Systematic Entomology (1998) **23**, 307–326

Evolution of the scarab hindwing articulation and wing base: a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera)

JONATHAN BROWNE and CLARKE H. SCHOLTZ Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

Abstract. A study is made of the articulation and base of hindwings of Scarabaeidae. The survey is based on an examination of over 150 genera from sixteen scarabaeid subfamilies and taxa of uncertain phylogenetic status. Relationships among all subfamilies of Scarabaeidae are examined here for the first time. The constructed phylogeny shows that the scarabaeid lineage (Scarabaeidae) is comprised of two major lines: an aphodiine line (containing Aphodiinae, including Aegialiini, *Aulonocnemis* and Scarabaeinae), and an orphnine line (containing Orphninae, Melolonthinae, *Acoma*, *Chnaunanthus*, Hopliini, *Oncerus*, Rutelinae, Dynastinae, Trichiinae, Cetoniinae, *Osmoderma* and Valginae).

Introduction

The Scarabaeidae is the largest of the thirteen families in the Scarabaeoidea and one of the largest and most diverse families of beetles. [The family and subfamily concepts of Scholtz (1990), Scholtz *et al*. (1994) and Browne & Scholtz (1995) are followed in this paper]. About 1725 of roughly 2000 described genera (86%), and 90% of the ≈ 30 000 known scarabaeoid species are found in the Scarabaeidae (Scholtz & Chown, 1995). The morphological and biological diversity of its members has led to the family being divided into numerous mostly well defined subfamilies and tribes, as well as into several groups of uncertain taxonomic status.

Several recent papers have reviewed, reconsidered or studied scarabaeoid adult and larval characters, commented on phylogenetic trends in the various groups and proposed general ground plans for most studied character suites (see Scholtz, 1990; Scholtz *et al*., 1994; Browne & Scholtz, 1995; Scholtz & Browne, 1996). In spite of the fact that the superfamily is one of the better studied beetle taxa, it has only recently been subjected to thorough phylogenetic analysis (Browne & Scholtz, 1998). The Scarabaeidae have not been analysed phylogenetically in any detail.

This paper is a sequel to Browne & Scholtz (1995), in which the families of the Scarabaeoidea were phylogenetically analysed using the characters of the hindwing articulation, hindwing base and wing venation. The same character suite which was used in that paper at superfamily level is used at family level in this one. We are fully aware of the criticism that could be levelled at phylogenetic studies based on characters from only one or two character suites; however, we are of the opinion that wing characters are the product of a deeply integrated portion of the genotype, and subject to a higher level of developmental canalization than the more conventional types of characters used in phylogenetic studies. They bear a higher, and more accurate, level of phylogenetic information than do conventional characters, and fit the accepted criteria of ‘good’ or ‘high weight’ taxonomic characters (as outlined by Mayr & Ashlock, 1991), whereas many conventional characters do not.

Materials and methods

Nomenclature

Terminology used in this paper was developed by Browne (1993) and published by Browne & Scholtz (1994). Reference is also made particularly to a study of the basal division of the Scarabaeoidea (Scholtz *et al*., 1994), a study of the evolution of the scarabaeoid wing (Browne & Scholtz, 1995) and a study of the evolution of all available scarabaeoid character suites (Browne & Scholtz, 1998).

Taxa studied

Hindwings of 153 genera from sixteen scarabaeid subfamilies and taxa of uncertain phylogenetic status were examined (Appendix 1). In addition, another ≈ 100 genera from the

Correspondence: Jonathan Browne, Common Ground Consulting, PO Box 1828, Cape Town 8000, South Africa.

remaining twelve scarabaeoid families were examined during the course of this study. Taxa with reduced wings (e.g. Phaenomeridinae) were not included.

Specimen preparation and examination

Various types of wing preparations were used. The most useful for examining the relative positions of the elements of articulation and base were simply drying the wing in an outstretched position and dry mounts on glass slides (see Kukalová-Peck & Lawrence, 1993). Axillary sclerites and basal plates were dissected and mounted on paper points, as it was necessary to rotate the specimen to fully appreciate the three-dimensional complexity. Vouchers were deposited in the collection of the Transvaal Museum, Pretoria. Illustrations were made using a Zeiss dissecting microscope and Zeiss 1,8 camera Lucida.

Cladistic analysis

Determination of character polarity and character state ordination is based on the polyphagan superfamilies Dascilloidea and Hydrophiloidea as outgroups. There has been much debate over which is the sister group of the Scarabaeoidea: Kukalová-Peck & Lawrence (1993), Scholtz *et al*. (1994) and Browne & Scholtz (1995) favour the latter, whereas other beetle workers, most notably Crowson (1967) and Scholtz (1990), have considered Dascilloidea to be the sister group of the superfamily. However, which of these taxa is used in the analysis makes no difference to the ordering or polarization of the character states.

Minimization of the number of character state changes is used to optimize the phylogram, through the use of PAUP/Mac version 3.1.2d5 (Swofford, 1985), licensed to Dr Peter Linder (Department of Botany, University of Cape Town). Trees were produced by the branch-and-bound algorithm, Farris optimization and outgroup rooting.

Categories and taxonomic ranking

In the past, the Scarabaeoidea have been divided into 'primitive', 'intermediate' and 'derived' groups. In this study, these arbitrary terms have been abandoned and replaced with ones derived from a genuine phylogenetic tree. We used the following hierarchical system when naming components of the phylogram: lineage, line, group, subgroup, infragroup. Where these comprise more than one terminal taxon, they are named for the most primitive included taxon.

Previous authors have, often arbitrarily, assigned taxon ranks which differ from those suggested by this analysis. Taxa assigned ranks by previous authors which are inconsistent with this analysis are indicated by quotation marks.

The character set

For multistate transformation series, non-redundant linear coding was favoured over binary or linear coding, as the former minimizes the number of character columns (Brooks & McLennan, 1991). Characters which were not present were coded 0, the primitive state, rather than 9, due to the inherent weaknesses of using 9 in phylogenetic analyses (Nixon & Davis, 1991). Autapomorphic character states were excluded from the analysis (except those of the family Scarabaeidae), as they are phylogenetically uninformative under the parsimony criterion (Swofford, 1985). These are described in the Results and discussion.

Character states used in cladistic analysis

In Browne's (1993) analysis, 146 characters of the hindwing articulation and wing base were coded as plesiomorphic or apomorphic for thirty-three higher scarabaeoid taxa (thirteen families, and thirty subfamilies and taxa of uncertain phylogenetic status); ninety-seven of these were judged to be relevant in the resolution of the Scarabaeidae phylogeny. Since Browne's (1993) study, all characters and states have been reassessed in the light of new data, and characters 73, 74, 80 and 95 have been deleted from the data matrix. Ninety-three characters, from sixteen taxa (Table 1; Appendix 2) were scored and thus subjected to cladistic analysis (Fig. 2).

Results and discussion

Overview

Branch-and-bound searching resulted in two equally parsimonious computer-generated trees (only the position of Orphninae differs), from which a strict consensus tree 147 steps long was produced (Fig. 2). The cladogram of fifteen taxa and ninety-three single- and multistate characters is 147 steps long, with a consistency index of 0.944 which is resolved at all nodes.

The phylogenetic analysis (Fig. 2) indicates that the Scarabaeidae comprises two lines: an aphodiine line (containing Aegialiini, *Aulonocnemis*, Aphodiinae, Scarabaeinae, which are united by forty-four derived states of the hindwing articulation and wing base), and an orphnine line (containing Orphninae, Melolonthinae, *Acoma*, *Chnaunanthus*, Hopliini, *Oncerus*, Rutelinae, Dynastinae, Trichiinae, Cetoniinae, *Osmoderma* and Valginae, which are united by twenty-two derived states of the hindwing articulation and wing base). The aphodiine line consists of the scarabaeine group (containing Scarabaeinae, which is united by twelve derived states of the hindwing articulation and wing base) and the aphodiine group (containing Aegialiini, *Aulonocnemis* and Aphodiinae, which are united by eight derived states of the hindwing articulation and wing base). The orphnine line consists of the orphnine group (containing Orphninae, which displays no derived states of the hindwing articulation or wing base), and the melolonthine group, united by four derived states of the hindwing articulation and wing base. The melolonthine group is comprised of the melolonthine subgroup (containing Melolonthinae, *Acoma*, *Chnaunanthus*, Hopliini and *Oncerus*, united by two derived states of the hindwing articulation and wing base), and the ruteline subgroup (containing Rutelinae, Dynastinae, Trichiinae, Cetoniinae, *Osmoderma* and Valginae, which are united by nineteen derived states of the hindwing articulation and wing base). The ruteline subgroup consists of the ruteline–dynastine infragroup (containing Rutelinae and Dynastinae, which are united by five derived states of the hindwing articulation and wing base) and the trichiine infragroup (containing Trichiinae, Cetoniinae, *Osmoderma* and Valginae, which are united by sixteen derived states of the hindwing articulation and wing base).

Convergences

Of 231 character states, only four (1.7%), characters 37, 59–60 and 71 (see below), are hypothesized to have evolved more than once. If the phylogeny were reconstructed to eliminate some of these convergences, others would result which would be more difficult to explain. For example, cetoniines and trichiines resemble each other in the presence of a narrowly digitate first axillary distal arch apex (37:2 = ch. 37, state 2). However, if this state is accepted as evidence of relationship, two derived character states of the first axillary (19:3) and the first basal plate (71:2) which cetoniines share with valgines would have to be accepted as independent derivations. Similarly, members of the ruteline–dynastine infragroup and *Osmoderma* resemble each other in convexity of the third axillary head (60:1). If this is taken as evidence of relationship, then the sixteen derived character states which *Osmoderma* shares with other members of the trichiine infragroup would have to be accepted as independently evolved states. A similar case can be made with character 71.

Reversals

We infer that reversals have occurred in the evolution of eight (3.4%) character states: characters 20, 21, 24, 58, 59, 62, 71 and 92. Most of these (ch. 20, 21, 58, 59, 62 and 71) are due to the unusual character state distribution in *Osmoderma*, currently classified as a member of the Trichiinae. This group displays a combination of highly derived and very primitive character states (see Trichiinae and *Osmoderma* below), but shares two derived character states with Cetoniinae.

In the primitive state the dorsal margin of FSc2 is flat (24:0). In the derived state this margin is enlarged and broad (24:1). The primitive state is found in members of the aphodiine line and as a reversal in members of the ruteline subgroup. The derived state is found in Orphninae and members of the melolonthine subgroup. To suppose that the character state in members of the ruteline subgroup was ancestral would require multiple evolution of other character states of related taxa, an unacceptable assumption. A similar situation occurs with character 92.

The evolution of the Scarabaeidae

This large cosmopolitan family is united by the following twenty-three apomorphic character states of the wing articulation (Browne & Scholtz, 1995): 1Ax – head proximal margin reduced, dorsal surface posteriorly reduced, anterior surface narrow, ventral projection long and narrow, distal embayment mesad, neck long; 2Ax – dorso-proximal and dorso-distal margins of dorso-proximal enlarged proximally and distally, antero-median to posterior sections of the dorso-proximal ridge enlarged laterad over dorso-distal ridge, anterior section of dorso-distal ridge basally curved distad, 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, subalare tendon attachment point very short, very broad, and apically deeply and broadly concave, with the base arising from the distal section of 2Ax and extends postero-proximad; 3Ax – distorted, moderately long to very short, tail curved, very short and very broad; 1BP – anterior section of proximal arch of BR reduced by a greatly enlarged br, distal arch of BR large and convex, HP curves postero-dorsad close to, or even over, BScA; 2BP – strongly reduced proximally, proximal arch of BMA strongly orientated antero-proximad and ventrad, BMP convex and very narrow, and the BMP-BCuA brace greatly enlarged, very broad and very convex.

Major divisions of the Scarabaeidae

Although the phylogeny presented in Fig. 2 is in broad agreement with those suggested by d'Hotman & Scholtz (1990a,b), Nel & Scholtz (1990), Scholtz (1990), Browne (1993), and to a certain extent with that presented by Howden (1982), there are several differences. These are briefly detailed below.

Howden (1982) places, as a possible option, Aphodiinae + Scarabaeinae, with Trogidae, Hybosoridae, Pleocomidae and Geotrupidae as an intermediate lineage. He further subdivides this lineage into three additional lineages, with either Aphodiinae + Scarabaeinae or Trogidae + Hybosoridae as the most primitive, Pleocomidae intermediate and Geotrupidae the most derived. d'Hotman & Scholtz (1990a) and Nel & Scholtz (1990) list Orphninae, Glaphyridae, Aegialiini, *Aulonocnemis*, Aclopinae and Aphodiinae as members of the intermediate lineage.

Howden (1982), Scholtz (1990), d'Hotman & Scholtz (1990a) and Nel & Scholtz (1990) are in broad agreement as to the taxa which constitute the derived scarabaeoid lineage. Howden (1982) listed Melolonthinae, Rutelinae, Dynastinae and Cetoniinae (and possibly Aphodiinae and Scarabaeinae). Scholtz (1990) added Scarabaeinae, and Nel & Scholtz (1990) and d'Hotman & Scholtz (1990a,b) further added Phaenomeridinae and 'Hopliinae'.

The topology presented in Fig. 2 agrees with that of Browne (1993), except for the arrangement of Trichiinae, *Osmoderma*, Cetoniinae and Valginae. Browne (1993) places *Osmoderma* as the sister group of (Trichiinae + Cetoniinae) + Valginae.

The aphodiine line

The aphodiine line displays the following forty-four apomorphic hindwing articulation and wing base character states: 1Ax – head strikingly reduced posteriorly (1:2), the antero-dorsal margin is orientated distad (3:2), and is reduced and extremely narrow (5:1), the proximal enlargement of the postero-proximal margin is absent (8:1), the anterior surface is strikingly short and narrow (11:1), FSc1 is short to long and broad, strongly convex (13:1), the ventral projection is strongly orientated postero-distad, weakly ventrad and not curved posteriad (17:1), FSc2 is reduced, small, round and partially or completely planate (23:1), the dorsal surface of the head and neck is extended anteriad (25:1), the neck is strikingly narrow (26:1) and strikingly long (28:2), the dorsal surface is orientated strongly distad and ventrad (29:1), the neck and tail articulation with 2Ax is strongly reduced anteriorly (30:1), the proximal arch of the tail is strikingly reduced anteriorly and posteriorly, expanded proximally (32:1), the distal arch is markedly reduced anteriorly and posteriorly but strikingly expanded distally (35:1); 2Ax – the body is extremely short (40:1), the dorso-proximal lobe is orientated postero-proximad (41:1) and enlarged dorsally (42:1), the posterior margin is strikingly enlarged (43:1) and straight (44:1), the posterior section of the dorso-proximal ridge is strikingly enlarged above and laterad over the dorso-distal ridge (47:2), the dorso-proximal and dorso-distal ridge apices are enlarged, very broad (49:1), partially to completely fused (50:1), antero-medially to posteriorly sinuate (51:1), the dorso-distal ridge apex is convex and strikingly narrowly falcate (53:1), the posterior wing process junction shifted posteriad to occupy the postero-proximal section of the lobe and is greatly lengthened anteriorly (55:2), the ventro-proximal ridge lies adjacent to the ventro-distal ridge (56:2); 3Ax – the head is strikingly reduced posteriorly (57:1), the anterior surface is broad, enlarged ventrally and is concave (61:1); 1BP – the proximal arch of BR is strikingly broad, deltoid, with proximal (66:1) and distal (67:1) extensions, the embayment is extremely narrow (69:1), the dorsal surface of BScA is slenderly ovoid and very convex (72:1), the apex is broadly spatulate, strongly curved ventrad beneath the postero-proximal margin of the ScA bulge (74:1); 2BP – very narrowly scaphoid (76:1), BMA is completely fused to BMP antero-distal section (77:1), the BMA-BMP junction is continuous and narrowly tubular (79:1), BMP-BCuA brace fused to form a narrow looping tube (80:2) the postero-distal section is reduced (81:1), the BMP-brace junction is broadly continuous (82:1), the BMP-BCuA brace is moderately shifted distad (84:1), the terminus is strongly shifted distad to fuse with the distal margin of BCuA (88:1), BCuA is orientated antero-distad (90:1) and moderately shifted anteriad to occupy the postero-distal section of 2 bp (91:1).

The aphodiine group

Members of the aphodiine group, Aegialiini, Aphodiinae and *Aulonocnemis*, are united by eight derived states of the hindwing articulation and wing base (see Aphodiinae below). No difference between the wings of these three taxa was found, therefore the two representatives of *Aulonocnemis* examined for this study, *Aulonocnemis crassecostata* and *A. vulgaris*, should be treated as aphodiines (see Aphodiinae below).

The scarabaeine group

Members of the scarabaeine group, those taxa traditionally included in the Scarabaeinae, are united by twelve derived states of the hindwing articulation and wing base.

The orphnine line

The orphnine line displays the following twenty-two apomorphic character states of the hindwing articulation and wing base: 1Ax – the postero-proximal margin of the head is enlarged (7:1), the anterior surface is long (10:1), the ventral projection is long and narrow, enlarged mesally, the base is narrow and the apex broader (14:2) and flared (15:1), the ventral projection is orientated ventrad and posteriad (16:1), and partially to completely convex (19:1), the distal embayment is orientated more ventrad (22:2), the dorsal margin of FSc2 is enlarged dorsally and is broad (24:1); 2Ax – the anterior margin of the dorso-distal lobe is reduced (45:1), the dorso-distal margin of the anterior section of the dorso-distal ridge is exposed (46:1), the posterior section is broadly curved postero-proximad (48:1), the apex is convex to planate, strikingly elongate and aciculate (52:1), the anterior section is straight and anteriad (54:2); 3Ax – the tail is curved postero-distad (65:1); 1BP – the distal arch of BR is orientated postero-

---

Fig. 1. Diagrammatic representations of hindwing articulation and wing base character/state transformations indicated in text and Table 1. 1–6, first axillary, dorsal view; 7,8, first axillary, proximal view; 9, first axillary, dorsal view; 10–18, first axillary, anterior view; 19, first axillary, ventral projection, longitudinal cross-section; 20–24, first axillary, anterior view; 25–38, first axillary, dorsal view; 39–54, second axillary, dorsal view; 55,56, second axillary, ventral view; 57–65, third axillary, dorso-lateral view; 66–70, first basal plate, BR, dorsal view; 71, first basal plate, BScA, dorsal view; 72, first basal plate, BScA, cross-sectional view; 73, first basal plate, BScA, dorsal view; 74, first basal plate, BScA and ScA bulge, postero-dorsal view; 75–89, second basal plate, dorsal view; 90,91, second basal plate, BCuA and CuA, dorsal view; 92,93, second basal plate, BCuA, dorsal view. Small arrows indicate regions of phylogenetic importance. Non-schematic illustrations of the hindwing articulations and wing bases of scarabaeid taxa can be found in Browne & Scholtz (1995).

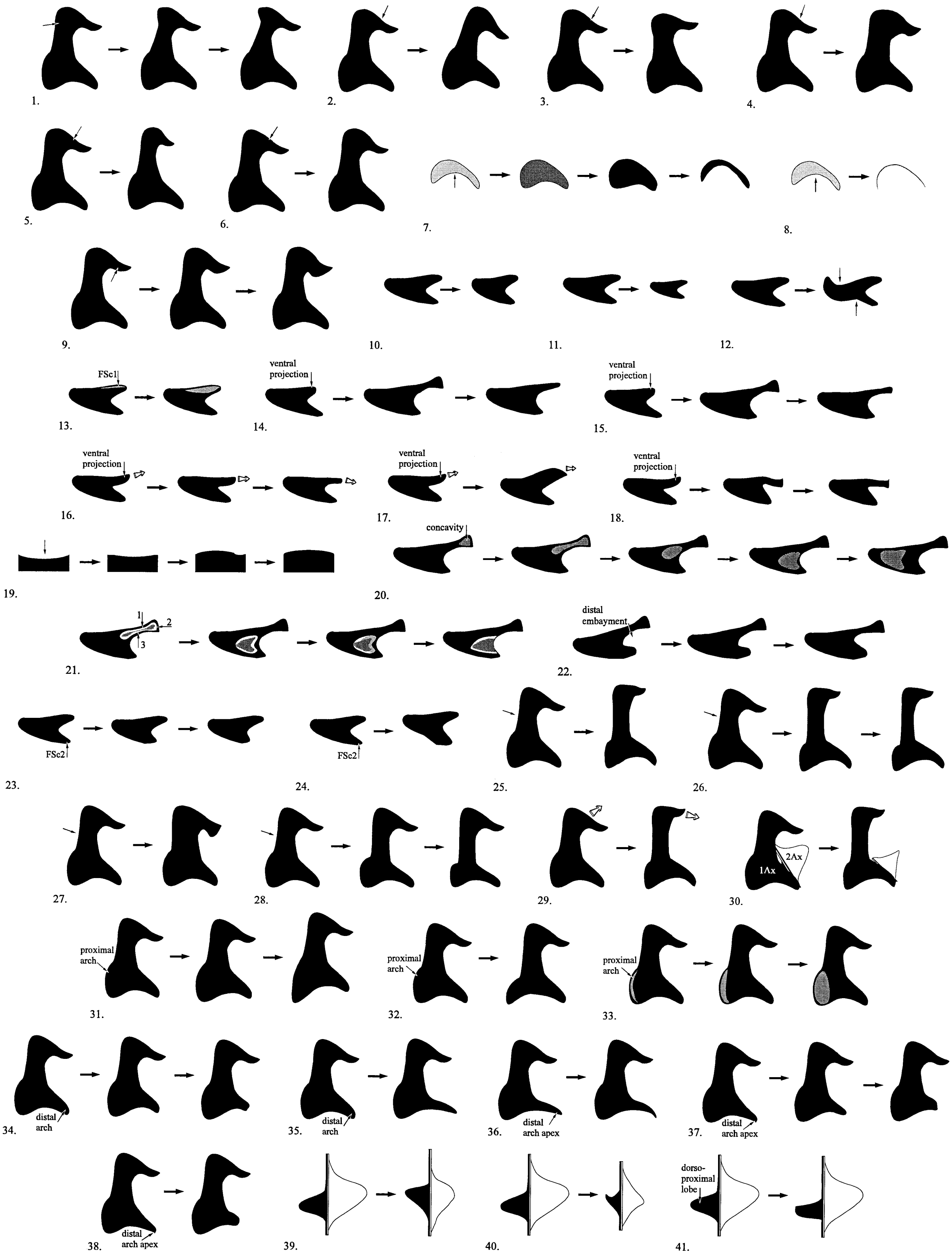
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
FSc1
13.
ventral projection
14.
ventral projection
15.
ventral projection
16.
ventral projection
17.
ventral projection
18.
19.
concavity
20.
1
2
3
21.
distal embayment
22.
FSc2
23.
FSc2
24.
25.
26.
27.
28.
29.
2Ax
1Ax
30.
proximal arch
31.
proximal arch
32.
proximal arch
33.
distal arch
34.
distal arch
35.
distal arch apex
36.
distal arch apex
37.
distal arch apex
38.
39.
40.
dorso-proximal lobe
41.

Fig. 1.

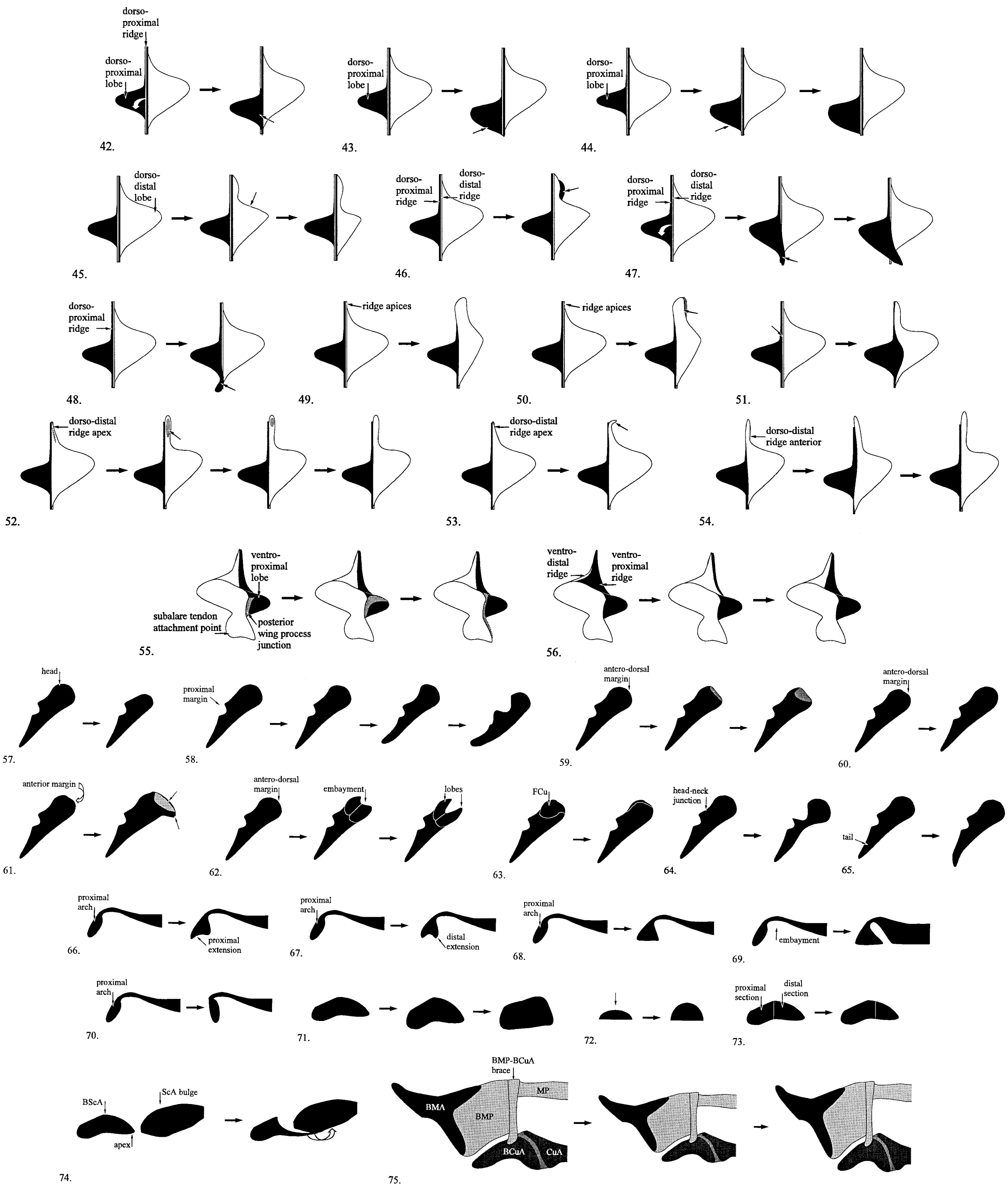

Fig. 1, continued.

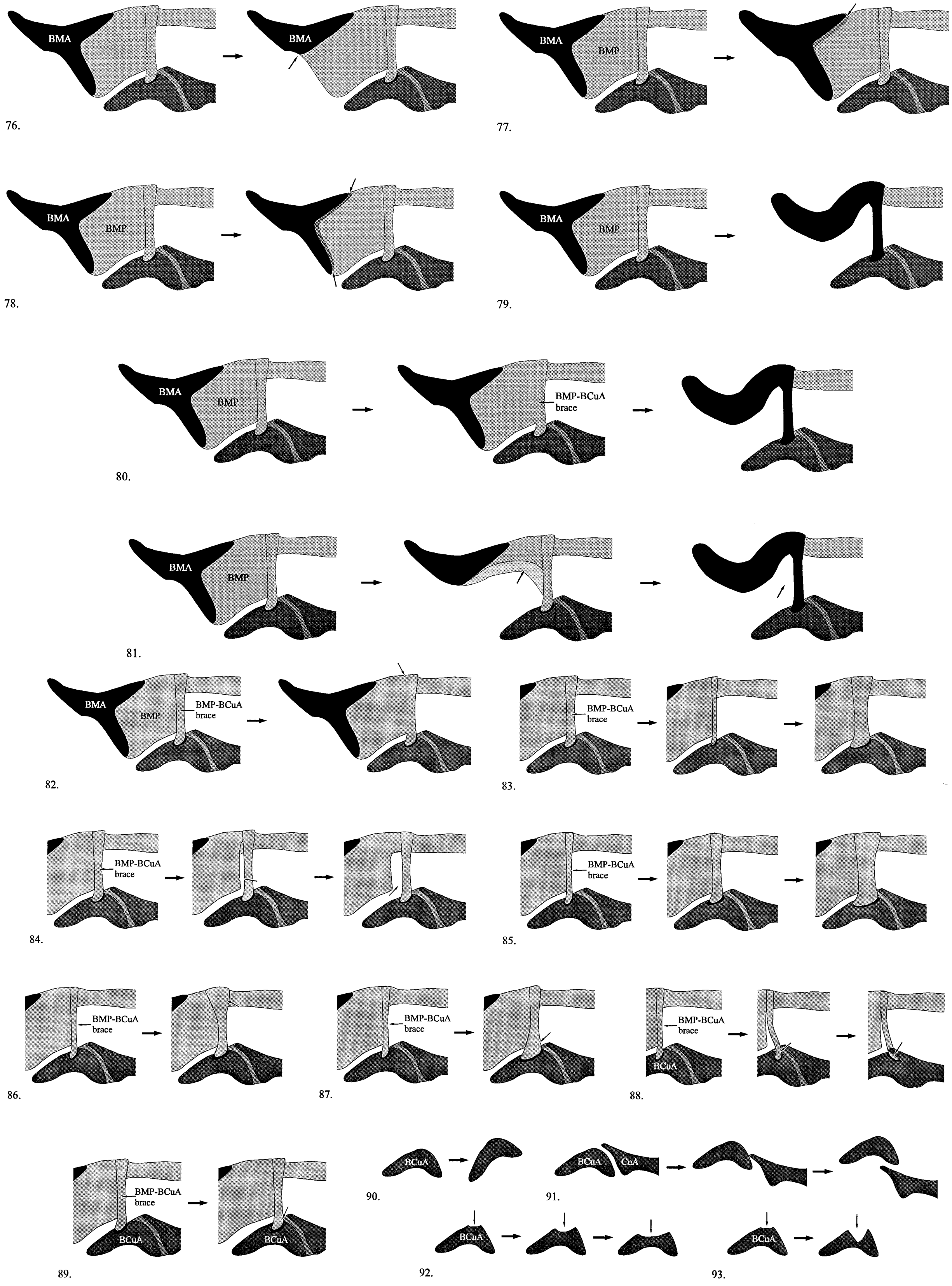

Fig. 1, continued.

Table 1. Characters and distribution of phylogenetically classified character states among Scarabaeidae taxa. Gl = Glaresidae, Ae = Aegialiini, Au = *Aulonocnemis*, Ap = Aphodiinae, Sc = Scarabaeinae, Or = Orphninae, Me = Melolonthinae, Ch = *Chnaunanthus*, On = *Oncerus*, Ac = *Acoma*, Ho = Hopliini, Ru = Rutelinae, Dy = Dynastinae, Os = *Osmoderma*, Tr = Trichiini, Ce = Cetoniinae, Va = Valginae.

	Taxa																
Character	Gl	Ae	Au	Ap	Sc	Or	Me	Ch	On	Ac	Ho	Ru	Dy	Os	Tr	Ce	Va
1	0	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
3	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
5	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
7	0	0	0	0	0	1	1	1	1	1	1	2	2	3	2	3	2
8	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	1	1	1	1	1	2	2	2	2	2	2
10	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
11	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
13	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
14	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
15	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2
16	0	0	0	0	0	1	1	1	1	1	1	2	2	2	2	2	2
17	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	2	1
19	0	0	0	0	0	1	1	1	1	1	1	2	2	3	2	3	3
20	0	0	0	0	0	0	1	1	1	1	1	2	2	3	4	4	4
21	0	0	0	0	0	0	0	0	0	0	0	1	1	2	3	3	3
22	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
23	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
25	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
26	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
28	0	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
29	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
30	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2
32	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2
34	0	0	0	0	0	0	0	0	0	0	0	2	2	1	1	1	1
35	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
36	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1
38	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
39	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
40	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
41	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
42	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
43	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
44	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	1	1	1	1	1	1	2	2	2	2	2	2
46	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
47	0	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
48	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
49	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
50	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
51	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	1	1	1	1	1	1	2	2	3	3	3	3
53	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
54	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
55	0	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1

Table 1 *continued*

	Taxa																
Character	Gl	Ae	Au	Ap	Sc	Or	Me	Ch	On	Ac	Ho	Ru	Dy	Os	Tr	Ce	Va
56	0	2	2	2	2	0	0	0	0	0	0	1	1	1	1	1	1
57	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
58	0	1	1	1	1	1	1	1	1	1	1	1	1	2	3	3	3
59	0	1	1	1	1	1	1	1	1	1	1	0	0	0	2	2	2
60	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
61	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2
63	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
64	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
65	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
66	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
67	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
69	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
71	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2
72	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
74	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
75	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
76	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
77	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
79	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
80	0	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
81	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
82	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
83	0	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
84	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
85	0	0	0	0	0	1	1	1	1	1	1	2	2	2	2	2	2
86	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
88	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
90	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
91	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
92	0	0	0	0	0	0	1	1	1	1	1	0	0	2	2	2	2
93	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0

proximad (70:2), BScA is broadly ovoid to rectangular (71:2C, convergence); 2BP – reduced proximally (75:2), the distal arch of BMA is indistinct, fused to the proximal section of BMP (78:1), the BMP-BCuA brace is entire, greatly strengthened (83:2), moderately enlarged (85:1) and terminally fused to the medial or disto-medial section of BCuA (89:1), and BCuA anterior surface with a broad concavity (92:1C).

The orphnine group

The orphnine group only contains Orphninae. This subfamily does not display any derived states of the hindwing articulation or wing base, but is instead characterized by a large number of plesiotypic character states.

The melolonthine group

This group contains the bulk of the Scarabaeidae taxa and is united by the following four derived states of the hindwing articulation and wing base: 1Ax – the FSc2 base is enlarged (9:1), the ventral projection concavity is shifted mesad of the preapical area (20:1); 2Ax – the body is slender and strikingly elongate (39:1); and 1BP – the postero-distal section of the proximal arch of BR is truncate (68:1).

The melolonthine subgroup

The melolonthine subgroup contains all those taxa traditionally placed in Melolonthinae, as well as *Acoma*,

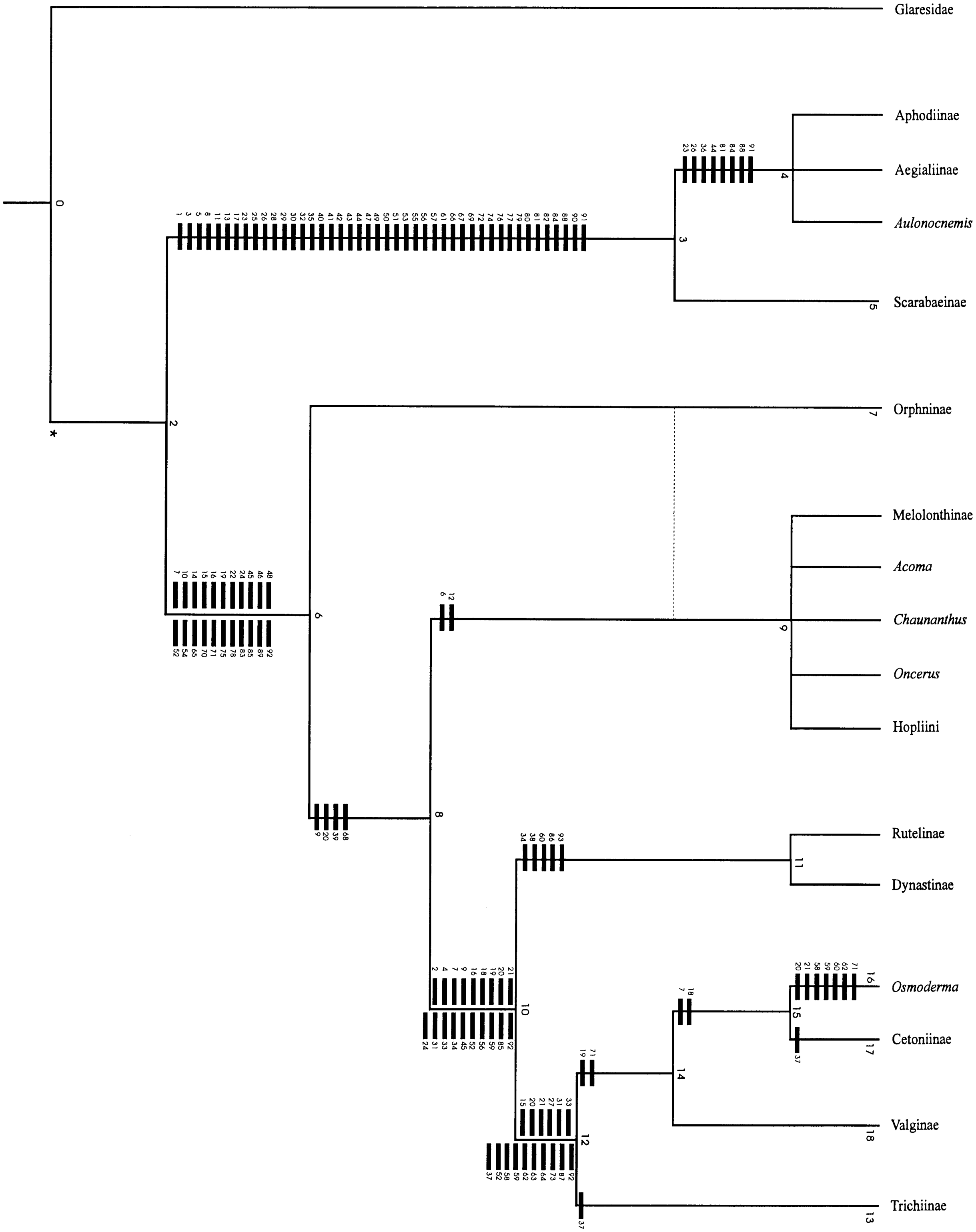

Fig. 2. Hypothesized branching patterns among members of Scarabaeidae based on ninety-three characters of the hindwing articulation and wing base (see Material and methods and Table 1). The tree shown here is the consensus tree of the two alternative trees produced by phylogenetic analysis; the first with the same topology as shown here, and the second with Orphninae as the sister group of the melolonthine subgroup, indicated by the dotted line. Solid boxes represent apotypic character states. Large numbers refer to branch points and smaller numbers refer to characters given in text (see Results and discussion). Characters which unite the Scarabaeidae (*) are given in Browne & Scholtz (1995).

'Chasmatopterinae', 'Hopliinae' and 'Oncerinae'. No differences between the hindwing articulation of wing base of these taxa were found and it is likely that *Acoma*, the monotypic subfamilies 'Chasmatopterinae' (as *Chnauanathus*) and 'Oncerinae' (as *Oncerus*), and 'Hopliinae' (as Hopliini) should be included within Melolonthinae. This subfamily displays only two derived states of the hindwing articulation and wing base (see Melolonthinae below).

The ruteline subgroup

This subgroup is united by the following nineteen derived states of the hindwing articulation and wing base: 1Ax – antero-dorsal margin of the head strikingly orientated postero-distad (2:1) and very broad (4:1), proximal enlargement of the postero-proximal margin of the head strongly enlarged (7:2), base of FSc2 moderately to very strongly enlarged (9:2), ventral projection orientated both ventrad and posteriad (16:2), partially or completely curved anteriad and/or posteriad (18:1), basally to subapically or basally to terminally convex (19:2), this concavity strongly shifted past the base of the ventral projection onto the anterior surface of the head (20:2) and the apical ridge reduced (21:1), dorsal margin of the anterior surface of FSc2 is not enlarged (24:0R, reversal), tail proximal arch moderately to strikingly expanded posteriorly and proximally (31:1), dorsal surface of the proximal arch moderately to deeply concave (33:1), distal arch reduced (34:1); 2Ax – dorso-distal lobe anterior margin strikingly reduced (45:2), dorso-distal ridge apex partially to completely planate, slender, strikingly elongate and aciculate (52:2), ventro-proximal ridge anterior section concealed by the ventro-distal ridge (56:1); 3Ax – antero-dorsal margin of the head weakly convex (59:0R); and 2BP – BMP-BCuA brace anteriorly or posteriorly strongly enlarged (85:2) and BCuA anterior surface concavity absent (92:0R).

The ruteline–dynastine infragroup

This infragroup is united by the following five derived character states of the hindwing articulation and wing base: 1Ax – tail distal arch strongly reduced (34:2) apex very broadly rounded (38:1); 3Ax – head convex (60:1C); 2BP – anterior and posterior sections of the BMP-BCuA brace anteriorly enlarged (86:1) and the concavity on the anterior surface of BCuA is extremely deep (93:1). No autapomorphic characters of the hindwing articulation or base support the separate origin of Rutelinae or Dynastinae.

The trichiine infragroup

The trichiine infragroup is united by the following sixteen derived states of the hindwing articulation and wing base: 1Ax – ventral projection basally, medially and apically of equal width (15:2), a convexity occurs from the base to the terminus which is strongly shifted dorso-mesad past the base of the ventral projection far onto the anterior surface of the head (20:4) with the apical ridge reduced (21:3), neck strikingly broad (27:1), tail proximal arch strongly expanded (31:2), dorsal surface of the proximal arch very deeply concave (33:2), distal arch apex moderately narrowly digitate (37:1); 2Ax – dorso-distal ridge apex completely planate, slender, strikingly elongate and aciculate (52:3); 3Ax – proximal margin of the head strikingly deeply concave (58:3), antero-dorsal margin strikingly deeply concave (59:2), head strikingly bi-lobed, embayment strong (62:2), FCu strikingly reduced distally (63:1), FCu-neck junction extremely narrow (64:1); 1BP – BScA proximal section of BScA much larger than the distal section (73:1); 2BP – posterior section of the BMP-BCuA brace enlarged (87:1) and the concavity on the anterior surface of BCuA is extremely broad (92:2).

Relationships between Trichiinae, Cetoniinae and Valginae are complex. *Osmoderma*, a very primitive trichiine genus (E. Holm, personal communication), is unusual in that it displays a unique mixture of primitive and derived character states that occur in different combinations in Rutelinae and Dynastinae, Trichiinae, Cetoniinae and Valginae. This analysis indicates that *Osmoderma* is the sister group of the Cetoniinae. The remaining trichiine species form the sister group of Valginae + Cetoniinae (including *Osmoderma*). *Osmoderma* shares two derived states of the hindwing articulation with Cetoniinae. It is likely that the former is a member of the latter (see Cetoniinae below). Valginae is a well defined subfamily, both in terms of wing and non-wing characters, and this analysis indicates it is the sister group of Cetoniinae + *Osmoderma* (see Valginae below).

The Scarabaeidae

Aegialiini

Aegialiini is a small, poorly defined tribe, but there is little doubt that it is one of the more primitive scarabaeid tribes (d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990). The diagnosis for this subfamily is virtually the same as that given for Aphodiinae (see below).

Although aegialiines do not exhibit any autapomorphic hindwing articulation or wing base characters, they do share eight derived character states of the wing articulation with *Aulonocnemis* and Aphodiinae, which together form a monophyletic group (see Aphodiinae below). It is likely that these three taxa together form Aphodiinae, as has been implied by other workers (Koshantschikov, 1913; Stebnicka, 1985; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990).

Aegialiini and Aphodiinae share apomorphic character states of the mouthparts (Nel & Scholtz, 1990), male genitalia (d'Hotman & Scholtz, 1990a), spiracles (Ritcher, 1969) and chromosomes (Virkki, 1967). Aegialiini also share many characters with *Aulonocnemis*, such as the shape of the wings (Balthasar, 1942), the shape of the male genitalia (d'Hotman & Scholtz, 1990a), larval morphology (Paulian & Lumaret, 1974), the general type of mouthparts (Scholtz, 1990), and food preferences and habits (Stebnicka, 1985).

Despite the lack of apomorphies which distinguish *Aulonocnemis* from Aphodiinae, and the lack of any reliable synapomorphies between Aegialiini and Aphodiinae, both Stebnicka (1985) and later Cambefort (1987) consider aegialiines to be intermediate between 'Aulonocneminae' and Aphodiinae. No wing articulation characters were found to support such a relationship. Therefore, we agree with Scholtz (1990) that Aegialiini is more correctly placed as a tribe of Aphodiinae.

'Aulonocneminae'

This is a small, poorly defined subfamily of four genera comprising about fifty 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). Adults are thought to be saproxylophagous (Cambefort, 1987). Because only two species of *Aulonocnemis* were available for this study, we felt that our discussion of phylogenetic placement of 'Aulonocneminae' should be restricted to *Aulonocnemis* alone.

The diagnosis of 'Aulonocneminae' is virtually the same as that of Aphodiinae (see below). Only a single derived character state separates *Aulonocnemis* from Aphodiinae, namely the presence of single apical spur on the hindtibia (Stebnicka, 1985), a convergent character state which is similarly used to separate *Leptohoplia* (Rutelinae) from Hopliini (Melolonthinae) (Howden & Hardy, 1971).

Many workers have regarded *Aulonocnemis* to be more closely related to Aegialiini than Aphodiinae (Stebnicka, 1985; Cambefort, 1987; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990). This was not supported in this study.

Aulonocnemis displays some apomorphic character states in common with Eupariini and secondarily with Psammodiini (both are derived aphodiine tribes) which are lacking in Aphodiini (a primitive aphodiine tribe) and Aegialiini. These include an elongate body shape, the antero-median area of the pronotum strongly elevated, a very small scutellum, middle and hindtibia flattened and without transverse carinae, and pygidium with transverse carinae. Similar synapomorphic character states prompted Koshantschikov (1913) to place a genus of 'Aulonocneminae', *Dialytoderus*, in Eupariini. Despite this seemingly clear distribution of non-wing character state distribution, *Aulonocnemis* is currently treated as a separate subfamily, 'Aluonocneminae', and considered to be most closely related to Aegialiini (Stebnicka, 1985; Cambefort, 1987). *Aulonocnemis* does not display any autapomorphic wing articulation character states, but does share eight derived wing articulation character states with Aphodiinae and Aegialiini, which together form a monophyletic group (see Aphodiinae below). The similarity shared between *Aulonocnemis* and Aphodiinae makes it desirable to place *Aulonocnemis* within Aphodiinae, probably within Eupariini. Furthermore, as Koshantschikov (1913) placed another 'aulonocnemine' genus, *Dialytoderus*, within Eupariini, it may also be desirable to provisionally place the two remaining 'aulonocnemine' genera in Aphodiinae.

Aphodiinae

Aphodiinae is a large cosmopolitan subfamily which has usually been considered one of the more primitive scarabaeid subfamilies (d'Hotman & Scholtz, 1990a; Scholtz, 1990). Aphodiinae species are small, brown or yellowish beetles. They have the pygidium covered and the hindtibia with two apical spurs. Larvae and adults are mostly dung feeders, but the larvae of some species feed on organic matter in the soil. Although Aphodiinae has long been accepted as the sister group of the Scarabaeinae, there has been some doubt as to the taxa which comprise the former (see above). Many workers have implied or suggested that aphodiines are most closely related to Aegialiini and 'Aulonocneminae' (Stebnicka, 1985; Cambefort, 1987; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990), a view which is supported by many synapomorphic character states, including those of the mouthparts (Nel & Scholtz, 1990), male genitalia (d'Hotman & Scholtz, 1990a), spiracles (Ritcher, 1969), chromosomes (Virkki, 1967), and wings.

Aphodiinae, together with Aegialiini and *Aulonocnemis*, display the following eight derived states of the hindwing articulation and wing base: 1Ax – FSc2 extremely small (23:2), neck extremely narrow (26:2), tail distal arch apex strongly curved posteriad (36:1); 2Ax – dorso-proximal lobe posterior margin broadly convex (44:2); 2BP – BMP postero-distal section absent (81:2), BMP-BCuA brace strongly shifted distad (84:2), terminus appears to fuse with the base of CuA (closer inspection shows that the brace posterior curves sharply mesad to fuse with the postero-proximal margin of BCuA) (88:2); and BCuA very strongly shifted anteriad in place of the postero-distal section of BMP (91:2).

Scarabaeinae

Scarabaeinae is a large, cosmopolitan, well defined subfamily that displays numerous derived character states, but is currently considered to be one of the more primitive scarabaeid subfamilies (d'Hotman & Scholtz, 1990a; Scholtz, 1990). Most adults and larvae are dung feeders. Adults provision brood chambers and in many instances remain with, and care for, the brood (Halffter & Matthews, 1966; Halffter & Edmonds, 1982). Many workers have suggested that scarabaeines occupy an intermediate position between Aphodiinae and Melolonthinae, but are more closely related to the former (for example see Howden, 1982). Many larval and adult character states support this relationship (Howden, 1982), including those of the mouthparts (Nel & Scholtz, 1990) and male genitalia (d'Hotman & Scholtz, 1990a).

Monophyly of the Scarabaeinae is supported by the fact that all of the taxa in this subfamily share the following twelve apomorphic character states of the wing articulation: 1Ax – FSc1 is very strongly elevated, long and orientated anterodorsad over the base of the ventral projection, FSc2 is completely planate, the neck is medially convex, the distal arch of the tail is strongly reduced anteriorly, strongly elongated distally and strongly reduced posteriorly; 2Ax – the posterior section of the dorso-proximal ridge is strikingly enlarged laterad, FM1 + FM2 together with the proximal extension of the 3Ax head are highly modified to form a ball-and-socket-like joint; 3Ax – the antero-proximal section of the head is narrowly enlarged proximally to form a long extension; 1BP – the proximal arch of BR is strikingly enlarged, the distal extension of the proximal arch is strikingly enlarged antero- to postero-distally, the BR embayment is strikingly narrow and falcate; and 2BP – extremely short and narrow.

Orphninae

The Orphninae is a small Old World group with a few genera (Nel & Scholtz, 1990). Adults and larvae have been recorded feeding on potatoes and sugar cane (Paulian & Lumaret, 1982). The Orphninae is a poorly defined subfamily, but there is little doubt that it is one of the more primitive members of the scarabaeid lineage (d'Hotman & Scholtz, 1990a). Orphninae have been associated with Hybosoridae (Iablokoff-Khnzorian, 1977; Paulian, 1984), Ochodaeidae (Blackwelder, 1944; Paulian, 1984) and Aphodiinae and Melolonthinae (Chalumeau & Gruner, 1974). d'Hotman & Scholtz (1990a) proposed that orphnines lie phylogenetically near Scarabaeinae and Melolonthinae. They found that the aedeagus resembles that of 'Hopliinae' and several Melolonthinae genera. This subfamily does not display any autapomorphic character states of the hindwing articulation or wing base.

Acoma

Acoma is a small genus which occurs in the western U.S.A. (Howden, 1958; Ritcher, 1969). Little is known about this genus and females have yet to be found (Howden, 1958). The diagnosis for *Acoma* is virtually the same as that of Melolonthinae (see below).

Both Arrow (1912, in Howden, 1958) and Leng (1920) placed *Acoma* in Pleocomidae. Davis (1924, in Howden, 1958) thought *Acoma* belonged near *Podolasia*, whereas Blackwelder (1944) listed it in the tribe Chasmatopterini of the subfamily Melolonthinae. Howden (1958) concluded that the phylogenetic placement of the genus is likely to remain in doubt until the morphology of the family is known. Ritcher (1969) has suggested that *Acoma* is related to one of the scarab subfamilies, but he does not elaborate. This genus does not display any autapomorphic hindwing articulation or wing base character states, but does share two apomorphic character states of the wing articulation with Melolonthinae, *Chnaunanthus*, *Oncerus*, and Hopliini (see Melolonthinae below). It is likely that these taxa together form a monophyletic group.

Chnaunanthus

Chnaunanthus is a well defined genus, based on non-wing characters, of uncertain phylogenetic status, but there is little doubt that it is one of the more derived scarab taxa closely related to Melolonthinae (Horn, 1867; Saylor, 1938; Blackwelder, 1944; d'Hotman & Scholtz, 1990a). The diagnosis for *Chnaunanthus* is virtually the same as that of Melolonthinae (see below).

Chnaunanthus was removed from Melolonthinae and elevated to subfamily status based on the position of the abdominal spiracles of the 7th and 8th segments in membrane (Saylor, 1938), but a re-examination of these by Ritcher (1969) found that the spiracles are actually situated in the lower parts of the tergites. *Chnaunanthus* is often commonly considered to belong to one of two melolonthine tribes, Chasmatopterini (Leng, 1920; Blackwelder, 1944; d'Hotman & Scholtz, 1990a), or Melolonthini (Nel & Scholtz, 1990). This genus does not display any autapomorphic hindwing articulation or wing base character states but does share two apomorphic character states of the wing articulation with Melolonthinae, *Acoma*, *Oncerus* and Hopliini, which together form a monophyletic group (see Melolonthinae below).

Oncerus

Oncerus is a well defined genus, based on non-wing characters, of uncertain phylogenetic status, but there is little doubt that it is one of the more derived scarab taxa closely related to Melolonthinae (Horn, 1867; Saylor, 1938). Although the diagnosis for *Oncerus* is virtually the same as that of Melolonthinae (see below), it has commonly been treated as a separate subfamily based on the non-melolonthine position of the abdominal spiracles (Horn, 1867). Leng (1920) placed *Oncerus* in a separate subfamily, 'Oncerinae', with *Chnaunanthus* and many other genera which are currently placed in Melolonthinae. This genus does not display any autapomorphic hindwing articulation or wing base character states, but does share two apomorphic character states of the wing articulation with Melolonthinae, *Acoma*, *Chnaunanthus*, and Hopliini which together form a monophyletic group (see Melolonthinae below).

Hopliini

Hopliini is small, ill defined tribe of uncertain phylogenetic status (d'Hotman & Scholtz, 1990a,b). This tribe is widespread and is found in the Palaearctic, Nearctic, Neotropical, Oriental and Afrotropical Regions (Hardy, 1977). Hopliines are usually active by day and use their well developed hind legs and claws to anchor and then to extract themselves from the composite flowers into which they tunnel and feed (Scholtz & Holm, 1985). The diagnosis for Hopliini is virtually the same as that of Melolonthinae (see below). Only a single autapomorphic character state separates Hopliini from other melolonthines, that is the presence of a pair of abdominal spiracles on the 7th segment in the tergite (Ritcher, 1969).

Members of this tribe are sometimes considered to be members of Rutelinae (Scholtz & Holm, 1985) or rarely 'Oncerinae' (Leng, 1920). However, this tribe is more often treated as a member of Melolonthinae (Blackwelder, 1944; Ritcher, 1969; Howden & Hardy, 1971; Hardy, 1977; Scholtz, 1990). Caveney (1986) found that the structure of the eye is similar to that of *Macrodactylus* (a primitive melolonthine). Analysis of hindwing articulation and wing base characters did not support such a specific relationship. This tribe does not display any autapomorphic hindwing articulation or wing base character states but does share two apomorphic character states of the wing articulation with Melolonthinae, *Acoma*, *Chnaunanthus* and *Oncerus*, with which it forms a monophyletic group (see Melolonthinae below).

Melolonthinae

Melolonthinae is a very large, diverse cosmopolitan, poorly defined subfamily. However, there is little doubt that it is one of the more derived scarab subfamilies (Yadav & Pillai, 1976; Howden, 1982; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990).

Melolonthines have been associated with Glaphyridae and 'Oncerinae' (Fowler, 1912, in Yadav & Pillai, 1976), Aphodiinae (Yadav, 1973) and Dynastinae (Howden, 1982). However, Melolonthinae is most commonly considered to be the sister group of Rutelinae or Rutelinae + Dynastinae (Ritcher, 1969; Meinecke, 1975; Yadav & Pillai, 1976; Caveney, 1986; Scholtz, 1990; Lawrence & Britton, 1991). This subfamily does not display any autapomorphic wing articulation character states but does share the following two apomorphic character states of the wing articulation with *Acoma*, *Chnaunanthus*, *Oncerus*, and Hopliini, which together form a monophyletic group: 1Ax – head antero-dorsal margin very convex (6:1) and the antero-distal surface narrows medially (12:1).

Rutelinae

Rutelinae is a well defined subfamily, based on non-wing characters, and there is little doubt that it is one of the more derived scarab subfamilies (Howden, 1982; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990). Some Anomalini (*Popilla*) differ from other rutelines in that the karyotype is 8 + Xy (Scholtz, 1990).

Rutelinae has usually been associated with both Melolonthinae and Dynastinae (Ritcher, 1969; Howden, 1982; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990). However, from the common tree, Rutelinae are more closely related to Dynastinae, and Melolonthinae the sister group of this lineage (Meinecke, 1975; Howden, 1982). This subfamily does not display any autapomorphic hindwing articulation or wing base character states but does share five apomorphic character states of the wing with Dynastinae, its sister group.

Dynastinae

Dynastinae is a well defined subfamily, based on non-wing characters, and there is little doubt that it is one of the more derived scarab subfamilies (Howden, 1982; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990). Dynastinae has usually been associated with Rutelinae (Ritcher, 1969; Howden, 1982; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990). This subfamily does not display any autapomorphic hindwing articulation or wing base character states but does share the following five apomorphic character states of the wing with Rutelinae, its sister group.

Trichiinae and Osmoderma

Trichiinae is a poorly defined subfamily of uncertain phylogenetic status (d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990). This is a medium-sized group with cosmopolitan distribution (Nel & Scholtz, 1990). Adults are usually flower or sap feeders. Larvae feed on decaying plant material (Nel & Scholtz, 1990).

Trichiinae (in this context including *Osmoderma*) is most commonly associated with Cetoniinae and Valginae, as either a cetoniine tribe (Leng, 1920; Ritcher, 1969; Caveney, 1986; Scholtz, 1990), or a separate subfamily (Blackwelder, 1944; Howden, 1968; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990). Trichiinae, with what was supposed to be its sister group, Valginae, is considered to be more primitive than Cetoniinae (Krikken, 1984).

Trichiinae have abdominal spiracle pair 1–3 in the pleural membrane and 6–7 in the sternites and six ovarioles per side (both primitive states). *Osmoderma* has abdominal pairs 1 and 2 in the pleural membrane and 3–6 in the sternites, whereas cetoniines have pairs 1–3 in the membrane and 4–6 in the sternites (all derived states) (Ritcher, 1969). *Osmoderma*, cetoniines and valgines have twelve ovarioles per side (the derived state) (Ritcher & Baker, 1974). The evidence indicates that Trichiinae is a polyphyletic subfamily with *Osmoderma* as a separate group, perhaps the sister group of Cetoniinae, and the remainder of Trichiinae the sister group of Cetoniinae (including Osmoderma) + Valginae.

Osmoderma displays the following nine autapomorphic hindwing articulation and wing base character states: 1Ax – ventral projection very short, concavity strongly shifted dorsomesad past the base of the ventral projection on the anterior surface of the head (20:3R) with the apical ridge weakly reduced (21:2R); 2Ax – subalare tendon attachment point strikingly enlarged; 3Ax – head moderately deeply concave (58:2R), antero-dorsal margin convex (59:0CR and 60:1C), anterior margin strikingly bi-lobed, embayment weak (62:1R); and 1BP – BScA broadly ovoid (71:1CR). *Osmoderma* shares two autapomorphic hindwing articulation character states with

Cetoniinae with which it forms a monophyletic group (see Cetoniinae below). Trichiinae displays only a single autapomorphic hindwing articulation character states: 1Ax – tail distal arch apex narrowly digitate, very weakly postero-distad (37:2C).

Cetoniinae

Cetoniinae is a well defined subfamily that displays several derived character states. It is commonly considered to be one of the more derived scarab subfamilies (d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990).

Cetoniines were once placed in Rutelinae (Leng, 1920) but are now most commonly regarded as the sister group of Rutelinae and/or Dynastinae (Ritcher, 1969; Meinecke, 1975; Howden, 1982; Caveney, 1986; d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990; Scholtz, 1990). Krikken (1984) considers Trichiinae + Valginae to be the primitive sister group of Cetoniinae, and Rutelinae + Dynastinae the sister group of Trichiinae + Valginae + Cetoniinae. Although there is no doubt that Cetoniinae, Trichiinae and Valginae are very closely related, there is some question as to the rank of these taxa.

Cetoniinae share the following two autapomorphic hindwing articulation character states with *Osmoderma*, with which it forms a monophyletic group: 1Ax – head postero-proximal margin strong but narrowly enlarged (7:3) and the ventral projection weakly curved anteriad (18:2). Cetoniinae (including *Osmoderma*) share two autapomorphic character states of the hindwing articulation and wing base with Valginae (see Valginae below). Cetoniines display only a single autapomorphic wing articulation character state: 1Ax – tail distal arch apex narrowly digitate, very weakly postero-distad (37:2C).

Valginae

Valginae is a well defined subfamily, often considered to be the most derived scarab subfamily (d'Hotman & Scholtz, 1990a; Nel & Scholtz, 1990), with 265 species in thirty-one genera (Krikken, 1978). This subfamily is widespread, occurring all the major zoogeographic regions except the Neotropics (Krikken, 1978). Most adults are usually small flower-visitors feeding on nectar and pollen (Krikken, 1978), but others are associated with termites (Scholtz, 1990). Larvae feed almost exclusively on decomposing vegetable debris, although some groups occur in termite nests (Scholtz, 1990).

Valgines differ from Cetoniinae in non-wing characters in that the larvae do not have maxillary and mandibular stridulatory areas. Valginae are the sister group of the Cetoniinae (including *Osmoderma*), with which they share the following two autapomorphic character states of the hindwing articulation and wing base: 1Ax – ventral projection base to terminus convex (19:3); and 1BP – BScA rectangular (71:2C).

Monophyly of the Valginae is supported by the fact that all members of this subfamily display ten apomorphic character states of the hindwing articulation and wing base: 1Ax – extremely narrow, head and neck much smaller than the tail, tail proximal arch strikingly enlarged posteriorly; 2Ax – subalare tendon attachment point strikingly long, narrow and acerose; 3Ax – proximal and distal lobes of head are exceedingly narrow and very long, embayment extremely deep and extends posteriorly to the head-neck junction, FCu-neck junction extremely narrow; 1BP – HP strongly lengthened distally as an extremely slender, sinuate sclerite, sclerotized section of ScA which lies between HP anteriorly, and BScA posteriorly and proximally, is completely reduced and membranous, and BScA distal section is extremely slender and the proximal section very broad.

Acknowledgements

For loan of material we thank Dr S. Endrödy-Younga (Transvaal Museum, Pretoria), Dr D. Carlson (California), Professor J. Doyen (University of California, Berkeley), Dr A. Hardy (Department of Food and Agriculture, California), Professor E. Holm (University of Pretoria), Professor H. Howden (Carleton University, Ottawa), Mr M. Kerley (The Natural History Museum, London), Mrs J. McNamara (Biosystematics Research Institute, Ottawa), Dr O. Merkl (Hungarian Museum of Natural History, Budapest) and Professor S. Peck (Carleton University, Ottawa). Dr J. Kukalová-Peck (Carleton University, Ottawa) offered incisive remarks and suggestions, as did an anonymous reviewer, incorporation of which contributed to a much improved manuscript. J.B. is especially grateful to the following people for extending their courtesies throughout the duration of this project: Ronald and Mary Browne (Ottawa), Catherine Yarymowich (Toronto), Steven Chown, Gustav Praekelt, Marianne and Clarke Scholtz (Pretoria), Ron Boyd, Henry Howden, Glen Kit, Jarmila Kukalová-Peck, Stewart Peck, Mike Weber (Ottawa), Lutz Auerswald, Pierre Janssens and Reinhard Predel (Cape Town). This project was funded by the Foundation for Research Development, Pretoria.

References

Balthasar, V. (1942) Über die Nervatur des Hinterflügels der Lamellicornien: eine Phylogenetisch-systematische und Vergleich-endmorphologische Studie. *Věstnik Československé Společnosti Nauk Praha*, **11**, 1–43.

Blackwelder, R.E. (1944) Checklist of the coleopterous insects of North America, Mexico, Central America, the West Indies and South America. *United States National Museum Bulletin*, **185**, 197–265.

Brooks, D.R. & McLennan, D.A. (1991) *Phylogeny, Ecology, and Behavior: a Research Program in Comparative Biology.* The University of Chicago Press, London.

Browne, D.J. (1993) *Phylogenetic significance of the hindwing basal articulation of the Scarabaeoidea* (*Coleoptera*). PhD thesis, University of Pretoria.

Browne, D.J. & Scholtz, C.H. (1994) The morphology and terminology of the hindwing articulation and wing base of the Coleoptera, with specific reference to the Scarabaeoidea. *Systematic Entomology*, **19**, 133–143.

Browne, D.J. & Scholtz, C.H. (1995) Phylogeny of the families of Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hindwing base and wing venation. *Systematic Entomology*, **20**, 145–173.

Browne, J. & Scholtz, C.H. (1998) A phylogeny of the families of Scarabaeoidea (Coleoptera). *Systematic Entomology* (in press).

Cambefort, Y. (1987) Insectes Coléoptères Aulonocneminae. *Faune de Madagascar*, **69**, 3086.

Caveney, S. (1986) The phylogenetic significance of ommatidium structure in the compound eyes of polyphagan beetles. *Canadian Journal of Zoology*, **64**, 1787–1819.

Chalumeau, F. & Gruner, L. (1974) Scarabaeoidea des Antilles Françaises. *Annales Société Entomologique de France*, **10**, 781–819.

Crowson, R.A. (1967) *The Natural Classification of the Families of Coleoptera*. Classey, Hampton.

Halffter, G. & Edmonds, W.D. (1982) *The Nesting Behaviour of Dung Beetles* (*Scarabaeinae*). Instituto de Ecologia, Mexico.

Halffter, G. & Matthews, E.G. (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologia Mexicana*, **12**–**14**, 3–312.

Hardy, A.R. (1977) A revision of the *Hoplia* of the Nearctic realm (Coleoptera: Scarabaeidae). *Occasional Papers in Entomology*, **23**, 1–48.

Horn, G.H. (1867) Descriptions of new genera and species of western Scarabaeidae, with notes on others already known. *Transactions of the American Entomological Society*, **22**, 163–169.

d'Hotman, D. & Scholtz, C.H. (1990a) Phylogenetic significance of the structure of the external male genitalia in Scarabaeoidea. *Entomology Memoirs*, **77**, 1–51.

d'Hotman, D. & Scholtz, C.H. (1990b) Comparative morphology of the male genitalia of derived groups of Scarabaeoidea (Coleoptera). *Elytron*, **4**, 3–39.

Howden, H.F. (1958) Species of *Acoma* having a three-segmented antennal club (Coleoptera: Scarabaeidae). *The Canadian Entomologist*, **95**, 377–401.

Howden, H.F. (1968) A review of the Trichiinae of North and Central America (Coleoptera: Scarabaeidae). *The Entomological Society of Canada*, **54**, 1–75.

Howden, H.F. (1982) Larval and adult characters of *Frickius* Germain, its relationship to the Geotrupini, and a phylogeny of some major taxa in the Scarabaeoidea (Insecta: Coleoptera). *Canadian Journal of Zoology*, **60**, 2713–2724.

Howden, H.F. & Hardy, A.R. (1971) Generic placement and adult behaviour of the genus *Leptohoplia* Saylor. *Proceedings of the Entomological Society of Washington*, **73**, 337–341.

Iablokoff-Khnzorian, S.M. (1977) Über die Phylogenie der Lamellicornia. *Entomologische Abhandlungen der Statlichen Museum für Tierkunde in Dresden*, **41**, 135–199.

Koshantschikov, W. (1913) Sescher Beitrag zur Kenntnis der Aphodiini (Coleoptera, Lamellicornia). *Archiv für Naturgeschichte*, **79A**, 186–203.

Krikken, J. (1978) Valgine beetles: a preliminary review of the genera, with descriptions of two novelties. *Zoologische Mendedelingen*, **15**, 153–164.

Krikken, J. (1984) A new key to the suprageneric taxa in the beetles family Cetoniidae, with annotated lists of the known genera. *Zoologishce Verhandelingen*, **210**, 3–75.

Kukalová-Peck, J. & Lawrence, J.F. (1993) Evolution of the hindwing in Coleoptera. *The Canadian Entomologist*, **125**, 181–258.

Lawrence, J.F. & Britton, E.B. (1991) Coleoptera. *Insects of Australia*. CSIRO, Canberra, Australia.

Leng, C.W. (1920) *Catalogue of the Coleoptera of America, North of Mexico*. John D. Sherman, New York.

Mayr, E. & Ashlock, P.D. (1991) *Principles of Systematic Zoology*, 2nd edn. McGraw-Hill, London.

Meinecke, C.C. (1975) Reichensensillen und Systematik der Lamellicornia (Insecta, Coleoptera). *Zoomorphologie*, **82**, 1–42.

Nel, A. & Scholtz, C.H. (1990) Comparative morphology of the mouthparts of adult Scarabaeoidea. *Entomology Memoirs*, **80**, 1–84.

Nixon, K.C. & Davis, J.I. (1991) Polymorphic taxa, missing values and cladistic analysis. *Cladistics*, **7**, 223–241.

Paulian, R. (1984) Les Orphnidae américains (Coléoptères, Scarabaeoidea). *Annales de la Société Entomologique de France*, **20**, 65–92.

Paulian, R. & Lumaret, J.-P. (1974) Les larves des Scarabaeidae: 4. Le genre *Aulonocnemis* Schaufuss. *Bulletin de la Société Entomologique de France*, **79**, 223–240.

Paulian, R. & Lumaret, J.-P. (1982) Le larve des Orphnidae (Col. Scarabaeoidea). *Bulletin de la Société Entomologique de France*, **87**, 263–272.

Ritcher, P.O. (1969) Spiracles of adult Scarabaeoidea (Coleoptera) and their phylogenetic significance. I. The abdominal spiracles. *Annals of the Entomological Society of America*, **62**, 869–880.

Ritcher, P.O. & Baker, C.W. (1974) Ovariole numbers in Scarabaeoidea (Coleoptera: Lucanidae, Passalidae, Scarabaeidae). *Proceedings of the Entomological Society of London*, **76**, 480–494.

Saylor, L.W. (1938) Revision of the subfamily Oncerinae with description of a new genus (Coleoptera: Scarabaeidae). *Proceedings of the Entomological Society of Washington*, **40**, 99–103.

Scholtz, C.H. (1990) Phylogenetic trends in the Scarabaeoidea. *Journal of Natural History*, **24**, 1027–1066.

Scholtz, C.H. & Browne, D.J. (1996) Polyphyly in the Geotrupidae (Coleoptera: Scarabaeoidea): a case for a new family. *Journal of Natural History*, **30**, 597–614.

Scholtz, C.H., Browne, D.J. & Kukalová-Peck, J. (1994) Glaresidae, archaeopteryx of the Scarabaeoidea (Coleoptera). *Systematic Entomology*, **19**, 259–277.

Scholtz, C.H. & Chown, S.L. (1995) The evolution of habitat use and diet in the Scarabaeoidea: a phylogenetic approach. *Biology, Phylogeny, and Classification of Coleoptera*. Muzeum i Instytut Zoologii PAN, Warszawa.

Scholtz, C.H. & Holm, E. (1985) *Insects of Southern Africa*. Butterworths, Durban.

Stebnicka, A.Z. (1985) A new genus and species of Aulonocneminae from India with notes on comparative morphology (Coleoptera: Scarabaeidae). *Revue Suisse Zoologique*, **92**, 649–658.

Swofford, D.L. (1985) *Phylogenetic Analysis using Parsimony.* Illinois Natural History Survey, Urbana, Illinois.

Virkki, N. (1967) Chromosome relationships in some North American scarabaeoid beetles, with special reference to *Pleocoma* and *Trox. Canadian Journal of Genetics and Cytology*, **9**, 107–125.

Yadav, J.S. (1973) Chromosome number and sex-determining mechanism in fourteen species of Coleoptera. *Current Science*, **42**, 514.

Yadav, J.S. & Pillai, R.K. (1976) Karyotypic studies on five species of Melolonthinae (Scarabaeidae: Coleoptera). *The Nucleus*, **19**, 195–200.

Accepted 4 November 1997

Appendix 1. Taxa studied.

Superfamily Hydrophiloidea
- Hydrophilidae: *Hydrophilus*, *Pseudohydrobius*, *Rygmodus*, Spercheus
- Synteliidae: *Syntelia*
- Sphaeritidae: *Sphaerites*
- Histeridae: *Hister*, *Teretriosoma*, *Pactolinus*

Superfamily Staphylinoidea
- Agyrtidae: *Necrophilus*
- Silphidae: *Diamesus*
- Staphylinidae: *Creophilus*, *Scaphidium*

Superfamily Dascilloidea
- Dascillidae: *Dascillus*

Superfamily Scarabaeoidea
- Glaresidae: *Glaresis*
- 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*, *Benedictia*, *Lichnanthe*, *Toxocerus*
- Trogidae: *Trox*, *Omorgus*, *Polynoncus*
- Bolboceratidae: *Athyreus*, *Australobolbus*, *Blackbolbus*, *Blackburnium*, *Bolbaineus*, *Bolbapium*, *Bolboceras*, *Bolbocerastes*, *Bolbocerosoma*, *Bolbocerosum*, *Bolbochromus*, *Bolbogonium*, *Bolbohamatum*, *Bolbelasmus*, *Bolboleaus*, *Bolborhachium*, *Bolborhinum*, *Bolborhombus*, *Bradycinetulus*, *Elephastomus*, *Eucanthus*, *Gilletinus*, *Neoathyreus*, *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*
- Ochodaeidae: *Chaetocanthus*, *Ochodaeus*, *Pseudochodaeus*, *Synochodaeus*
- Scarabaeidae: *Acognatha*, *Acoma*, *Aegialia*, *Agamopus*, *Alaberoides*, *Allokotarsa*, *Amphimallon*, *Anachalcos*, *Anatochilus*, *Anisonyx*, *Anomala*, *Anomaluera*, *Aphodius*, *Aphonides*, *Apogonia*, *Archophileurus*, *Asthenopholis*, A*taenius*, *Aulonocnemis*, *Bolax*, *Brachymacroma*, *Callirhinus*, *Camenta*, *Camentoserica*, *Campilipus*, *Campsiura*, *Catharsius*, *Canthidium*, *Canthon*, *Cartwrightia*, *Chironitis*, *Chlorocala*, *Chnaunanthus*, *Circellium*, *Coenochilus*, *Colobopterus*, *Comythovalgus*, *Copris*, *Coprophanaeus*, *Coptorhina*, *Cotinus*, *Cyclocephala*, *Cyclomera*, *Cymophorus*, *Cyphonistes*, *Cyptochirus*, *Cyrioperta*, *Deltochilum*, *Deltorrhinum*, *Diastictus*, *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*, *Macrodactylus*, *Melinesthes*, *Milichus*, *Neoserica*, *Nyassinus*, *Olbaberoides*, *Oncerus*, *Oniticellus*, *Onitis*, *Onthophagus*, *Oplostomus*, *Orizabus*, *Orphnidus*, *Orphnus*, *Osmoderma*, *Oxygrylius*, *Oxysternon*, *Pachycnema*, *Paracotalpa*, *Parathyce*, *Pedaria*, *Pedaridium*, *Pelidnota*, *Peritrichia*, *Phacosoma*, *Phalogogonia*, *Phalops*, *Phanaeus*, *Phileurus*, *Philoscaptus*, *Phobetus*, *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*, *Uroxys*, *Valgus*, *Xinidium*, *Xyloryctes*

Appendix 2. Character states used in cladistic analysis.

The format followed in this section enables cross-referencing of each transformation series with the phylogram (Fig. 2), for example: 1. *Head – dorsal surface, proportions*: (0) normal; (1) strongly reduced posteriorly; (2) strikingly reduced posteriorly. $[0_0 \rightarrow 1_2 \rightarrow 2_3]$. CI 1.000. In this case $[0_0 \rightarrow 1_2 \rightarrow 2_3]$ denotes that 0 is the primitive state, 1 the intermediate state and 2 the derived state. The transformation series progresses from branch point 0 to branch point 2 to branch point 3 on the phylogram (Fig. 2). The consistency index (CI) of this character is 1.000. The following are descriptions of the plesiomorphic (0) and apomorphic (1, 2, 3, 4) character states for the characters used in this analysis.

Hindwing articulation, first axillary (Fig. 1: 1–38)

1. *Head – dorsal surface, proportions*: (0) normal; (1) strongly reduced posteriorly; (2) strikingly reduced posteriorly. $[0_0 \rightarrow 1_2 \rightarrow 2_3]$. CI 1.000.
2. *Head – antero-dorsal margin, orientation*: (0) weakly to moderately postero-distad; (1) strikingly postero-distad. $[0_8 \rightarrow 1_{10}]$. CI 1.000.
3. *Head – antero-dorsal margin, orientation*: (0) weakly to moderately postero-distad; (1) distad. $[0_2 \rightarrow 1_3]$. CI 1.000.
4. *Head – antero-dorsal margin, width*: (0) normal; (1) very broad. $[0_8 \rightarrow 1_{10}]$. CI 1.000.
5. *Head – antero-dorsal margin, width*: (0) normal; (1) reduced, extremely narrow. $[0_2 \rightarrow 1_3]$. CI 1.000.
6. *Head – antero-dorsal margin, form*: (0) planate to weakly deplanate; (1) very convex. $[0_8 \rightarrow 1_9]$. CI 1.000.
7. *Head – postero-proximal margin, degree and width of proximal enlargement*: (0) weak and narrow; (1) moderate and broad; (2) strong and very broad; (3) strong but very narrow. $[0_2 \rightarrow 1_6{:}1_8 \rightarrow 2_{10}{:}2_{14} \rightarrow 3_{15}]$. CI 1.000.
8. *Head – postero-proximal margin, degree and width of proximal enlargement*: (0) weak and narrow; (1) absent. $[0_2 \rightarrow 1_3]$. CI 1.000.
9. *Head – postero-dorsal surface, FSc2, base, width*: (0) normal; (1) weakly enlarged; (2) moderately to very strongly enlarged. $[0_6 \rightarrow 1_8 \rightarrow 2_{10}]$. CI 1.000.
10. *Head – anterior surface, length*: (0) very long; (1) long. $[0_2 \rightarrow 1_6]$. CI 1.000.
11. *Head – anterior surface, length*: (0) very long; (1) strikingly short and narrow. $[0_2 \rightarrow 1_3]$. CI 1.000.
12. *Head – antero-distal surface, width*: (0) not waisted; (1) waisted. $[0_8 \rightarrow 1_9]$. CI 1.000.
13. *Head – anterior surface, FSc1, shape and form*: (0) absent or very weak; (1) short or long, broad, strongly convex. $[0_2 \rightarrow 1_3]$. CI 1.000.
14. *Head – anterior surface, ventral projection, relative proportions*: (0) short but of normal width, base very broad, median broad, apex less broad; (1) long and narrow, enlarged mesally, base very broad, median broad, apex less broad; (2) long and narrow, enlarged mesally, base narrow, apex broader. $[0_0 \rightarrow 1_2 \rightarrow 2_6]$. CI 1.000.
15. *Head – anterior surface, ventral projection, apex, width*: (0) narrow; (1) strongly flared; (2) flare reduced. $[0_2 \rightarrow 1_6{:}1_{10} \rightarrow 2_{12}]$. CI 1.000.
16. *Head – anterior surface, ventral projection, orientation*: (0) orientated disto-ventrad and curved posteriad; (1) more strongly orientated ventrad and weakly curved posteriad; (2) strongly orientated both ventrad and posteriad. $[0_2 \rightarrow 1_6{:}1_8 \rightarrow 2_{10}]$. CI 1.000.
17. *Head – anterior surface, ventral projection, orientation*: (0) orientated disto-ventrad and curved posteriad; (1) more strongly orientated postero-distad, weakly ventrad and not curved posteriad. $[0_2 \rightarrow 1_3]$. CI 1.000.
18. *Head – anterior surface, ventral projection, form*: (0) broadly curved posteriad; (1) basally to subapically curved anteriad, apically curved posteriad; (2) straight or weakly curved anteriad. $[0_8 \rightarrow 1_{10}{:}1_{14} \rightarrow 2_{15}]$. CI 1.000.
19. *Head – anterior surface, ventral projection, shape*: (0) deeply concave; (1) base to median concave or partially convex; (2) base to subapical area convex; (3) base to terminus convex. $[0_2 \rightarrow 1_6{:}1_8 \rightarrow 2_{10}{:}2_{12} \rightarrow 3_{14}]$. CI 1.000.
20. *Head – anterior surface, ventral projection, concavity, position and shape*: (0) concavity in preapical area; (1) concavity basad and weakly to strongly extended apicad from the base of the ventral projection; (2) concavity strongly shifted mesad just past the base of the ventral projection onto the anterior surface of the head, and not extended apicad; (3) concavity strongly shifted dorso-mesad past the base of the ventral projection on the anterior surface of the head, and not extended apicad; (4) concavity very strongly shifted dorso-mesad past the base of the ventral projection far onto the anterior surface of the head, not extended apicad. $[0_6 \rightarrow 1_8 \rightarrow 2_{10} \rightarrow 4_{12}{:}4_{15} \rightarrow 3_{16}]$. CI 1.000.
21. *Head – anterior surface, ventral projection, concavity, structure*: (0) concavity surrounded by three unequally strong ridges of unequal length; (1) concavity surrounded by three equally strong ridges of equal length; (2) concavity surrounded by three ridges of equal length with the apical ridge weakly reduced; (3) concavity surrounded by three ridges of equal length with the apical ridge strongly reduced to absent. $[0_8 \rightarrow 1_{10} \rightarrow 3_{12}{:}3_{15} \rightarrow 2_{16}]$. CI 1.000.
22. *Head – anterior surface, distal embayment, orientation*: (0) more dorsad; (1) more mesad; (2) more ventrad. $[0_0 \rightarrow 1_2 \rightarrow 2_6]$. CI 1.000.
23. *Head – anterior surface, FSc2, shape and form*: (0) deltoid and very convex; (1) reduced, small, round and partially or completely planate; (2) even smaller. $[0_2 \rightarrow 1_3 \rightarrow 2_4]$. CI 1.000.
24. *Head – anterior surface, FSc2, dorsal margin, relative size*: (0) not enlarged; (1) enlarged dorsally, broad. $[0_2 \rightarrow 1_6{:}1_8 \rightarrow 0_{10}]$. CI 0.500.
25. *Head and neck – dorsal surface, form*: (0) weakly curved proximad; (1) extended anteriad. $[0_2 \rightarrow 1_3]$. CI 1.000.
26. *Neck – width*: (0) normal; (1) very narrow; (2) strikingly narrow. $[0_2 \rightarrow 1_3 \rightarrow 2_4]$. CI 1.000.
27. *Neck – width*: (0) normal; (1) strikingly broad. $[0_{10} \rightarrow 1_{12}]$. CI 1.000.
28. *Neck – length*: (0) normal; (1) long; (2) strikingly long. $[0_0 \rightarrow 1_2 \rightarrow 2_3]$. CI 1.000.
29. *Neck – dorsal surface, orientation*: (0) weakly antero-distad; (1) very strongly distad and ventrad. $[0_2 \rightarrow 1_3]$. CI 1.000.
30. *Neck and tail – articulation with 2Ax*: (0) articulation extends along the distal margin of the neck and tail; (1) reduced anteriorly, articulation extends along the distal margin of the tail. $[0_2 \rightarrow 1_3]$. CI 1.000.
31. *Tail – proximal arch, size*: (0) normal; (1) moderately expanded posteriorly and proximally; (2) strikingly expanded posteriorly and proximally. $[0_8 \rightarrow 1_{10} \rightarrow 2_{12}]$. CI 1.000.
32. *Tail – proximal arch, size*: (0) normal; (1) strikingly reduced anteriorly and posteriorly, expanded proximally. $[0_2 \rightarrow 1_3]$. CI 1.000.

33. *Tail – proximal arch, dorsal surface, form*: (0) weakly concave; (1) moderately concave; (2) deeply concave. $[0_{8}\rightarrow 1_{10}\rightarrow 2_{12}]$. CI 1.000.
34. *Tail – distal arch, size*: (0) normal; (1) moderately reduced anteriorly, distally and posteriorly; (2) strikingly reduced anteriorly, distally and posteriorly. $[0_{8}\rightarrow 1_{10}\rightarrow 2_{11}]$. CI 1.000.
35. *Tail – distal arch, size*: (0) normal; (1) markedly reduced anteriorly and posteriorly, strikingly expanded or elongated distally. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
36. *Tail – distal arch, apex, form*: (0) weakly curved posteriad; (1) strongly curved posteriad. $[0_{3}\rightarrow 1_{4}]$. CI 1.000.
37. *Tail – distal arch, apex, shape and orientation*: (0) aciculate; (1) moderately narrowly digitate, weakly postero-distad; (2) narrowly digitate, very weakly postero-distad. $[0_{10}\rightarrow 1_{12}:1_{15}\rightarrow 2_{17}:1_{12}\rightarrow 2_{13}]$. CI 0.667.
38. *Tail – distal arch, apex, shape and orientation*: (0) aciculate; (1) very broadly rounded. $[0_{10}\rightarrow 1_{11}]$. CI 1.000.

Hindwing articulation, second axillary (Fig. 1: 39–56)

39. *2Ax – body, relative proportions*: (0) about as long as broad; (1) slender and strikingly elongate. $[0_{6}\rightarrow 1_{8}]$. CI 1.000.
40. *2Ax – body, relative proportions*: (0) about as long as broad; (1) extremely short. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
41. *Dorso-proximal lobe – orientation*: (0) proximad; (1) postero-proximad. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
42. *Dorso-proximal lobe – position relative to dorso-proximal ridge*: (0) arises from the postero-medial section of ridge, depressed below the ridge; (1) arises from the posterior section of ridge, enlarged to the same dorsal plane as the ridge. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
43. *Dorso-proximal lobe – posterior margin, degree of posterior enlargement*: (0) weakly enlarged; (1) strikingly enlarged. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
44. *Dorso-proximal lobe – posterior margin, form*: (0) concave; (1) straight; (2) broadly convex. $[0_{2}\rightarrow 1_{3}\rightarrow 2_{4}]$. CI 1.000.
45. *Dorso-distal lobe – anterior margin, length*: (0) normal; (1) moderately reduced; (2) strikingly reduced. $[0_{2}\rightarrow 1_{6}:1_{8}\rightarrow 2_{10}]$. CI 1.000.
46. *Dorso-proximal ridge – anterior section, position*: (0) completely concealed by the dorso-distal ridge; (1) dorso-distal margin exposed. $[0_{2}\rightarrow 1_{6}]$. CI 1.000.
47. *Dorso-proximal ridge – antero-median to postero-median section, position*: (0) depressed below the dorso-distal ridge; (1) moderately enlarged above and laterad over the dorso-distal ridge; (2) strongly to strikingly enlarged above and laterad over the dorso-distal ridge. $[0_{0}\rightarrow 1_{2}\rightarrow 2_{3}]$. CI 1.000.
48. *Dorso-proximal ridge – posterior section, orientation*: (0) posteriad or postero-distad; (1) broadly curved postero-proximad. $[0_{2}\rightarrow 1_{6}]$. CI 1.000.
49. *Ridge apices – dorsal surface, width*: (0) narrow; (1) enlarged, very broad. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
50. *Ridge apices – apices, degree of fusion*: (0) not fused; (1) partially to completely fused. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
51. *Dorso-proximal and dorso-distal ridges – antero-median to posterior, shape*: (0) straight; (1) sinuate. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
52. *Dorso-distal ridge – apex, form and shape*: (0) convex and broadly falcate; (1) convex, slender, strikingly elongate; (2) partially planate, slender, strikingly elongate; (3) completely planate, slender, strikingly elongate. $[0_{2}\rightarrow 1_{6}:1_{8}\rightarrow 2_{10}\rightarrow 3_{12}]$. CI 1.000.
53. *Dorso-distal ridge – apex, form and shape*: (0) convex and broadly falcate; (1) convex and strikingly narrowly falcate. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
54. *Dorso-distal ridge – anterior section, form*: (0) curved proximad; (1) extended antero-proximad or curved distad; (2) straight and anteriad. $[0_{0}\rightarrow 1_{2}\rightarrow 2_{6}]$. CI 1.000.
55. *Ventro-proximal lobe – posterior wing process junction, position*: (0) occupies the posterior margin of the lobe; (10 occupies the postero-proximal section of the lobe and is greatly lengthened anteriorly, extending to, and running along the anterior margin of the lobe; (2) shifted posteriad to occupy the extreme postero-proximal corner of the subalare tendon attachment point. $[0_{0}\rightarrow 1_{2}\rightarrow 2_{3}]$. CI 1.000.
56. *Ventro-proximal ridge – anterior section, position*: (0) completely or partially conceals the ventro-distal ridge; (1) concealed by the ventro-distal ridge; (2) lies adjacent to the ventro-distal ridge. $[0_{8}\rightarrow 1_{10}:0_{2}\rightarrow 2_{3}]$. CI 1.000.

Hindwing articulation, third axillary (Fig. 1: 57–65)

57. *Head – length*: (0) normal; (1) strikingly reduced posteriorly. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
58. *Head – proximal margin, form*: (0) convex or straight; (1) shallowly concave; (2) moderately deeply concave; (3) strikingly deeply concave. $[0_{0}\rightarrow 1_{2}:1_{10}\rightarrow 3_{12}:3_{15}\rightarrow 2_{16}]$. CI 1.000.
59. *Head – antero-dorsal margin, form*: (0) weakly convex or straight; (1) weakly concave; (2) very deeply concave. $[0_{0}\rightarrow 1_{2}:1_{8}\rightarrow 0_{10}\rightarrow 2_{12}:2_{15}\rightarrow 0_{16}]$. CI 0.500.
60. *Head – antero-dorsal margin, form*: (0) weakly convex or straight; (1) convex. $[0_{10}\rightarrow 1_{11}:0_{15}\rightarrow 1_{16}]$. CI 0.500.
61. *Head – anterior surface, form*: (0) narrow, not enlarged ventrally, convex; (1) broad, enlarged ventrally, concave. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
62. *Head – shape*: (0) formed as a single lobe or very weakly bi-lobed, embayment absent; (1) strikingly bi-lobed, embayment weak; (2) strikingly bi-lobed, embayment strong. $[0_{10}\rightarrow 2_{12}:2_{15}\rightarrow 1_{16}]$. CI 1.000.
63. *Head – FCu, size*: (0) normal; (1) strikingly reduced distally. $[0_{10}\rightarrow 1_{12}]$. CI 1.000.
64. *Head-neck junction – width*: (0) very broad; (1) strikingly reduced, extremely narrow. $[0_{10}\rightarrow 1_{12}]$. CI 1.000.
65. *Tail – AXA, form*: (0) straight; (1) curved postero-distad. $[0_{2}\rightarrow 1_{6}]$. CI 1.000.

Hindwing base, first basal plate (Fig. 1: 66–74)

66. *BR – proximal arch, size and shape*: (0) slenderly deltoid; (1) strikingly broad, deltoid, with a proximal extension. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
67. *BR – proximal arch, distal extension*: (0) absent; (1) present. $[0_{2}\rightarrow 1_{3}]$. CI 1.000.
68. *BR – proximal arch, postero-distal section, form*: (0) rounded; (1) truncate. $[0_{6}\rightarrow 1_{8}]$. CI 1.000.

69. *BR – embayment, size*: (0) normal; (1) extremely narrow. [$0_2 \rightarrow 1_3$]. CI 1.000.
70. *BR – distal arch, orientation*: (0) postero-proximad; (1) postero-distad. [$0_2 \rightarrow 1_6$]. CI 1.000.
71. *BScA – shape*: (0) slenderly ovoid; (1) broadly ovoid; (2) rectangular. [$0_2 \rightarrow 1_6 : 1_{12} \rightarrow 2_{14} : 2_{15} \rightarrow 1_{16}$]. CI 0.667.
72. *BScA – dorsal surface, shape and form*: (0) slenderly ovoid, weakly convex; (1) slenderly ovoid and very convex. [$0_2 \rightarrow 1_3$]. CI 1.000.
73. *BScA – proximal and distal sections, relative size*: (0) proximal section as large as, or smaller than the distal section; (1) proximal section much larger than the distal section. [$0_{10} \rightarrow 1_{12}$]. CI 1.000.
74. *BScA – apex, shape and orientation*: (0) broadly rounded, distad; (1) broadly spatulate, strongly curved ventrad beneath the postero-proximal margin of the ScA bulge. [$0_2 \rightarrow 1_3$]. CI 1.000.

Hindwing base, second basal plate (Fig. 1: 75–93)

75. *2BP – size*: (0) massive or very large; (1) very strongly reduced on all margins; (2) reduced proximally. [$0_0 \rightarrow 1_2 \rightarrow 2_6$]. CI 1.000.
76. *BMA – shape*: (0) broadly scaphoid; (1) very narrowly scaphoid. [$0_2 \rightarrow 1_3$]. CI 1.000.
77. *BMA – distal arch*: (0) distinct; (1) indistinct, completely fused to BMP antero-distal section. [$0_2 \rightarrow 1_3$]. CI 1.000.
78. *BMA – distal arch*: (0) distinct; (1) indistinct, fused to BMP proximal section. [$0_2 \rightarrow 1_6$]. CI 1.000.
79. *BMA and BMP – junction, degree of fusion and shape*: (0) discontinuous and very broad; (1) continuous and narrowly tubular. [$0_2 \rightarrow 1_3$]. CI 1.000.
80. *BMP – form*: (0) planate; (1) BMP fused to brace, markedly convex; (2) BMP and brace fused to form a narrow, looping tube. [$0_0 \rightarrow 1_2 \rightarrow 2_3$]. CI 1.000.
81. *BMP – postero-distal section, presence*: (0) present; (1) partially reduced; (2) very weakly sclerotized to absent. [$0_2 \rightarrow 1_3 \rightarrow 2_4$]. CI 1.000.
82. *BMP – junction with brace, degree of fusion*: (0) discontinuous; (1) broadly continuous. [$0_2 \rightarrow 1_3$]. CI 1.000.
83. *BMP-BCuA brace – relative strength*: (0) entire and strong; (1) entire but only moderately strong; (2) entire and greatly strengthened. [$0_0 \rightarrow 1_2 \rightarrow 2_6$]. CI 1.000.
84. *BMP-BCuA brace – position*: (0) extends posteriad; (1) moderately shifted distad; (2) strongly shifted distad. [$0_2 \rightarrow 1_3 \rightarrow 2_4$]. CI 1.000.
85. *BMP-BCuA brace – width*: (0) slender; (1) moderately enlarged; (2) anteriorly or posteriorly strongly enlarged. [$0_2 \rightarrow 1_6 : 1_8 \rightarrow 2_{10}$]. CI 1.000.
86. *BMP-BCuA brace – anterior and posterior sections, relative width*: (0) equally broad; (1) anteriorly enlarged. [$0_{10} \rightarrow 1_{11}$]. CI 1.000.
87. *BMP-BCuA brace – anterior and posterior sections, relative width*: (0) equally broad; (1) posteriorly enlarged. [$0_{10} \rightarrow 1_{12}$]. CI 1.000.
88. *BMP-BCuA brace – terminus, position*: (0) fused to the proximal section of BCuA; (1) strongly shifted distad to fuse with the distal margin of BCuA; (2) appears to fused with the base of CuA. [$0_2 \rightarrow 1_3 \rightarrow 2_4$]. CI 1.000.
89. *BMP-BCuA brace – terminus, position*: (0) fused to the proximal section of BCuA; (1) fused to the medial or the disto-medial section of BCuA. [$0_2 \rightarrow 1_6$]. CI 1.000.
90. *BCuA – orientation*: (0) postero-distad or distad; (1) antero-distad. [$0_2 \rightarrow 1_3$]. CI 1.000.
91. *BCuA – position*: (0) posteriad of BMP; (1) moderately shifted anteriad to occupy the postero-distal section of 2BP; (2) strongly shifted anteriad to occupy the postero-distal section of 2BP. [$0_2 \rightarrow 1_3 \rightarrow 2_4$]. CI 1.000.
92. *BCuA – anterior surface, concavity, form*: (0) absent to moderately broad; (1) broad; (2) extremely broad. [$0_2 \rightarrow 1_6 : 1_8 \rightarrow 0_{10} \rightarrow 2_{12}$]. CI 0.667.
93. *BCuA – anterior surface, concavity, form*: (0) absent to shallow; (1) extremely deep. [$0_{10} \rightarrow 1_{11}$]. CI 1.000.