight. - Ventral view: Proximal margin with a very strong ridge. Distal margin with a weak ridge. Posterior margin with a prominent ridge.

Second Axillary (Fig.193)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; weakly distinct from lobe. *Apex* obscured by the distal ridge; waisted. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; extremely short; distinct from lobe; weakly extended past the posterior margin of lobe. Distal ridge distinct from lobe. *Apex* narrow; completely planate; slender; strikingly elongate; acuminate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and antierad. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely concealed by the distal ridge. *Median to posterior section* obscured by the distal ridge. Distal ridge *apex* broadly rounded. *Anterior section* very broad and short; curved distad. *Median and posterior sections* moderately broad; long. *Antero-median section* weakly waisted. *Median section* very strongly convex to form a ridge. *Postero-proximal angle* strongly extended postero-proximad. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* long and moderately broad; apically not curved ventrad; posterior margin narrowly rounded; postero-distal margin reduced; dorsally concave; surrounds the dorso-proximal ridge posterior within the concavity; extends postero-proximad from the median; postero-dorsal section of the proximal ridge is very weakly extended past the terminus of the subalare tendon attachment point; strongly visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe moderately; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* broad. *Apex* rounded; curved antierad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe very short and moderately broad; deltoid; shorter than proximal lobe; moderately sclerotized; planate; very strongly sloped ventrad. *Anterior margin* weakly convex; oriented postero-distad; strikingly reduced. *Apex* broadly rounded; strongly reduced. *Posterior margin* straight; moderately reduced. - Ventral view: Proximal lobe short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly,

extending to, and running along the anterior margin of the lobe. Distal lobe extremely small; weakly discontinuous with ridge; concave.

Median Plate (Fig.194)

FMI oriented strongly postero-proximad. *Anterior to posterior section* extremely narrow and very long. *Proximal margin* straight. Articulation with 2Ax extends along the distal margin of the distal ridge over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 absent.

Third Axillary (Fig.195)

Head weakly convex; normal length; strikingly bi-lobed, embayment weak. Proximal margin moderately deeply concave. Anterior margin convex; broad; narrow, not enlarged ventrally; from the proximal angle it slopes very strongly antero-distad. *Antero-proximal margin* broadly extended proximad as a lobe. Proximal lobe weakly convex; short. *Antero-distal margin* broadly extended anteriorly as a lobe. Distal lobe very strongly convex; short. AXCu occupies the proximal one-third of the proximal lobe; convex. FCu strikingly reduced distally; moderately large; distinct; occupies distal two-thirds of the proximal lobe and the proximal one-half of the distal lobe. FA moderately narrow; occupies the distal one-half of the distal lobe. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent. Head and neck junction strikingly reduced, extremely narrow.

Neck elevated proximally and weakly so distally. FCu section of neck absent. AXCu forms entire neck; extremely small. Proximal margin elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is strongly curved distad over the distal margin of the tail and strongly curved ventrad reducing the width of the tail; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; extremely narrow; very short. *Dorsal surface* oriented laterad. *Window* absent. FJ+AXJ extremely narrow and short; occupies the anterior half of the tail; moderately sclerotized; curved ventrad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.196)

Humeral Plate moderately broad and long. Anterior margin strongly sinuate; strongly sclerotized; adjacent to BScA. Apex broadly rounded; clavate; curved ventrad. Dorsal margin convex. Proximal margin convex; strongly curved ventro-proximad. Ventral margin concave. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; broadly ovoid; convex; moderately elevated dorsad. Proximal and distal sections separated by a prominent suture. *Proximal section* strongly and extremely broadly extended anteriorly and postero-proximally as a very broad convexity; much larger than the distal section. *Distal section* discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior moderately convex; moderately extended posteriad. Bulge moderately broad.

Radial Basivenale convex; open; discontinuous with radial stem; angled proximad; rectangular. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin depressed below the posterior margin of ScA bulge; moderately broad; straight; angled proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. br strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* slender; short; concave; weakly distinct from BScA.

Second Basal Plate (Fig.197)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; posteriorly enlarged; convex; distinct from BMP. Terminus fused to a deep concavity on the disto-medial section of BCuA. *Point of fusion* discontinuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* planate. *Anterior margin* concave. *Proximal arch* very short; planate and straight; oriented antero-proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both IBP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia broadly fused. Posterior margin of BCuA fused with the anterior margin of BCuP. *Suture line* present. BCuA very narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized. *Anterior margin* with an extremely broad extremely deep concavity. *Distal margin* continuous with CuA. BCuP weakly deltoid; convex; oriented posteriad; moderately sclerotized. Distal embayment very narrow but deep. – Cubitus Anterior fused to BCuA. Junction indistinct.

Basalare (Fig.198)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* rectangular; weakly convex; polished; depressed from neck; slopes

ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale weakly rectangular; polished.

Discussion

Trichiinae do not display any apomorphic character states of the wing articulation and wing base. In addition, it is quite likely that this subfamily is polyphyletic and comprised by at least two distinct lineages (E. Holm pers. comm. 1992), formed by *Osmoderma* and all other Trichiinae (Browne 1993). The latter share two autapomorphic character states of the wing articulation and wing base with Cetoniinae.

Trichiines are most commonly associated with Cetoniinae and Valginae, as either a cetoniine tribe (Leng 1920; Ritcher 1969ab; Caveney 1986) or a separate subfamily (Blackwelder 1944; Howden 1968; d'Hotman & Scholtz 1990a; Nel & Scholtz 1990; Scholtz 1990). Trichiinae, together with their sister group Valginae, are considered to be more archaic than Cetoniinae (Krikken 1984). Krikken (1984) suggested that Trichiinae are the sister group of Valginae and that together they are the sister group of Cetoniinae.

Trichiinae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Dynastinae, Oncerinae, Chasmatopterinae, *Acoma*, Hopliinae, Cetoniinae and Valginae (Browne 1993)

Valginae

Introduction

This subfamily consists of about 200 species world wide. Adults are usually associated with flowers. In North America all stages of *Valgus* have been found beneath loose bark at the base of trees in damp, rotten wood, in association with termites (Ritcher 1966), and in Australia large numbers of *Microvalgus* have been reared from termite mound material (Britton 1970). The relationship between the valgines and termites is unknown. In central Europe, *Valgus hemipterus* is common where termites are absent.

Hind Wing Articulation Description

First Axillary (Fig.199)

Head - Dorsal surface strongly reduced posteriorly; broad; clavate; convex. *Antero-dorsal margin* oriented strikingly postero-distad; very broad; weakly deplanate. *Antero-proximal margin* with ventral enlargement reduced. *Postero-proximal margin* enlargement strong and very broad. *FSc2* base moderately enlarged. Apex oriented postero-distad; rounded but narrowly so. Anterior surface narrow; long; not waisted medially. *FSc1* absent. *Ventral projection* extremely long and narrow; enlarged mesally; basally to subapically curved anteriorly; apically curved posteriorly. Dorsal surface base to terminus convex. - Ventral surface convex. Apex convex; wider than base; flare reduced; truncate. Concavity strongly shifted dorso-mesad past the base of the ventral projection far onto the anterior surface of the head, and not extended apicad; surrounded by three ridges of equal length; the apical ridge is absent. *Distal embayment* oriented ventro-mesad. *FSc2* oriented distad and

weakly dorsad; deltoid; convex; broad; long. Dorsal surface not enlarged dorsally; convex; not twisted. Ventral surface convex. Base proximally with a convexity. Apex aciculate. Head and neck dorsal surface extended anteriorly.

Neck strikingly broad; long; weakly oriented antero-distad; articulation with 2Ax extends along the distal margin of the neck and tail; continuous with tail. Proximal margin sinuate; curved ventrad; only the anterior is very weakly reduced. Distal margin concave. *Distal embayment* broadly but very shallowly concave.

Tail - Dorsal view: Proximal arch strikingly enlarged posteriorly. *Dorsal surface* deeply concave. *Antero-proximal margin* weakly concave. *Postero-proximal margin* convex. *Postero-proximal angle* very broadly rounded. Articulation with PRR extremely strong along the entire length of the proximal arch; very long but narrow; very strongly recurved. Antero-dorsal surface deeply concave. Postero-dorsal surface deeply concave. Posterior margin deeply concave; angled antero-distad. Distal arch moderately reduced anteriorly, distally and posteriorly. *Apex* very narrow; digitate; weakly oriented postero-distad; weakly curved ventrad. *Distal margin* convex. - Ventral view: Proximal, distal and posterior ridges indistinct; form a single very broad ridge.

Second Axillary (Fig.200)

Radial Fulcalare absent.

Ridges - Dorsal view: Proximal ridge entire; weakly distinct from lobe. *Apex* obscured by the distal ridge. *Anterior section* distal margin exposed. *Antero-median to postero-median section* moderately enlarged above and laterad over the distal ridge. *Posterior section* weakly enlarged above the distal ridge; broadly curved postero-proximad; moderately short; weakly extended past the posterior margin of lobe. Distal ridge distinct from lobe. *Apex* narrow; completely planate; slender; strikingly elongate; aciculate; strongly curved ventro-proximad; the distal margin is reduced revealing the ventral section of the distal lobe. *Anterior section* slender and strikingly elongate; straight and anteriorly. *Median to posterior section* dorsally concealed by the proximal ridge. *Posterior section* weakly extended past the posterior margin of lobe. - Ventral view: Proximal ridge anteriorly completely concealed by the distal ridge. *Median to postero-median section* obscured by the distal ridge. *Postero-median to terminus* acerose; extremely long; extends ventro-distad from the proximal lobe; much longer than the subalare tendon attachment point. Distal ridge *apex* broadly rounded. *Anterior section* broad and short; curved distad. *Median and posterior sections* extremely narrow; acerose; long. *Antero-median section* not waisted. *Median section* very strongly convex to form a ridge. *Postero-proximal angle* very strongly extended postero-proximad. *Postero-distal angle* not extended postero-distad. *Subalare tendon attachment point* strikingly long, narrow and acerose; apically not curved ventrad; posterior margin aciculate; extends postero-proximad from the median; postero-dorsal section of the proximal ridge is strongly extended past the terminus of the subalare tendon attachment point; strongly visible dorsally.

Body - Dorsal view: slender and strikingly elongate. Proximal lobe moderately; deltoid; oriented proximad; arises from the postero-medial section of the ridge; depressed below the ridge; strongly sclerotized; weakly concave. *Base* broad. *Apex* rounded; curved

anteriad. *Anterior margin* concave. *Posterior margin* weakly enlarged; concave. Distal lobe extremely small; deltoid; shorter than proximal lobe; moderately sclerotized; planate. *Anterior margin* straight; oriented distad; strikingly reduced. *Apex* broadly rounded. *Posterior margin* convex; strongly reduced. - Ventral view: Proximal lobe short; convex. *Posterior wing process junction* formed as a slender, ridge-like convexity; occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe. Distal lobe extremely small; weakly discontinuous with ridge; concave.

Median Plate (Fig.201)

FM1 oriented strongly postero-proximad. *Anterior to posterior section* extremely narrow and very long. *Proximal margin* straight. Articulation with 2Ax extends along the distal margin of the distal ridge over the posterior section of the ventral ridge. *Distal margin* extremely narrowly and weakly fused to 3Ax. FM2 absent.

Third Axillary (Fig.202)

Head weakly convex; normal length; strikingly bi-lobed; lobes exceedingly narrow and very long. Proximal margin strikingly deeply concave. Anterior margin very deeply concave; broad; narrow, not enlarged ventrally; from the proximal angle it slopes very strongly antero-distad. *Embayment* extremely deep and extends posteriorly to the head-neck junction; deltoid. *Antero-proximal margin* very strongly extended proximad as a lobe. Proximal lobe convex; strikingly long; narrow; acerose. *Antero-distal margin* very strongly extended anteriad as a lobe. Distal lobe convex; strikingly long; narrow; acerose. AXCu occupies the proximal one-third of the proximal lobe; convex. FCu strikingly reduced distally; distinct; occupies distal two-thirds of the proximal lobe and the proximal one-half of the distal lobe. FA moderately narrow; occupies the distal one-half of the distal lobe. *Anterior margin* entire. Suture line between FCu and FA present. Suture line between FCu and AXCu present. Suture line between FA and FJ absent. Head and neck junction extremely narrow.

Neck strongly elevated, extremely long and narrow; curved postero-distad. FCu section of neck absent. AXCu forms entire neck; extremely small. Posterior section elevated as a very narrow and short ridge. *Ridge* extends to median of the proximal margin of tail; very short. Dorsal surface of ridge is strongly curved distad over the distal margin of the tail; enlarged dorsally relative to AXA. Prong armed with a single broad but short tooth; oriented postero-dorsad. Detached AXCu fragment saddle-shaped; strongly curved ventrad both anteriorly and posteriorly; slender; moderately sclerotized.

Tail reduced; extremely narrow; very short. *Dorsal surface* oriented laterad. *Window* absent. FJ+AXJ extremely narrow and short; occupies the anterior half of the tail; moderately sclerotized; curved ventrad. Suture line between FJ and AXJ absent. Suture line between FA+AXJ and AXA present. AXA extremely short and narrow; more strongly sclerotized than FA+AXJ; occupies the posterior half of the tail; curved postero-distad. Suture line between AXA and AXCu present.

Hind Wing Base Description

First Basal Plate (Fig.203)

Humeral Plate strongly lengthened distally as an extremely slender, sinuate sclerite. Anterior margin sinuate; strongly sclerotized; adjacent to, and almost fused with BScA. *Antero-distal surface* membranous. Apex broadly deltoid; curved ventrad. Dorsal margin sinuate. Proximal margin deeply concave; strongly curved ventro-proximad. Ventral margin sinuate. Suture line between FPC+BPC and FC+BC absent.

Anterior Subcostal Basivenale oriented distad; rectangular; small; convex. Proximal and distal sections separated by a prominent suture. *Proximal section* strongly and extremely broadly extended anteriorly and postero-proximally as a broad convexity; much larger than the distal section. *Distal section* extremely narrow; discontinuous with the ScA bulge; separated by a moderately deep concavity. Apex broadly rounded; oriented distad. – Subcosta Anterior extremely broad; both concave and convex; extended posteriorly. Bulge moderately broad; fused to BR.

Radial Basivenale very strongly convex; open; discontinuous with radial stem; angled proximad; rectangular to ovoid. Proximal arch slenderly deltoid; curved postero-distad. *Anterior section* strikingly reduced by a greatly enlarged br; discontinuous with the anterior margin of BR. *Posterior margin* weakly concave; surrounds the BMA arch apex. *Postero-distal margin* truncate. Anterior margin fused to the posterior margin of ScA; extremely narrow; strongly convex; angled antero-proximad. Embayment normal size. Distal arch discontinuous with radial stem; moderately broad; convex; broadly curved proximad; oriented postero-proximad. br strongly sclerotized; occupies about one-third of the proximal arch; discontinuous with BR. *br projection* slender; short; weakly distinct from BScA.

Second Basal Plate (Fig.204)

MA-BMA Junction absent. – MP-BMP Junction: MP broadly continuous with BMP; arises from below the BMP-BCuA brace. – Crimp Patterns absent. – BMP-CuA Brace absent. – BMP-BCuA Brace present but modified; discontinuous with BMP; entire and greatly strengthened; extends posteriad; posteriorly enlarged; convex; distinct from BMP. Terminus fused to a deep concavity on the disto-medial section of BCuA. *Point of fusion* discontinuous.

Medial Basivenalia reduced proximally. BMA broadly scaphoid; completely fused to BMP. *Proximal surface* convex. *Medial and distal surfaces* weakly convex. *Anterior margin* weakly concave. *Proximal arch* extremely short; planate and straight; oriented antero-proximad; strongly curved ventrad. Apex terminates below BR proximal arch apex. *Distal arch* indistinct; fused to the proximal section of BMP. BMP junction with BMA discontinuous and very broad; fused to brace; markedly convex; separated from both IBP and BCu by membrane. *Proximal section* broadly deltoid; planate; slopes ventro-distad. *Distal section* indistinguishable from BMP-BCuA brace; long; broad; rectangular; strongly convex.

Cubital Basivenalia narrowly fused. Postero-proximal margin of BCuA fused with the antero-proximal margin of BÇuP. *Suture line* present. BCuA very narrow and long; convex; oriented distad; lies posteriad of BMP; strongly sclerotized. *Anterior margin* with an extremely broad extremely deep concavity. *Distal margin* continuous with CuA. BCuP ovoid; convex; oriented posteriad; moderately sclerotized. Distal embayment very narrow but deep. – Cubitus Anterior fused to BCuA. Junction indistinct.

Basalare (Fig.205)

Head - HP lobe large; continuous with neck. *Apex* broadly truncate. *Dorsal surface* weakly elevated from neck; not polished. BScP lobe claviform; weakly projects posteriad from neck. *Dorsal surface* rectangular; weakly convex; polished; depressed from neck; slopes ventrad. *Ventral surface* polished. – Posterior Subcostal Basivenale weakly deltoid; polished.

Discussion

Monophyly of the Valginae is supported by the fact that all members of this subfamily display 10 apomorphic character states of the wing articulation and wing base:

1. 1Ax: the postero-proximal margin of the head displays a strong and very broad proximal enlargement,
2. the anterior surface of the ventral projection is basally to subapically curved anteriorly and apically curved posteriad,
3. the proximal arch is strikingly enlarged posteriorly;
4. 2Ax: the subalare tendon attachment point is strikingly long, narrow and acerose;
5. 3Ax: the proximal and distal lobes of the head are exceedingly narrow and very long,
6. the embayment is extremely deep and extends posteriorly to the head-neck junction,
7. the FCu-neck junction is extremely narrow;
8. 1BP: HP is strongly lengthened distally as an extremely slender, sinuate sclerite,
9. the sclerotized section of ScA which lies between HP anteriorly, and BScA posteriorly and proximally, is completely reduced and membranous,
10. the BScA distal section is extremely slender and the proximal section very broad.

Krikken (1984) considers Valginae to be the sister group of "Trichiinae" and together the sister group of Cetoniinae. d'Hotman & Scholtz (1990a) consider Valginae to be the most transformed scarabaeoid subfamily.

Valginae share 22 apomorphic character states of the wing articulation and wing base with Orphninae, Melolonthinae, Rutelinae, Dynastinae, Oncerinae, Chasmatopterinae, *Acoma*, Hopliini, Cetoniinae and Trichiinae (Browne 1993).

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APPENDIX

List of abbreviations

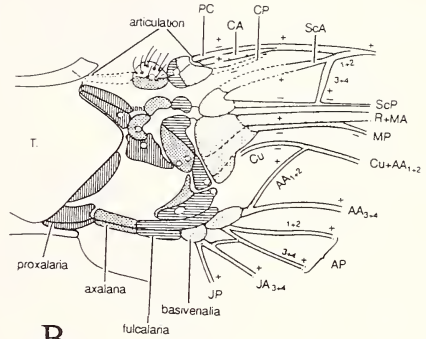
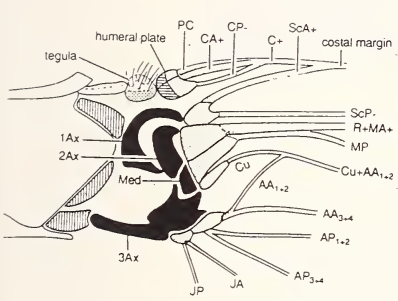
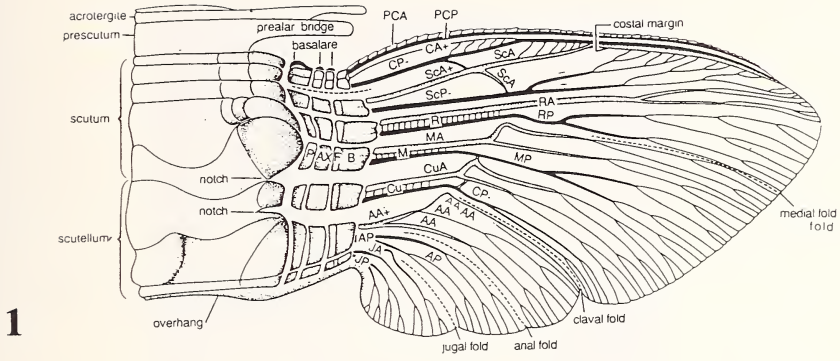
- 1Ax – first axillary
 1BP – first basal plate
 2Ax – second axillary
 2BP – second basal plate
 3Ax – third axillary
 4Ax – fourth axillary
 A – anal vein
 AA – anterior anal vein
 AP – posterior anal vein
 AX – axalare
 AXA – anal axalare
 AXAA – anterior anal axalare
 AXAP – posterior anal axalare
 AXC – costal axalare
 AXCA – anterior costal axalare
 AXCP – posterior costal axalare
 AXCu – cubital axalare
 AXCuA – anterior cubital axalare
 AXCuP – posterior cubital axalare
 AXJ – jugal axalare
 AXJA – anterior jugal axalare
 AXJP – posterior jugal axalare
 AXM – medial axalare
 AXMA – anterior medial axalare
 AXMP – posterior medial axalare
 AXPC – precostal axalare
 AXPCA – anterior precostal axalare
 AXPCP – posterior precostal axalare
 AXR – radial axalare
 AXRA – anterior radial axalare
 AXRP – posterior radial axalare
 AXSc – subcostal axalare
 AXScA – anterior subcostal axalare
 AXScP – posterior subcostal axalare
 B – basivenale
 BA – anal basivenale
 BAA – anterior anal basivenale
 BAP – posterior anal basivenale
 BAS – basalare
 BC – costal basivenale
 BCA – anterior costal basivenale
 BCP – posterior costal basivenale
 BCu – cubital basivenale
 BCuA – anterior cubital basivenale
 BCuP – posterior cubital basivenale
 BJ – jugal basivenale
 BJA – anterior jugal basivenale
 BJP – posterior jugal basivenale
 BM – medial basivenale
 BMA – anterior medial basivenale
 BMP – posterior medial basivenale
 BPC – precostal basivenale
 BPCA – anterior precostal basivenale
 BPCP – posterior precostal basivenale
 br – proximal sub-section of proximal arch of
 BR
 BR – radial basivenale
 BRA – anterior radial basivenale
 BRP – posterior radial basivenale
 BSc – subcostal basivenale
 BScA – anterior subcostal basivenale
 BScP – posterior subcostal basivenale
 C – costal vein
 CA – anterior costal vein
 CP – posterior costal vein
 Cu – cubital vein
 CuA – anterior cubital vein
 CuP – posterior cubital vein
 d-dl – dorso-distal lobe
 d-dr – dorso-distal ridge
 d-nr – distal neck ridge
 d-pl – dorso-proximal lobe
 d-pr – dorso-proximal ridge
 d-tr – distal tail ridge
 F – fulcalare
 FA – anal fulcalare
 FAA – anterior anal fulcalare
 FAP – posterior anal fulcalare
 FC – costal fulcalare
 FCA – anterior costal fulcalare
 FCP – posterior costal fulcalare
 FCu – cubital fulcalare
 FCuA – anterior cubital fulcalare
 FCuP – posterior cubital fulcalare
 FJ – jugal fulcalare
 FJA – anterior jugal fulcalare
 FJP – posterior jugal fulcalare
 FM – medial fulcalare

- FM1 – the distal portion of FM which articulates with BMA
FM2 – the proximal portion of FM which articulates with BMP
FMA – anterior medial fulcalare
FMP – posterior medial fulcalare
FPC – precostal fulcalare
FPCA – anterior precostal fulcalare
FPCP – posterior precostal fulcalare
FR – radial fulcalare
FRA – anterior radial fulcalare
FRP – posterior radial fulcalare
FSc – subcostal fulcalare
FSc1 – ventral tooth of 1Ax head
FSc2 – dorsal tooth of 1Ax head
FScA – anterior subcostal fulcalare
FScP – posterior subcostal fulcalare
HP – humeral plate
J – jugal vein
JA – anterior jugal vein
JP – posterior jugal vein
M – medial vein
MA – anterior medial vein
MED – medial plate
mg – medial groove
MP – posterior medial vein
p-nr – proximal neck ridge
p-tr – proximal tail ridge
PC – precostal vein
PCA – anterior precostal vein
PCP – posterior precostal vein
post-tr – posterior tail ridge
PR – proxalare
PRA – anal proxalare
PRAA – anterior anal proxalare
PRAP – posterior anal proxalare
PRC – costal proxalare
PRCA – anterior costal proxalare
PRCP – posterior costal proxalare
PRCu – cubital proxalare
PRCuA – anterior cubital proxalare
PRCuP – posterior cubital proxalare
PRJ – jugal proxalare
PRJA – anterior jugal proxalare
PRJP – posterior jugal proxalare
PRM – medial proxalare
PRMA – anterior medial proxalare
PRMP – posterior medial proxalare
PRPC – precostal proxalare
PRPCA – anterior medial proxalare
PRPCP – posterior medial proxalare
PRR – radial proxalare
PRRA – anterior radial proxalare
PRRP – posterior radial proxalare
PRSc – subcostal proxalare
PRScA – anterior subcostal proxalare
PRScP – posterior subcostal proxalare
PWP – posterior wing process junction
R – radial vein
RA – anterior radial vein
RP – posterior radial vein
Sc – subcostal vein
ScA – anterior subcostal vein
ScP – posterior subcostal vein
STAP – subalare tendon attachment point
v-dl – ventro-distal lobe
v-dr – ventro-distal ridge
v-pl – ventro-proximal lobe
v-pr – ventro-proximal ridge

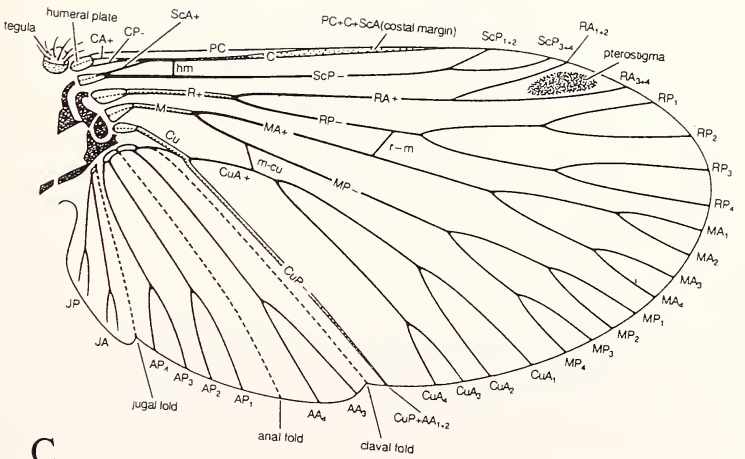
Authors' address:

D.J. Browne and C.H. Scholtz, Department of Entomology, University of Pretoria, Pretoria 0002, South Africa.

Figs.1-2: **1:** Scheme of ancestral Pterygote wing articulation, wing base and wing venation; the ancestral band of unfused sclerites (P=proxalare, AX=axalare, F=fulcalare, B=basivenale) gave rise to all Recent types of wing articulation and wing base (from Kukalová-Peck 1983). – **2:** Wing articulation and wing base of Neoptera (diagrammatic): a, showing the three axillary sclerites and median plate and their associations with basivenalia; b, showing homologies with the original band sclerites illustrated in Figure 1; c, showing the position of the axillary sclerites in relation to the wing venation (a from Lawrence et al. 1991; b from Kukalová-Peck 1991; c from Kukalová-Peck & Lawrence 1993).



2



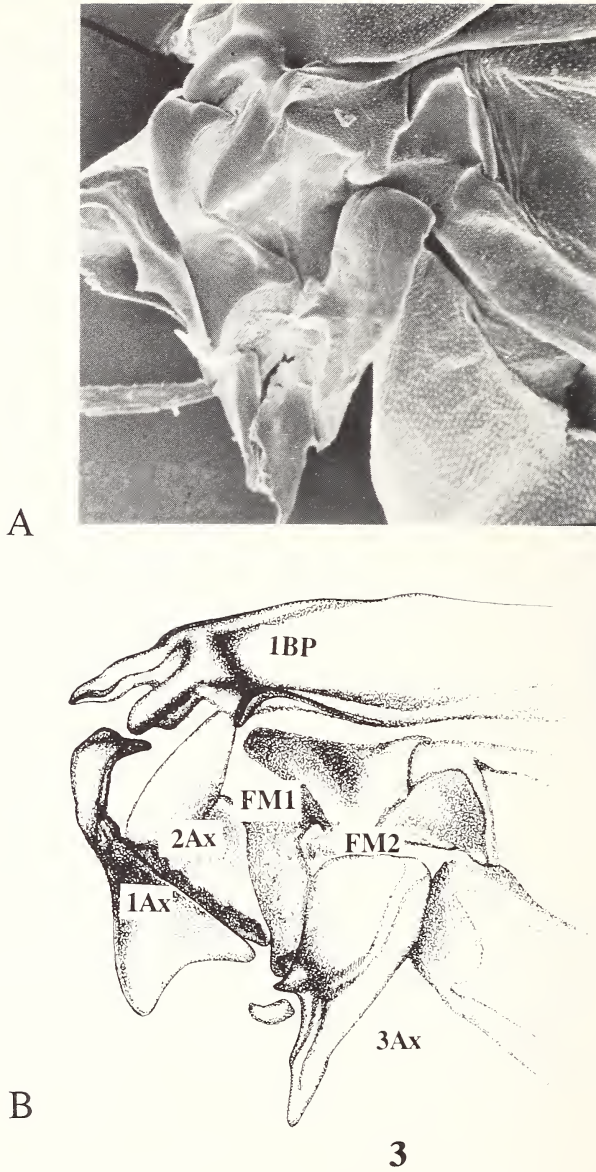
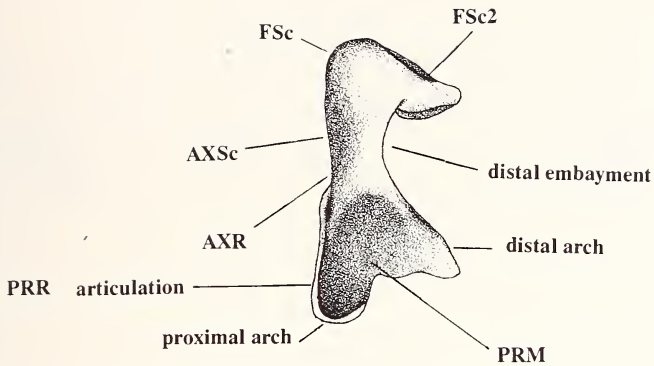
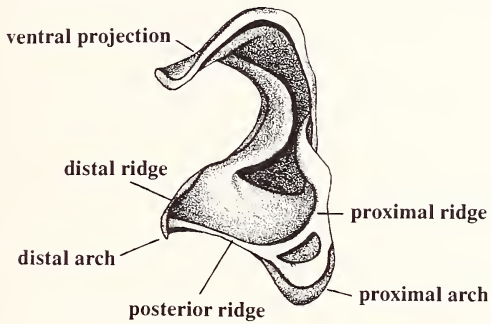


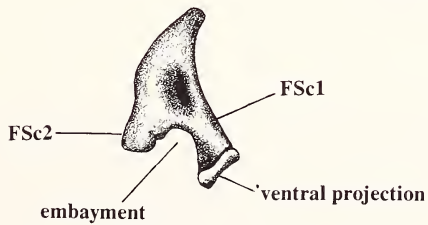
Fig.3: Hind wing articulation and wing base of *Glaresis walzlae* (Glaresidae): a, scanning electron micrograph (1000x); b, showing relative positions of axillaries and basal plates, first axillary (1Ax), second axillary (2Ax), FR, AXM, the position of the 2Ax proximal lobe beneath 1Ax (stippled region on the distal arch of the 1Ax tail), third axillary (3Ax), detached AXCu fragment of 3Ax, first basal plate (1BP), HP, PC+C, BScA, ScA, BRP, second basal plate (2BP), BMA, BMP, MP, BMP-BCuA brace, BCuA, BCuP, and median plate (MED=FM1+FM2) (slightly diagrammatic).



4



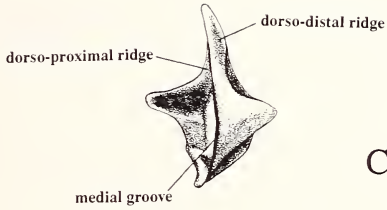
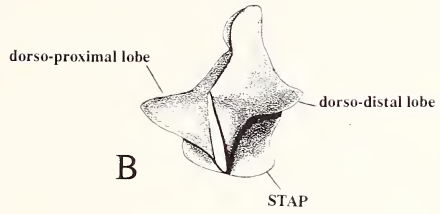
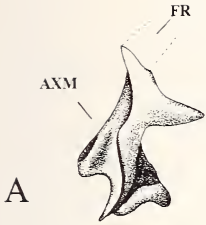
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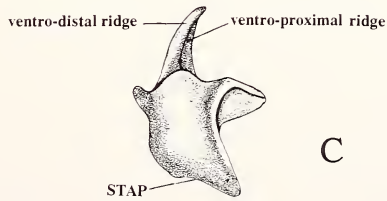
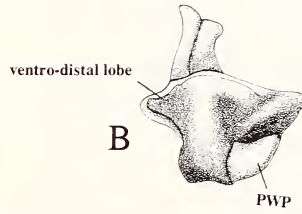
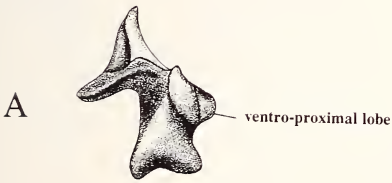
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Figs.4-6: First axillary of Rutelinae (Scarabaeidae) showing the position of the original band sclerites: **4:** dorsal, showing FSc1, FSc2, AXSc, AXR, PRM, head, neck, distal embayment, tail, PRR articulation, proximal arch, distal arch and posterior margin of the tail. – **5:** ventral, showing ventral projection, distal neck ridge, proximal neck ridge, distal tail ridge, distal arch, posterior tail ridge, posterior margin of the tail, proximal arch, and proximal tail ridge. – **6:** anterior, showing FSc1, FSc2, ventral projection and embayment. Not to scale. Originals Browne (1993).

Figs.7-8: Second axillary of Scarabaeoidea: **7**: dorsal: a. Bolboceratidae showing the position of FR and AXM; b. Scarabaeinae (Scarabaeidae), showing dorso-proximal ridge (d-pr), dorso-distal ridge (d-dr), dorso-proximal lobe (d-pl), dorso-distal lobe (d-dl) and the part of the subalare tendon attachment point (STAP); c. Rutelinae (Scarabaeidae), showing the dorso-proximal ridge (d-pr), dorsal distal ridge (d-dr), and the apex of the dorsal distal ridge, anterior section of the dorsal distal ridge, medial section of the dorso-proximal and dorso-distal ridges, and terminus of the dorso-proximal and dorso-distal ridges, medial groove (mg) and part of the subalare tendon attachment point (STAP). – **8**: ventral: a. Bolboceratidae, showing the ventral proximal lobe (v-pl), ventro-distal lobe (v-dl), ventro-proximal ridge (v-pr), ventro-distal ridge (v-dr), posterior wing process (PWP) and the subalare tendon attachment point (STAP); b. Scarabaeinae (Scarabaeidae), showing the ventro-proximal lobe (v-pl), ventro-distal lobe (v-dl), ventro-proximal ridge (v-pr), ventro-distal ridge (v-dr), posterior wing process (PWP) and the subalare tendon attachment point (STAP); c. Rutelinae (Scarabaeidae), showing the ventro-proximal lobe (v-pl), ventro-distal lobe (v-dl), ventro-proximal ridge (v-pr), ventro-distal ridge (v-dr), posterior wing process (PWP) and subalare tendon attachment point (STAP). Not to scale. Originals Browne (1993).

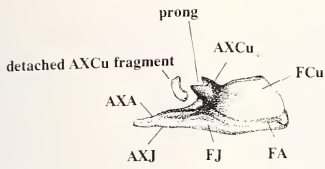


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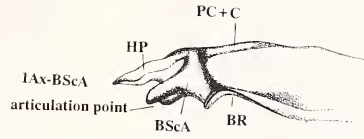


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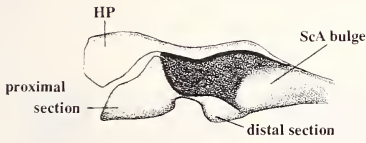
Figs.9-15: **9:** Dorso-lateral view of the third axillary of *Glaresis walzlae* (Glaresidae) showing original band sclerites and detached AXCu fragment of 3Ax. – **10:** Dorsal view of the first basal plate of *Glaresis walzlae* (Glaresidae) showing HP, PC+C, 1Ax-BScA articulation point, BScA, ScA and BRP. – **11:** Dorsal view of the first basal plate (excluding BRP) of Scarabaeinae (Scarabaeidae) showing the humeral plate (HP); the proximal and distal sections of BScA, and ScA bulge. – **12:** Anterior view of the humeral plate of Scarabaeinae (Scarabaeidae) showing the proximal, dorsal, ventral and distal margins. – **13:** Second basal plate (including BRP) of Scarabaeoidea: a, *Glaresis walzlae* (Glaresidae) showing BRP, proximal and distal arches of BRP, embayment (open), RP, brp, brp projection, BMA, BMP, BMP-BCuA brace and BCuA; b, Bolboceratidae showing BRP, embayment (closed), RP, BMA, the proximal and distal arches of BMA, BMP, MP, BMP-CuA brace, BCuA, BCuP, distal embayment and CuA. – **14:** Dorso-lateral view of the basalare of Bolboceratidae (Geotrupidae) showing the HP lobe and BScP lobe. – **15:** Dorso-lateral view of BScP of Bolboceratidae, showing BScP and ScP. Not to scale. Originals Browne (1993).



9



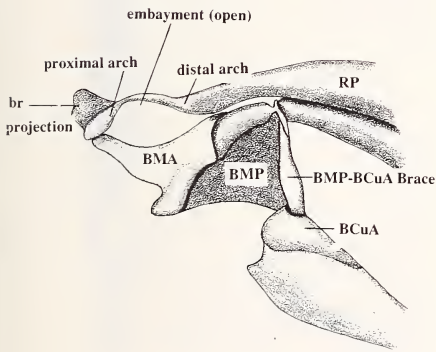
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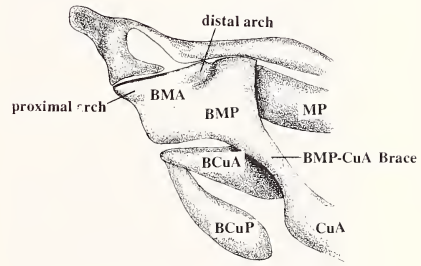
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12



A



B

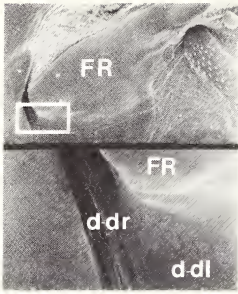
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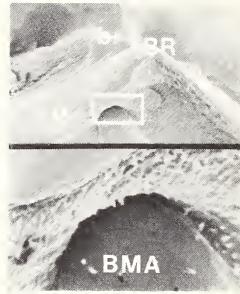
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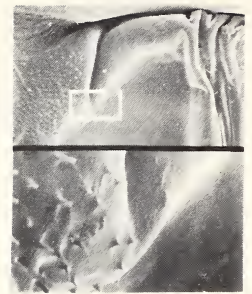
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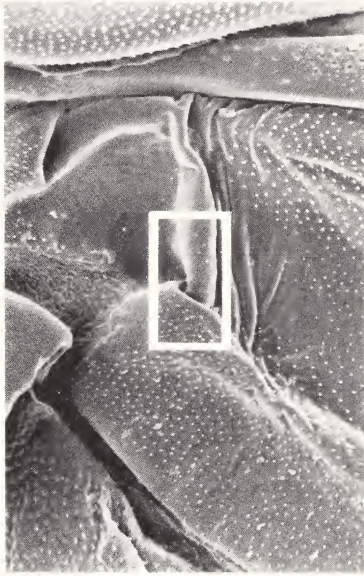
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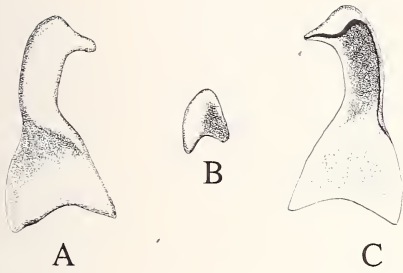


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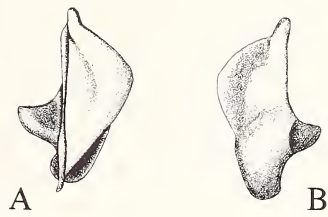


19

Figs.16-19: Scanning electron micrographs of some basal articulation structures of *Glareis walzlae* (Glaresidae). – **16**: Second axillary showing the anterior section of the distal lobe and ridge of 2Ax and FR. – **17**: First and second basal plates showing the relative positions of BRP, brp, FR, and apex of the proximal arch of BMA. – **18**: Second basal plate showing the incomplete junction between BMA and BMP. – **19**: Second basal plate showing the BMP-BCuA brace. Not to scale. Originals Browne (1993).



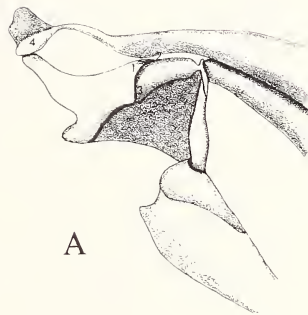
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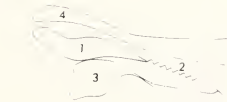
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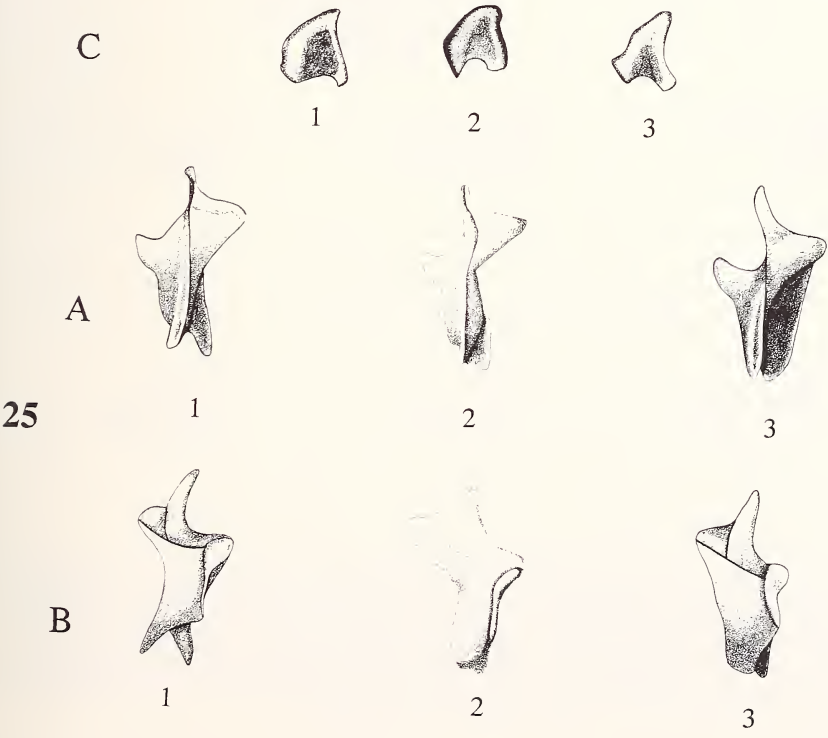
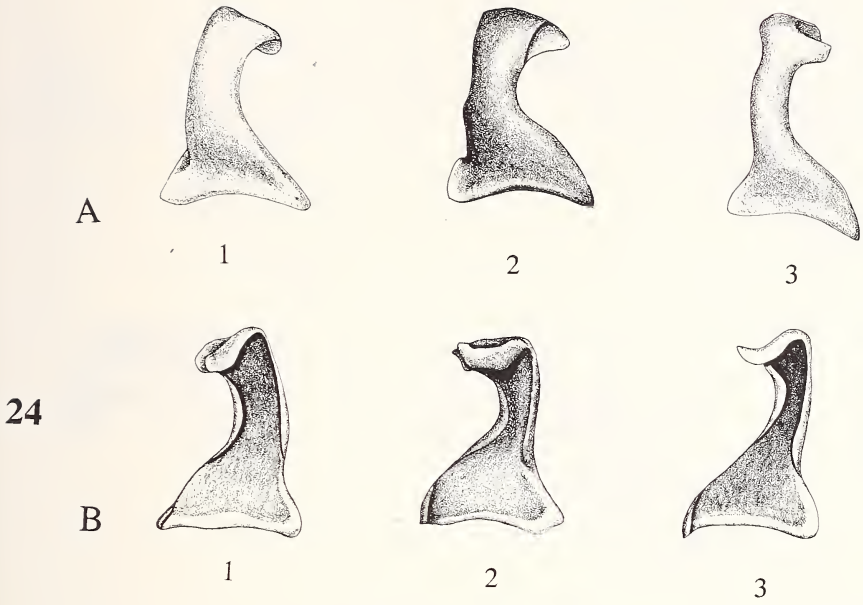
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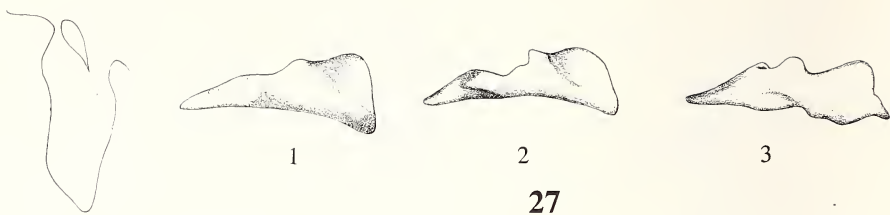
B

Figs.20-23: Hind wing articulation and wing base of *Glareis walzlae* (Glareisidae). – 20: First axillary: a, dorsal; b, ventral; c, anterior. – 21: Second axillary: a, dorsal; b, ventral. – 22: Dorsolateral view of the third axillary. – 23: Second basal plate (including BR); a, dorsal; b, ventral showing RA (serrated line); 1, BMA, 2, RA, 3, BMP, 4, BR. Not to scale. Originals Browne (1993).

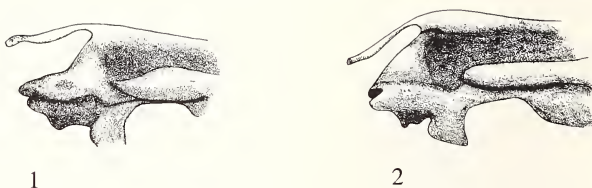
Figs.24-25: Hind wing articulation and wing base of Passalidae. – **24**: First axillary: a, dorsal; b, ventral; c, anterior: 1, *Veturius tuberculifrons* (Proculini: Passalinae); 2, *Passalus punctatostratus* (Passalini: Passalinae); 3, *Ceracupes arrowi* (Aulacoeylinae). – **25**: Second axillary: a, dorsal; b, ventral: 1, *Oileus sargi* (Proculini: Passalinae); 2, *Passalus punctatostratus* (Passalini: Passalinae); 3, *Ceracupes arrowi* (Aulacoeylinae). Not to scale. Originals Browne (1993).



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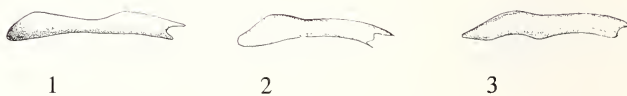
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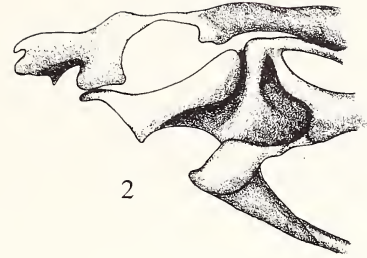
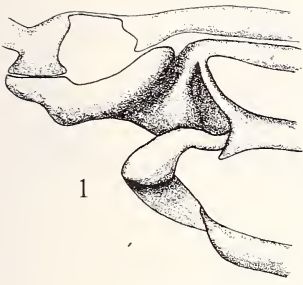
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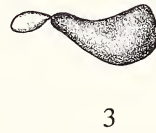
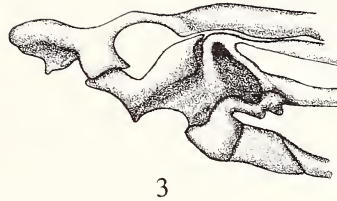
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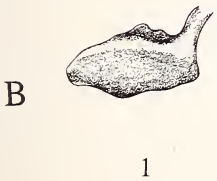
Figs.26-28: Hind wing articulation and wing base of Passalidae. – 26: Outline of the median plate of *Ceracupes arrowi* (Aulacocyclinae). – 27: Dorso-lateral view of the third axillary of Passalidae: 1, *Oileus sargi* (Proculini: Passalinae); 2, *Aceraius grandis hirsutus* (Passalini: Passalinae); 3, *Aulacocyclus errans* (Aulacocyclinae). – 28: First basal plate: a, dorsal; b, anterior: 1, *Odontotaenius disjunctus* (Proculini: Passalinae); 2, *Passalus punctatostriatus* (Passalini: Passalinae); 3, *Aulacocyclus errans* (Aulacocyclinae). Not to scale. Originals Browne (1993).



29

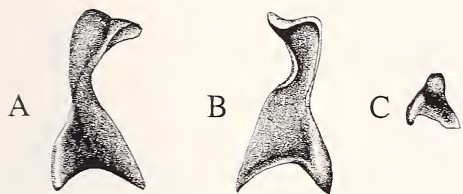


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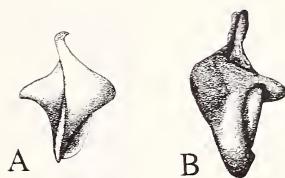


Figs.29-30: Hind wing articulation and wing base of Passalidae. – 29: Dorsal view of the second basal plate (including BR): 1, *Odontotaenius disjunctus* (Proculini: Passalinae); 2, *Passalus punctatostrigatus* (Passalini: Passalinae); 3, *Aulacocyclus errans* (Aulacocyclusinae). – 30: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP: 1, *Odontotaenius disjunctus* (Proculini: Passalinae); 2, *Aceraius grandis hirsutus* (Passalini: Passalinae); 3, *Aulacocyclus errans* (Aulacocyclusinae). Not to scale. Originals Browne (1993).

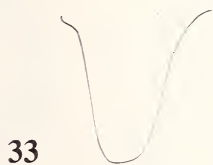
Figs.31-37: Hind wing articulation and wing base of Diphyllostomatidae. – **31**: First axillary: a, dorsal; b, ventral; c, anterior. – **32**: Second axillary: a, dorsal; b, ventral. – **33**: Outline of the median plate. – **34**: Outline of the dorso-lateral view of the third axillary. – **35**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **36**: Dorsal view of the second basal plate (including BR). – **37**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).



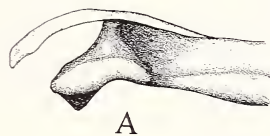
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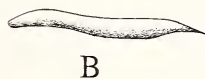
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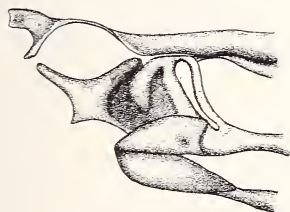
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B



34



36



A



B

37



1



2



3



4

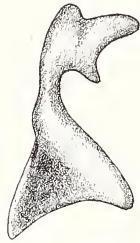


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38 A



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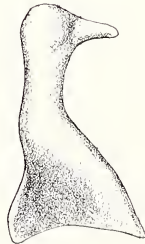
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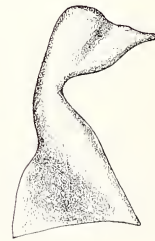
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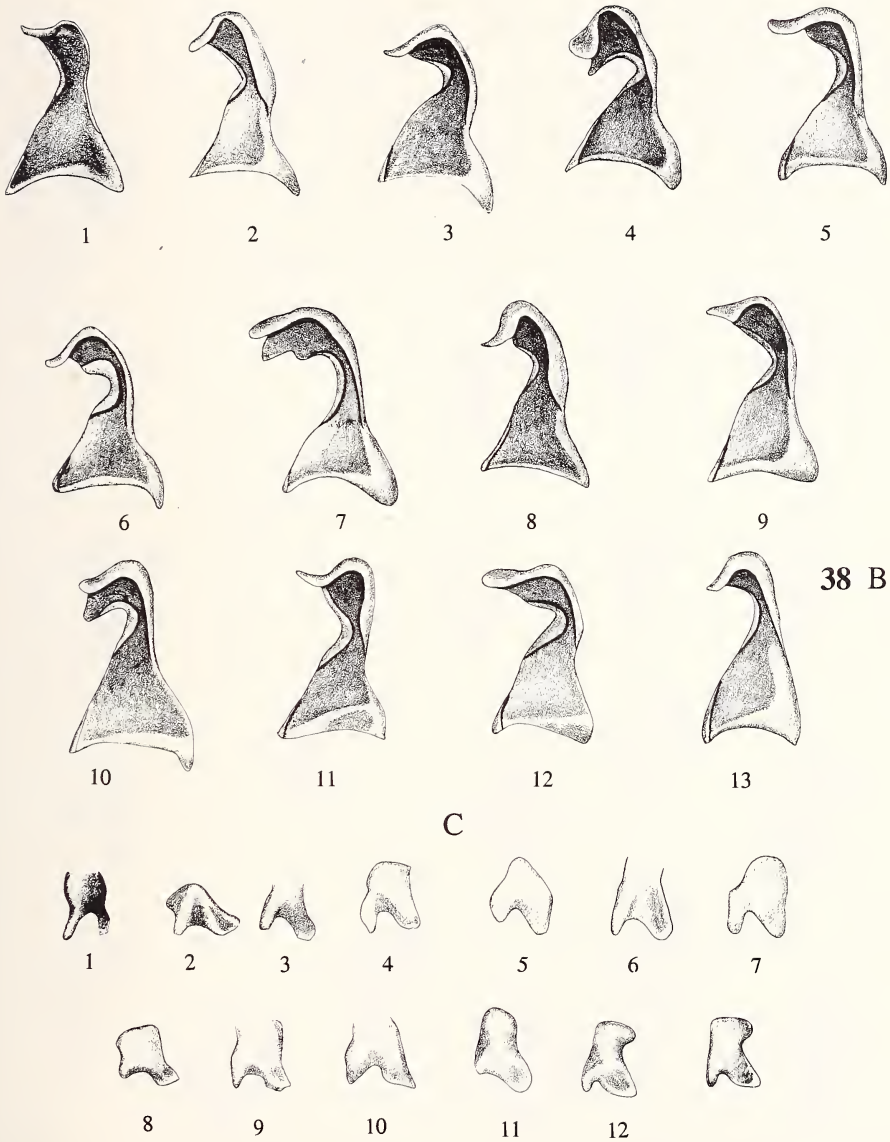


Fig.38: Hind wing articulation and wing base of Lucanidae. First axillary: a, dorsal; b, ventral; c, anterior 1, *Aesalus asiaticus* (Aesalinae); 2, *Lamprima aurata* (Lampriminae); 3, *Platycerus* spec. (Platycerini: Lucaninae); 4, *Aegus formosa* (Dorcini: Lucaninae); 5, *Neolucanus castanopterus* (Lucanini: Lucaninae); 6, *Nigidius bubalus* (Figulini: Lucaninae); 7, *Prosopocoilus savagei* (Cladognathini: Lucaninae); 8, *Chiasognathus* spec. (Chiasognathini: Lucaninae); 9, *Nicagus japonicus* (Nicaginae); 10, *Penichrolucanus leveri* (Penichrolucaninae); 11, *Sinodendron cylindricum* (Sinodendrini: Syndesinae); 12, *Syndesus cornutus* (Syndesini: Syndesinae); 13, *Ceruchus* spec. (Ceruchini: Syndesinae); a, dorsal; b, ventral; c, anterior. Not to scale. Originals Browne (1993).

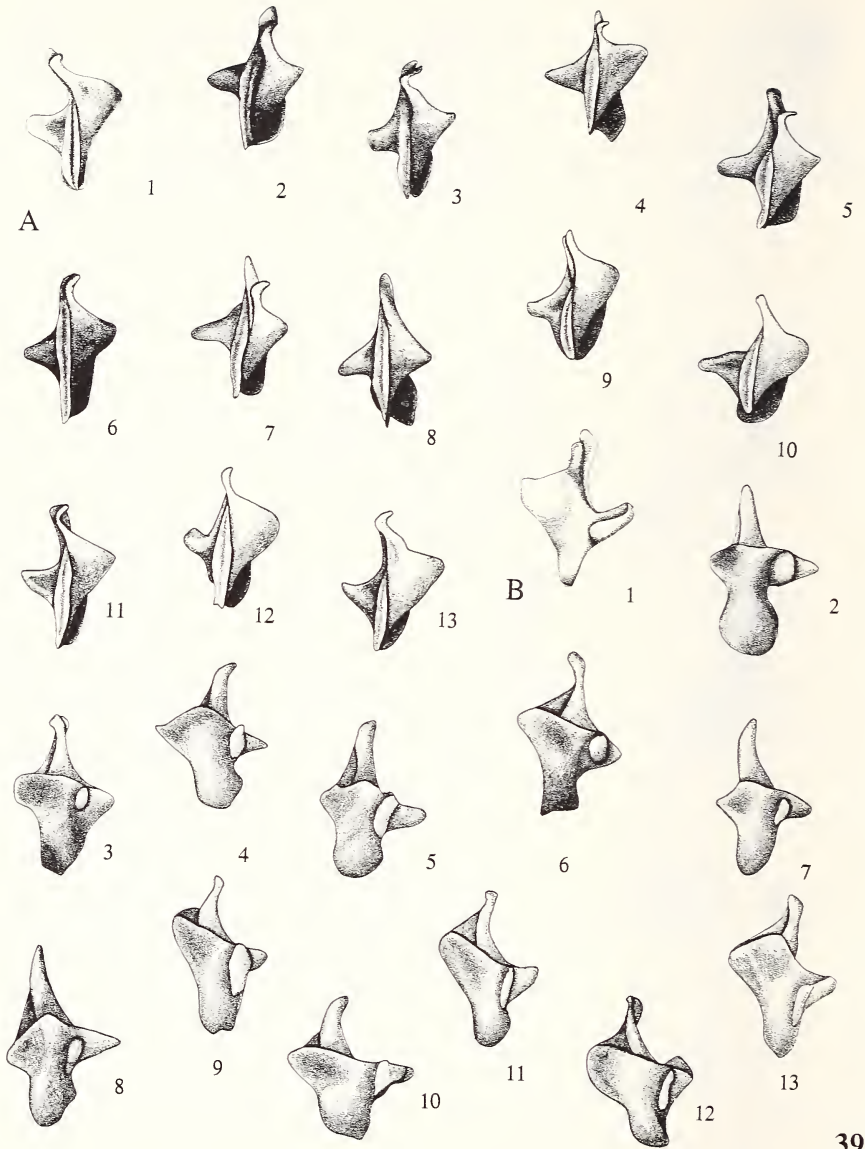
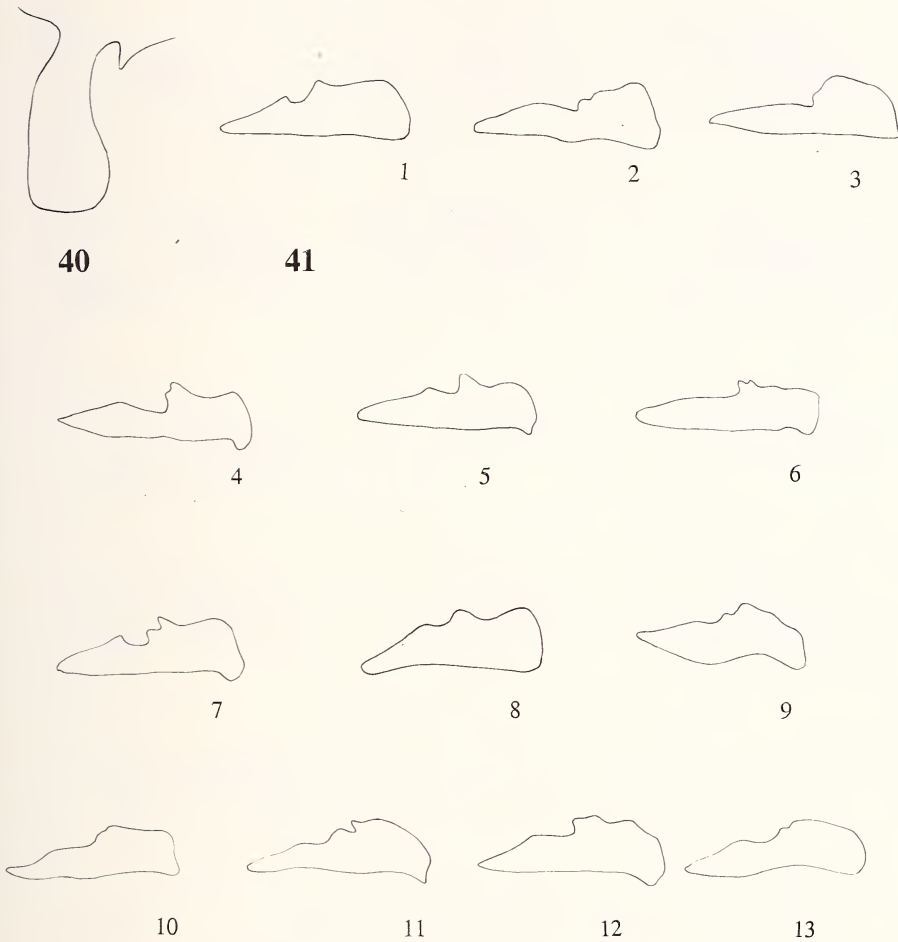
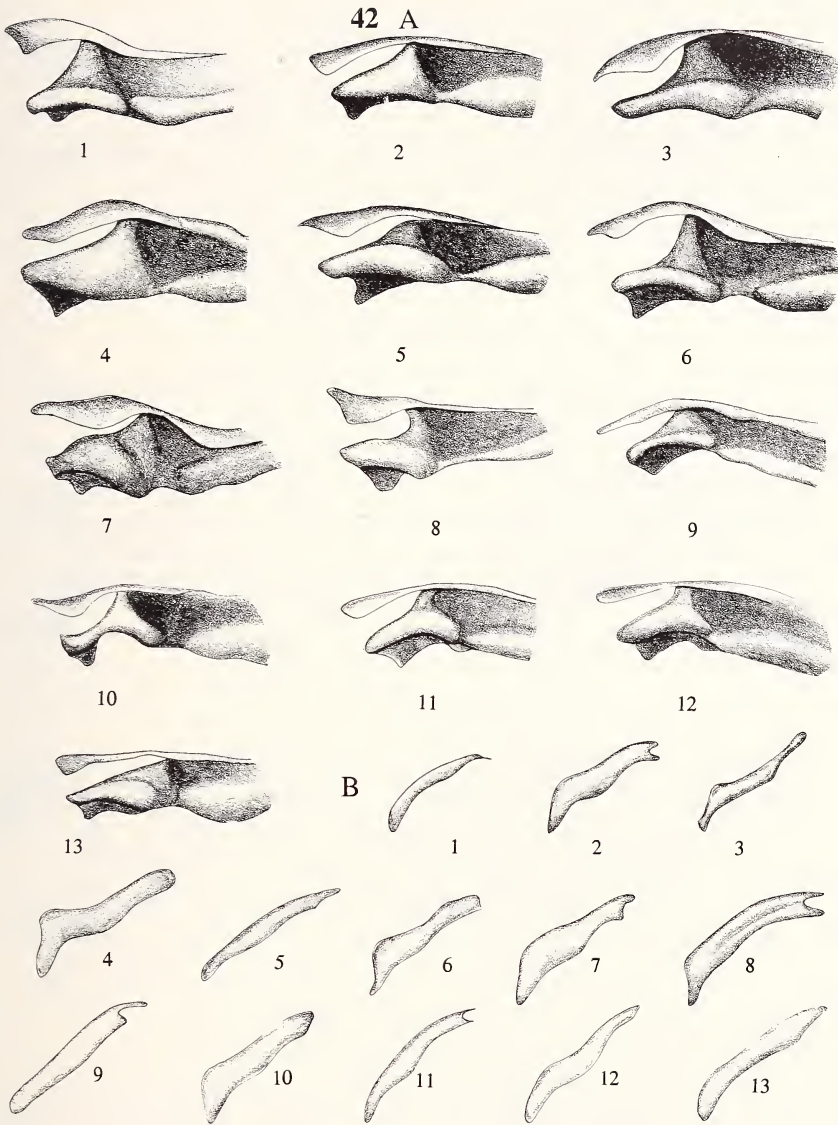


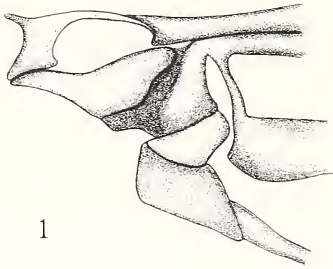
Fig.39: Hind wing articulation and wing base of Lucanidae. Second axillary: a, dorsal; b, ventral: 1, *Aesalus asiaticus* (Aesalinae); 2, *Lamprina aurata* (Lampriminae); 3, *Platycerus* spec. (Platycerini: Lucaninae); 4, *Dorcus parallelipedus* (Dorcini: Lucaninae); 5, *Neolucanus castanopterus* (Lucanini: Lucaninae); 6, *Figulus binodulus* (Figulini: Lucaninae); 7, *Prosopocoilus savagei* (Cladognathini: Lucaninae); 8, *Chiasognathus* spec. (Chiasognathini: Lucaninae); 9, *Nicagus japonicus* (Nicaginae); 10, *Penichrolucanus leverii* (Penichrolucaninae); 11, *Sinodendron cylindricum* (Sinodendrini: Syndesinae); 12, *Syndesus cornutus* (Syndesini: Syndesinae); 13, *Ceruchus* spec. (Ceruchini: Syndesinae). Not to scale. Originals Browne (1993).



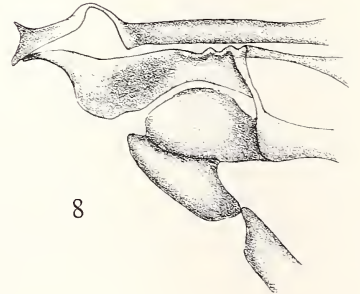
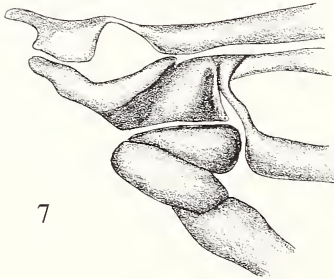
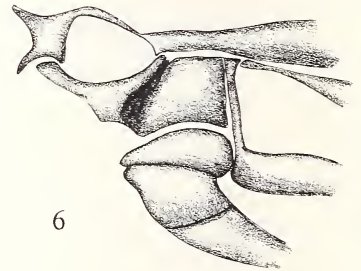
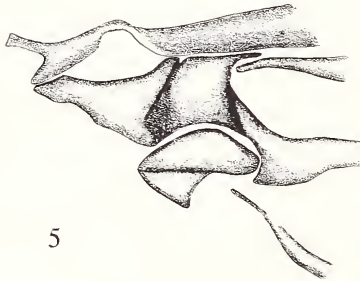
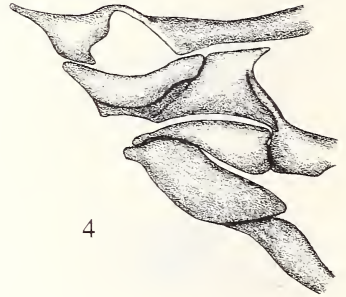
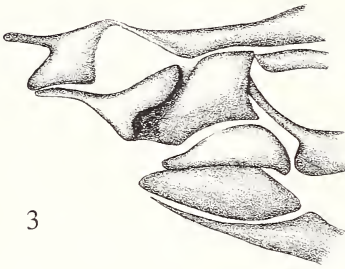
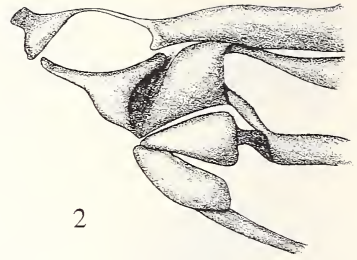
Figs.40-41: Hind wing articulation and wing base of Lucanidae. – **40**: Outline of the median plate.
 – **41**: Outline of the dorso-lateral view of the third axillary: 1, *Aesalus asiaticus* (Aesalinae); 2, *Lamprima latreillei* (Lampriminae); 3, *Platycerus* spec. (Platycerini: Lucaninae); 4, *Aegus formosa* (Dorcini: Lucaninae); 5, *Neolucanus castanopterus* (Lucanini: Lucaninae); 6, *Figulus binodulus* (Figulini: Lucaninae); 7, *Prosopocoilus savagei* (Cladognathini: Lucaninae); 8, *Chiasognathus* spec. (Chiasognathini: Lucaninae); 9, *Nicagus japonicus* (Nicaginae); 10, *Penichrolucanus leveri* (Penichrolucaninae); 11, *Sinodendron cylindricum* (Sinodendrini: Syndesinae); 12, *Syndesus cornutus* (Syndesini: Syndesinae); 13, *Ceruchus* spec. (Ceruchini: Syndesinae). Not to scale. Originals Browne (1993).

Fig.42: Hind wing articulation and wing base of Lucanidae. First basal plate (excluding BR): a, dorsal; b, anterior: 1, *Aesalus asiaticus* (Aesalinae); 2, *Lamprima latreillei* (Lampriminae); 3, *Platycerus* spec. (Platycerini: Lucaninae); 4, *Dorcus parallelipedus* (Dorcini: Lucaninae); 5, *Neolucanus castanopterus* (Lucanini: Lucaninae); 6, *Nigidius bubalus* (Figulini: Lucaninae); 7, *Prosopocoilus fabre* (Cladognathini: Lucaninae); 8, *Chiasognathus* spec. (Chiasognathini: Lucaninae); 9, *Nicagus japonicus* (Nicaginae); 10, *Penichrolucanus leveri* (Penichrolucaninae); 11, *Sinodendron cylindricum* (Sinodendrini: Syndesinae); 12, *Syndesus cornutus* (Syndesini: Syndesinae); 13, *Ceruchus* spec. (Ceruchini: Syndesinae). Not to scale. Originals Browne (1993).





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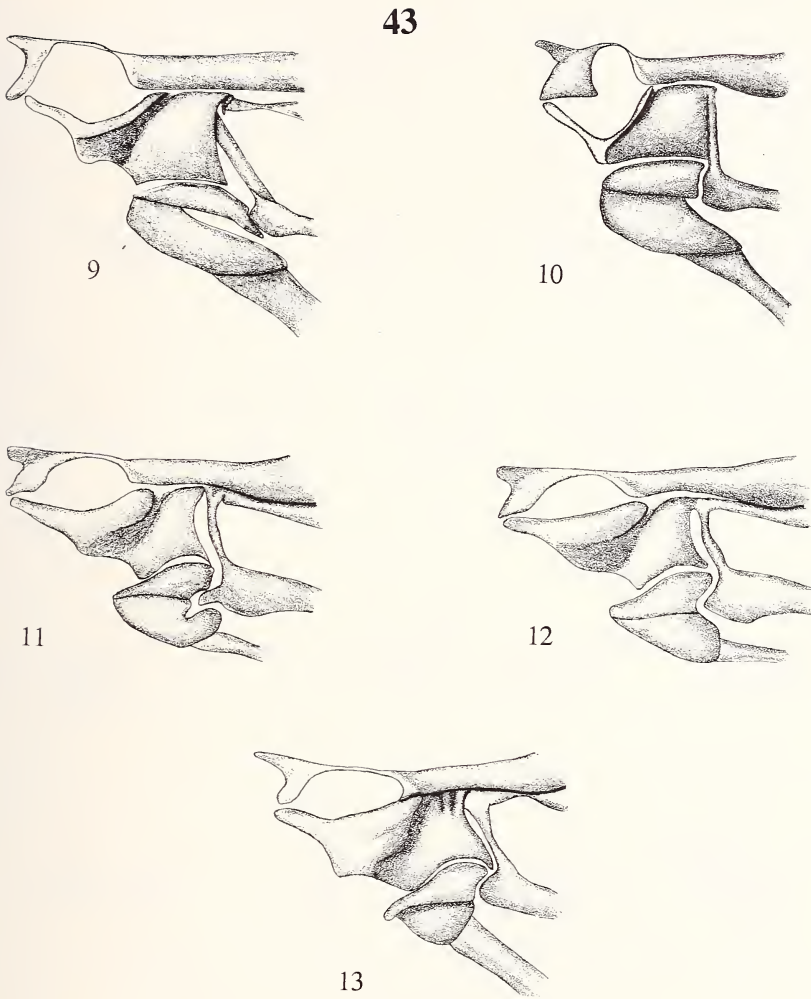
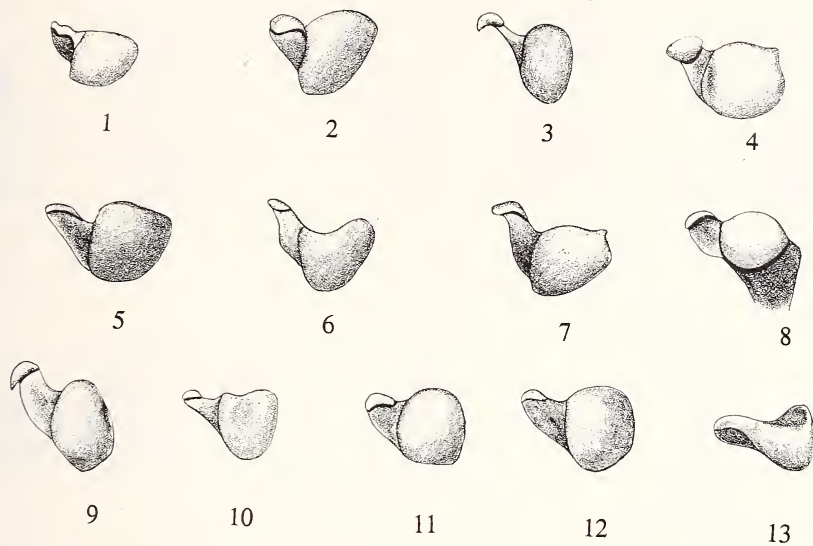


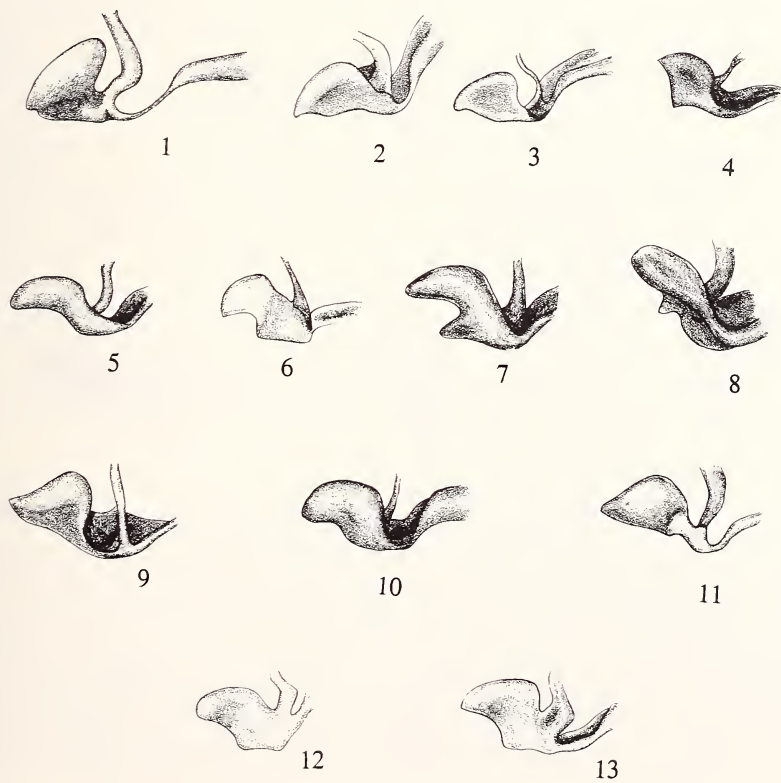
Fig.43: Hind wing articulation and wing base of Lucanidae. Dorsal view of the second basal plate (including BR): 1, *Aesalus asiaticus* (Aesalinae); 2, *Lamprima latreillei* (Lampriminae); 3, *Platycerus* spec. (Platycerini: Lucaninae); 4, *Dorcus parallelipedus* (Dorcini: Lucaninae); 5, *Neolucanus castanopterus* (Lucanini: Lucaninae); 6, *Nigidius bubalus* (Figulini: Lucaninae); 7, *Prosopocoilus fabre* (Cladognathini: Lucaninae); 8, *Chiasognathus* spec. (Chiasognathini: Lucaninae); 9, *Nicagus japonicus* (Nicaginae); 10, *Penichrolucanus leveri* (Penichrolucaninae); 11, *Sinodendron cylindricum* (Sinodendrini: Syndesinae); 12, *Syndesus cornutus* (Syndesini: Syndesinae); 13, *Ceruchus* spec. (Ceruchini: Syndesinae). Not to scale. Originals Browne (1993).

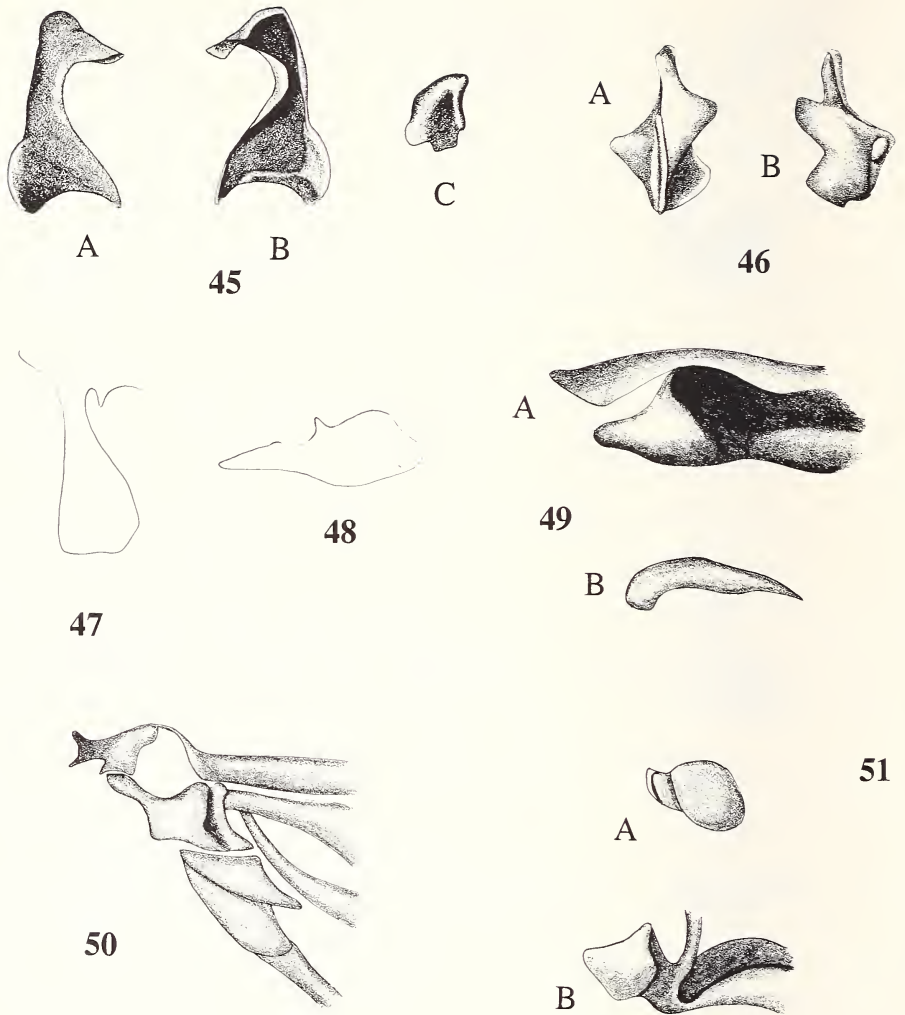
Fig.44: Hind wing articulation and wing base of Lucanidae. Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP: 1, *Aesalus asiaticus* (Aesalinae); 2, *Lamprima latreillei* (Lampriminae); 3, *Platycerus* spec. (Platycerini: Lucaninae); 4, *Dorcus parallelipedus* (Dorcini: Lucaninae); 5, *Neolucanus castanopterus* (Lucanini: Lucaninae); 6, *Nigidius bubalus* (Figulini: Lucaninae); 7, *Prosopocoilus fabre* (Cladognathini: Lucaninae); 8, *Chiasognathus* spec. (Chiasognathini: Lucaninae); 9, *Nicagus japonicus* (Nicaginae); 10, *Penichrolucanus leveri* (Penichrolucaninae); 11, *Sinodendron cylindricum* (Sinodendrini: Syndesinae); 12, *Syndesus cornutus* (Syndesini: Syndesinae); 13, *Ceruchus* spec. (Ceruchini: Syndesinae) with the basalare in the dorsal view. Not to scale. Originals Browne (1993).

A



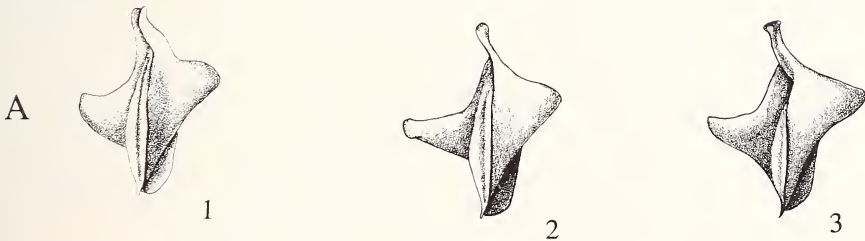
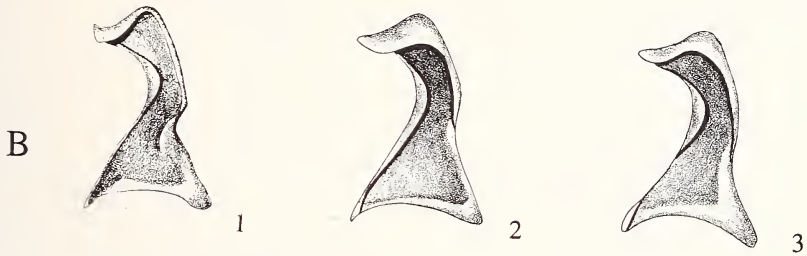
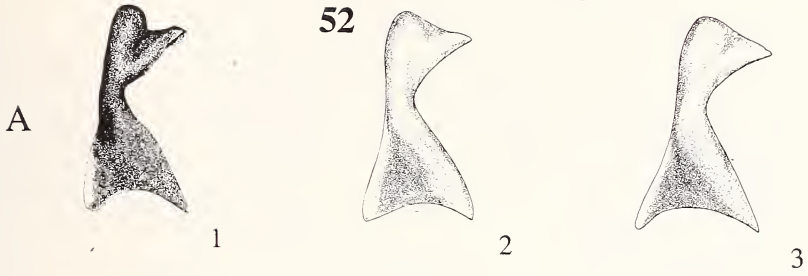
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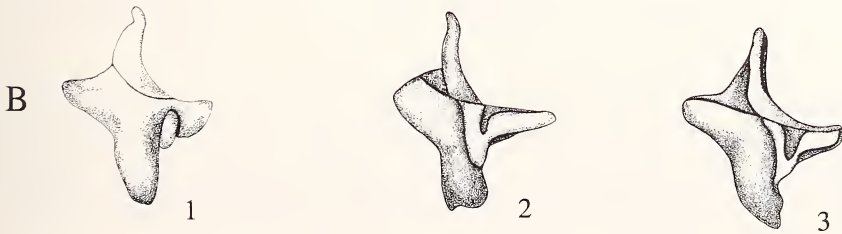


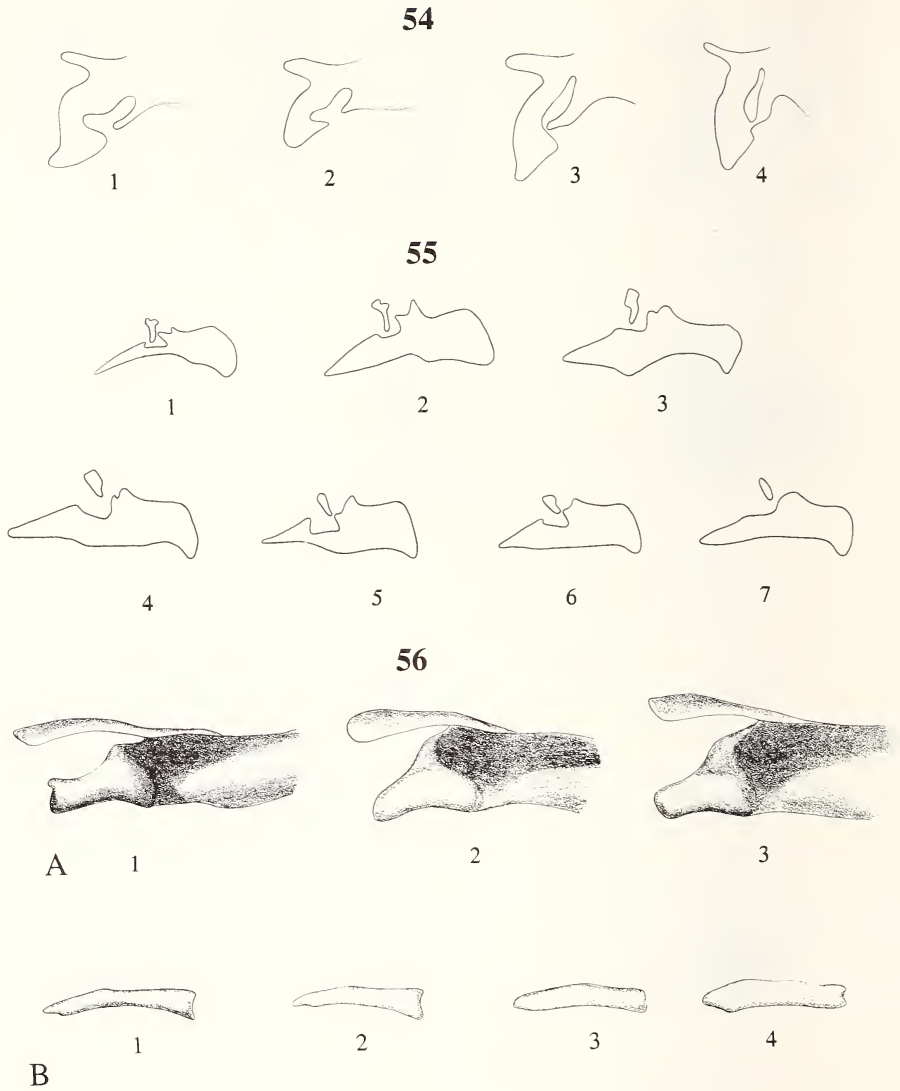
Figs.45-51: Hind wing articulation and wing base of *Lichnanthe apina* (Glaphyridae). – **45**: First axillary: a, dorsal; b, ventral; c, anterior. – **46**: Second axillary: a, dorsal; b, ventral. – **47**: Outline of the median plate. – **48**: Outline of the dorso-lateral view of the third axillary. – **49**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **50**: Dorsal view of the second basal plate (including BR). – **51**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).

Figs.52-53: Hind wing articulation and wing base of Trogidae. – **52**: First axillary: a, dorsal; b, ventral; c, anterior: 1, *Trox montanus*; 2, *Polynoncus longitarsus*; 3, *Omorgus villosus*. – **53**: Second axillary: a, dorsal; b, ventral; 1, *Trox montanus*; 2, *Polynoncus longitarsus*; 3, *Omorgus villosus*. Not to scale. Originals Browne (1993).



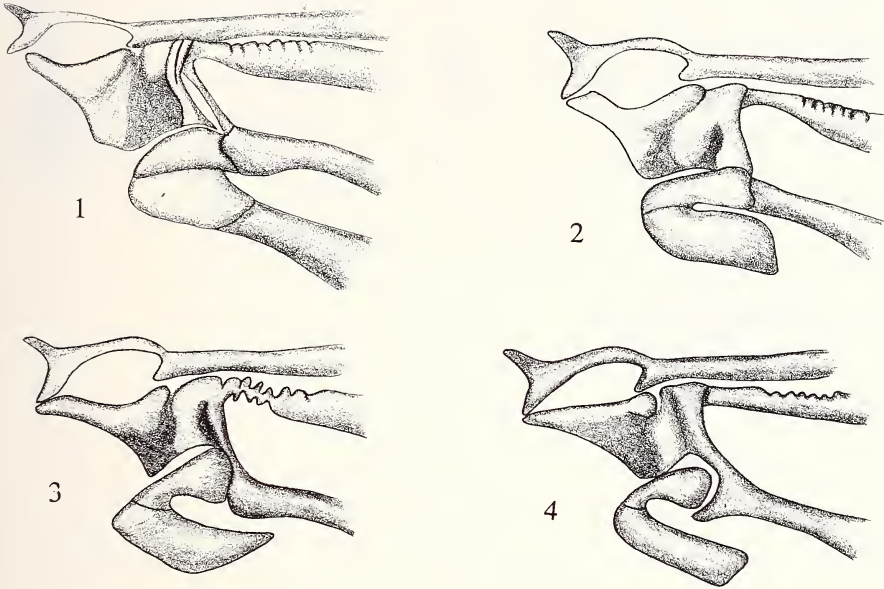
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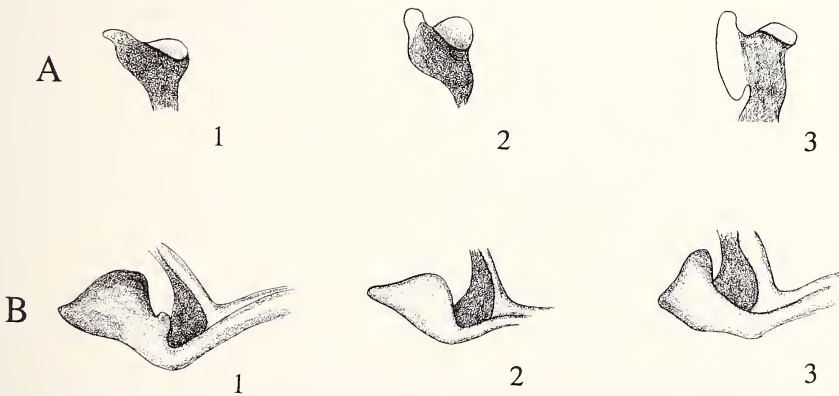


Figs.54-56: Hind wing articulation and wing base of Trogidae. – **54**: Outline of the median plate: 1, *Trox plicatus*; 2, *Trox sulcatus*; 3, *Polynoncus longitarsus*; 4, *Omorgus quadridens*. – **55**: Outline of the dorso-lateral view of the third axillary: 1, *Trox plicatus*; 2, *Trox luridus*; 3, *Polynoncus gemmingeri*; 4, *Omorgus euclensis*; 5, *Omorgus suberosus*; 6, *Omorgus squalidus*; 7, *Omorgus (Haroldomorgus) batesi*. – **56**: First basal plate (excluding BR): a, dorsal; b, anterior: 1, *Trox plicatus*; 2, *Trox sulcatus*; 3, *Polynoncus longitarsus*. Not to scale. Originals Browne (1993).

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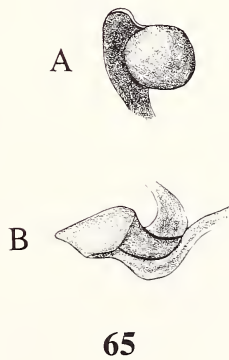
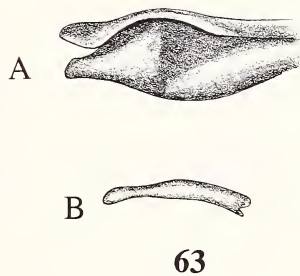
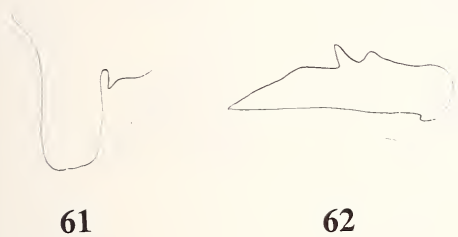
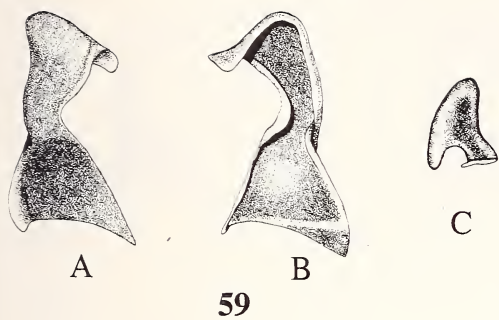


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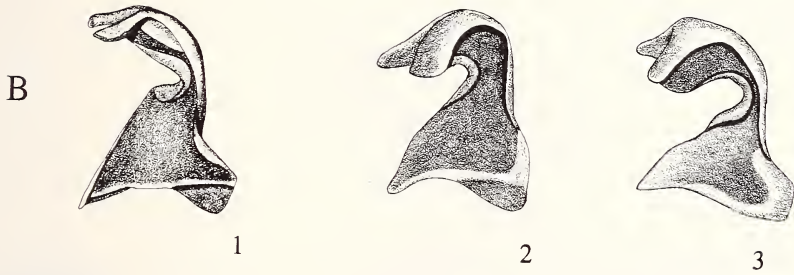
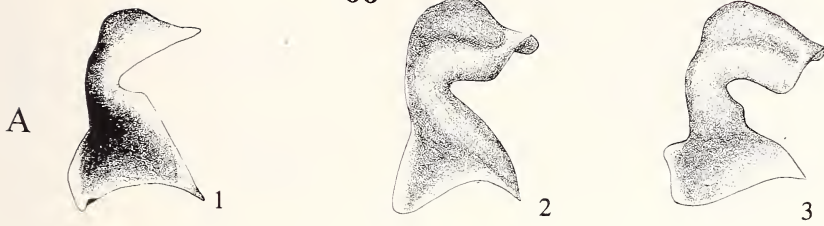
Figs.57-58: Hind wing articulation and wing base of Trogidae. – 57: Dorsal view of the second basal plate (including BR): 1, *Trox plicatus*; 2, *Trox sulcatus*; 3, *Polynoncus longitarsus*; 4, *Omorgus quadridens*. – 58: Lateral view of the basalare and BScP: a, basalare; b, BScP: 1, *Trox montanus*; 2, *Polynoncus longitarsus*; 3, *Omorgus squalidus*. Not to scale. Originals Browne (1993).

Figs.59-65: Hind wing articulation and wing base of *Pleocoma linsleyi* (Pleocomidae). – **59**: First axillary: a, dorsal; b, ventral; c, anterior. – **60**: Second axillary: a, dorsal; b, ventral. – **61**: Outline of the median plate. – **62**: Outline of the dorso-lateral view of the third axillary. – **63**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **64**: Dorsal view of the second basal plate (including BR). – **65**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).

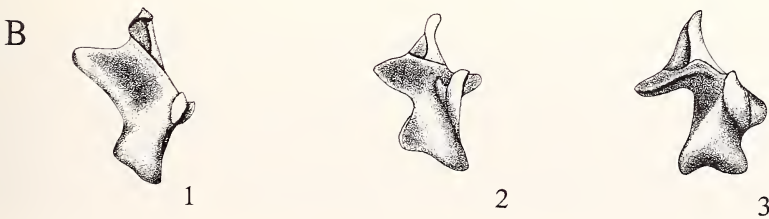
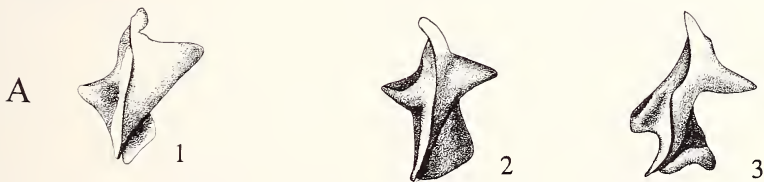


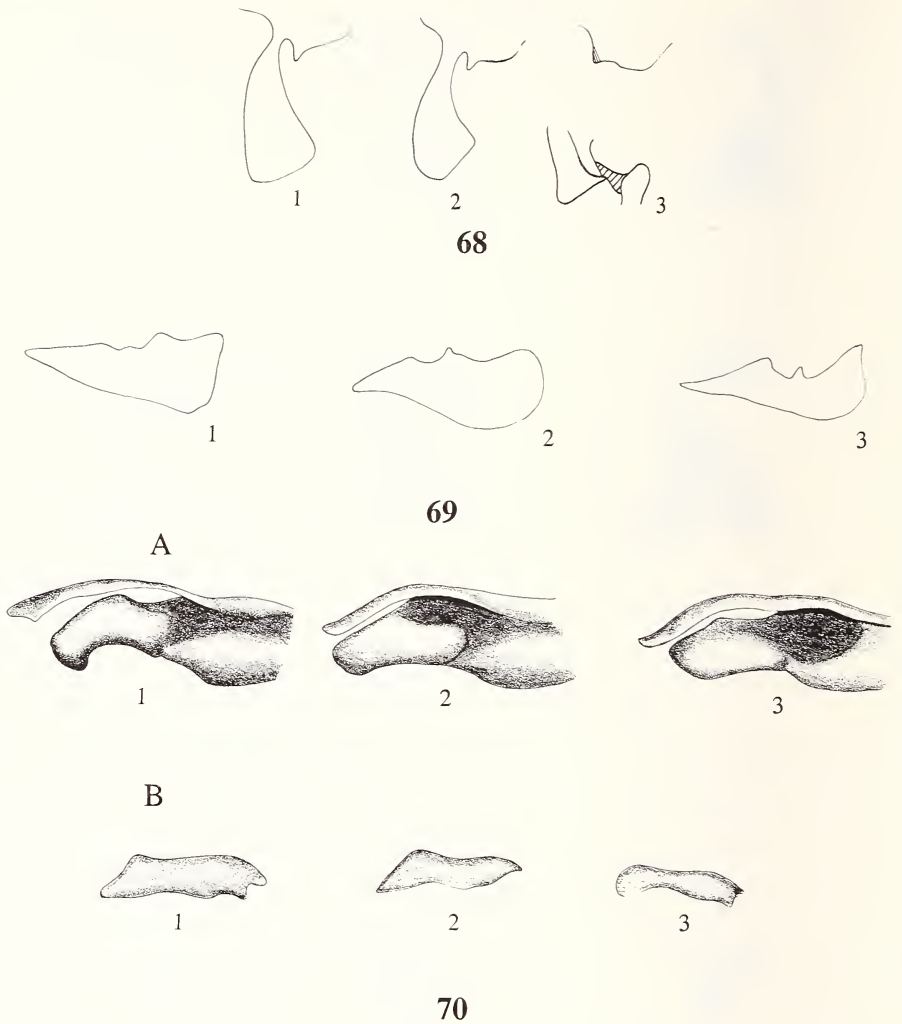
Figs.66-67: Hind wing articulation and wing base of Bolboceratidae. – **66**: First axillary: a, dorsal; b, ventral; c, anterior: 1, *Eucanthus felschei* (Bolboceratini); 2, *Bolborhinum binasutum* (Bolboceratini); 3, *Neoathyreus panamaensis* (Athyreini). – **67**: Second axillary: a, dorsal; b, ventral: 1, *Eucanthus felschei* (Bolboceratini); 2, *Bolborhinum binasutum* (Bolboceratini); 3, *Neoathyreus panamaensis* (Athyreini). Not to scale. Originals Browne (1993).

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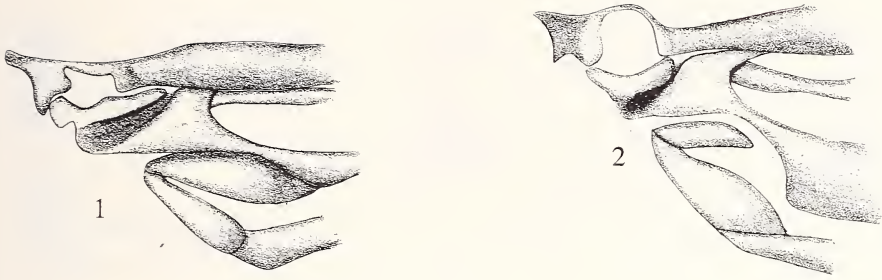


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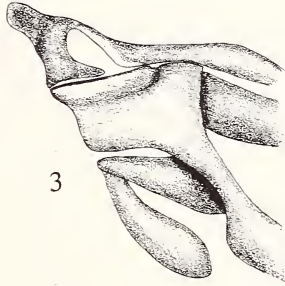




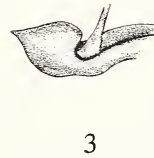
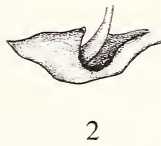
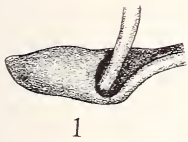
Figs.68-70: Hind wing articulation and wing base of Bolboceratidae. – **68**: Outline of the median plate: 1, *Eucanthus felschei* (Bolboceratini); 2, *Bolborhinum binasutum* (Bolboceratini); 3, *Neoathyreus panamaensis* (Athyreini) showing the relative positions of 1Ax+2Ax, the anterior and posterior remnants of MED (shaded areas) and 3Ax. – **69**: Outline of the dorso-lateral view of the third axillary: 1, *Eucanthus subtropicus* (Bolboceratini); 2, *Bolborhinum binasutum* (Bolboceratini); 3, *Neoathyreus panamaensis* (Athyreini). – **70**: First basal plate (excluding BR) of Bolboceratidae: a, dorsal; b, anterior: 1, *Eucanthus felschei* (Bolboceratini); 2, *Bolborhinum binasutum* (Bolboceratini); 3, *Neoathyreus panamaensis* (Athyreini). Not to scale. Originals Browne (1993).



71



A

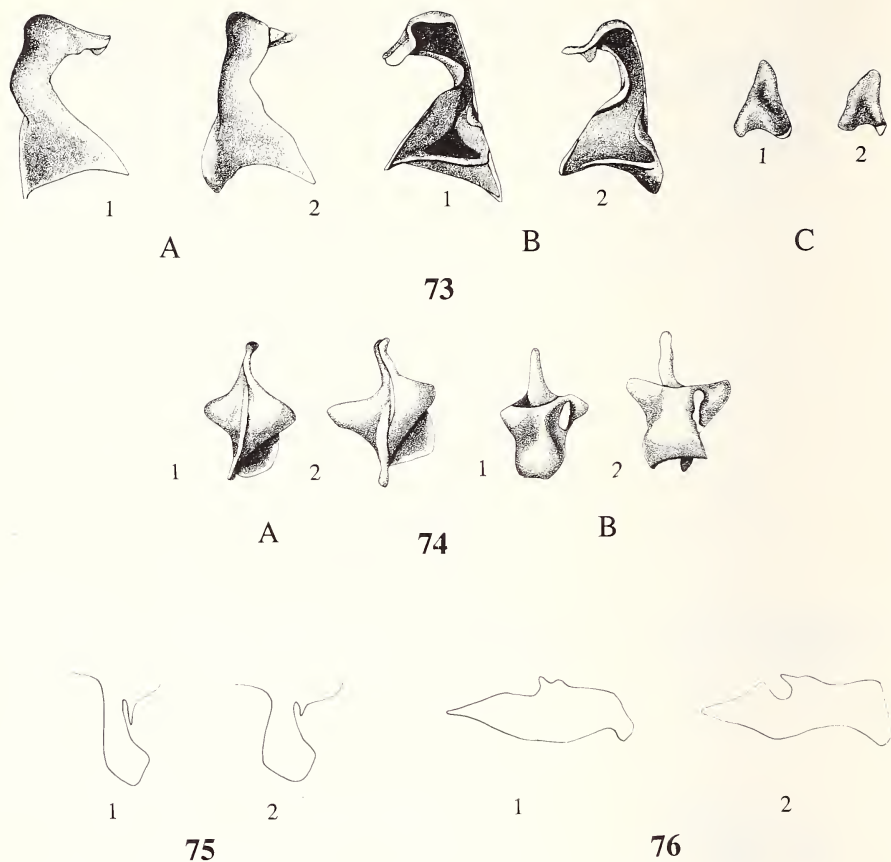


B



72

Figs.71-72: Hind wing articulation and wing base of Bolboceratidae. – 71: Dorsal view of the second basal plate (including BR): 1, *Eucanthus felschei* (Bolboceratini); 2, *Bolborhinum binasutum* (Bolboceratini); 3, *Neoathyreus panamaensis* (Athyreini). – 72: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP: 1, *Eucanthus felschei* (Bolboceratini); 2, *Bolborhinum binasutum* (Bolboceratini); 3, *Neoathyreus panamaensis* (Athyreini). Not to scale. Originals Browne (1993).



Figs.73-76: Hind wing articulation and wing base of Geotrupidae. – **73:** First axillary: a, dorsal; b, ventral; c, anterior: 1, *Cnemotrupes splendidus* (Geotrupinae: Geotrupidae); 2, *Frickius* spec. (Taurocerastinae: Geotrupidae). – **74:** Second axillary: a, dorsal; b, ventral: 1, *Cnemotrupes splendidus* (Geotrupinae: Geotrupidae); 2, *Frickius* spec. (Taurocerastinae: Geotrupidae). – **75:** Outline of the median plate: 1, *Cnemotrupes splendidus* (Geotrupinae: Geotrupidae); 2, *Frickius* spec. (Taurocerastinae: Geotrupidae). – **76:** Outline of the dorso-lateral view of the third axillary: 1, *Cnemotrupes splendidus* (Geotrupinae: Geotrupidae); 2, *Frickius* spec. (Taurocerastinae: Geotrupidae). Not to scale. Originals Browne (1993)



1



2

A



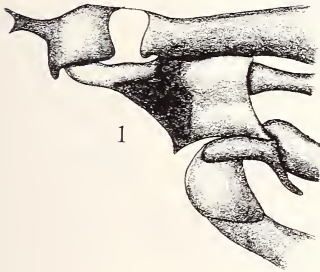
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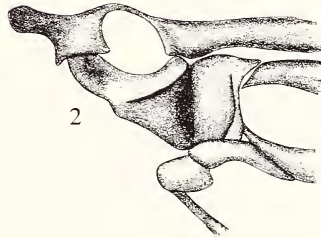
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1



2

78



1



2

A



1

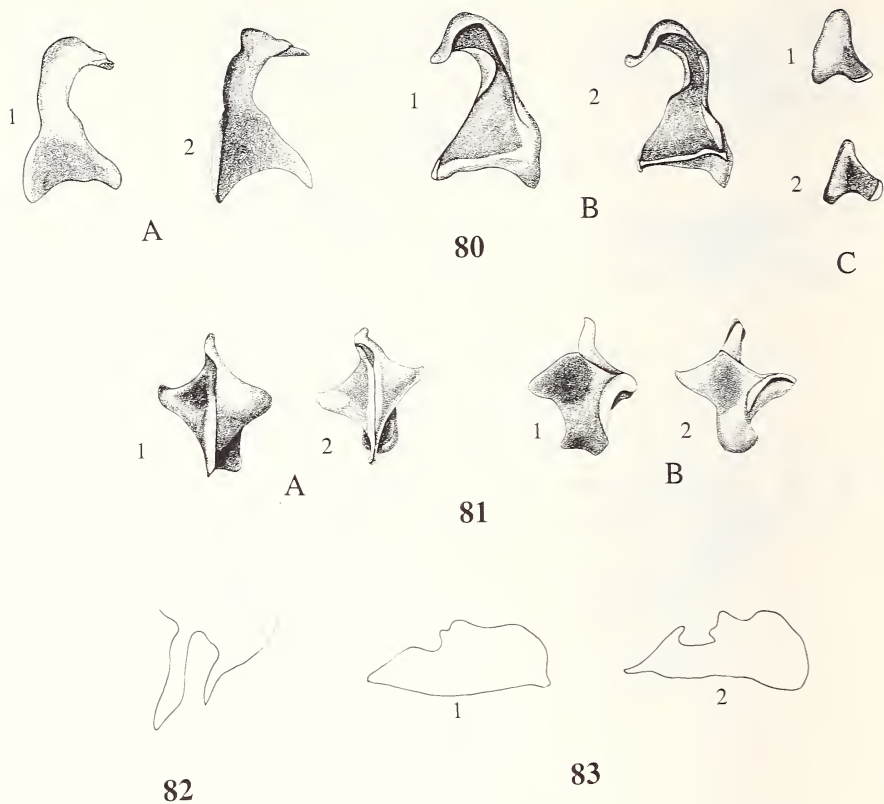


2

B

79

Figs.77-79: Hind wing articulation and wing base of Geotrupidae. – 77: First basal plate (excluding BR): a, dorsal; b, anterior: 1, *Cnemotrupes splendidus* (Geotrupinae: Geotrupidae); 2, *Frickius* spec. (Taurocerastinae: Geotrupidae). – 78: Dorsal view of the second basal plate (including BR): 1, *Cnemotrupes splendidus* (Geotrupinae: Geotrupidae); 2, *Frickius* spec. (Taurocerastinae: Geotrupidae). – 79: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP: 1, *Cnemotrupes splendidus* (Geotrupinae: Geotrupidae); 2, *Frickius* spec. (Taurocerastinae: Geotrupidae). Not to scale. Originals Browne (1993).



Figs.80-83: Hind wing articulation and wing base of Hybosoridae. – **80**: First axillary: a. dorsal; b. ventral; c. anterior: 1, *Hybosorus ruficornis* (Old World); 2, *Anaides simplicicollis* (New World). – **81**: Second axillary: a. dorsal; b. ventral: 1, *Hybosorus ruficornis* (Old World); 2, *Anaides simplicicollis* (New World). – **82**: Outline of the median plate. – **83**: Outline of the dorso-lateral view of the third axillary: 1, *Hybosorus ruficornis* (Old World); 2, *Anaides simplicicollis* (New World). Not to scale. Originals Browne (1993).

Figs.84-86: Hind wing articulation and wing base of Hybosoridae. – **84**: First basal plate (excluding BR): a. dorsal; b. anterior: 1, *Phaeochrous mashunus* (Old World); 2, *Anaides simplicicollis* (New World). – **85**: Dorsal view of the second basal plate (including BR): 1, *Phaeochrous mashunus* (Old World); 2, *Anaides simplicicollis* (New World). – **86**: Dorso-lateral view of the basalare and BScP: a. basalare; b. BScP: 1, *Phaeochrous mashunus* (Old World); 2, *Anaides simplicicollis* (New World). Not to scale. Originals Browne (1993).

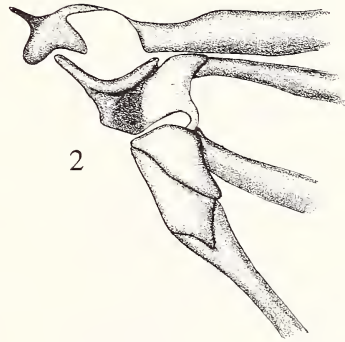
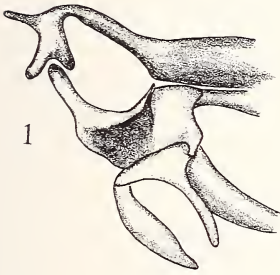


A



B

84



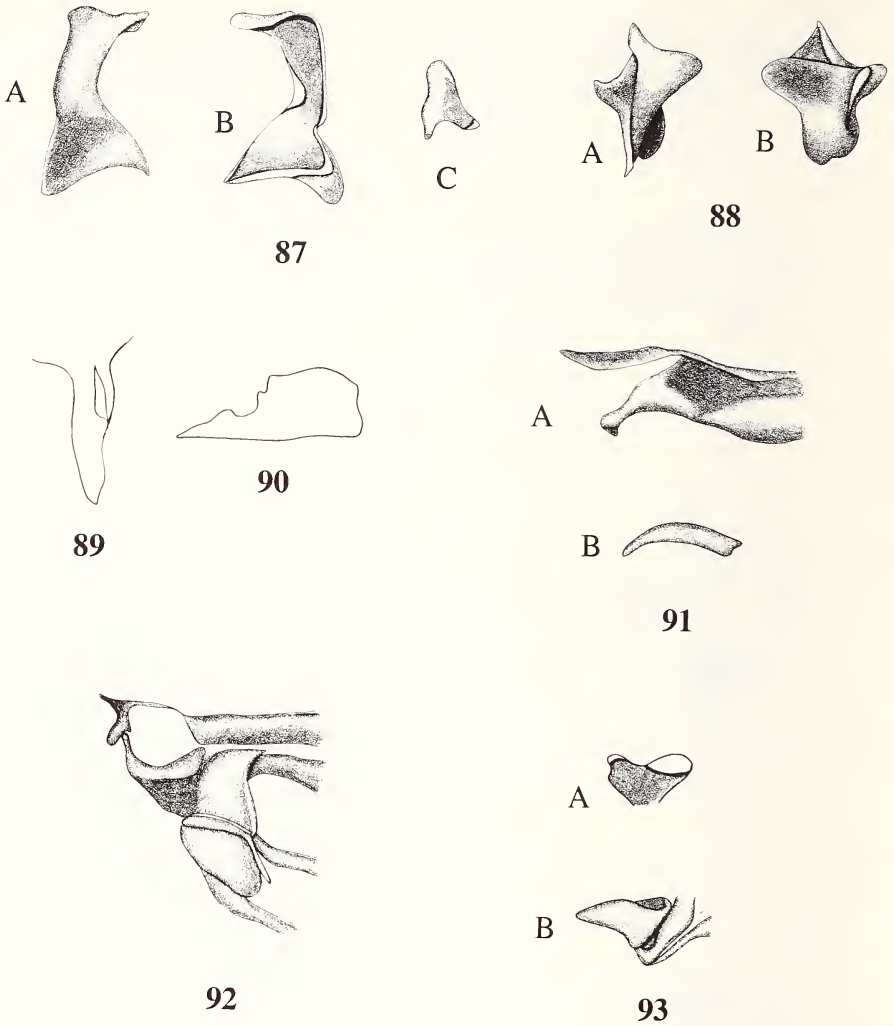
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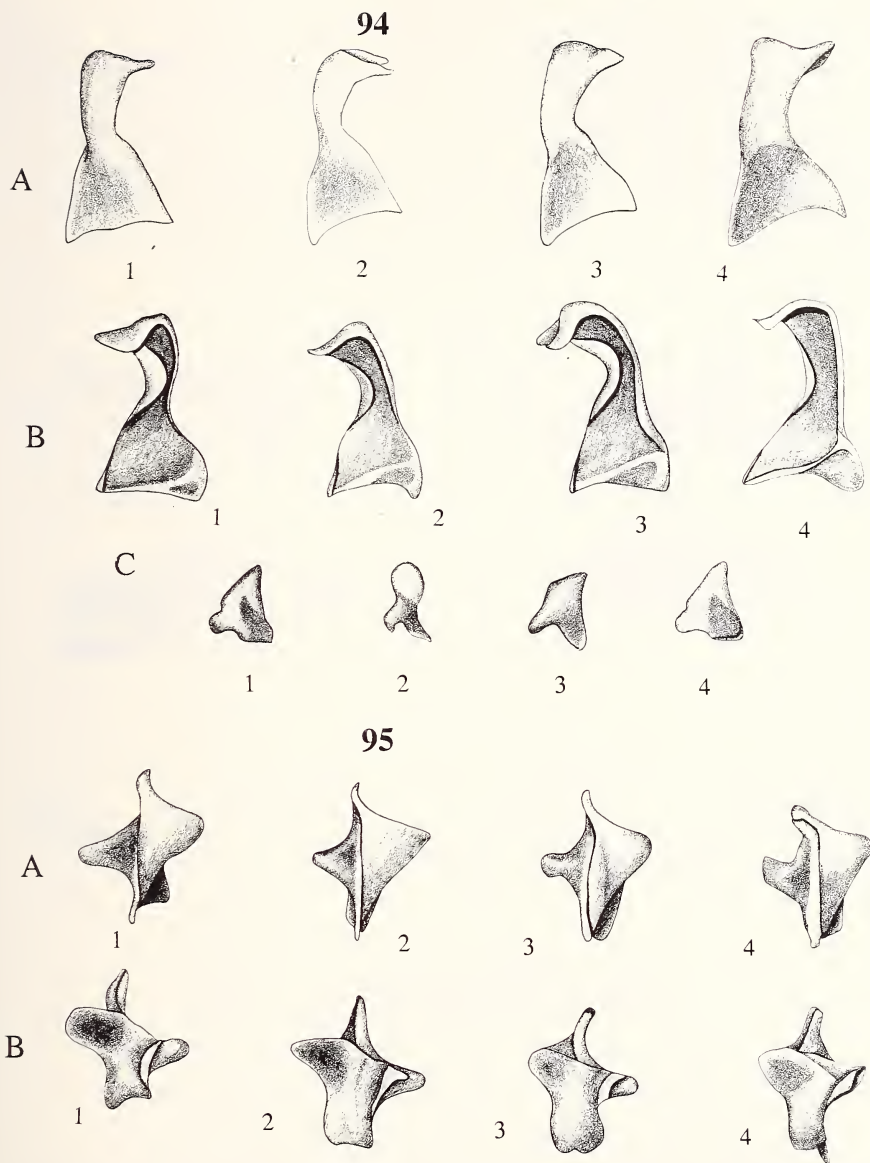
A

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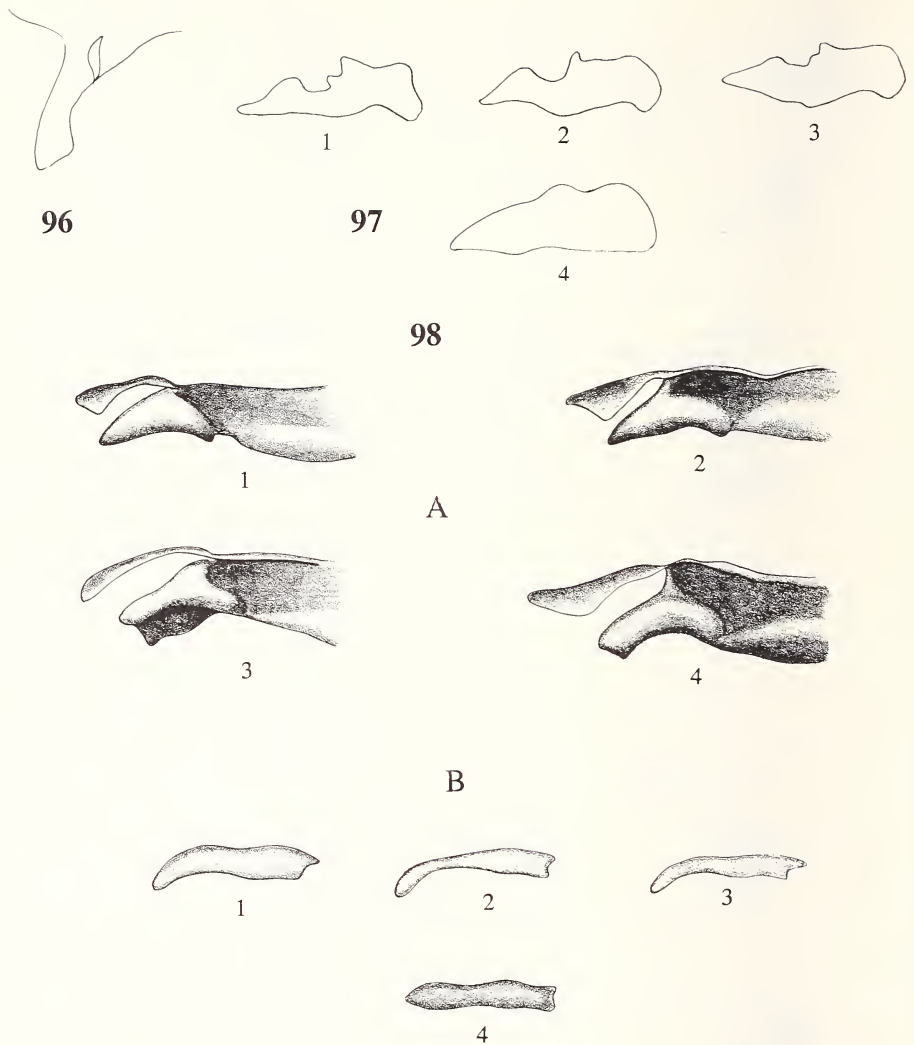
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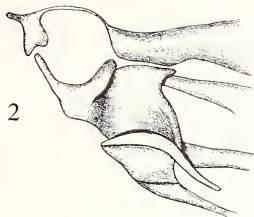
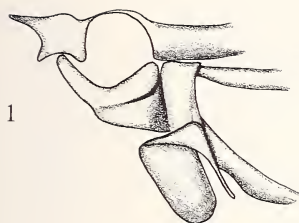
Figs.87-93: Hind wing articulation and wing base of *Ceratocanthus nitidus* (Ceratocanthidae). – 87: First axillary: a, dorsal; b, ventral; c, anterior. – 88: Second axillary: a, dorsal; b, ventral. – 89: Outline of the median plate. – 90: Outline of the dorso-lateral view of the third axillary. – 91: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – 92: Dorsal view of the second basal plate (including BR). – 93: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).



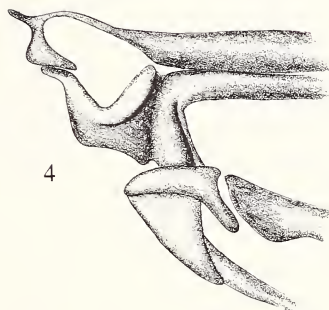
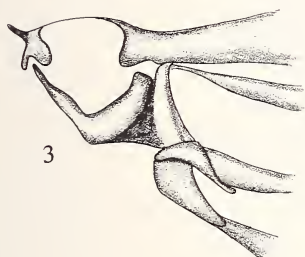
Figs.94-95: Hind wing articulation and wing base of Ochodaecidae. – **94**: First axillary: a, dorsal; b, ventral; c, anterior; 1, *Ochodaecus* spec. (Ochodainae); 2, *Chaetocanthus insuetus* (Chaetocanthini: Chaetocanthinae); 3, *Pseudochodaecus estriatus* (Pseudochodaecini: Chaetocanthinae); 4, *Synochodaecus modestus* (Synochodaecini: Chaetocanthinae). – **95**: Second axillary: a, dorsal; b, ventral; 1, *Ochodaecus* spec. (Ochodainae); 2, *Chaetocanthus insuetus* (Chaetocanthini: Chaetocanthinae); 3, *Pseudochodaecus estriatus* (Pseudochodaecini: Chaetocanthinae); 4, *Synochodaecus modestus* (Synochodaecini: Chaetocanthinae). Not to scale. Originals Browne (1993).



Figs.96-98: Hind wing articulation and wing base of Ochodaevidae. – **96**: Outline of the median plate. – **97**: Outline of the dorso-lateral view of the third axillary: 1, *Ochodaevus* spec. (Ochodainae); 2, *Chaetocanthus insuetus* (Chaetocanthini: Chaetocanthinae); 3, *Pseudochodaevus estriatus* (Pseudochodaevini: Chaetocanthinae); 4, *Synochodaevus modestus* (Synochodaevini: Chaetocanthinae). – **98**: First basal plate (excluding BR): a, dorsal; b, anterior: 1, *Ochodaevus* spec. (Ochodainae); 2, *Chaetocanthus insuetus* (Chaetocanthini: Chaetocanthinae); 3, *Pseudochodaevus estriatus* (Pseudochodaevini: Chaetocanthinae); 4, *Synochodaevus modestus* (Synochodaevini: Chaetocanthinae). Not to scale. Originals Browne (1993).



99



B



A

1

2

3

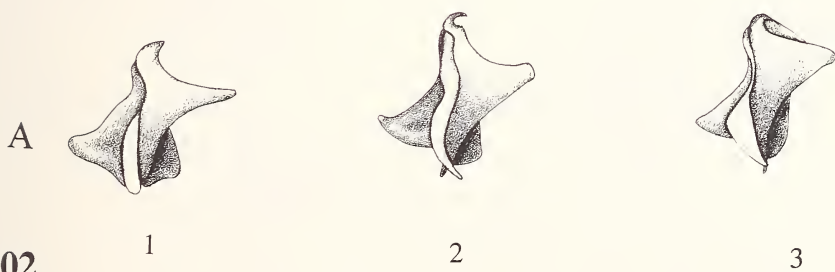
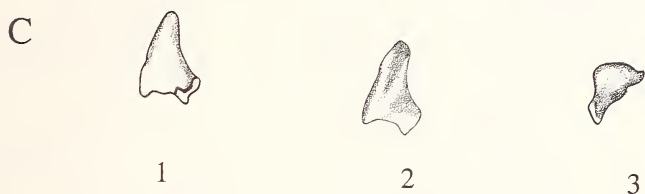
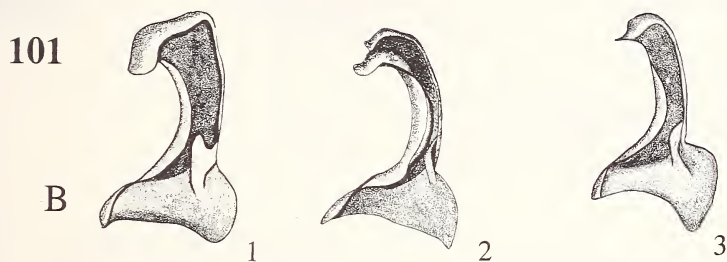
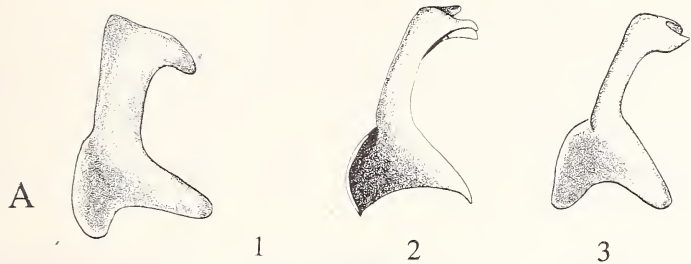
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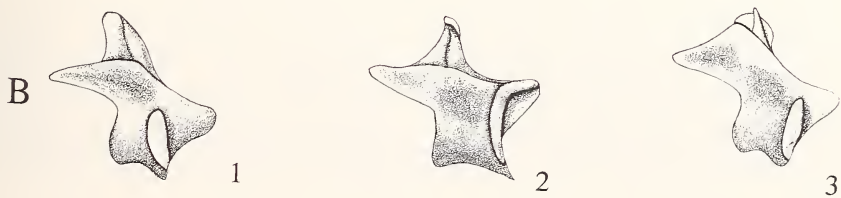
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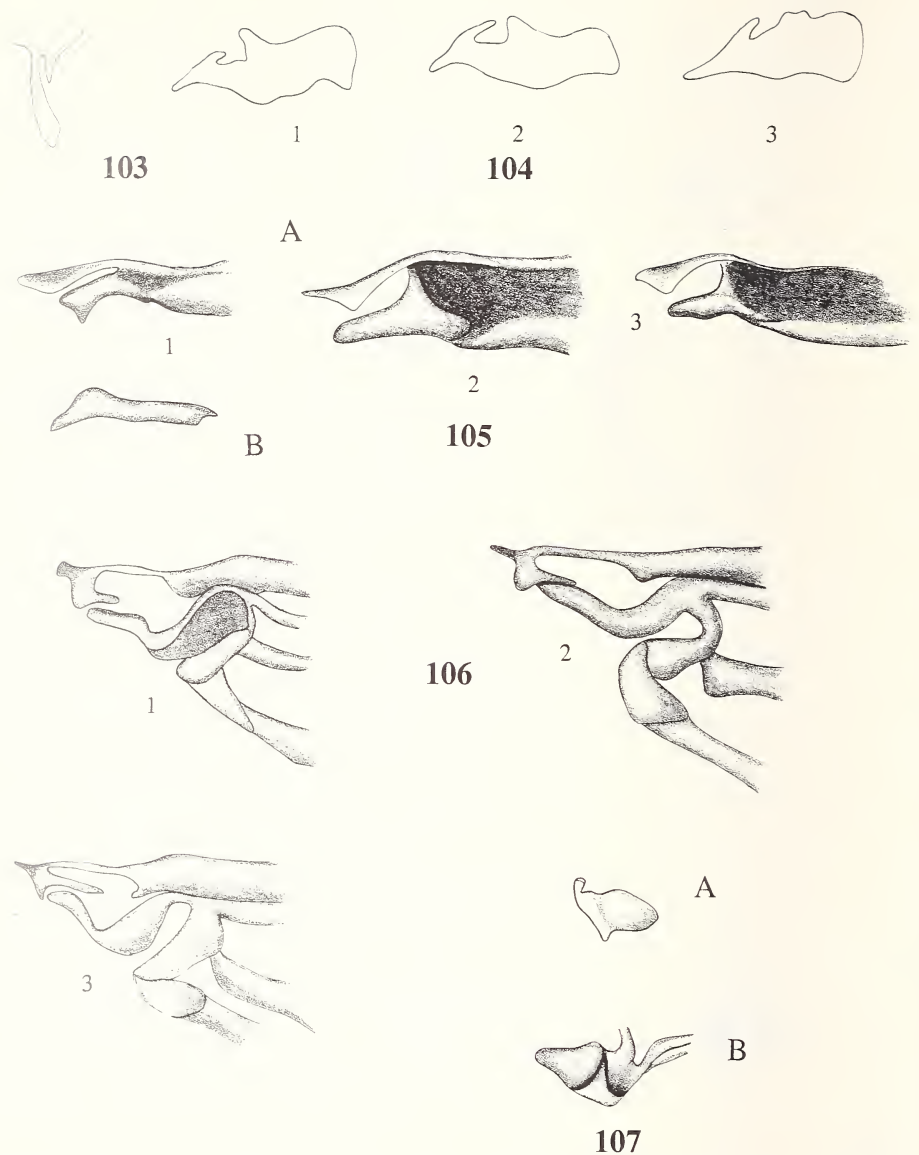
Figs.99-100: Hind wing articulation and wing base of Ochodaidae. – **99**: Dorsal view of the second basal plate (including BR): 1, *Ochodaus* spec. (Ochodainae); 2, *Chaetocanthus insuetus* (Chaetocanthini: Chaetocanthinae); 3, *Pseudochodaus estriatus* (Pseudochodaeni: Chaetocanthinae); 4, *Synochodaus modestus* (Synochodaeni: Chaetocanthinae). – **100**: Dorsolateral view of the basalare and BScP: a, basalare; b, BScP: 1, *Ochodaus* spec. (Ochodainae); 2, *Chaetocanthus insuetus* (Chaetocanthini: Chaetocanthinae); 3, *Pseudochodaus estriatus* (Pseudochodaeni: Chaetocanthinae); 4, *Synochodaus modestus* (Synochodaeni: Chaetocanthinae). Not to scale. Originals Browne (1993).

Figs.101-102: Hind wing articulation and wing base of Aphodiinae (Scarabaeidae). – **101:** First axillary of Aphodiinae (Scarabaeidae): a, dorsal; b, ventral; c, anterior: 1, *Colobopterus* spec. (Aphodiini); 2, *Ataenius desertus* (Eupariini); 3, *Rhyssemus hamatus* (Psammodiini). – **102:** Second axillary of Aphodiinae (Scarabaeidae): a, dorsal; b, ventral: 1, *Colobopterus* spec. (Aphodiini); 2, *Ataenius desertus* (Eupariini); 3, *Rhyssemus hamatus* (Psammodiini). Not to scale. Originals Browne (1993).

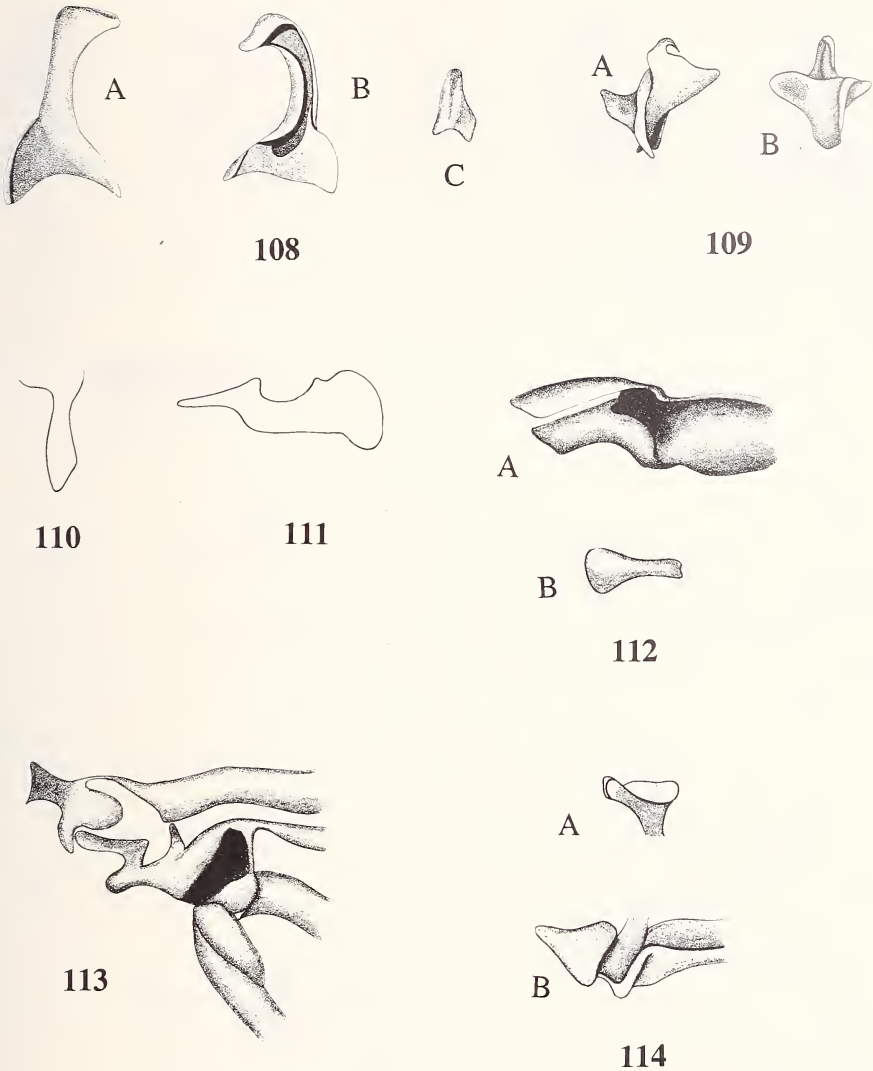


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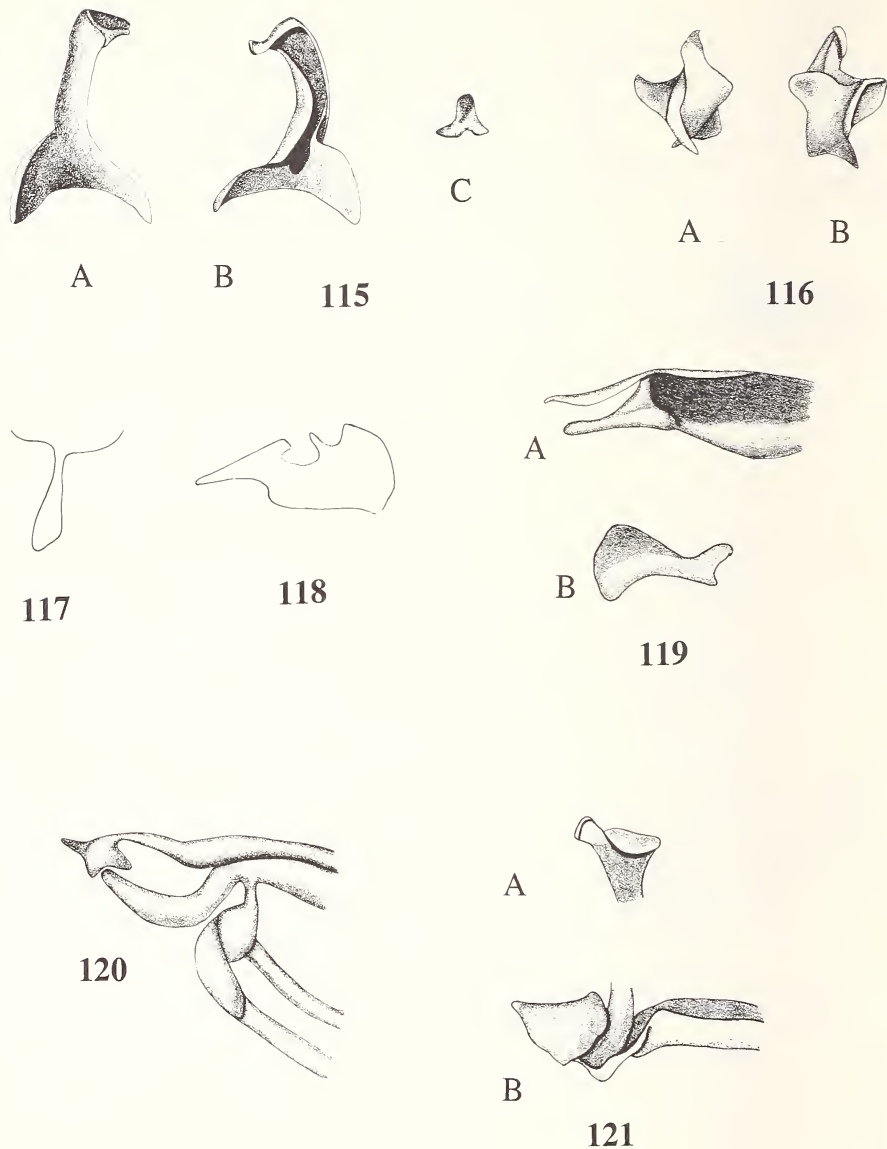


Figs.103-107: Hind wing articulation and wing base of Aphodiinae (Scarabaeidae). – **103**: Outline of the median plate. – **104**: Outline of the dorso-lateral view of the third axillary: 1, *Colobocterus* spec. (Aphodiini); 2, *Ataenius desertus* (Eupariini); 3, *Rhyssemus hamatus* (Psammodiini). – **105**: First basal plate (excluding BR): a, dorsal; b, anterior: 1, *Colobocterus* spec. (Aphodiini); 2, *Ataenius desertus* (Eupariini); 3, *Rhyssemus hamatus* (Psammodiini). – **106**: Dorsal view of the second basal plate (including BR): 1, *Colobocterus* spec. (Aphodiini); 2, *Ataenius desertus* (Eupariini); 3, *Rhyssemus hamatus* (Psammodiini). – **107**: Dorso-lateral view of the basalare and BScP of Aphodiinae (Scarabaeidae): a, basalare; b, BScP. Not to scale. Originals Browne (1993).

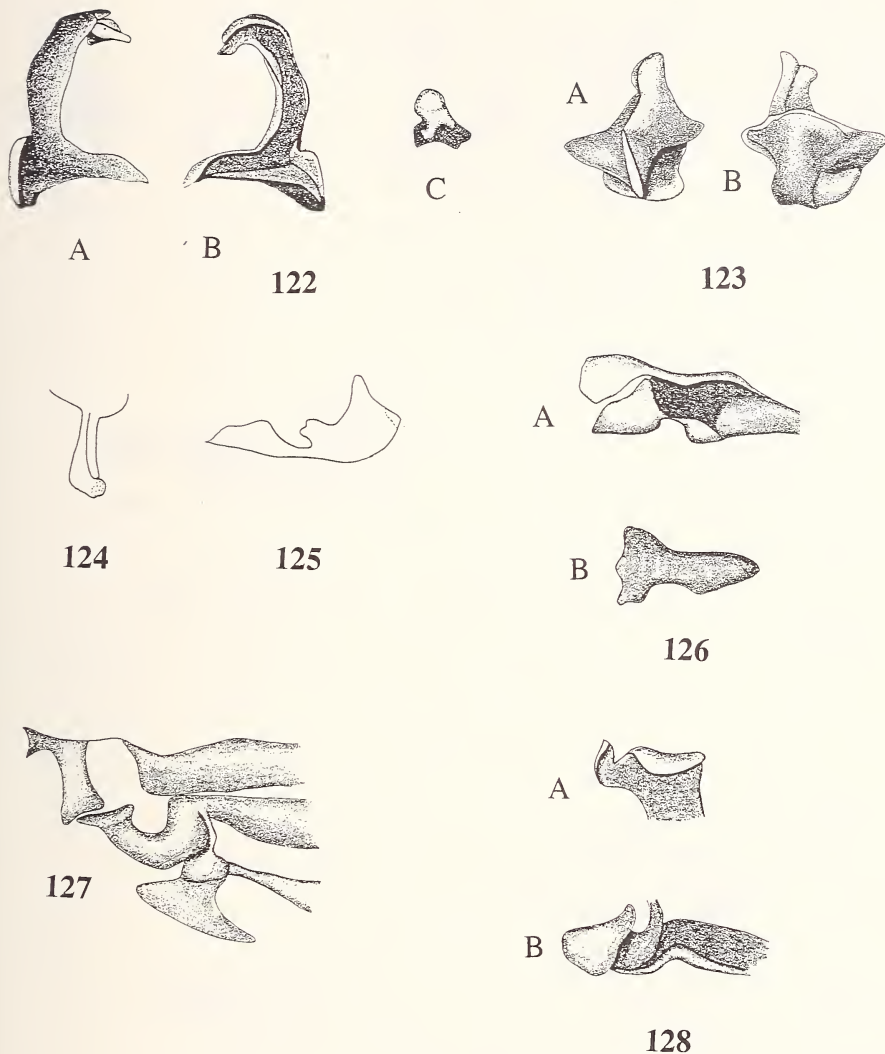


Figs.108-114: Hind wing articulation and wing base of *Aegialia crossa* (Aegialiinae: Scarabaeidae). – **108**: First axillary: a, dorsal; b, ventral; c, anterior. – **109**: Second axillary: a, dorsal; b, ventral. – **110**: Outline of the median plate. – **111**: Outline of the dorso-lateral view of the third axillary. – **112**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **113**: Dorsal view of the second basal plate (including BR). – **114**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).

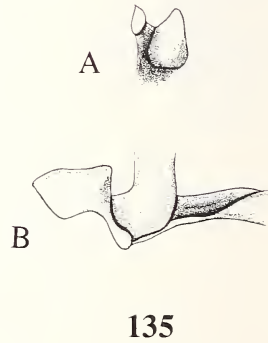
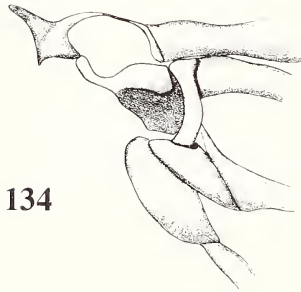
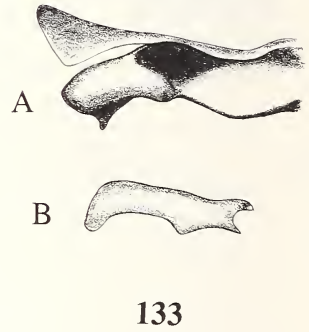
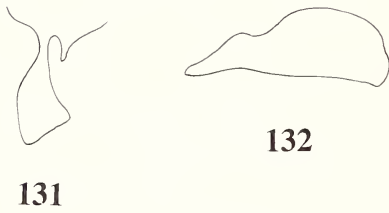
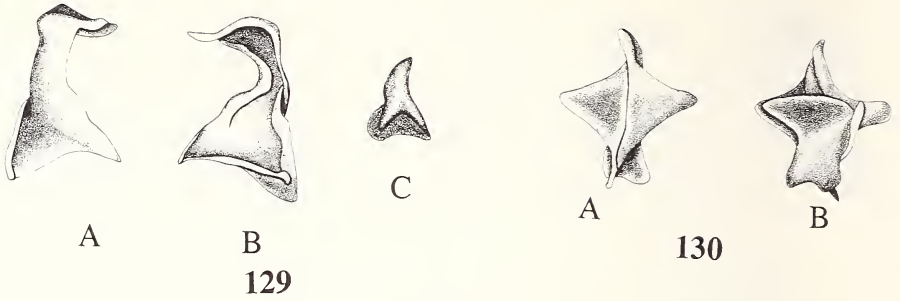
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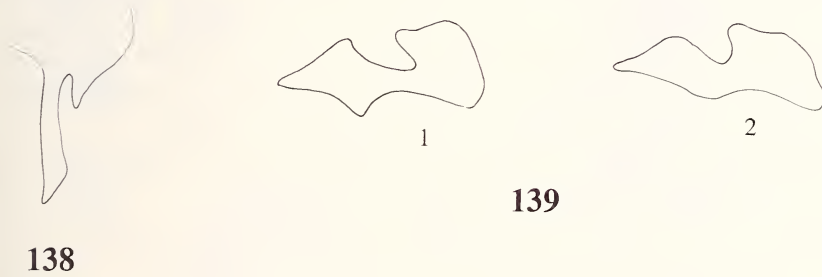
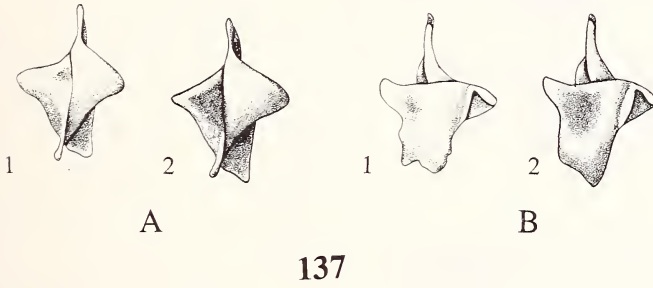
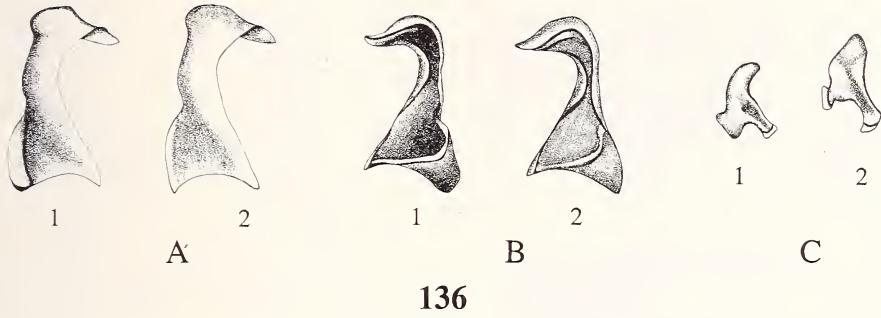
Figs.115-121: Hind wing articulation and wing base of *Aulonocnemis vulgaris* (Aulonocneminae: Scarabaeidae). – **115**: First axillary: a, dorsal; b, ventral; c, anterior. – **116**: Second axillary: a, dorsal; b, ventral. – **117**: Outline of the median plate. – **118**: Outline of the dorso-lateral view of the third axillary. – **119**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **120**: Dorsal view of the second basal plate (including BR). – **121**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).



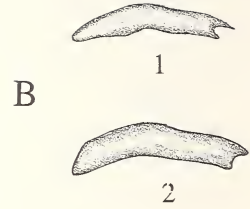
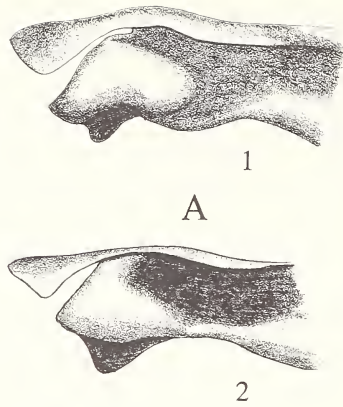
Figs.122-128: Hind wing articulation and wing base of *Eurysternus caribaeus* (Scarabaeinae: Scarabaeidae). – **122**: First axillary: a, dorsal; b, ventral; c, anterior. – **123**: Second axillary: a, dorsal; b, ventral. – **124**: Outline of the median plate. – **125**: Outline of the dorso-lateral view of the third axillary. – **126**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **127**: Dorsal view of the second basal plate (including BR). – **128**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).



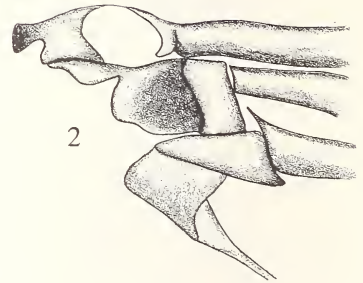
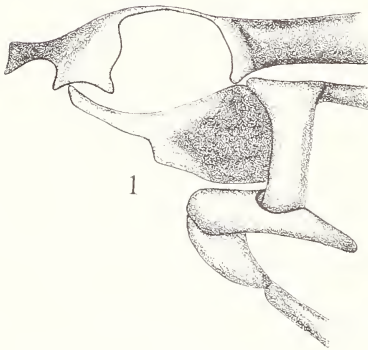
Figs.129-135: Hind wing articulation and wing base of *Orphnidus capensis* (Orphninae: Scarabaeidae). – **129**: First axillary: a, dorsal; b, ventral; c, anterior. – **130**: Second axillary: a, dorsal; b, ventral. – **131**: Outline of the median plate. – **132**: Outline of the dorso-lateral view of the third axillary. – **133**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **134**: Dorsal view of the second basal plate (including BR). – **135**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).



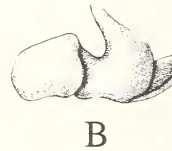
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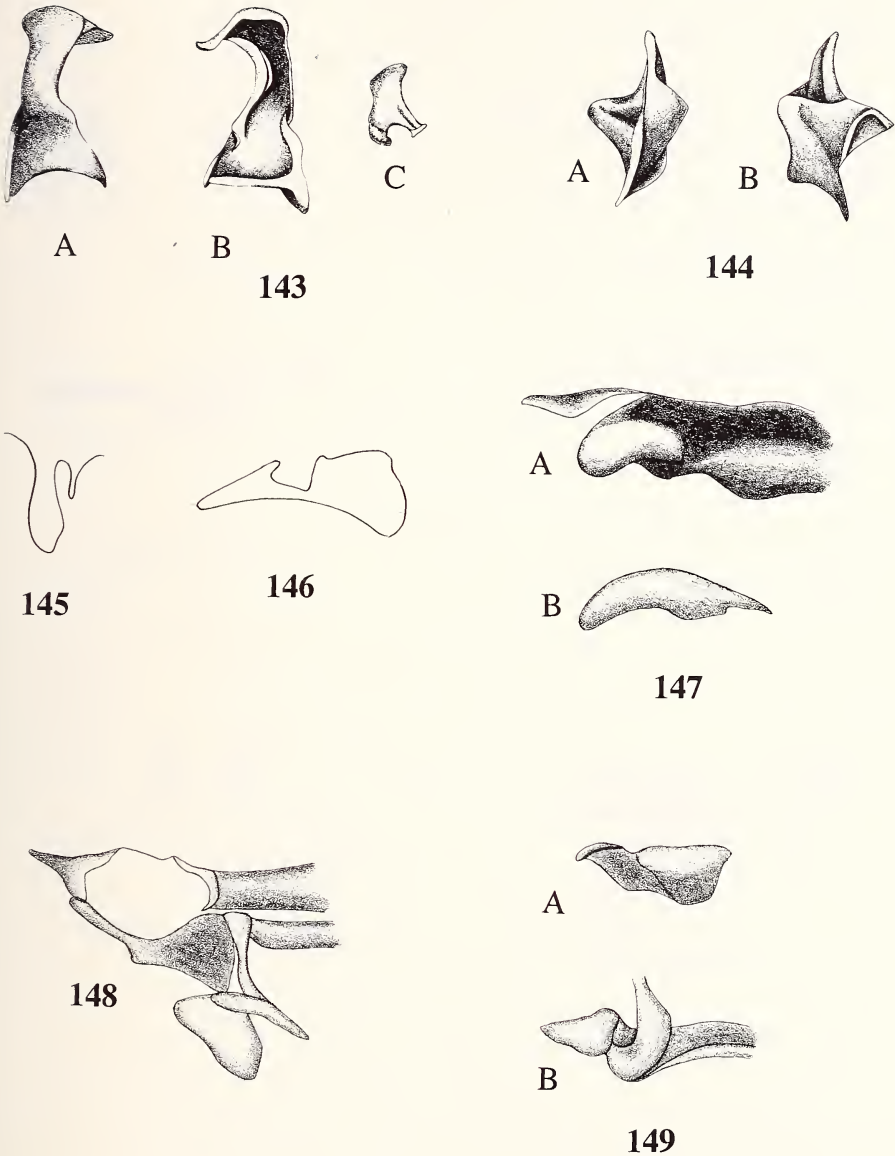


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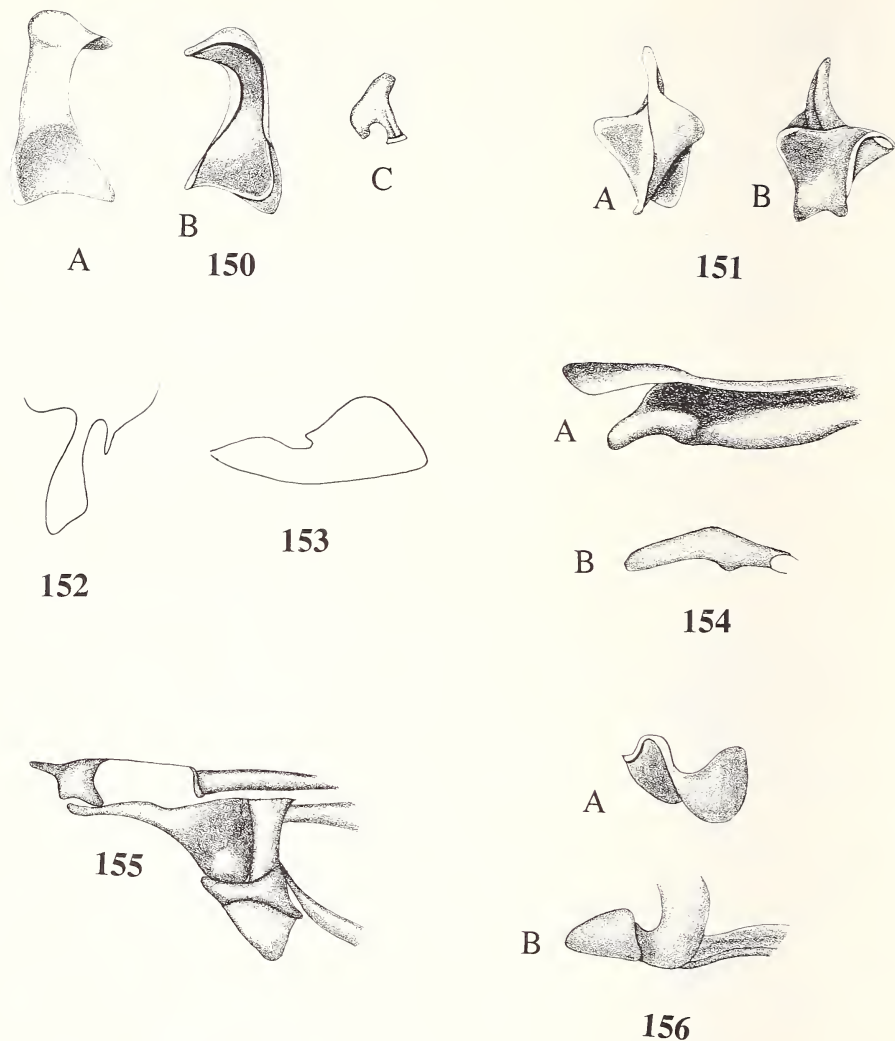


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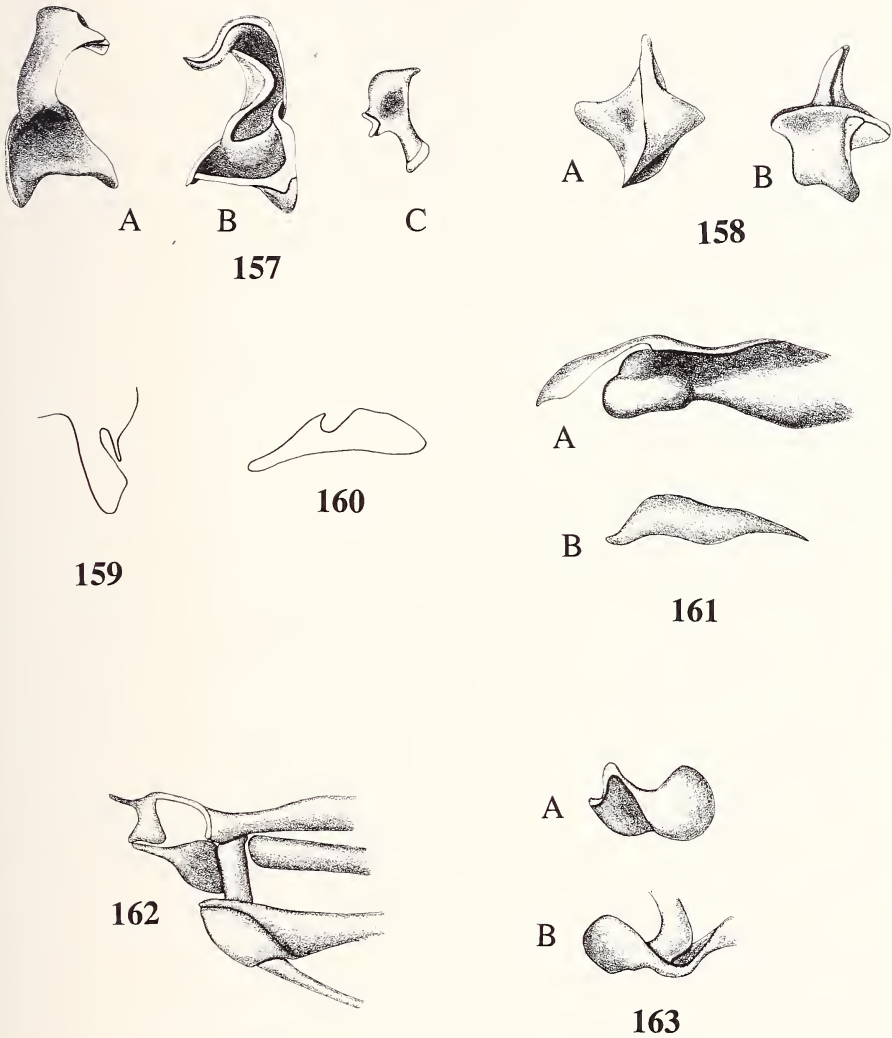
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Figs.143-149: Hind wing articulation and wing base of *Acoma glabrata* (Scarabaeidae). – **143**: First axillary: a, dorsal; b, ventral; c, anterior. – **144**: Second axillary: a, dorsal; b, ventral. – **145**: Outline of the median plate. – **146**: Outline of the dorso-lateral view of the third axillary. – **147**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **148**: Dorsal view of the second basal plate (including BR). – **149**: Dorso-lateral view of the basalare and BSCP: a, basalare; b, BSCP. Not to scale. Originals Browne (1993).

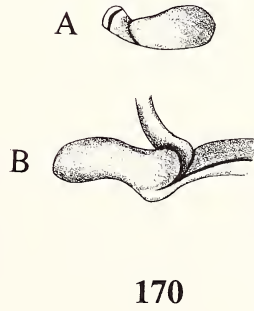
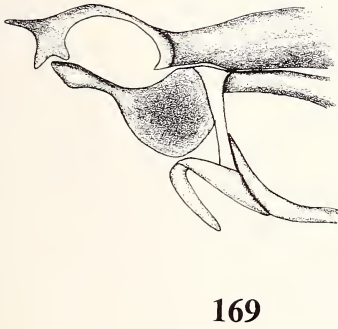
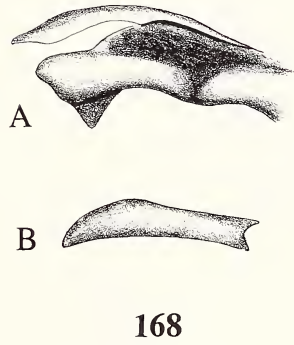
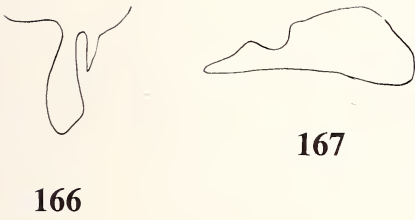
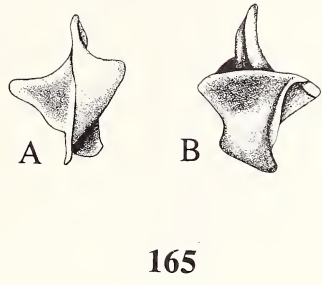
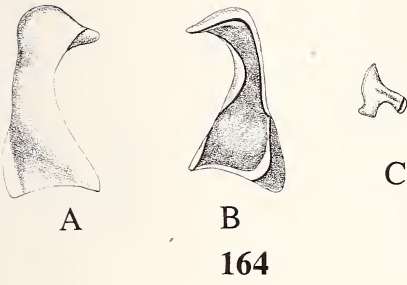


Figs.150-156: Hind wing articulation and wing base of *Chnaunanthus chapini* (Scarabaeidae). – **150**: First axillary: a, dorsal; b, ventral; c, anterior. – **151**: Second axillary: a, dorsal; b, ventral. – **152**: Outline of the median plate. – **153**: Outline of the dorso-lateral view of the third axillary. – **154**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **155**: Dorsal view of the second basal plate (including BR). – **156**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).



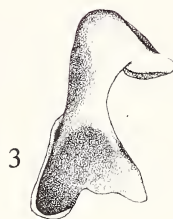
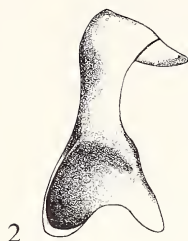
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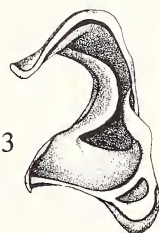
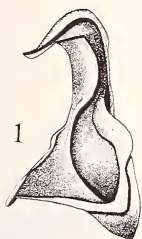


Figs.171-172: Hind wing articulation and wing base of Rutelinae (Scarabaeidae). – **171**: First axillary: a, dorsal; b, ventral; c, anterior: 1, *Leptohoplia testacepennis*; 2, *Popillia basalis*; 3, *Pelidnota punctulata*. – **172**: Second axillary: a, dorsal; b, ventral: 1, *Leptohoplia testacepennis*; 2, *Popillia basalis*; 3, *Pelidnota punctulata*. Not to scale. Originals Browne (1993).

171



B

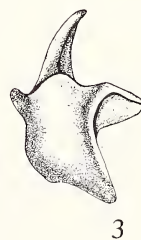


C



172

A



B



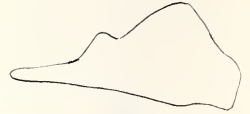
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173



1



2

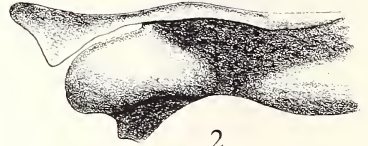


3

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1



2

A



3

B



1



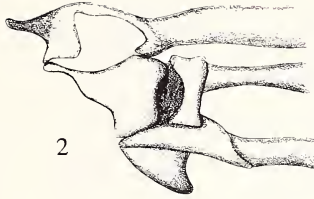
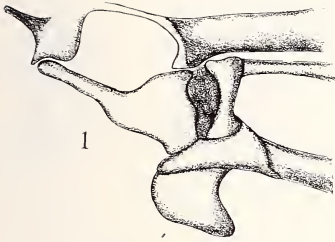
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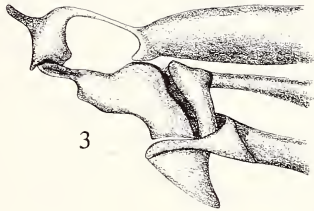
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Figs.173-175: Hind wing articulation and wing base of Rutelinae (Scarabaeidae). – 173: Outline of the median plate. – 174: Outline of the dorso-lateral view of the third axillary: 1, *Leptohoplia testaceipennis*; 2, *Popillia basalis*; 3, *Pelidnota punctulata*. – 175: First basal plate (excluding BR): a, dorsal; b, anterior: 1, *Leptohoplia testaceipennis*; 2, *Popillia basalis*; 3, *Pelidnota punctulata*. Not to scale. Originals Browne (1993).



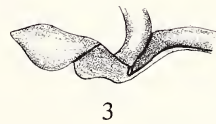
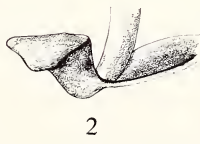
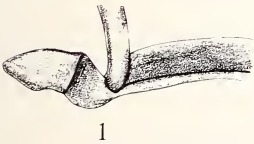
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A

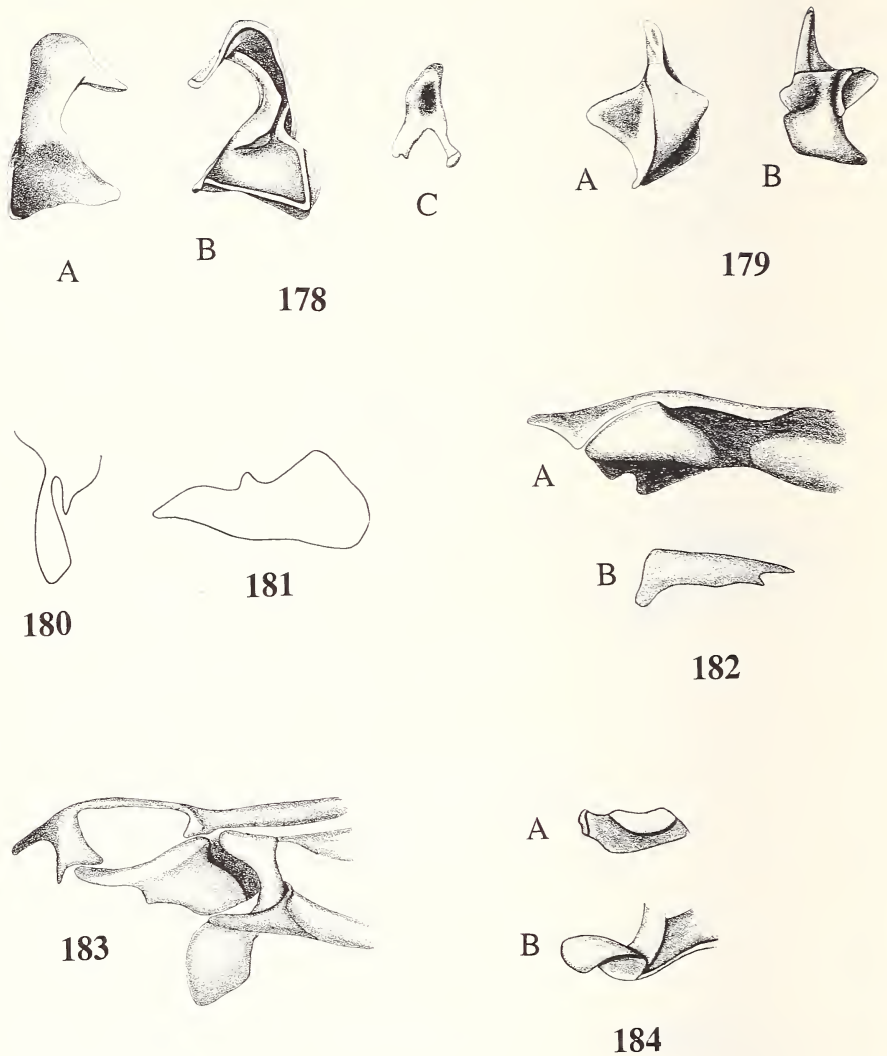


B

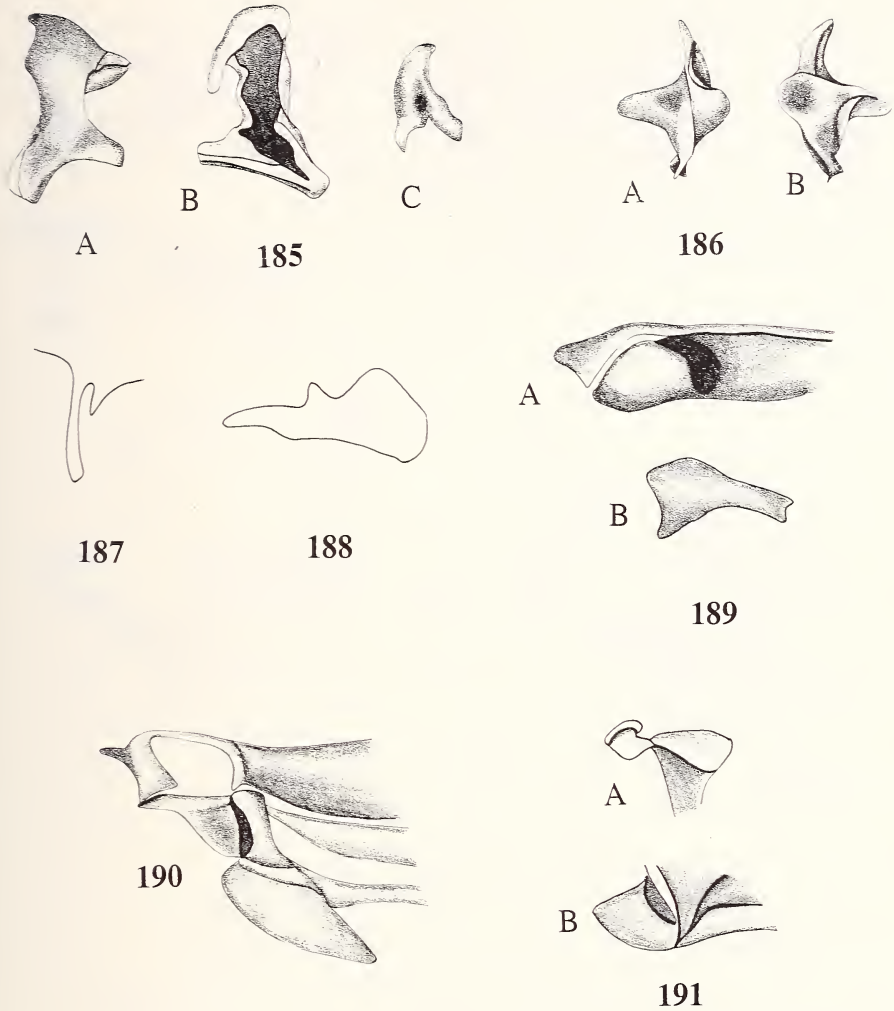


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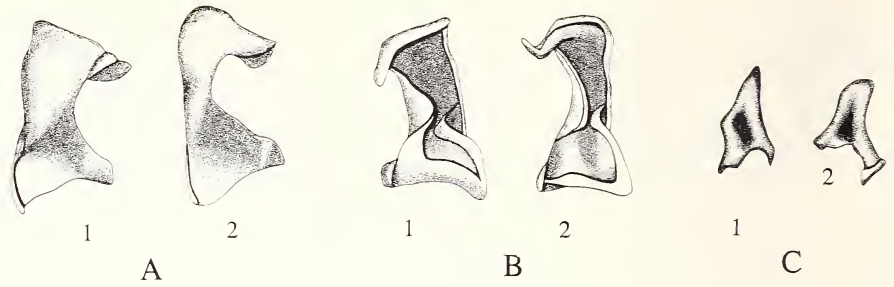


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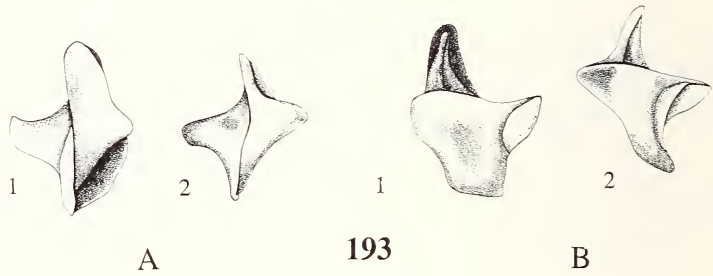


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 - **185**: First axillary: a, dorsal; b, ventral; c, anterior. - **186**: Second axillary: a, dorsal; b, ventral. -
187: Outline of the median plate. - **188**: Outline of the dorso-lateral view of the third axillary. - **189**:
 Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. - **190**: Dorsal
 view of the second basal plate (including BR). - **191**: Dorso-lateral view of the basalare and BScP:
 a, basalare; b, BScP. Not to scale. Originals Browne (1993).

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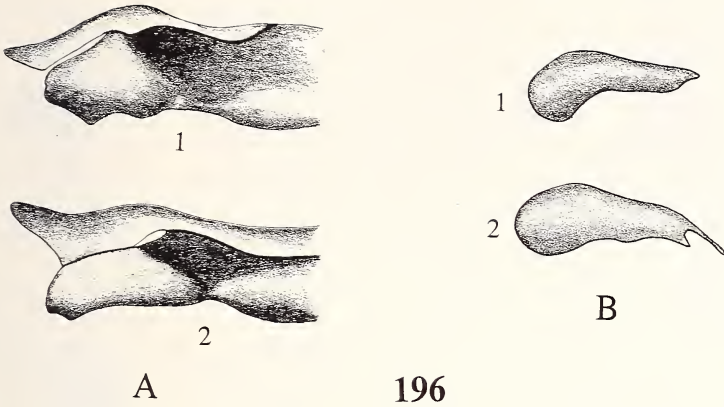


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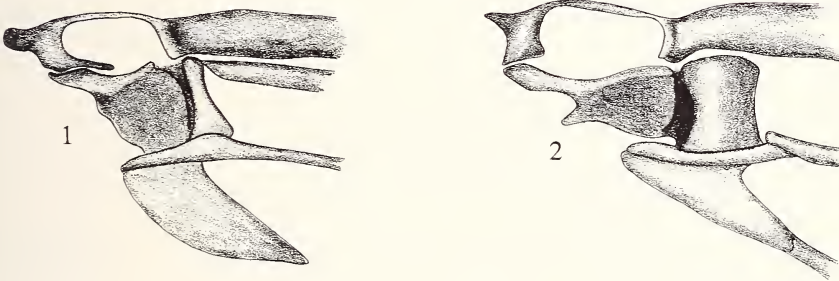
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Figs.192-195: Hind wing articulation and wing base of Trichiinae (Scarabaeidae). - **192**: First axillary: a, dorsal; b, ventral; c, anterior: 1, *Osmoderma scabrum*; 2, *Campilipus* spec. - **193**: Second axillary: a, dorsal; b, ventral: 1, *Osmoderma scabrum*; 2, *Campilipus* spec. - **194**: Outline of the median plate of Trichiinae (Scarabaeidae). - **195**: Outline of the dorso-lateral view of the third axillary: 1, *Osmoderma scabrum*; 2, *Campilipus* spec. Not to scale. Originals Browne (1993).



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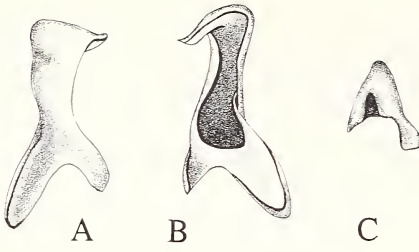
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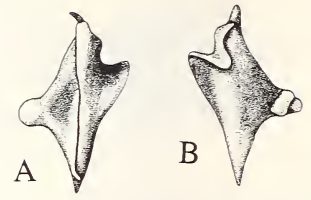
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Figs.196-198: Hind wing articulation and wing base of Trichiinae (Scarabaeidae). – 196: First basal plate (excluding BR): a, dorsal; b, ventral: 1, *Osmoderma scabrum*; 2, *Campilipus* spec. – 197: Dorsal view of the second basal plate (including BR): 1, *Osmoderma scabrum*; 2, *Campilipus* spec. – 198: Dorso-lateral view of the basalare and BScP: a, basalare of Trichiinae; b, BScP of *Osmoderma scabrum*; c, BScP of *Campilipus* spec. Not to scale. Originals Browne (1993).

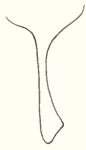
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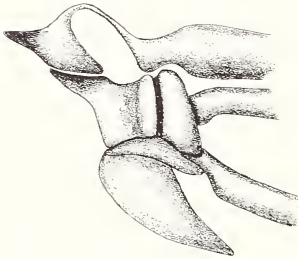


A



B

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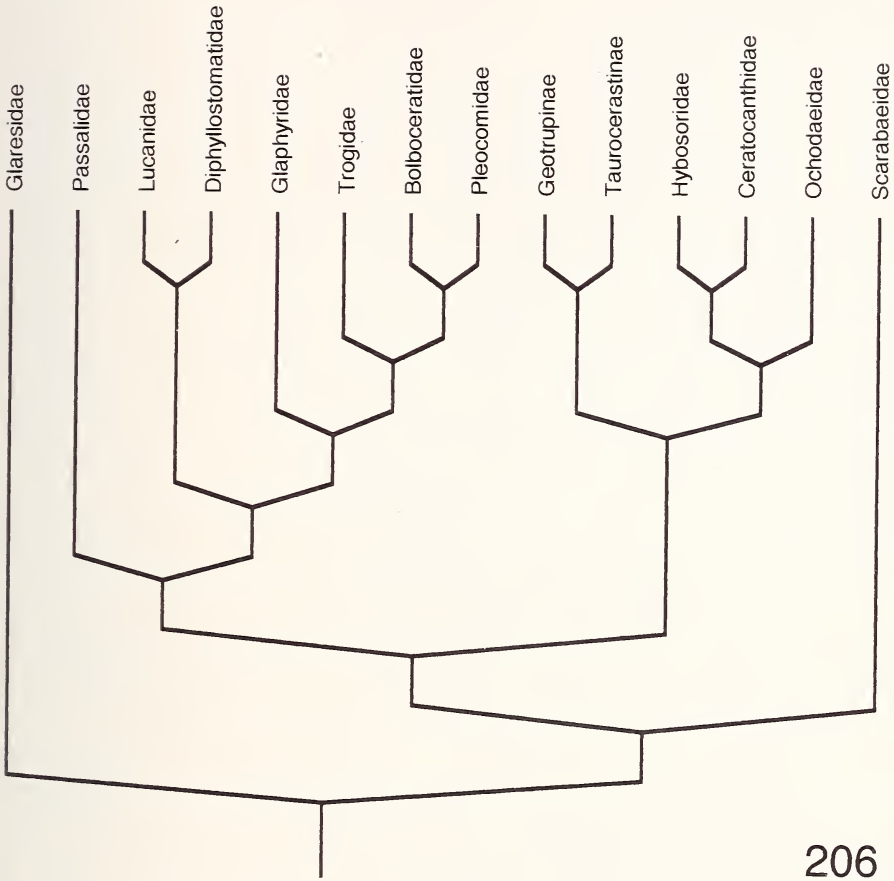
A



B

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Figs.199-205: Hind wing articulation and wing base of *Comythovalgus* spec. (Valginae: Scarabaeidae). – **199**: First axillary: a, dorsal; b, ventral; c, anterior. – **200**: Second axillary: a, dorsal; b, ventral. – **201**: Outline of the median plate. – **202**: Outline of the dorso-lateral view of the third axillary. – **203**: Dorsal view of the first basal plate (excluding BR): a, dorsal; b, anterior view of HP. – **204**: Dorsal view of the second basal plate (including BR). – **205**: Dorso-lateral view of the basalare and BScP: a, basalare; b, BScP. Not to scale. Originals Browne (1993).



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Fig.206: Hypothesised branching patterns among members of Scarabaeoidea based on characters of the hind wing articulation, wing base and wing venation (Browne 1993; Browne & Scholtz 1995).

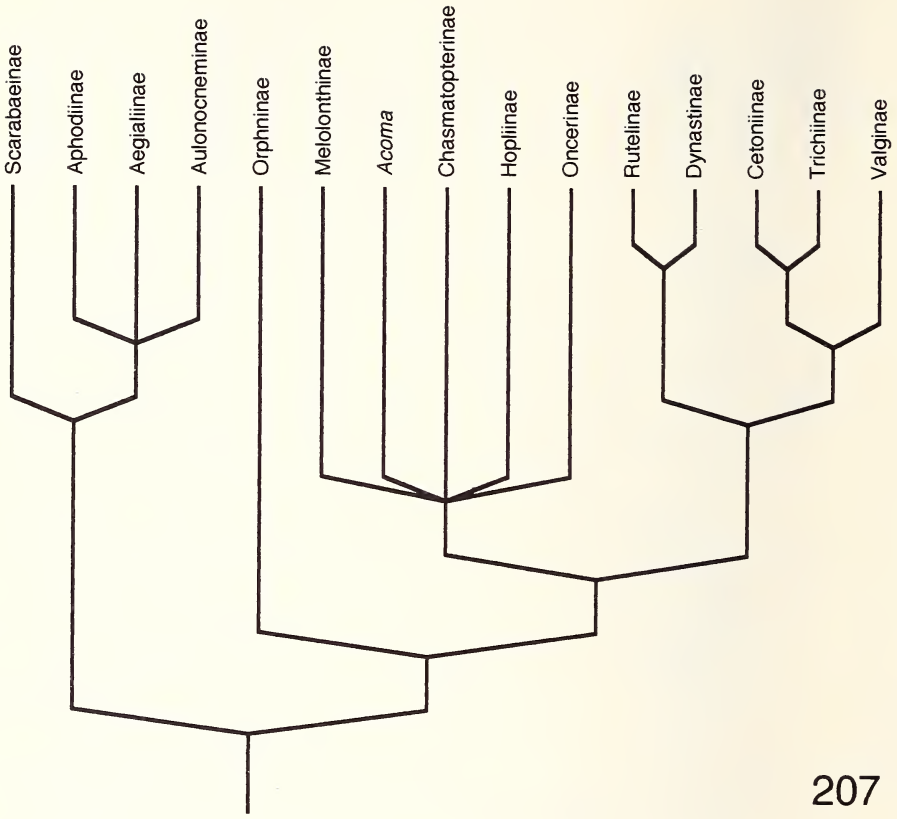


Fig.207: Hypothesised branching patterns among members of Scarabaeidae based on characters of the hind wing articulation and wing base (Browne 1993).

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