

# The species-level phylogeny of archostematan beetles—where do *Micromalthus debilis* and *Crowsoniella relictata* belong?

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**Abstract.** A species-level phylogenetic analysis comprising 37 of the 45 known extant species of archostematan beetles and a total of 110 morphological characters from adults and larvae is presented. For the first time, characters of the male genitalia are included in a phylogenetic analysis of Archostemata. The dataset is analysed with parsimony as well as with Bayesian algorithms. Analyses with differently arranged datasets, with larval characters included or excluded, and including or excluding *Micromalthus debilis* and *Crowsoniella relictata* are conducted. The resulting hypothesis of the species-level phylogeny of Archostemata confirms Cupedidae and Ommatidae as monophyletic taxa. Within Cupedidae, the South American *Paracupes* and the North American *Priacma* together are the sister group to all remaining Cupedidae. Among the latter, the identification of a clade comprising *Rhipsideigma*, *Cupes capitatus* and *Tenomerga leucophaea* renders *Tenomerga* polyphyletic. *Ascioplaga scalena* **comb. nov.** is transferred from *Adinolepis*. Characters of the male genitalia support phylogenetic affinities of *Micromalthus debilis* with Ommatidae and of *Crowsoniella relictata* with Cupedidae.

## Introduction

Archostemata is one of four suborders of beetles (Coleoptera) (e.g. Crowson, 1960; Lawrence & Newton, 1995), and constitutes the smallest and the least investigated of these suborders. Recent investigations of the basal phylogeny of Coleoptera place Archostemata as sister group to all other extant beetles (i.e. the Adephaga and Myxophaga and Polyphaga: Beutel & Haas 2000; Caterino *et al.*, 2002; Hughes *et al.*, 2006). There are other interpretations, for example with Polyphaga as sister group to all other beetles and Archostemata as sister group to Adephaga or Myxophaga (e.g. Baehr, 1976; Kukalová-Peck & Lawrence, 1993, 2004), or together with Myxophaga as sister group to Adephaga + Polyphaga (Hunt *et al.*, 2007). However, at present the position as sister group to the remaining Coleoptera seems to be the best supported.

Currently, 45 extant archostematan species are known worldwide, and five families are recognized: Ommatidae, containing two genera and six species; Cupedidae with nine genera

and 36 species; and the monotypic families Crowsoniellidae, Micromalthidae and possibly Jurodidae (Lawrence & Newton, 1995; Kirejtshuk, 1999; Hörnschemeyer, 2005).

*Crowsoniella relictata* and *Micromalthus debilis* are remarkable for different reasons. *Crowsoniella relictata* is known only from three male specimens collected in 1973 in Italy by Roberto Pace (Pace, 1975). With a total length of approximately 1.5 mm, the species is comparatively small for an archostematan beetle. Furthermore, there are many special morphological features, for example missing alae, modified and reduced mouth parts, and smooth elytra without the otherwise characteristic archostematan window punctures. Nothing is known about its biology, and, although many have tried, it has not been possible to collect additional specimens. *Micromalthus debilis* is of a similar small size and also shows numerous modifications. However, in habitus it is very different from *C. relictata*. The biology and many aspects of the anatomy of larvae and adults are quite well known. *Micromalthus debilis* shows the most complex life cycle among Coleoptera, comprising four externally different larval forms, including a paedogenetic larva, an arrhenotokous reproductive pathway and a thelytokous pathway (Pollock & Normark, 2002).

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Whether the adults are capable of reproducing is still uncertain (for summary and references see Hörschemeyer, 2005).

Another aberrant, probably archostematan, species is *Sikhotealinia zhiltzovae* (Lafer, 1996), currently placed in its own family Jurodidae (Kirejtshuk, 1999). It is known only from the holotype and shows a combination of polyphagan-like wing venation and morphological characteristics of abdomen, thorax and head that are otherwise found in Adephaga and Archostemata.

The phylogeny of Archostemata has so far been studied only at the family or genus level, with moderate taxon sampling (e.g. Hörschemeyer *et al.*, 2002; Beutel & Hörschemeyer, 2002a, b; Hörschemeyer *et al.*, 2006; Beutel *et al.*, 2008), and the phylogenetic relationships of *C. relictata*, *M. debilis* and *S. zhiltzovae* are still not satisfactorily resolved. Hörschemeyer *et al.* (2002) and Beutel & Hörschemeyer (2002a) found *M. debilis* to be the sister group of Cupedidae, and *C. relictata* as the sister group of Ommatidae. This position of *C. relictata* is in agreement with Crowson (1975), who associated it with *Tetrapteralerus*, at least partially because of the presence of lateral antennal grooves on the heads of *Crowsoniella* and *Tetrapteralerus*. The close relationship of *M. debilis* to Cupedidae is based mainly on larval characters. Beutel & Hörschemeyer (2002b) and Hörschemeyer *et al.* (2006) also determined *M. debilis* to be closely related to Cupedidae. However, *Crowsoniella* turned out as sister group to *M. debilis* + Cupedidae. Beutel *et al.* (2008) included extinct taxa in their analysis and established a clade comprising some fossil groups, *S. zhiltzovae*, *C. relictata* and *M. debilis*. This clade was the sister group to Cupedidae. Even though the character sampling of that study was very comprehensive, the problem remained that most support for this clade was due to loss of characters.

The present study aims to reconstruct the species-level phylogeny of Archostemata based on a comprehensive morphological dataset utilizing characters from structures such as the male genitalia that so far have not been used in analyses of archostematan phylogeny, and comprising as many extant species as possible.

## Materials and methods

### Material

Specimens from the following collections were examined.

ANIC: Australian National Insect Collection, Canberra City, Australia.  
 BMNH: The Natural History Museum, London, England.  
 BPBM: Bernice P. Bishop Museum, Honolulu, Hawaii.  
 FMNH: Field Museum of Natural History, Chicago, USA.  
 LACM: Natural History Museum of Los Angeles County, Los Angeles, USA.  
 MCZC: Museum of Comparative Zoology, Cambridge, USA.  
 MSNV: Museo Civico di Storia Naturale, Verona, Italy.  
 MTEC: Montana Entomology Collection, Bozeman, USA.  
 NMV: Museum Victoria, Entomology, Melbourne, Australia.

QMBA: Queensland Museum, South Brisbane, Australia.  
 SMTD: Staatliches Museum für Tierkunde, Dresden, Germany

TMSA: Transvaal Museum, Pretoria, South Africa.

UMRM: Wilbur R. Enns Entomology Museum, University of Missouri, Columbia, USA.

USNM: National Museum of Natural History, Washington D.C., USA.

WAM: Western Australian Museum, Perth, Australia.

ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

ZMHB: Museum für Naturkunde der Humboldt-Universität zu Berlin, Institut für Systematische Zoologie, Berlin, Germany.

ZSMC: Zoologische Staatssammlung München, München, Germany.

In addition to specimens from scientific collections, the author received specimens for preparation from the following persons: Dr R. G. Beutel (Jena, Germany; p-BEUT), Dr M. Hauser (Urbana, USA; p-MH), Dr J. F. Lawrence (Gympie, Australia), S. Lubkin (Ithaca, USA), Dr M. A. Perotti (Bangor, UK), Dr D. A. Pollock (Portales, USA), Dr R. Staals (Pretoria, South Africa), Dr W. Steiner (Washington, USA), Dr D. K. Young (Madison, USA).

Specimens now in the collection of the author are labelled with p-ThH.

Altogether, more than 400 specimens from 37 species of Archostemata were investigated.

In the following, the species are listed in alphabetical order. The information is arranged as follows: genus species; biogeographic realm; collection, type status (if applicable).

*Adinolepis apodema* (Neboiss, 1987): Australasian; WAM, Holotype.

*Adinolepis eumana* (Neboiss, 1960): Australasian; NMV, Holotype, ANIC, Paratype

*Adinolepis mathesonae* (Neboiss, 1960): Australasian; NMV, Holotype; ANIC.

*Adinolepis youanga* (Neboiss, 1960): Australasian; NMV, Holotype; ANIC, Paratype; ANIC; p-ThH.

*Ascioplaga mimeta* (Neboiss, 1984): Australasian; QMBA; p-MH.

*Ascioplaga scalena* (Neboiss, 1984) **comb. nov.** (previously in *Adinolepis*): Australasian; ANIC, Holotype.

*Ascioplaga sciasma* (Neboiss, 1984): Australasian; BPBM, Holotype; QMBA.

*Crowsoniella relictata* (Pace, 1975): western Palearctic; MSNV, Holotype; Paratype.

*Cupes capitatus* (Fabricius, 1801): Nearctic; FMNH; SMTD; USNM; p-ThH.

*Distocupes varians* (Lea, 1902): Australasian; ANIC, Holotype; ANIC; p-ThH.

*Micromalthus debilis* (LeConte, 1878): Nearctic; SMTD; MTEC, Dominican Amber, foss.; UMRM.

*Omma mastersii* (Macleay, 1869): Australasian; ANIC.

*Omma sagitta* (Neboiss, 1989): Australasian; BMNH.

*Omma stanleyi* (Newman, 1839): Australasian; ANIC; SMTD; USNM, p-BEUT.  
*Paracupes brasiliensis* (Kolbe, 1898): Neotropical; BMNH; ZSMC; ZMHB, Holotype.  
*Priacma serrata* (Leconte, 1861): Nearctic; MCZC, Holotype; FMNH; LACM; p-MH; p-ThH.  
*Prolixocupes latreillei* (Solier, 1849): Neotropical; SMTD; FMNH; USNM; BMNH; p-MH.  
*Prolixocupes lobiceps* (Leconte, 1874): Nearctic; MCZC, Holotype; FMNH; LACM; USNM; LACM, Paratype of *C. boycei*.  
*Rhipsideigma cretaceotincta* (Kolbe, 1897): Afrotropic; ZSMC; BMNH; FMNH.  
*Rhipsideigma lugubris* (Fairmaire, 1895): Afrotropic; FMNH.  
*Rhipsideigma raffrayi* (Fairmaire, 1884): Afrotropic; FMNH; ZFMK; BMNH.  
*Tenomerga anguliscutis* (Kolbe, 1886): eastern Palearctic; ZFMK; ZMHB, Lectotype.  
*Tenomerga cinerea* (Say, 1831): Nearctic; LACM; USNM; ZSMC; p-ThH; p-MH; SMTD; *Cupes oculatus*: USNM, Paratype; FMNH.  
*Tenomerga favella* (Neboiss, 1984): eastern Indo-malay; BMNH, Holotype.  
*Tenomerga japonica* (Tamanuki, 1928): eastern Palearctic; LACM; BMNH.  
*Tenomerga kapnodes* (Neboiss, 1984): northern Australasia, eastern Indo-malay; BPBM, Holotype; BPBM.  
*Tenomerga leucophaea* (Newman, 1839): Afrotropic; TMSA; p-ThH; ZMHB, Holotype.  
*Tenomerga moultoni* (Gestro, 1910): eastern Indo-malay; BMNH; SMTD.  
*Tenomerga mucida* (Chevrolat, 1829): eastern Palearctic; USNM; *Cupes ocellaris*: BMNH, Holotype; *Cupes clathratus*: BMNH; SMTD; ZFMK.  
*Tenomerga sibyllae* (Klapperich, 1950): eastern Palearctic; ZFMK, Holotype; ZFMK, Paratype.  
*Tenomerga trabecula* (Neboiss, 1984): eastern Palearctic; ZFMK, Paratype; ZMHB, Holotype.  
*Tenomerga yamato* (Miyatake, 1985): eastern Indo-malay; ZMHB.  
*Tetraphalerus bruchi* (Heller, 1913): Neotropical; SMTD, Holotype; NMNH; USNM, p-BEUT; BMNH.  
*Tetraphalerus wagneri* (Waterhouse, 1901): Neotropical; BMNH, Holotype; NMNH.

## Methods

One specimen of each of the following species was investigated by high-resolution computed X-ray tomography ( $\mu$ CT): *Cupes capitatus*, *Tenomerga cinerea*, *Distocupes varians*, *Ascioplaga mimeta*, *Priacma serrata*, *Tetraphalerus bruchi* and *Micromalthus debilis*. The specimens designated for  $\mu$ CT investigation were treated with Dubosq-Brasil (Romeis, 1968) for 2 days, then gradually transferred to 100% ethanol and dried at the critical point (Balzers CPD 030 Critical Point Dryer). The  $\mu$ CT data for *Cu. capitatus*, *Tet. bruchi* and *As.*

*mimeta* (Hörschemeyer *et al.*, 2006) were obtained by Dr J. Goebbels and J. Nötel at the Federal Institute for Materials Research and Testing (BAM), Berlin, Germany. *Priacma serrata* was scanned at SkyScan by F. Pasop (Hörschemeyer *et al.*, 2002), and the datasets for *D. varians*, *M. debilis* and *T. cinerea* were produced at the Advanced Photon Source (APS) of the Argonne National Laboratory (ANL), USA with the help of Dr F. De Carlo.

Specimens for SEM investigation were either dehydrated with ethanol, dried at the critical point and sputter-coated with gold (Balzers SCD050) and studied and imaged with a LEO 438 VP scanning electron microscope, or they were studied in the high-pressure mode of the SEM without prior drying and coating.

TGS AMIRA 4.1 software was used for the processing of  $\mu$ CT data and images.

The terminology for muscles of the head follows Kéler (1963). Character handling and analysis were carried out with MESQUITE (Maddison & Maddison, 2007), PAUP\* 4.0b10 (Swofford, 2001) and MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Bremer-support values were calculated with AUTODECAY 5.0 (Eriksson, 2003). *Blattella germanica* (Linnaeus, 1767) (Blattodea), *Sialis lutaria* (Linnaeus, 1758) (Megaloptera: Sialidae), *Trachypachus* sp. (Adephaga: Trachypachidae) and *Elateroides dermestoides* (Linnaeus, 1761) (Polyphaga: Lymexylidae) were used as out-group taxa and treated as all other groups in the analysis (simultaneous analysis; Nixon & Carpenter, 1993).

The parsimony analysis was performed with the heuristic search algorithm of PAUP\* 4.0b10 (Swofford, 2001), with the parameter addseq set to random and nreps set to 1000. Characters 48, 53 and 62 were coded as ordered (=Wagner parsimony; Wagner, 1961; Kluge & Farris, 1969; Farris, 1970; Wiley *et al.*, 1991), and the remaining characters were coded as unordered (Fitch parsimony; Fitch, 1971). All characters were equally weighted (weight set to 1). The bootstrap values were calculated with PAUP\* (addseq set to simple, 1000 bootstrap replicates).

For the Bayesian analysis with MRBAYES, polymorphous character representations were replaced by '?' to represent uncertain character states. The standard model for morphological characters as implemented in MRBAYES 3.1.2 and proposed by Lewis (2001) and Nylander *et al.* (2004) was employed in its simplest version, with all state frequencies (change rates) set equal, all topologies with equal probabilities and with unconstrained branch length. Two parallel runs with multiple chains were calculated with a ratio of 1 cold to 3 heated chains. Two distinct analyses were run, one with one million generations, a burn-in of 250 000 and the temperature parameter set to 0.20, and the second with ten million generations, a burn-in of two million and the temperature set to 0.10.

To identify the influence of the larval characters and of the presence or absence of *Micromalthus debilis* and *Crowsoniella relicta* on the result of the phylogenetic analysis, seven additional analyses with modified data matrices were conducted with the heuristic search algorithm of PAUP\* with the parameters set as explained above: from the dataset containing

**Table 1.** Statistical parameters for the results of phylogenetic analyses of modified datasets on PAUP\*.

	All characters included	Without larval characters
All taxa included	Steps = 263 No. trees = 1695 CI = 0.6768 RC = 0.5831	Steps = 229 No. trees = 490 CI = 0.6594 RC = 0.5696
Without <i>M. debilis</i> and <i>C. relicta</i>	Steps = 239  No. trees = 486 CI = 0.7113 RC = 0.6238	Steps = 209  No. trees = 162 CI = 0.6890 RC = 0.6039
With <i>M. debilis</i> , without <i>C. relicta</i>	Steps = 255  No. trees = 1458 CI = 0.6902 RC = 0.5976	Steps = 221  No. trees = 162 CI = 0.6742 RC = 0.5856
Without <i>M. debilis</i> , with <i>C. relicta</i>	Steps = 249  No. trees = 1720 CI = 0.7068 RC = 0.6182	Steps = 220  No. trees = 648 CI = 0.6818 RC = 0.5946

all characters, *M. debilis* and *C. relicta* were both removed or were removed individually. For a dataset without larval characters, analyses were run with all taxa included, with *M. debilis* and *C. relicta* removed from the matrix, and with only one of these species removed. Owing to the lack of data for the larvae of most species, no analyses with exclusively larval characters were carried out. The results of the various analyses are listed in Table 1. Figure 1 shows strict consensus trees for all analyses.

## Results

With all characters (see Appendix 1) and all taxa (for matrix see Appendix 2) included, the parsimony analysis produced 1695 trees of 263 steps each. The consistency index (CI) is 0.68, and the rescaled consistency index (RC) is 0.58 for these trees. A majority-rule consensus tree of all trees is shown in Fig. 2.

The results of the two Bayesian analyses are virtually identical (Fig. 3), with differences of  $\pm 0.01$  in the posterior probability of a few nodes.

Following is a list of potential autapomorphies for the monophyletic groups represented in Fig. 2. If not otherwise noted, only autapomorphies reconstructed for the respective node under delayed (DELTRAN) and under accelerated (ACCTRAN) character transformation are considered. The consistency index of a character (ci) is noted when it is lower than 1.0.

*Clade i (Archostemata).* 2-1 (character 2 - state 1) (ci = 0.5) cuticle of head capsule with micro-tubercles; 38-1 (only

DELTRAN) Prementum with deep central cavity; 86-1 larval head capsule with postero-median emarginations; 94-1 mola of larval mandible quadrangular and with well-defined boundary; 95-1 cardo of larvae with separate, lateral, semi-membranous part; 96-1 larval ligula sclerotized, enlarged and wedge-shaped; 97-1 larval mentum and submentum fused; 104-1 second and later instars with tergal ampullae; 110-1 larval segment 10 not visible externally.

*Clade ii (Ommatidae).* 8-3 (ci = 0.6) dorsal margin of antennal insertions slightly elevated and extended (head protuberances P1); 22-1 only scapus with dense scale coverage; 27-1 (ci = 0.75) cutting edge of mandible with 3 vertically arranged teeth; 33-1 (ci = 0.5) apical palpomere of maxilla with dorso-lateral field of sensilla in deep pit; 49-1 (ci = 0.5) and 50-1 (ci = 0.33) elytra with 10 longitudinal rows of window punctures (in homoplasy to Clade xxvii).

*Clade iii (Cupedidae).* 8-1 (ci = 0.6) head protuberances P1 distinct; 36-1 (only DELTRAN) galea capitate, with slender base; 47-1 (only DELTRAN) subapical tarsomere wider than apical tarsomere; 76-1 parameres with apical hooks.

*Clade iv (Cupedidae without Priacma + Paracupes).* 28-1 ventral surface of mandible with at least two areas with different surface structures separated by a ridge or a groove; 72-1 (ci = 0.5) parameres with ventro-marginal spines.

*Clade v (Cupedidae without Priacma, Paracupes, Prolixocupes).* 9-2 (ci = 0.8) head protuberances P1 slightly tilted anteriorly over antennal insertion (in homoplasy to Clade xxvii); 10-3 (ci = 0.7) protuberances P1 conical and acute; 11-2 (ci = 0.8) protuberances P2 with cranial and caudal halves of different shape (in homoplasy to Clade xxvii); 22-2 scapus and pedicellus with dense scale cover but cuticle visible (in homoplasy to Clade xxvii); 90-1 (only ACCTRAN) larval head with tentorial bridge missing, gular ridges distinct and posterior tentorial arms membranous; 98-1 (only ACCTRAN) larvae without labial muscles; 100-1 (only ACCTRAN) larvae with proventriculus.

*Clade vi (Cupes, Distocupes, Tenomerga, Rhipsideigma).* 12-1 anterior tips of protuberances P2 small, acute and upright; 85-1 (ci = 0.5) head of second and later instars transverse and lateral narrowly rounded; 102-1 second and later instars with glabrous patches on prosternum; 105-1 (ci = 0.5) second and later instars with sternal asperities; 108-1 (ci = 0.5) larval tergum nine with terminal process.

*Clade vii (Cupes, Tenomerga, Rhipsideigma).* 40-2 (ci = 0.75) ligula subdivided in many digital appendages (in homoplasy to Clade xxii); 64-1 (ci = 0.5) sternite nine triangular and half as long as tergite nine; 66-1 (ci = 0.5) tergite nine with two lateral and one central lobe; 101-1 second and later instars with prothorax wider than following segments;



107-1 larvae with lateral longitudinal bulges on segments one to seven.

*Clade viii* (*Tenomerga* without *T. leucophaea*). 79-2 penis short, does not reach base of apical hooks; 81-1 (ci = 0.4) apex of penis with dorso-ventral notch.

*Clade ix* [*Tenomerga* without (*T. leucophaea*, *T. favella*, *T. kapnodes*, *T. moultoni*)]. 10-5 (ci = 0.7) protuberances P1 acute, basally wide and slightly onion-shaped; 12-4 (ci = 0.8) protuberances P2 blunt to acute conical and of intermediate size, similar to posterior tip.

*Clade x* (*Tenomerga japonica*, *T. trabecula*, *T. kurosawai*, *T. yamato*). 49-1 (ci = 0.3) elytra with 10 longitudinal rows of window punctures (in homoplasy to Ommatidae); 50-1 (ci = 0.4) elytral window punctures transverse.

*Clade xi* (*Tenomerga trabecula*, *T. kurosawai*, *T. yamato*). 10-2 (ci = 0.7) protuberances P1 blunt and conical (in homoplasy to Clade xvii).

*Clade xii* (*Tenomerga kurosawai*, *T. yamato*). 14-2 (ci = 0.75) protuberances P3 low and wide (in homoplasy to Clade xv).

*Clade xiii* (*Tenomerga anguliscutis*, *T. mucida*, *T. sibyllae*). 71-1 (ci = 0.5) bifurcate process of aedeagus Y-shaped; 75-1 ventro-marginal spines of parameres reach tips of apical hooks.

*Clade xiv* (*Tenomerga mucida*, *T. sibyllae*). 50-4 (ci = 0.4) elytral window punctures irregular, rounded (in homoplasy to Clade xxviii).

*Clade xv* (*Tenomerga favella*, *T. kapnodes*, *T. moultoni*). 5-1 (ci = 0.3) dorso-central area of head with markedly large scales; 13-4 (ci = 0.8) posterior tip of protuberances P2 small; 14-2 (ci = 0.75) protuberances P3 low and wide (in homoplasy to Clade XII); 23-1 three to four apical antennomeres with light, silvery setae; 41-4 (ci = 0.4) mentum and submentum fused without suture.

*Clade xvi* (*Tenomerga kapnodes*, *T. moultoni*). 57-1 elytral apex with triangular, white markings.

*Clade xvii* (*Tenomerga leucophaea*, *Cupes capitatus*, *Rhipsideigma*). 10-2 (ci = 0.7) protuberances P1 blunt, conical (in homoplasy to Clade XI); 12-3 (ci = 0.8) anterior tips of protuberances P2 big and upright; 14-3 (ci = 0.75) protuberances P3 narrow, longitudinal and high; 22-3 cuticle of scapus and pedicellus hidden by dense scale coverage; 77-1 (ci = 0.4) basal opening of aedeagus dorso-cranial oriented.

*Clade xviii* (*Cupes capitatus*, *Rhipsideigma*). 8-2 (ci = 0.6) and 9-1 (ci = 0.8) protuberances P1 big and towering (in homoplasy to clade xxvi); 73-1 (ci = 0.3) ventro-marginal spines of parameres originate in the apical half of the aedeagus.

*Clade xix* (*Rhipsideigma*). 53-2 elytra with apical tip and with an additional tip where the intervals 3 and 7 fuse; 54-1 tip on the elytral apex bigger than or as big as the tip at the fusion of intervals 3 and 7; 61-1 apical two-thirds of sternite 9 thin and needle-like; 66-1 tergite 9 with two short lateral lobes and a long, slender central lobe; 74-1 ventro-marginal spines of parameres are very short and uncinat; 82-1 dorsal plate with narrow apical half and with lateral extensions.

*Clade xx* (*Rhipsideigma adjuncta*, *R. anosibense*, *R. lugubris*). 81-2 (ci = 0.4) penis with truncated apex.

*Clade xxi* (*Rhipsideigma anosibense*, *R. lugubris*). 54-2 tip at the fusion of intervals 3 and 7 bigger than the tip at the elytral apex; 83-1 lateral extensions of the dorsal plate rotated and widened apically.

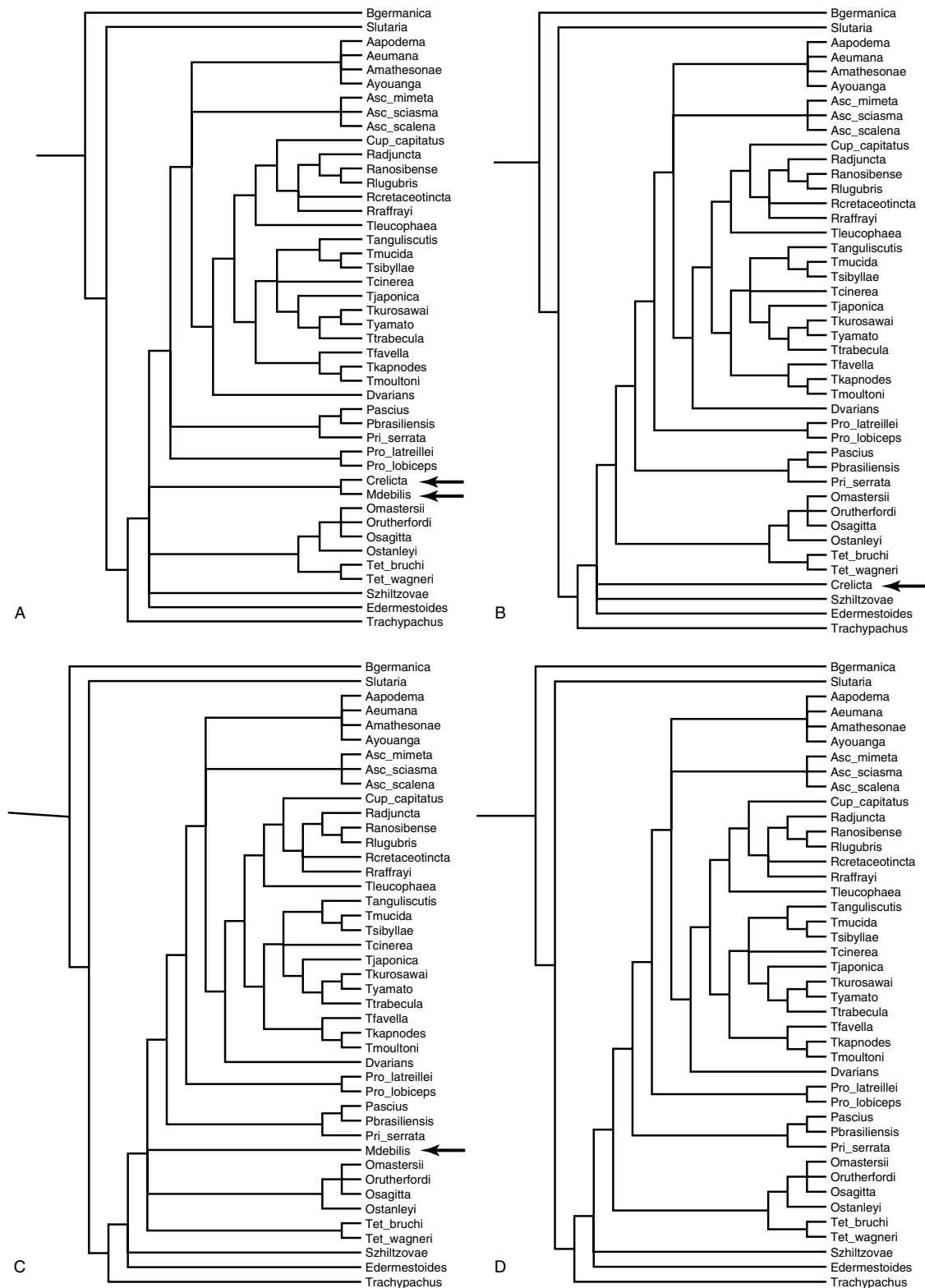
*Clade xxii* (*Adinolepis*, *Ascioplaga*). 11-0 (only DELTRAN, ci = 0.8) protuberances P2 missing; 29-1 (only ACCTRAN) ventral surface of mandible with deep pit; 40-2 (ci = 0.75) ligula subdivided into many digitiform appendages (in homoplasy to clade VII); 62-1 (only DELTRAN) sternite 9 caudally narrow and tapering, approximately onion-shaped.

*Clade xxiii* (*Adinolepis*). 4-1 (only ACCTRAN, ci = 0.5) head densely set with special, thick scales (in homoplasy to clade xxvi); 22-6 (only DELTRAN) six to ten basal antennomeres with ST2 scales; 44-1 (only DELTRAN) pronotum without distinct tips at anterior corners, lateral margins converging anteriorly; 62-2 (only DELTRAN) sternite 9 very long and narrow triangular; 68-1 (only DELTRAN) tergite 9 with constriction in basal third; 84-1 (only DELTRAN) penis very slender with more or less parallel sides.

*Clade xxiv* (*Ascioplaga*). 7-1 head with lateral projections below and above the anterior margins of the eyes; 12-2 (ci = 0.8) anterior tips of protuberances P2 small and horizontal; 13-2 (ci = 0.8) posterior tips of protuberances P2 small and horizontal; 22-5 cuticle of three to five basal antennomeres hidden by dense scale coverage.

*Clade xxv* (*Ascioplaga mimeta*, *A. sciasma*). 9-4 (ci = 0.8) protuberances P1 strongly tilted, tip pointing cranial; 51-5 (ci = 0.4) bottom of window punctures more or less completely covered by dense ring of large scales.

*Clade xxvi* (*Prolixocupes*). 4-1 (only ACCTRAN, ci = 0.5) head densely set with special type of thick scales (in homoplasy to clade xxiii); 9-1 (ci = 0.8) protuberances P1



**Fig. 1.** Strict consensus trees of results of datasets with all characters included: A, all taxa included; B, without *Micromalthus debilis*; C, without *Crownsoniella relicta*; D, without *M. debilis* and *C. relicta*. The arrows indicate the positions of *M. debilis* and *C. relicta*. Strict consensus trees of results of datasets without larval characters: E, all taxa included; F, without *M. debilis*; G, without *C. relicta*; H, without *M. debilis* and *C. relicta*. The arrows indicate the positions of *M. debilis* and *C. relicta*.

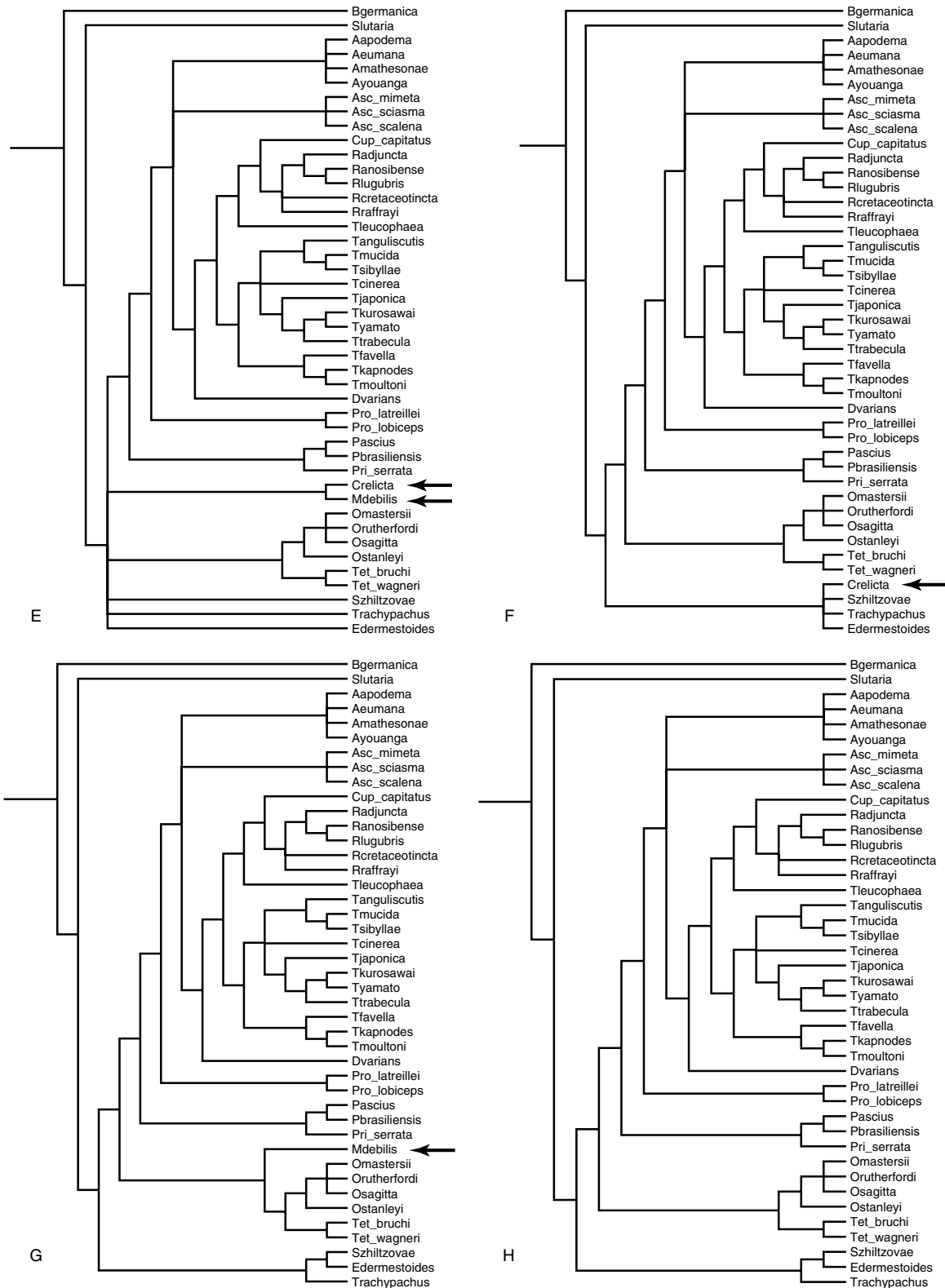
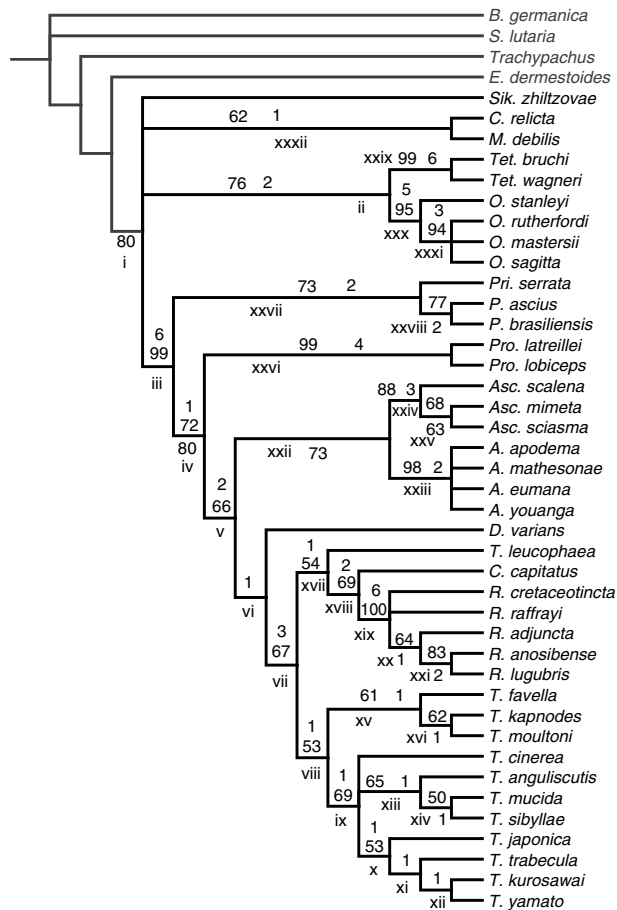


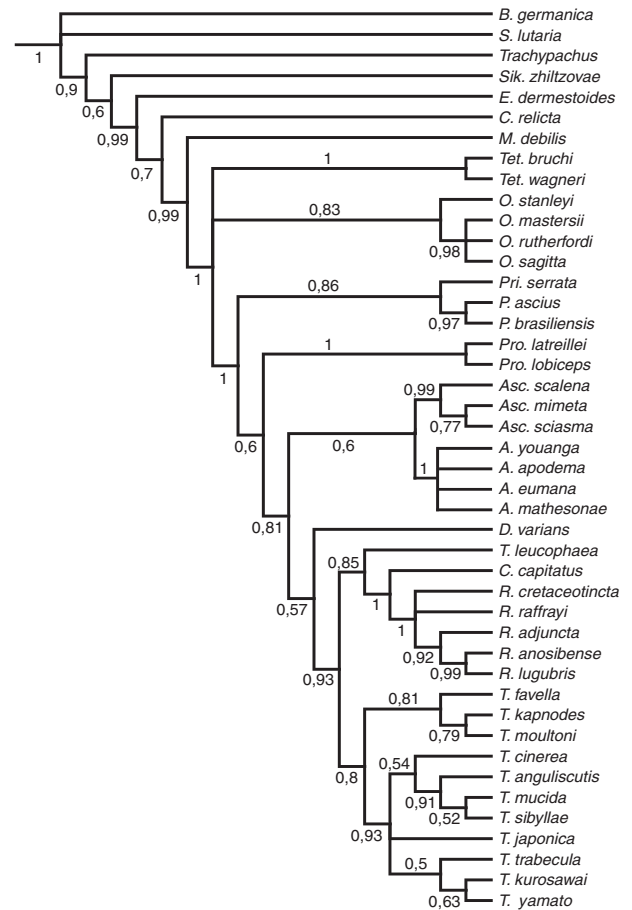
Fig. 1. (Continued).



**Fig. 2.** Majority-rule consensus tree of 1695 shortest trees (263 steps, CI = 0.68) from PAUP\* parsimony analysis with all characters and all taxa included. The two-digit numbers below branches give the percentage of cladograms that contain the respective node where the value differs from 100%. Nodes with values less than 50% are collapsed. Two-digit numbers above branches give the bootstrap values where they are greater than 50%. Single-digit values above or below branches represent Bremer support values. A list of potential autapomorphies for monophyla marked with roman numbers is given in the Results section.

steeply rising (in homoplasy to Clade xviii); 10-1 (ci = 0.7) protuberances P1 blunt and rounded; 11-1 (ci = 0.8) protuberances P2 a simple longitudinal bulge; 22-4 three to four basal antennomeres densely set with special scales; 63-1 sternite 9 very short, with two apical lobes; 81-3 (ci = 0.4) penis with widened apex.

**Clade xxvii** (Priaema, Paracupes). 9-2 (ci = 0.8) protuberances P1 slightly tilted anteriorly over antennal insertions (in homoplasy to Clade V); 11-2 (ci = 0.8) cranial and caudal halves of protuberances P2 of different shape (in homoplasy to Clade V); 22-2 scapus and pedicellus with densely set scales but visible cuticle (in homoplasy to Clade V); 25-1 mandible large and elongated; 49-1 (ci = 0.3) elytra



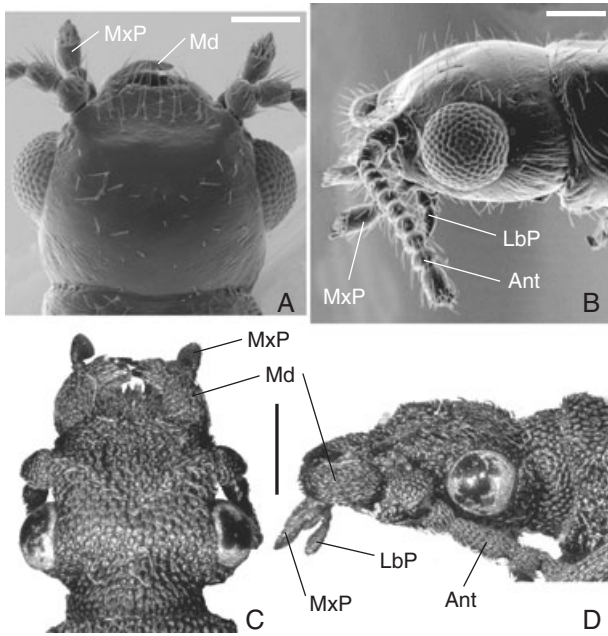
**Fig. 3.** Majority-rule consensus tree from Bayesian analysis (ten million generations). Numbers on the branches represent posterior probabilities.

with ten longitudinal rows of window punctures (in homoplasy to Clade II); 51-1 (ci = 0.4) bottom and inner wall of punctures without scales; 52-1 (ci = 0.3) closed elytra do not form a common apex; 55-1 elytral apex strongly serrated.

**Clade xxviii** (Paracupes). 10-4 (ci = 0.7) protuberances P1 more or less acute, with flattened posterior dorsal surface; 50-4 (ci = 0.4) window punctures of elytra are irregular and rounded (in homoplasy to Clade XIV).

**Clade xxix** (Tetraphalerus). 6-1 scales minute, like setae on mushroom-shaped micro-tubercles; 11-3 (ci = 0.8) protuberances P2 ridge-like, at least in cranial part; 15-1 head more than 1.3× longer than wide; 18-1 head with antennal grooves below the eyes; 37-8 (ci = 0.7) gula sutures not visible; 39-2 (ci = 0.8) prementum more than 1.5× longer than wide at the apex, with narrow oval apex; 77-2 (ci = 0.4) basal opening of aedeagus lies anteriorly.





**Fig. 4.** A, B, scanning electron microscope images of head of *Micromalthus debilis*: A, dorsal view; B, left lateral view. Scale 100  $\mu$ m. C, D, head of *Omnia stanleyi*: C, dorsal view; D, left lateral view. Scale 1 mm. Ant, antenna; Ga, galea; LbP, labial palpus; Md, mandible; MxP, maxilla palpus.

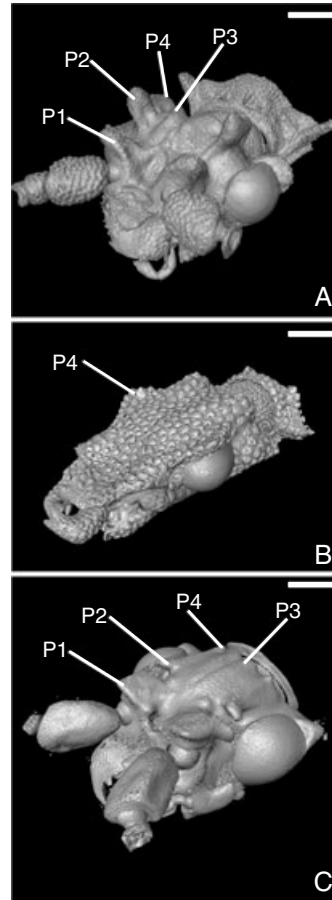
*Clade xxx* (*Omnia*). 21-1 third antennomere more than 1.5 $\times$  longer than fourth; 24-2 (ci = 0.7) labrum, clypeus and frons fused (in homoplasy to Clade XXXI); 34-1 pit of dorso-lateral sensillary field on apical palpomeres with very small opening; 42-1 (ci = 0.5) anterior corners of pronotum rounded; 78-1 (ci = 0.5) apex of parameres not sclerotized, sub-apically widened and emarginated.

*Clade xxxi* (*Omnia* without *O. stanleyi*). 30-1 apical palpomeres of maxilla approximately as long as the diameter of an eye and strongly wedge-shaped; 45-1 caudal margin of pronotum with narrowly triangular white markings; 56-1 middle and / or anterior area of elytra with white transverse or X-shaped markings.

*xxxii* (*Crowsoniella*, *Micromalthus*). 23-2 (ci=0.7) labrum, clypeus and frons fused (in homoplasy to Clade xxx); 36-2 galea missing; 38-2 and 39-5 (ci = 0.8) prementum reduced; 40-3 (ci = 0.75) ligula missing.

## Discussion

With more than 1600 trees of equal length, the relatively good resolution of the strict consensus trees (Fig. 1) from the parsimony analyses is quite astonishing. The topography of the strict and majority-rule (Fig. 2) consensus trees is supported by the results of the Bayesian analyses (Fig. 3).

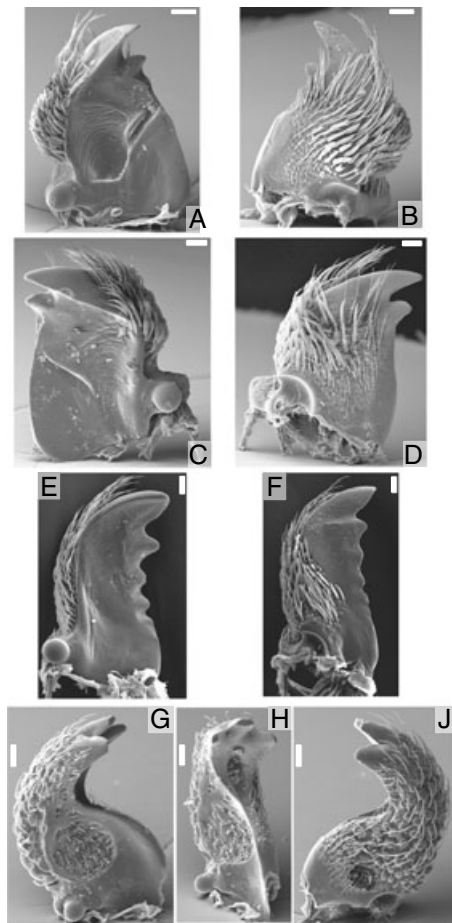


**Fig. 5.** Protuberances on the heads of Archostemata: A, *Cupes capitatus*; B, *Tetraphalerus bruchi*; C, *Ascioptaga mimeta*. Surface views reconstructed from high-resolution X-ray tomography data (all BAM). For *C. capitatus* and *A. mimeta* scales are removed so that the surface of the cuticle is visible. Scales 0.5 mm. P1–P4, head protuberances 1 to 4.

Comparison of the analyses in which *M. debilis* and *C. relictus* were removed from the dataset clearly shows where the source of the large number of equally parsimonious trees lies. Removing both species reduces the number of trees of equal length. Without the larval characters, even the removal of only *C. relictus* results in a reduction of two-thirds in the number of equally parsimonious trees. The removal of only *M. debilis* results in even more trees of equal length.

The latter may be explained by the absence of synapomorphies of *C. relictus* with other taxa when *M. debilis* is absent. When both species are present, the parsimony analysis joins them in a monophylum that is supported by five unambiguous autapomorphies, all of which are reductions of mouthpart characters of the adults that do not occur in other Archostemata. If *M. debilis* is removed from the dataset no characters remain that could join *C. relictus* consistently to any other taxon.

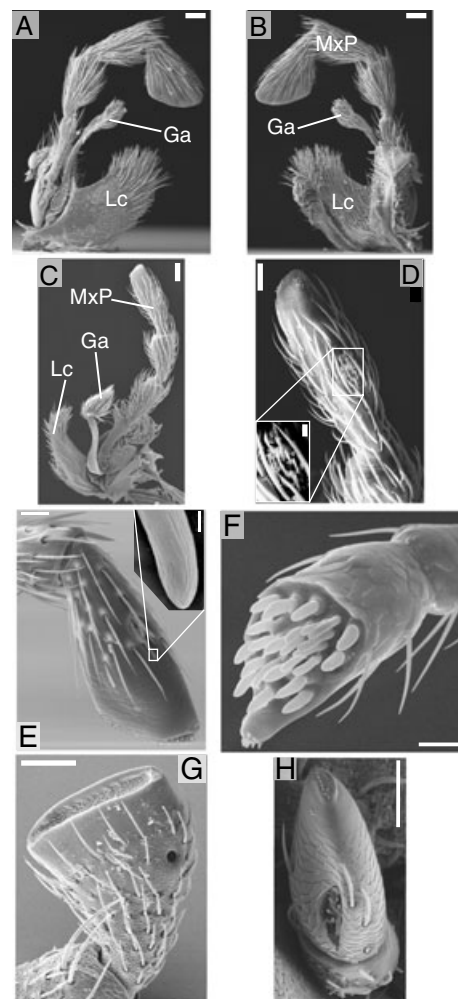
If only *C. relictus* is removed, the effect is different, because *M. debilis* has at least a few derived characters in common with Ommatidae or Cupedidae. Some characters of



**Fig. 6.** Mandibles of Archostemata. A, B, *Ascioplaga mimeta*: A, ventral; B, dorsal. C, D, *Tenomerga leucophaea*: C, ventral; D, dorsal. E, F, *Priacma serrata*: E, ventral; F, dorsal. G, H, J, *Omma stanleyi*: G, ventral; H, mesal; J, dorsal. All scales 100  $\mu$ m.

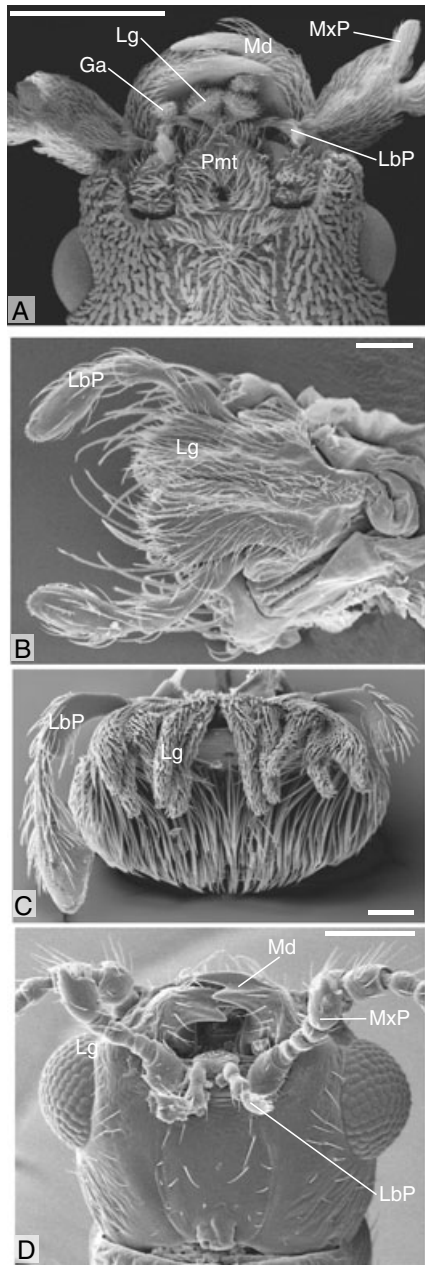
the head, mouthparts and genitalia (8, 16, 24, 26, 27, 78, 80) of *M. debilis* are similar to the conditions in Ommatidae. Thus, when *C. relictata* and larval characters are excluded, *M. debilis* is placed as the sister group of Ommatidae (Fig. 1). The aedeagus of *M. debilis* shows characters that are also present in *Tetraphalerus* and *Omma*. For example, the ventro-marginal spines (VMS) are absent (char. 72), which is probably the plesiomorphic condition. Potential synapomorphies of *M. debilis* and *Omma* are the presence of emarginations in the distal thirds of the median surfaces of the parameres (char. 78) and the distinct lateral compression of the penis (char. 80). Similar subapical emarginations are unknown in other Archostemata, and the penis usually is well rounded. In combination with the shape of the mandible (chars 25, 26, 27) and the length of the antenna (char. 16), the adult characters support a close relationship of *M. debilis* and Ommatidae.

Because the characters of the larvae (from 85 onwards) of *M. debilis* are as in Cupedidae, the analysis without *C. relictata* but with larval characters included is strongly influenced by



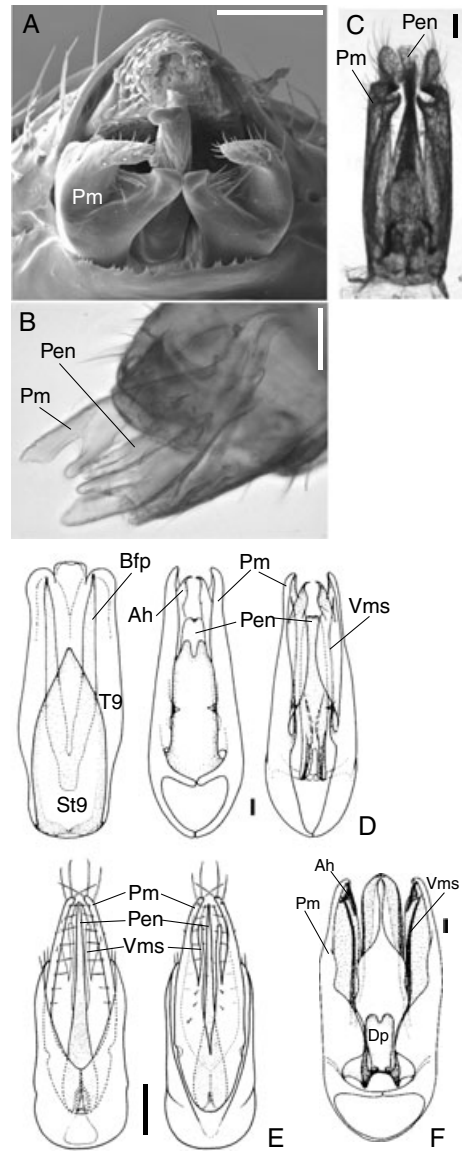
**Fig. 7.** Maxillae of Archostemata. A, B, *Tenomerga leucophaea*: A, dorsal; B, ventral, scales 100  $\mu$ m. C, D, *Priacma serrata*: C, right maxilla, dorsal, scale 100  $\mu$ m; D, apical palpomere of right maxilla, dorsal, showing fields of sensilla, scale 50  $\mu$ m, inset scale 2  $\mu$ m. E, *Cupes capitatus*, apical palpomere of left maxilla showing fields of sensilla, scale 20  $\mu$ m, inset scale 1  $\mu$ m. F, *Micromalthus debilis*, apical palpomere of right maxilla with large field of sensilla, scale 6  $\mu$ m. G, *Omma stanleyi*, apical palpomere of right maxilla with narrow opening to cavity containing sensilla, scale 100  $\mu$ m. H, *Tetraphalerus bruchi*, apical palpomere of right maxilla with deep cavity of sensilla, scale 50  $\mu$ m. Ga, galea; LbP, labial palpus; Lc, lacinia; Lg, ligula; MxP, maxilla palpus; Pmt, prementum.

the conflict between adult and larval characters, and no well-supported phylogenetic placement of *M. debilis* is obtained. Because larval characters are available for only six species of Archostemata (*Omma* sp., *M. debilis*, *Priacma serrata*, *Distocupes varians*, *Rhysideigma raffrayi*, *Tenomerga cinerea*; see Grebennikov, 2004), and for Ommatidae only one larva of unknown stage and uncertain species identity (Lawrence, 1999) is known, it is quite difficult to interpret the observed states. Most larval characters of *M. debilis* are as otherwise found in larvae of Cupedidae. Nevertheless, the differing states in



**Fig. 8.** Scanning electron microscope images of labiae of Archostemata. A, B, *Priacma serrata*: A, ventral view of head with mouthparts in situ, note enlarged prementum with deep central cavity, scale 1 mm; B, dorsal view of labium, scale 100  $\mu$ m. C, frontal view of labium of *Ascioplaga mimeta*, scale 100  $\mu$ m. D, ventral view of head of *Micromalthus debilis* showing reduced labium and maxillae, scale 100  $\mu$ m. Ga, galea; LbP, labial palpus; Lg, ligula; Md, mandible; MxP, maxilla palpus; Pmt, prementum.

the ommatid larva may well be autapomorphies of *Omma* or Ommatinae. However, the currently available information is not sufficient to decide whether this is the case. Consequently, it is not possible to present a very robust hypothesis on the



**Fig. 9.** Male genitalia of Archostemata. A, B, *Micromalthus debilis*: A, scanning electron microscope image of tip of abdomen with partly extruded aedeagus, scale 50  $\mu$ m; B, transmitted light microscopic image of tip of abdomen with partly extruded aedeagus, scale 50  $\mu$ m. C, dorsal view of aedeagus of *Omma stanleyi*, scale 100  $\mu$ m. D, slightly schematic drawings of aedeagus of *Tenomergera cinerea* (after Neboiss, 1984), from left to right: segment 9 ventral, aedeagus dorsal, ditto, ventral, scale 100  $\mu$ m. E, drawings of aedeagus of *Crowsoniella relictata* (after Pace, 1975), left: dorsal, right: ventral, scale 50  $\mu$ m. F, slightly schematic drawings of aedeagus of *Distocupes varians* (after Neboiss, 1984), aedeagus dorsal, scale 100  $\mu$ m. Ah, apical hook; Bfp, bifurcate process; Dp, dorsal plate; Pen, penis; Pm, paramere; St9, sternite 9; T9, tergite 9; Vms, ventromarginal spine.

phylogenetic relationships of *M. debilis* based on the present dataset.

With *C. relictata* the situation is similar, although even fewer synapomorphies with other Archostemata could be identified.



A derived character of the male genitalia is shared with a sub-group of Cupedidae: the presence of VMS (chars 72, 73) is a potential synapomorphy of *C. relictata* and Cupedidae without *Paracupes* and *Priacma*. A closer relationship of *C. relictata* with *Tetraphalerus* as proposed by Crowson (1975), Beutel & Hörschemeyer (2002a) and Hörschemeyer *et al.* (2002) is not supported by this analysis. The lateral antennal grooves of *Crowsoniella* and *Tetraphalerus* are morphologically quite different (above the eyes in *Crowsoniella*, below the eyes in *Tetraphalerus*) and probably have evolved independently. However, numerous autapomorphies of *C. relictata* in combination with homoplasies in other characters prevent a well-founded reconstruction of the relationships of *C. relictata* in this analysis.

The analysis in Beutel *et al.* (2008) placed *C. relictata* and *M. debilis* in a monophylum together with *S. zhiltzovae* and four extinct taxa. In that analysis, this monophylum was the sister group of Cupedidae. Beutel *et al.* (2008) mentioned that this monophylum was largely based on reductions and that the interpretation of the characters of the fossils was difficult in some cases. It is possible that the potential autapomorphies of this monophylum are in fact homoplasies. At least, the support for a closer relationship of *S. zhiltzovae*, *C. relictata* and *M. debilis* was quite weak and the characters of the male genitalia do not at all support such a relationship.

*Sikhotealinia zhiltzovae* shows an unusual combination of characters: the prothorax with exposed pleural sutures and the presence of free trochantins on all three pairs of legs are clearly plesiomorphic among Coleoptera (cf. Beutel, 1997). The head with its abruptly constricted neck and bulging eyes and the shape and surface structure of the pronotum are similar to what is found in Cupedidae. However, important autapomorphies of Archostemata, such as characters of the mouthparts, are absent. Only an enlarged, plate-like prementum is present, but without a central cavity (chars 38, 39), whereas the remaining mouthparts appear quite plesiomorphic. In the parsimony analyses, *S. zhiltzovae* is placed at the base of Archostemata or, depending on the composition of the dataset (Fig. 1), together with outgroup taxa. The Bayesian analysis places the species one branch lower, with the polyphagan outgroup as sister group to Archostemata (Fig. 3).

As mentioned above, Beutel *et al.* (2008) found *S. zhiltzovae* within Archostemata in a monophylum together with some extinct taxa and *M. debilis* and *C. relictata*. But here its position also depended on the composition of the dataset, and the Bayesian analysis placed it together with its fossil relatives, Jurodidae, outside Archostemata.

Obviously, our current knowledge of *S. zhiltzovae* does not allow for a well-supported reconstruction of its phylogenetic relationships. As suggested by Beutel *et al.* (2008), an extensive reinvestigation of the holotype, probably with the help of high-resolution X-ray tomography, is highly desirable.

Apart from the positions of *S. zhiltzovae*, *C. relictata* and *M. debilis*, the different analyses consistently yield the same relationships of archostematan genera and species. The strict consensus trees are well resolved, with uncertainties restricted

mainly to relationships of species within genera. The compositions of higher-level taxa, especially of Ommatidae and Cupedidae, are in agreement with the family definitions given by Lawrence & Newton (1995).

At lower taxonomic levels, however, there are significant differences from the assumptions of Neboiss (1984): for instance, the genus *Tenomerga* is not monophyletic in its present designation, and *Priacma* and *Paracupes* are sister groups.

#### The phylogeny of *Omma*

The relationships among the species of *Omma* are unequivocal as far as the sister-group relationship of *O. stanleyi* to the remaining species is concerned. Among *O. rutherfordi*, *O. mastersii* and *O. sagitta* the latter two species are very similar in size and habitus, and show similar white markings on the elytra (char. 56), which are probably correlated with their mimicking a mutillid hymenopteran in body shape, colour pattern and behaviour (Lawrence, 1999; Geoff Monteith, personal communication). Based on these data it seems most likely that *O. mastersii* and *O. sagitta* are sister groups. Even though *O. rutherfordi* is less similar in body shape to the latter two species than *O. stanleyi*, characters such as its white markings on the elytra and especially the shape and relative size of the apical maxillary and labial palpomeres (char. 30) support its sister-group relationship with *O. mastersii* + *O. sagitta*.

#### The Cupedidae of the Australian region

*Adinolepis* and *Ascioplaga* emerged as sister groups from the Bayesian analysis with a posterior probability of 0.6. The parsimony analysis recovered this grouping in 73% of the equally parsimonious trees. This monophylum (Clade xxii) is characterized by autapomorphies of the head and of the mouthparts. The species belonging to these genera occur only on the Australian mainland and on the island Grande Terre of New Caledonia, which is located east of Australia. A characteristic feature is a deep pit on the ventral surface of each mandible (char. 29). Otherwise, a similar pit is found only in *Distocupes varians*, also occurring only in Australia.

Hörschemeyer *et al.* (2006) obtained a sister-group relationship between *Distocupes varians* and *Adinolepis* + *Ascioplaga*. The present analyses do not support such a relationship however. *Distocupes varians* is placed consistently as sister group of the monophylum composed of *Cupes*, *Rhipsideigma* and *Tenomerga* (Clade vii). Thus, the special shape of the ventral mandibular surface must have evolved independently in the stem lineages of *Adinolepis* + *Ascioplaga* and *D. varians* + (*Cupes*, *Rhipsideigma*, *Tenomerga*) or it is a character that was present already in the last common ancestor of (*Adinolepis*, *Ascioplaga*, *Cupes*, *Rhipsideigma*, *Tenomerga*). In this case it must have been lost in the last common ancestor of (*Cupes*, *Rhipsideigma*, *Tenomerga*).

*Ascioplaga scalena* **comb. nov.** was described by Neboiss (1984) as *Adinolepis scalena*. The present analyses consistently associate the species with *Ascioplaga*, as it shows all apomorphies of the genus (see Results). Hence, the species is hereby transferred to *Ascioplaga*.

#### The phylogeny of *Adinolepis*

The monophyly of *Adinolepis* is well supported by a number of autapomorphies in the male genitalia and the head. However, because of homoplasies in characters of the head and of the prothorax, the relationships among the species of *Adinolepis* could not be resolved fully in either Bayesian or parsimony analyses.

The description of *Adinolepis apodema* (Neboiss, 1989) was based on a single specimen. The diagnostic character for this species is the presence of only one spot with light scales in the otherwise dark scales of the third interval of each elytron in contrast to two such spots in *A. mathesonae*. Furthermore, the type locality of *A. apodema* is separated by more than 2000 km from the range of *A. mathesonae*.

Unfortunately, the holotype of *A. apodema* is a female, so that characters of the male genitalia were not available at the time of description. Furthermore, in *A. mathesonae* and in *A. eumana*, which also have two light spots in the otherwise dark third interval, there are intermediate states of this character. In some specimens the anterior light spot is very short, composed of only a few scales, whereas in another specimen this spot was missing on one elytron. This shows that the coloration of the elytra might be slightly variable in *Adinolepis*, thus suggesting that *A. apodema* is only a colour variant of *A. mathesonae*.

#### The phylogenetic relationships of *Tenomerga*, *Cupes* and *Rhipsideigma*

A striking result is the polyphyly of *Tenomerga*, because *Tenomerga leucophaea* consistently forms a clade (xvii) together with *Cupes capitatus* and *Rhipsideigma*. This monophylum is the sister group of the remaining *Tenomerga* species and is well supported by five unambiguous autapomorphies (see Results).

Neboiss (1984: 457) recognized that *T. leucophaea* is distinctly different from the remaining *Tenomerga* species in a number of characters. He judged these differences as important enough to put *T. leucophaea* in a subgenus of its own (Neboiss 1984: 448), but this subgenus was never formally established.

The inclusion of the North American *Cupes capitatus* in a monophylum together with the South African *T. leucophaea* and the species of *Rhipsideigma* that occur in eastern Africa and Madagascar might seem surprising. However, *Cu. capitatus* has all the apomorphies mentioned above. Especially conspicuous are the pronounced protuberances on the head.

The large geographic distance between the present ranges of *Cu. capitatus*, *T. leucophaea* and *Rhipsideigma* is not a substantial argument against *Cu. capitatus*' belonging to

this taxon. For instance, there are Baltic amber fossils (de Motschulsky, 1856; de Peyerimhoff, 1909; Kirejtshuk, 2005), fossils from the middle Eocene of Messel (near Darmstadt, Germany) (Tröster, 1993) and of Eckfeld (Germany) (Wappler, 2003) as well as fossils from the upper Oligocene of Enspel (Wedmann, 2000) and from the Pliocene of Willershausen (Germany) (Gersdorf, 1976) that are closely related to *Cu. capitatus*. These fossils close the distribution gap between North America and Africa. Besides the fossils that are related to *Cu. capitatus*, there are also a few specimens that seem to be more closely related to *T. leucophaea* (Kirejtshuk, 2005). Thus, fossil and extant species together show a previously much wider distribution of *Tenomerga* (sensu lato), with one Afro-American and one Asiatic clade.

#### The relationships of the species of *Tenomerga* (Clade viii)

The differences among *T. anguliscutis*, *T. mucida* and *T. sibyllae*, which are restricted to eastern Asia, are restricted to variations in colouring. For *T. anguliscutis* and *T. mucida*, Neboiss (1984: 452) mentioned that the male genitalia of both species are identical and allow no species distinction. For *T. sibyllae* no males are known. This species is very similar to the other two in all available characters. Consequently, one might suspect that *T. anguliscutis*, *T. mucida* and *T. sibyllae* are only colour variants of one species.

The bootstrap values for the nodes within *Tenomerga* (Clade viii) are quite low. This probably not only reflects a lack of informative characters in this study but may also be a result of the high similarity and close relationship of all species that belong to this clade. An investigation of the relationships of this group with molecular data would be useful. Such a study could also help to determine how many individual species of *Tenomerga* are really present in East Asia.

## Conclusions

This exclusively morphology-based phylogenetic analysis resulted in a reasonably well-resolved species-level phylogeny of extant Archostemata. The generally recognized taxa Cupedidae and Ommatidae (e.g. Lawrence & Newton, 1995) were confirmed. Within Cupedidae, noteworthy results are the sister-group relationship of the South American *Paracupes* and the North American *Priacma*. Together they are the sister group to all remaining Cupedidae and they are probably close to the morphological ground-pattern of Cupedidae.

An Australian monophylum containing *Ascioplaga*, *Adinolepis* and *Distocupes*, as described by Hörschemeyer *et al.* (2006), could not be confirmed fully. According to the present analysis, *Distocupes* is more closely related to *Tenomerga* (sensu lato) than to the other Australian genera. The identification of a monophylum comprising *Rhipsideigma*, *Cupes capitatus* and *Tenomerga leucophaea* renders *Tenomerga* polyphyletic in its present composition and establishes two evolutionary lineages within this clade (vii). The Afro-American



lineage with *Rhipsideigma*, *Cupes capitatus* and *Tenomerga leucophaea* was present in Europe until the ice ages, as documented by Pliocene fossils (Gersdorf, 1976). The Asian lineage, comprising the remaining species of *Tenomerga*, is currently found in eastern Asia and North America.

Characters of the male genitalia indicate a relationship of *Micromalthus debilis* with Ommatidae and of *Crowsoniella relictata* with Cupedidae. However, owing to numerous homoplastic characters of other body parts and of the larvae these positions of *C. relictata* and *M. debilis* among the extant Archostemata are not very well supported. For *Sikhotealinia zhiltzovae* no stable position among the other Archostemata could be determined. All three species have so many autapomorphies, or, in other words, so few potential synapomorphies with other clades, that it is not possible to identify their sister groups unequivocally, based on the morphological characters utilized in this study. Here, new, freshly collected specimens for more detailed morphological and especially for genetic investigation seems to be the only way to progress.

The derived features of the archostematan mouthparts only in part belong to the ground-pattern of Archostemata. For instance, the complex structures on the ventral surfaces of the mandibles of Cupedidae (Fig. 6) evolved within the taxon, as the reconstructions of the autapomorphies for the different nodes show. Furthermore, the clubbed galea and the ligula with numerous digitiform appendages are autapomorphies of monophyla within Cupedidae. The only derived mouthpart characters that obviously belong to the ground-pattern of Archostemata are the modified labium with its central apodeme of the prementum (char. 38) and the associated muscles (M28 and M30, Hörnschemeyer *et al.*, 2002, 2006) that insert on this apodeme. These characters are present in Cupedidae as well as in Ommatidae and probably were also present in their last common ancestor. The species of the genera *Paracupes* and *Priacma* might serve as a model for the ground-pattern of archostematan morphology. They show the characteristic prementum but otherwise fairly plesiomorphic mouthparts.

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## Appendix 1. List of characters used in the phylogenetic analysis.

In total, 110 morphological characters from the head, thorax and male genitalia of adults, and from the head, thorax and abdomen of the larvae were compiled. Characters are uniformly weighted and coded as non-additive (=‘Fitch parsimony’: Fitch, 1971; Wiley *et al.*, 1991) if not noted otherwise.

Characters of the adult head: 1–23

### 1 Number of ocelli: (0) 1 to 3 ocelli; (1) no ocelli.

For the ground pattern of Pterygota it can be assumed that three ocelli were present. Most Coleoptera do not have ocelli, but three probably are present in *Sikhotealinia zhit-zovae* and two or one in representatives of some groups of Polyphaga (Leschen & Beutel, 2004).

### 2 Cuticle of head with micro-tubercles (Fig. 4): (0) no; (1) yes.

The cuticle of most Archostemata has a structure of micro-tubercles. Typically each tubercle bears one scale. The presence of micro-tubercles is probably a derived condition of Archostemata or a subgroup thereof, since in most other insects the cuticle lacks such tubercles.

### 3 Scales on head approximately cylindrical, rod-like (ST2): (0) no; (1) yes.

On the head and prothorax of *Adinolepis* there are numerous approximately cylindrical scales with rounded apex, which tower slightly above the surrounding scales. These rod-like scales are scattered among the ‘normal’ scales. This type of scales is missing in other Archostemata.

### 4 Head densely set with thick, inflated scales: (0) no; (1) yes.

The scales on the heads of *Adinolepis* and *Prolixocupes* are markedly thick and inflated. The scales are so densely

set that the cuticle is not visible. Similarly dense scale coverage is also present in *Rhipsideigma* and *Cupes* but there the scales are not inflated.

### 5 Central dorsal area of head set with markedly large scales: (0) no; (1) yes.

Some Asiatic species of Cupedidae have wide, oval scales on the central, dorsal surfaces of their heads. These scales are at least as wide as long, whereas in other species the scales on the head are usually longer than wide.

### 6 Scales minute and slender, inserted on mushroom-shaped micro-tubercles (Fig. 5B): (0) no; (1) yes.

In *Tetraphalerus* the cuticle of at least the head and thorax has enlarged micro-tubercles with radial grooves. In cross-section, the mushroom-shape of the micro-tubercles, with extended cap and narrower base, becomes apparent. On each of these modified micro-tubercles a short and stout seta is present. These setae are probably homologous to the scales of other Archostemata.

### 7 Head with lateral projections below and above the anterior margins of the eyes (Fig. 5C): (0) no; (1) yes.

*Ascioplaga* has relatively small projections at the dorsal and ventral anterior margins of the eyes. These small tenons are visible only after the scales have been removed. With intact scale-coverage only a slight indentation is visible in the area between the two tenons.

### 8 Head protuberances above the antennal insertions (P1) (Fig. 5): (0) absent; (1) distinct; (2) markedly large; (3) only dorsal margin of antennal insertions slightly elevated and extended.

Big protuberances on the dorsal side of the head are a prominent character that, in this form, is present only in Archostemata. The protuberances are present in three areas of the head: above the antennal insertions (P1), above the eyes (P2), and medial of P2 (P3). The P1 protuberances are present in more or less distinct form in all



Archostemata with the exception of *Crowsoniella relictata* and *Sikhotealinia zhiltzovae* (cf. Neboiss, 1984).

- 9 Shape of protuberances above antennal insertions (P1)** (Fig. 5): (0) unobtrusive or absent; (1) steeply rising; (2) slightly tilted anteriorly over antennal insertion; (3) distinctly tilted anteriorly, slightly flattened dorsally; (4) strongly tilted, tip pointing cranial.

- 10 Tips of protuberances above antennal insertions (P1)** (Fig. 5): (0) unobtrusive or absent; (1) blunt, rounded; (2) blunt, conical; (3) acute, conical; (4) more or less acute, posterior dorsal surface flattened; (5) wide basally, acute, slightly onion-shaped.

- 11 Protuberances above the eyes (P2)** (Fig. 5): (0) absent; (1) simple longitudinal bulge; (2) cranial and caudal halves of bulge of different shape; (3) ridge-like, at least in cranial part; (4) low, wide bulge.

The protuberances above the eyes (P2) are very variable between species. In most species the anterior and the posterior halves of the longitudinal bulge are of different shape (cf. Neboiss, 1984).

- 12 Anterior tip of protuberances P2** (Fig. 5): (0) absent; (1) small, acute and upright (max. one-third of height of eye); (2) small, horizontal; (3) big and upright (ca. half height of eye); (4) intermediate size, blunt to acute conical, of similar size to posterior tip.

- 13 Posterior tip of protuberances P2** (Fig. 5): (0) absent; (1) acute, upright and relatively small; (2) small, horizontal; (3) blunt, bulging; (4) inconspicuous.

- 14 Median protuberances (P3)** (Fig. 5): (0) absent; (1) distinct pair, low and wide; (2) more or less indistinct pair, low and wide; (3) narrow, longitudinal, may be very high pair.

In Cupedidae the median protuberances (P3) are distinct and of variable shape. In *Rhypsodeigma* they are high whereas in the Asian species of *Tenomerga* they are low and wide.

- 15 Ratio of length to width of head** (Figs 4, 5): (0) head as long as wide or wider than long; (1) head more than 1.3× longer than wide.

In many insects the head is approximately as long as it is wide. In contrast to this the *Tetraphalerus* species have a strongly elongated head.

- 16 Ratio of body length to length of antenna:** (0) body less than 3× longer than antenna; (1) body more than 3× longer than antenna.

In many insects the antennae are more than a third of the body length. In some species of Archostemata “(*C. relictata*, *M. debilis*, *S. zhiltzovae*, *Omma*, *Tetraphalerus*)” short antennae of less than one-third of the length of the body are present.

- 17 Antennal insertions:** (0) separated by more than three diameters of the scapus; (1) separated by ca. two diameters of the scapus; (2) separated by one or less than one diameter of the scapus; (3) separated by more than two but less than three diameters of the scapus; (4) separated by slightly more than one diameter of the scapus.

In many Endopterygota such as, for example, *Sialis*, *Trachypachus*, *Omma*, the antennal sockets are relatively far apart, whereas in the Cupedidae they are strongly approximated.

- 18 Head with lateral antennal grooves:** (0) absent; (1) below the eyes; (2) above the eyes.

Antennal grooves on the sides of the head are present only in *Tetraphalerus* and *Crowsoniella*.

- 19 Number of muscles inserting on the scapus:** (0) 3; (1) 4; (2) 2.

In adults of Endopterygota the scapus usually has three muscles (Kéler, 1963). In contrast to this, four muscles are present in *Tenomerga cinerea*, *Distocupes varians* and *Ascioplaga mimeta*, as well as in the polyphagan beetle *Lytta vesicatoria* L., 1758 (Schneider, 1981). In *Micromalthus debilis* only two muscles are present.

- 20 Antennal muscle M3:** (0) missing; (1) present.

Among the investigated Cupedidae, *Priacma serrata* and *Cupes capitatus* have three muscles connecting the scapus with the head. However, the combination of muscles present is not identical in these two species. Based on the positions of origins and insertions of the muscles and on their relation to the origins of other muscles it can be concluded that in *Cup. capitatus* the *Musculus tentorioscapalis lateralis* (M3) is present whereas in *P. serrata* it is missing (Hörnschemeyer *et al.*, 2002, 2006).

- 21 Length of third antennomere:** (0) third antennomere approximately as long as fourth; (1) third antennomere more than 1.5× longer than fourth.

In *Omma* the first flagellomere (=third antennomere) is distinctly longer than the following flagellomeres.

- 22 Number of antennomeres with dense scale cover:** (0) none; (1) only scapus; (2) scapus and pedicellus with cuticle visible; (3) cuticle of scapus and pedicellus hidden; (4) 3 to 4 basal antennomeres with special scales; (5) 3 to 5 basal antennomeres with cuticle hidden; (6) 6 to 10 basal antennomeres with ST2 (see char. 3) scales.

Many species of Archostemata have a dense scale coverage on the scapus and pedicellus, whereas the flagellomeres only have slender setae. However, in some species also one or more flagellomeres have scales.

- 23 Three to four apical antennomeres with light silvery setae:** (0) no; (1) yes.

In most species the coloration of the distal flagellomeres is similar to that of the more proximal flagellomeres. However, in *Tenomerga favella*, *T. kapnodes* and *T. moultoni* the apical three to four flagellomeres are coloured conspicuously light and silvery.

Characters of the adult mouthparts: 24–41

- 24 Clypeus, labrum:** (0) clypeus and labrum free; (1) clypeus and frons fused, labrum free; (2) labrum, clypeus and frons fused.

In the ground pattern of Insecta, the clypeus and labrum are connected to one another and to the frons via membranes so that they are moveable. In Archostemata the clypeus is

absent as a separate sclerite. The labrum is moveable in most species but in Ommatidae and in *Micromalthus* and *Crowsoniella* it is fused to the frons.

- 25 Shape of mandible** (Fig. 6): (0) short and compact; (1) large, elongated; (2) small, reduced.

In *Priacma* and *Paracupes* the mandibles are exceptionally long with nearly straight cutting edges. In most other Archostemata the mandibles are relatively short with strongly curved apex.

- 26 Mandible: smooth ventral surface rotated inwards** (Fig. 6G): (0) no; (1) yes.

In *Omma*, *Tetrapterus*, *Micromalthus* and *Prolixocupes* the smooth, functional, ventral surface of the mandible is rotated inwards. Thus, these surfaces of both mandibles are facing each other. This rotation also has the effect that the structured outer surface with its setae or scales extends between the smooth ventral surface and the posterior condylus of the mandible.

- 27 Cutting edge of mandible** (Fig. 6): (0) horizontal; (1) with 3 vertically arranged teeth; (2) nearly vertical with 2 blunt teeth; (3) approximately crescent-shaped.

Most Coleoptera have mandibles with horizontal cutting edges. In Ommatidae and *Micromalthus* the cutting edge is more or less perpendicular with three vertically arranged teeth.

- 28 Ventral surface of mandible with at least two differently structured areas separated by a ridge or a groove** (Fig. 6): (0) no; (1) yes.

Some species of Cupedidae have the functional ventral surface of the mandible separated into two to three differently structured areas.

- 29 Ventral surface of mandible with deep cavity** (Fig. 6A): (0) no; (1) yes.

The mandibles of *Ascioplaga*, *Adinolepis* and *Distocupes* have conspicuous, deep cavities in their ventral surfaces.

- 30 Apical palpomere of maxilla:** (0) not conspicuously large, i.e. shorter than two-thirds of the diameter of an eye; (1) approximately as long as the diameter of an eye and strongly wedge-shaped.

In *Omma sagitta*, *O. rutherfordi* and *O. mastersii* the palps of maxilla and labium are conspicuously long. The apical palpomere of the maxilla is about as long as the diameter of one eye. In other Archostemata such prominent palpomeres are absent.

- 31 Apical segment of maxillary palp** (Fig. 7): (0) with only one apical field of sensilla (campaniform sensilla); (1) with an apical and a dorso-lateral field of sensilla.

The apical segment of the maxillary and labial palps of most insects has an apical field of sensilla, which usually are of campaniform type. In Coleoptera an additional field of sensilla is present. It is located in the dorso-lateral area of the apical palpomere and contains long, strong sensilla with blunt, rounded tips (Guse & Honomichl, 1980; Honomichl, 1980; Honomichl & Guse, 1981; Mann & Crowson, 1984; Hörnschemeyer *et al.*, 2002; Beutel & Hörnschemeyer, 2002a). Similar fields of

sensilla are known also from some basal Hymenoptera (Vilhelmsen, 1996).

- 32 Apical palpomere of maxilla with digitiform sensilla** (Honomichl, 1980): (0) no; (1) yes.

In all Coleoptera examined with the exception of Archostemata and at least some Cantharidae (Polyphaga) the dorso-lateral sensillary field of the apical palpomere contains countersunk digitiform sensilla (Honomichl, 1980; T. Hörnschemeyer, unpublished data).

- 33 Dorso-lateral field of sensilla on apical maxillary palpomere in deep cavity** (Fig. 7G): (0) no; (1) yes.

The dorso-lateral field of sensilla on the apical palpomere is placed in a cavity in *Prolixocupes* and Ommatidae. This cavity is at least as deep as its sensilla are long.

- 34 Cavity of dorso-lateral field of sensilla on apical palpomeres with very small opening** (Fig. 7G): (0) no; (1) yes.

The opening of the cavity of the dorso-lateral field of sensilla on the apical palpomeres is very small in *Omma*. In *O. rutherfordi* the diameter of the opening is nearly as small as the socket of a seta.

- 35 The dorso-lateral field of sensilla on the maxillary palpus with fewer than 4 sensilla:** (0) no; (1) yes.

In most species of Archostemata the dorso-lateral field of sensilla of the apical palpomere of the maxilla contains 8–20 sensilla. Only in some species of Cupedidae and in *Crowsoniella* are there fewer than eight sensilla. *Adinolepis mathesonae* has no sensilla at all of this special type and in this area of the palps.

- 36 Galea** (Figs 7, 8): (0) not slender or capitate; (1) capitate, with slender base; (2) missing.

The shape of the galea is characteristic for Cupedidae, with a slender, rod-like basal part and a distinct setose terminal club. In the ground pattern of insects the galea is broad and more or less spatulate.

- 37 Gula-sutures:** (0) no gula; (1) diverging caudally, reaching the posterior margin of the head; (2) approximately trapezoid, converging caudally, reaching the posterior margin of the head; (3) approximately parallel, reaching the posterior margin of the head; (4) approximately parallel, not reaching the posterior margin of the head; (5) convex; (6) distinctly converging to the posterior tentorial pits, parallel from there on; (7) V-like, not reaching the posterior margin of the head; (8) not visible.

Insects with a prognathous head usually have secondary sclerotizations and/or fusions of the submentum with the head capsule, which close and protect the functional ventral side of the head. This so-called gula is bordered by distinct sutures in most Coleoptera.

- 38 Prementum with deep central cavity** (Fig. 8): (0) no; (1) yes; (2) prementum reduced.

In the ground pattern of insects the prementum is a relatively small, simple sclerite with the insertions of the glossa and paraglossa and of the labial palps on its dorsal surface. In Archostemata the prementum is enlarged and it has a long apodeme in the centre of its caudal half, which



is visible externally as a cavity. *Sikhotealinia* also has an enlarged prementum but without the central apodeme.

- 39 Shape of prementum:** (0) small, not lid-like; (1) less than 1.5× longer than wide at the apex, with oval apex; (2) more than 1.5× as long as wide at the apex, with narrow oval apex; (3) large and lid-like (as wide as long or wide than long), with wide, rounded apex, without transverse ridge; (4) approximately shield-like (as wide as long or wider than long), with transverse ridge in caudal third; (5) small, reduced.

In most species of Archostemata the prementum is a more or less flat plate. Some species of Cupedidae have a prominent transverse ridge in the caudal third of the prementum (see character 38).

- 40 Ligula** (Fig. 8): (0) glossa and paraglossa not fused; (1) ligula with two parts of equal shape and size; (2) ligula subdivided into many digitiform appendages; (3) missing. The ligula is the product of the fusion of the labial glossa and paraglossa and it is present in all taxa of Coleoptera. Many species of Cupedidae have a characteristic ligula that is subdivided into several digitiform appendages.

- 41 Mentum, submentum:** (0) free, unfused; (1) submentum fused to head capsule; (2) mentum, submentum and head capsule fused, with transverse suture between mentum and submentum; (3) mentum, submentum and head capsule fused, with deep, arcuate sutures between mentum and submentum; (4) mentum, submentum and head capsule fused, without suture.

As with most other Coleoptera, the submentum of Archostemata is fused to the head capsule as part of the ventral closure of the head. Most species of Archostemata do not have a separate mentum, only in *Tetraphalerus* is it recognizable (Beutel *et al.*, 2008). In some Cupedidae a distinct suture is present in the anterior area of the submentum. Probably the mentum is fused to the submentum, which has been integrated into the head capsule.

Characters of the adult thorax and its appendages: 42–57

- 42 Anterior corners of pronotum rounded:** (0) no; (1) yes. The shape of the pronotum and of its anterior and lateral borders varies significantly among taxa. Cupedidae often have distinct tips at the anterior corners, whereas in Ommatidae the pronotum is smoothly rounded as in many other insects.

- 43 Anterior corners of pronotum with double tips:** (0) no; (1) yes.

In Cupedidae the anterior corners of the pronotum usually have distinct tips. In some species, i.e. in *Rhipsideigma* spp., there are even double tips.

- 44 Pronotum without distinct tips at anterior corners, lateral margins converging anteriorly:** (0) no; (1) yes.

The lateral margins of the pronotum of *Adinolepis* converge evenly from the caudal to the cranial margin. Distinct tips on the anterior corners are missing.

- 45 Caudal margin of pronotum with narrowly triangular white markings:** (0) no; (1) yes.

In *Omma sagitta*, *O. rutherfordi* and *O. mastersii* the caudal margin of the pronotum bears white markings that are not present in other Archostemata.

- 46 Prosternal process:** (0) does not reach mesoventrite; (1) reaches into small cavity on mesosternum.

In most species of Archostemata the prosternal process separates the procoxae and reaches into a small cavity on the mesoventrite. In Ommatidae, *Micromalthus*, *Crowsoniella* and *Sikhotealinia* the prosternal process is short and does not reach the mesoventrite.

- 47 Subapical tarsomere:** (0) narrower than or as wide as the apical tarsomere; (1) wider than the apical tarsomere.

Like many Polyphaga, Cupedidae have dense pads of adhesive setae on their tarsomeres and tarsomeres 1 to 4 are often enlarged. In Ommatidae and in some other Archostemata there are no such adhesive pads and all tarsomeres are cylindrical.

- 48 Elytra** (coded as ordered and additive (Kluge & Farris, 1969; Farris, 1970; Wiley *et al.*, 1991)): (0) absent; (1) with rows of window-punctures (pits with transparent, membranous bottom); (2) completely sclerotized, without rows of window-punctures.

The presence of elytra is a distinctive autapomorphy of Coleoptera. With the inclusion of information from the fossil record one can reconstruct the evolution of the elytra of Coleoptera as a gradual increase of the sclerotization of the previously membranous forewings. The sclerotization extended from the wing veins and the window-punctures of Archostemata can be interpreted as an intermediate step to the completely sclerotized elytra.

- 49 Elytra with 10 longitudinal rows of window-punctures:** (0) no; (1) yes.

Ommatidae, *Priacma*, *Paracupes* and some other Cupedidae have ten longitudinal rows of window-punctures on the elytra. In the other species only nine rows are present.

- 50 Shape of window-punctures:** (0) absent; (1) transverse; (2) approximately round to square; (3) longitudinal; (4) irregular, rounded.

The window-punctures of the Archostemata are of different shape. Irregular, rounded pits are common but some species of *Tenomerga* have distinctly transverse, rectangular pits.

- 51 Scale cover of window-punctures:** (0) no window-punctures present; (1) bottom and inner wall of punctures without scales; (2) small scales hanging into the puncture from projections of the wall, but not reaching the bottom; (3) up to 4 scales 'flowing' from the wall onto the ground of the puncture; (4) loose ring of small scales covers most of the bottom of the puncture; (5) dense ring of large scales covers the bottom more or less completely.

The window-punctures of the elytra of Archostemata are set with scales in different ways. Quite common is a configuration with small scales that stand on projections of the wall of the puncture and hang into it. Conspicuously, the scales in the window-punctures usually have a different surface structure from the scales surrounding the punctures.

- 52 Closed elytra do not form a common apex:** (0) no; (1) yes.

In *Omma rutherfordi*, *Paracupes* and *Priacma* the elytra do not end in a common apex. Instead, each elytron has a more or less pronounced tip.

- 53 Elytra with apical tip and with an additional tip where the intervals 3 and 7 fuse** (coded as ordered and additive (Kluge & Farris, 1969; Farris, 1970; Wiley *et al.*, 1991)): (0) no elytra; (1) elytra without double tip; (2) elytra with two tips.

The elytra of *Rhipsideigma* have a distinct projection where intervals 3 and 7 fuse. In addition, the apex of each elytron is extended into a pronounced tip. The size ratio of these tips varies among species (see character 54).

- 54 Size ratio of apical projections of elytra:** (0) no elytra or no projections present; (1) tip on the elytral apex bigger or as big as the tip at the fusion of intervals 3 and 7; (2) tip at fusion of intervals 3 and 7 bigger than elytral apex.

- 55 Elytral apex strongly serrate:** (0) no; (1) yes.

In *Paracupes* and *Priacma* the otherwise smooth outer margin of the elytra is strongly serrate apically.

- 56 Middle and/or anterior area of the elytra with white transverse or X-shaped markings:** (0) no; (1) yes.

In *Omma sagitta*, *O. rutherfordi* and *O. mastersii* the elytra bear characteristic white markings that are not present in other Archostemata.

- 57 Triangular white markings on the elytral apex:** (0) no; (1) yes.

*Tenomerga kapnodes* and *T. moultoni* have very similar white markings in the apical third of the elytra. Such a colour pattern is not present in any other archostematan species.

Characters of the male genital complex were adopted from Sharp & Muir (1912), Edwards (1953a, b), Vidal Sarmiento (1969), Pace (1975), Vulcano & Pereira (1975), Neboiss (1984, 1989), Miyatake (1985, 1986) and Lawrence (1999) for most species. For *Omma stanleyi*, *Tetraphalerus bruchi*, *Priacma serrata*, *Tenomerga cinerea* and *Micromaltus debilis* original investigations were possible (Fig. 9): 58–84

- 58 Dorsal plate** (Fig. 9F): (0) absent; (1) present.

In the male genitalia of some Cupedidae a so-called dorsal plate is present, which lies on the penis. In *Rhipsideigma* the dorsal plate is comparatively large and has long lateral extensions (see chars 82 and 83). The shape of the dorsal plate varies distinctly among species.

- 59 Dorsal plate short, with two short apical lobes:** (0) no; (1) yes.

In *Distocupes* and *Ascioplaga* the dorsal plate has only about a quarter of the length of the aedeagus. In most other species it is approximately half as long as the aedeagus.

- 60 Dorsal plate long, with two apical lobes:** (0) no; (1) yes.

- 61 Apical two-thirds of sternite 9 very thin, needle-like:** (0) no; (1) yes.

The usually quite broad ninth sternite is conspicuously thin and needle-like in *Rhipsideigma*.

- 62 Sternite 9 caudally narrow and tapering (coded as ordered and additive** (Kluge & Farris, 1969; Farris, 1970; Wiley *et al.*, 1991)): (0) no; (1) approximately onion-shaped; (2) narrowly triangular and about 3× longer than it is wide at the base.

In *Distocupes*, *Ascioplaga* and *Adinolepis* the ninth sternite tapers strongly towards its apex.

- 63 Sternite 9 short, with 2 apical lobes:** (0) no; (1) yes.

In *Prolixocupes* the ninth sternite is less than one-third of the length of the aedeagus and its apex is deeply emarginate.

- 64 Sternite 9 rounded triangular and approximately half as long as tergite 9:** (0) no; (1) yes.

This is the most common shape of sternite 9 in Cupedidae.

- 65 Tergite 9 with 2 lateral lobes and one central lobe:** (0) no; (1) yes.

In many Cupedidae the apex of the ninth tergite has three lobes, whereas in Ommatidae it is evenly rounded.

- 66 Tergite 9 with 2 short, somewhat acute lateral lobes and a long, slender central lobe:** (0) no; (1) yes.

The apex of the ninth tergite of *Rhipsideigma* has a long and slender central lobe with rounded or blunt tip. The lateral lobes are short and, in ventral view, acute.

- 67 The lateral lobes of tergite 9 are short and merge perpendicular with the long central lobe:** (0) no; (1) yes.

The ninth tergite of *Ascioplaga* has a long central lobe with rounded apex. The lateral lobes are short and merge perpendicular with the central lobe. The central lobe is only weakly sclerotized.

- 68 Tergite 9 with constriction in its basal third:** (0) no; (1) yes.

The ninth segment and the aedeagus of *Adinolepis* are conspicuously slender. The ninth tergite is distinctly constricted in its basal third.

- 69 Bifurcate process** (Fig. 9D): (0) absent; (1) present.

Many Cupedidae have a V-shaped sclerite between the ninth sternite and the aedeagus. The shape of this sclerite is slightly variable between species.

- 70 Bifurcate process V-shaped:** (0) no; (1) yes.

- 71 Bifurcate process Y-shaped:** (0) no; (1) yes.

In *Tenomerga anguliscutis*, *T. kapnodes* and *T. mucida* the bifurcate process has a short, central extension at the proximal end.

- 72 Parameres with ventro-marginal spines** (Fig. 9): (0) no; (1) yes.

Many species of Cupedidae have long, slender processes on the ventral, inner margin of the parameres (VMS, Neboiss, 1984). The tips of the VMS often lie near the apex of the parameres.

- 73 Ventro-marginal spines of the parameres originate in the apical half of the aedeagus:** (0) no; (1) yes.

In most species the ventro-marginal spines originate in the basal half of the aedeagus. In *Cupes capitatus* and *Rhipsideigma* spp., their origin is shifted distally.

**74 Ventro-marginal spines of the parameres short and uncinatate:** (0) no; (1) yes.

In *Rhipsideigma* spp. the VMS are very short and their origins lie only a short distance behind the tips of the parameres. These short VMS look like a second pair of apical hooks (Neboiss, 1984).

**75 Ventro-marginal spines of parameres end close to the tips of the apical hooks:** (0) no; (1) yes.

The length of the ventro-marginal spines varies slightly among species. In some species they end close to the tips of the parameres and the apical hooks, but in most species they hardly reach the base of the apical hooks.

**76 Parameres with apical hooks** (Fig. 9): (0) no; (1) yes.

In Cupedidae each paramere has a strongly sclerotized, small subapical hook on its inner surface. Ommatidae, *Micromalthus* and *Crowsoniella* have no such hooks.

**77 Position of the basal opening of the aedeagus** (Fig. 9): (0) dorsal; (1) dorso-anteriorly; (2) anteriorly.

The basal opening through which the ductus ejaculatorius enters the aedeagus is positioned dorsally in most species, whereas in *Rhipsideigma* spp. the opening lies at the anterior apex of the aedeagus.

**78 Parameres with un-sclerotized apex, sub-apically widened and emarginate** (Fig. 9): (0) no; (1) yes.

In *Micromalthus* and *Omma* the parameres have large sub-apical emarginations on the mesal sides. Similar structures are rare among Coleoptera. They are, for example, present in *Atractocerus* spp. (Lymexylidae) (Sharp & Muir, 1912).

**79 Penis (=mesal lobe sensu Neboiss, 1984):** (0) nearly reaches up to the tips of the parameres; (1) reaches up to the base of the apical hooks; (2) does not reach up to the base of the apical hooks.

Most Coleoptera have quite a long penis that nearly reaches up to the tips of the parameres (Sharp & Muir, 1912; Jeanne, 1955; Iablokoff-Khnzorian, 1980). In some species of Archostemata the penis is so short that it only comes up to the distal third of each paramere.

**80 Penis distinctly compressed:** (0) no; (1) yes.

The apex of the penis is usually rounded. In *Micromalthus* and *Omma stanleyi* it is distinctly compressed.

**81 Shape of apex of penis:** (0) rounded; (1) with dorsoventral notch; (2) truncated; (3) widened.**82 Dorsal plate nearly as long as parameres, apically constricted and with lateral extensions:** (0) no; (1) yes.

The apical third to half of the dorsal plate of *Rhipsideigma* spp. has only about a third or less of the width of its base. The sides of the dorsal plate are turned dorsally and form long lateral extensions. The shape of these extensions varies between species. See also character 58.

**83 Lateral extensions of dorsal plate apically rotated and widened:** (0) no; (1) yes.**84 Penis slender with more or less parallel sides:** (0) no; (1) yes.

In *Adinolepis* spp. the penis is conspicuously slender.

**85 Head of second and later instars:** (0) parallel-sided, slightly converging anteriorly or evenly rounded; (1) transverse, laterally narrowly rounded, greatest width near caudal margin; (2) transverse with distinctly protruding eye region.

The larvae of *Omma*, *Sialis*, *Trachypachus* and of most Coleoptera have an approximately parallel-sided head, whereas *Micromalthus* and the Cupedidae have a short and wide head with distinctly rounded sides.

**86 Postero-median emarginations of head capsule:** (0) absent; (1) present.

All known larvae of the Archostemata have deep V-shaped emarginations in the middle of the dorsal and ventral posterior margins of the head capsule.

**87 Endocarina:** (0) absent; (1) present; (2) present and Y-shaped.

In all known larvae of Archostemata a distinct endocarina is present. In *Omma* spp. it is Y-shaped, whereas in the other species it is simple. In Lymexylidae and some other Coleoptera this suture is present but indistinct.

**88 Frontal suture in second and later instars:** (0) distinct; (1) indistinct or missing.

The frontal suture is quite distinct in most larvae of Coleoptera. It is missing in the later instars of Archostemata and of Lymexylidae (Beutel & Hörnschemeyer, 2002a).

**89 Stemmata:** (0) more than one pair; (1) only one pair or no stemmata.

The larvae of most Coleoptera have five to six stemmata, whereas the larva of *Omma* sp. has only four stemmata, and in the other Archostemata stemmata are missing.

**90 Endoskeleton of larval head:** (0) with tentorial bridge and posterior tentorial arms, gular ridges missing; (1) tentorial bridge missing, gular ridges distinct, posterior tentorial arms membranous.

Known larvae of the Archostemata have a reduced tentorium. The tentorial bridge, the dorsal arms and the anterior arms are missing. The posterior tentorial arms are a membranous extension of the gular ridges. A similar condition is also present in the adults of Cupedidae (Hörnschemeyer *et al.*, 2002; Hörnschemeyer *et al.*, 2006).

In the larvae the apex of the posterior tentorial arms is connected to the anatomical mouth opening. Such a connection is not known from the larvae of other Coleoptera.

**91 Length of antennae:** (0) at least 20% of the width of the head; (1) less than 20% of the width of the head.

Similarly short larval antennae as in *Micromalthus* and Cupedidae are also present in xylobiont larvae of other beetle taxa, for example Lymexylidae and Cerambycidae.

**92 Antennal muscles:** (0) more than one; (1) one.

The larvae of *Micromalthus debilis* have only one antennal muscle. The larvae of *Rhipsideigma* and *Distocupes* and those of many other Coleoptera have three antennal muscles. In *Elateroides dermestoides* (Lymexylidae) at least two muscles are present.

**93 Apex of mandibles:** (0) with fewer than 3 apical teeth; (1) with 3 apical teeth.

*Larval characters* (Beutel & Hörnschemeyer, 2002a, b): 85–110

In all known larvae of the Archostemata the mandible has three strong apical teeth.

- 94 Shape of the mola:** (0) not quadrangular, without distinct boundary; (1) quadrangular, with well-defined boundary.

The mandibles of the known larvae of the Archostemata have well-defined quadrangular molas, which, in this form, are not known from other taxa. However in *Omma* the distinct boundary of the mola is absent.

- 95 Cardio:** (0) undivided; (1) with separate, lateral, semi-membranous part.

In all known archostematan larvae the cardo is separated into a well-sclerotized mesal part and a soft lateral part.

- 96 Ligula:** (0) unsclerotized; (1) sclerotized, enlarged and wedge-shaped.

The ligula of archostematan larvae is relatively large, well sclerotized and wedge-shaped. This condition was interpreted as an autapomorphy of this taxon by Lawrence (1999) and Beutel & Haas (2000).

- 97 Mentum and submentum:** (0) separate; (1) fused.

The mentum and submentum of larvae of the Archostemata are fused and characteristically constricted in the area of the maxillary grooves.

- 98 Labial muscles:** (0) present; (1) absent.

Labial muscles are absent in larvae of *Rhipsideigma*, *Distocupes* and *Micromalthus*.

- 99 Transverse muscle between the gular ridges:** (0) absent; (1) present.

A transverse muscle that stretches between the gular ridges is only known to occur in the larvae of *Micromalthus* and *Tenomerga* and in *Orchesia* Latreille (Polyphaga: Melandryidae) (Beutel & Hörnschemeyer, 2002a).

- 100 Proventriculus:** (0) present; (1) absent.

The larvae of *Micromalthus*, *Tenomerga* and *Distocupes* have a proventriculus with strong cuticular teeth (Beutel & Hörnschemeyer, 2002a).

- 101 Width of prothorax in second and later instars:** (0) as wide as or narrower than the following segments; (1) wider than the following segments.

In the second and later instars of *Tenomerga* and *Rhipsideigma* the prothorax is wider than the following segments.

- 102 Glabrous patches on the prosternum of second and later instars:** (0) absent; (1) present.

Beginning with the second instars there are glabrous patches on the prosternum anterior of the asperities (see char. 105).

- 103 Abdominal segments 1 to 3 of second and later instars:** (0) shorter than the thorax; (1) longer than the thorax.

The abdomen of the larvae of the Archostemata is conspicuously elongated.

- 104 Tergal ampullae of second and later instars:** (0) absent; (1) present.

Tergal ampullae are known from all larvae of the Archostemata.

- 105 Sternal asperities of second and later instars:** (0) absent; (1) present.

Asperities are present on the prosternum of the first instar of *Priacma serrata* and on all sternites of the larvae of *Micromalthus debilis*. In the larva of *Omma* spp. asperities are absent.

- 106 Number of leg segments:** (0) 6; (1) 5.

Larvae of Polyphaga and Myxophaga usually have five segments, whereas the larvae of Adephaga and Archostemata have six segments.

- 107 Lateral longitudinal bulges on abdominal segments 1 to 7:** (0) absent; (1) present.

The larvae of *Tenomerga* and *Rhipsideigma* have lateral longitudinal bulges on the abdominal segments 1 to 7.

- 108 Sclerotized terminal process on tergum 9:** (0) absent; (1) present.

An arcuate, well-sclerotized process with numerous small teeth is present at the end of tergum 9 of the larvae of Cupedidae and of *Micromalthus debilis*. The larva of *Omma* spp. and the larvae of other Coleoptera do not have such a tergal process (Böving & Craighead, 1931; Lawrence, 1999).

In *M. debilis* a similar process is also present on the ninth sternum. The tergal and the sternal processes are arranged like pliers. As the sternal process is present only in *M. debilis* it is probably an autapomorphy of this species.

- 109 Urogomphi:** (0) absent; (1) present.

Urogomphi are absent on the ninth segment of all known larvae of the Archostemata. They are present in the larvae of the Adephaga, of the Torridincolidae and of many Polyphaga.

- 110 Segment 10:** (0) visible externally; (1) not visible externally.

The tenth segment is not visible in the larvae of the Archostemata, whereas it is visible externally in the larvae of most other beetles.

Appendix 2. Data matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>B. germanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
<i>S. lutaria</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	1	3	0	0	0
<i>A. apodema</i>	1	1	1	1	0	0	0	1	3	3	0	0	0	0	0	0	2	0	?	?	0	6	0	1	0	0	0	1	1	0
<i>A. eumana</i>	1	1	1	1	0	0	0	1	2	3	0	0	0	0	0	0	2	0	?	?	0	6	0	1	0	0	0	1	1	0
<i>A. mathesonae</i>	1	1	1	1	0	0	0	1	3	3	0	0	0	0	0	0	2	0	?	?	0	6	0	1	0	0	0	1	1	0
<i>A. youanga</i>	1	1	1	1	0	0	0	1	3	3	0	0	0	0	0	0	2	0	?	?	0	6	0	1	0	0	0	1	1	0
<i>Asc. mimeta</i>	1	1	0	1	0	0	1	1	4	3	0	2	2	0	0	0	2	0	1	1	0	5	0	1	0	0	0	1	1	0
<i>Asc. sciasma</i>	1	1	0	1	0	0	1	1	4	3	0	2	2	0	0	0	2	0	?	?	0	5	0	1	0	0	0	1	1	0
<i>Asc. scalena</i>	1	1	0	1	1	0	1	1	2	3	0	2	2	0	0	0	2	0	?	?	0	5	0	1	0	0	0	1	1	0
<i>C. relictata</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2	?	?	0	0	0	2	2	?	?	0	0	0
<i>Cup. capitatus</i>	1	1	0	0	0	0	0	2	1	2	2	3	3	3	0	0	2	0	0	1	0	3	0	1	0	0	0	1	0	0
<i>D. varians</i>	1	1	0	0	1	0	0	1	2	3	2	1	0	0	0	0	2	0	1	1	0	2	0	1	0	0	0	1	1	0
<i>M. debilis</i>	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	2	0	1	1	0	0	0
<i>O. mastersii</i>	1	1	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	?	?	1	1	0	2	0	1	1	0	0	1
<i>O. rutherfordi</i>	1	1	0	0	0	0	0	1	?	2	0	0	0	0	0	1	4	0	?	?	1	1	0	2	0	1	1	0	0	1
<i>O. sagitta</i>	1	1	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	?	?	1	1	0	2	0	1	1	0	0	1
<i>O. stanleyi</i>	1	1	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	?	?	1	1	0	2	0	1	1	0	0	0
<i>P. ascius</i>	1	1	0	0	0	0	0	1	2	4	2	0	0	0	0	0	2	0	?	?	0	2	0	1	1	0	0	0	0	0
<i>P. brasiliensis</i>	1	1	0	0	0	0	0	1	2	4	2	0	0	0	0	0	2	0	?	?	0	2	0	1	1	0	0	0	0	0
<i>Pri. serrata</i>	1	1	0	0	0	0	0	1	2	3	2	0	1	0	0	0	1	0	0	0	0	2	0	1	1	0	0	0	0	0
<i>Pro. latreillei</i>	1	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0	2	0	?	?	0	4	0	1	0	1	0	1	0	0
<i>Pro. lobiceps</i>	1	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0	2	0	?	?	0	4	0	1	0	1	0	1	0	0
<i>R. adjuncta</i>	1	1	0	0	0	0	0	2	1	2	2	3	3	3	0	0	2	0	?	?	0	3	0	1	0	0	0	1	0	0
<i>R. anosibense</i>	1	1	0	0	0	0	0	2	1	2	2	3	3	3	0	0	2	0	?	?	0	3	0	1	0	0	0	1	0	0
<i>R. cretaceotincta</i>	1	1	0	0	0	0	0	2	1	2	2	3	3	3	0	0	2	0	?	?	0	3	0	1	0	0	0	1	0	0
<i>R. lugubris</i>	1	1	0	0	0	0	0	2	1	2	2	3	3	3	0	0	2	0	?	?	0	3	0	1	0	0	0	1	0	0
<i>R. raffrayi</i>	1	1	0	0	0	0	0	2	1	2	2	3	3	3	0	0	2	0	?	?	0	3	0	1	0	0	0	1	0	0
<i>S. zhiltzovae</i>	0	?	0	0	0	0	0	0	0	0	0	4	0	0	0	1	3	0	?	?	0	0	0	1	0	0	0	?	?	0
<i>T. anguliscutis</i>	1	1	0	0	0	0	0	1	2	5	2	4	3	1	0	0	2	0	?	?	0	2	0	1	0	0	0	1	0	0
<i>T. cinerea</i>	1	1	0	0	0	0	0	1	2	5	2	4	3	1	0	0	2	0	1	1	0	2	0	1	0	0	0	1	0	0
<i>T. favella</i>	1	1	0	0	1	0	0	1	2	3	2	1	4	2	0	0	2	0	?	?	0	2	1	1	0	0	0	1	0	0
<i>T. japonica</i>	1	1	0	0	0	0	0	1	2	5	2	4	3	1	0	0	2	0	?	?	0	2	0	1	0	0	0	1	0	0
<i>T. kapnodes</i>	1	1	0	0	1	0	0	1	2	3	2	1	4	2	0	0	2	0	?	?	0	2	1	1	0	0	0	1	0	0
<i>T. kurosawai</i>	1	1	0	0	0	0	0	1	2	?	2	4	?	2	0	0	2	0	?	?	0	2	0	1	0	0	0	1	0	0
<i>T. leucophaea</i>	1	1	0	0	0	0	0	1	2	2	2	3	0	3	0	0	2	0	?	?	0	3	0	1	0	0	0	1	0	0
<i>T. moultoni</i>	1	1	0	0	1	0	0	1	2	3	2	1	4	2	0	0	2	0	?	?	0	2	1	1	0	0	0	1	0	0
<i>T. mucida</i>	1	1	0	0	0	0	0	1	2	5	2	4	3	1	0	0	2	0	?	?	0	2	0	1	0	0	0	1	0	0
<i>T. sibyllae</i>	1	1	0	0	0	0	0	1	2	5	2	4	3	1	0	0	2	0	?	?	0	2	0	1	0	0	0	1	0	0
<i>T. trabecula</i>	1	1	0	0	0	0	0	1	2	2	2	4	3	1	0	0	2	0	?	?	0	2	0	1	0	0	0	1	0	0
<i>T. yamato</i>	1	1	0	0	0	0	0	1	2	2	2	4	3	2	0	0	2	0	?	?	0	2	0	1	0	0	0	1	0	0
<i>Tet. bruchi</i>	1	1	0	0	0	1	0	3	0	0	3	0	0	0	1	1	0	1	2	0	0	1	0	1	0	1	1	0	0	0
<i>Tet. wagneri</i>	1	1	0	0	0	1	0	3	0	0	3	0	0	0	1	1	0	1	?	?	0	1	0	1	0	1	1	0	0	0
<i>Trachypachus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	1	0	0	0	0	0	0
<i>E. dermestoides</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	?	0	0	0	1	0	0	2	0	0	0



Data matrix (Continued).

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	
<i>B. germanica</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>S. lutaria</i>	0	0	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>A. apodema</i>	?	0	0	0	?	?	2	1	?	?	4	0	0	1	0	1	1	1	0	?	?	0	1	0	0	0	0	?	?	?	
<i>A. eumana</i>	1	0	0	0	1	?	2	1	4	?	4	0	0	1	0	1	1	1	0	3	3	0	1	0	0	0	0	?	0	0	
<i>A. mathesonae</i>	0	0	0	0	1	1	2	1	4	?	4	0	0	1	0	1	1	1	0	2	1	0	1	0	0	0	0	?	0	0	
<i>A. youanga</i>	1	0	0	0	1	1	2	1	4	?	4	0	0	0	0	1	1	1	0	3	3	0	1	0	0	0	0	?	0	0	
<i>Asc. mimeta</i>	1	0	0	0	0	1	2	1	4	2	4	0	0	0	0	1	1	1	0	2	5	0	1	0	0	0	0	1	1	0	
<i>Asc. sciasma</i>	1	0	0	0	?	1	3	1	4	?	2	0	0	0	0	1	1	1	0	?	5	0	1	0	0	0	0	1	1	0	
<i>Asc. scalena</i>	?	0	0	0	?	?	2	1	?	?	2	0	0	0	0	1	1	1	0	3	2	0	1	0	0	0	0	?	?	?	
<i>C. relict</i>	1	0	0	0	1	2	3	2	5	3	?	1	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	?	?	?	
<i>Cup. capitatus</i>	1	0	0	0	0	1	2	1	4	2	4	0	0	0	0	1	1	1	0	2	4	0	1	0	0	0	0	?	0	0	
<i>D. varians</i>	1	0	0	0	0	1	2	1	4	?	4	0	0	0	0	1	1	1	0	2	2	0	1	0	0	0	0	1	1	0	
<i>M. debilis</i>	1	0	0	0	0	2	5	2	5	3	4	1	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	?	?	?	
<i>O. mastersii</i>	1	0	1	1	?	0	4	1	1	?	4	1	0	0	1	0	0	1	1	2	1	0	1	0	0	1	0	0	0	0	
<i>O. rutherfordi</i>	1	0	1	1	?	?	?	1	?	?	4	1	0	0	1	?	0	1	?	4	1	1	1	0	0	1	0	0	0	0	
<i>O. sagitta</i>	1	0	1	1	?	?	?	1	?	?	4	1	0	0	1	0	0	1	1	?	?	0	1	0	0	1	0	?	?	?	
<i>O. stanleyi</i>	1	0	1	1	0	0	4	1	1	1	4	1	0	0	0	0	0	1	1	4	1	0	1	0	0	0	0	0	0	0	
<i>P. ascius</i>	?	0	0	0	?	?	3	1	?	?	4	0	0	0	0	1	1	1	1	4	1	1	1	0	1	0	0	?	?	?	
<i>P. brasiliensis</i>	1	0	0	0	0	1	3	1	1	1	4	0	0	0	0	1	1	1	1	4	1	1	1	0	1	0	0	0	0	0	
<i>Pri. serrata</i>	1	0	0	0	0	1	2	1	1	1	4	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	
<i>Pro. latreillei</i>	1	0	1	0	0	1	7	1	1	1	2	0	0	0	0	1	1	1	0	2	5	0	1	0	0	0	0	?	0	0	
<i>Pro. lobiceps</i>	1	0	?	0	?	?	6	1	1	1	3	0	0	0	0	1	1	1	0	2	3	0	1	0	0	0	?	0	0	0	
<i>R. adjuncta</i>	?	0	0	0	?	?	2	1	?	?	3	0	1	0	0	1	1	1	0	?	?	1	2	1	0	0	0	1	0	0	
<i>R. anosibense</i>	?	0	0	0	?	?	2	1	?	?	3	0	1	0	0	1	1	1	0	?	?	1	2	2	0	0	0	1	0	0	
<i>R. cretaceotincta</i>	1	0	0	0	0	1	2	1	4	?	3	0	1	0	0	1	1	1	0	2	5	1	2	1	0	0	0	1	0	0	
<i>R. lugubris</i>	1	0	0	0	?	1	2	1	4	2	3	0	1	0	0	1	1	1	0	2	5	1	2	2	0	0	0	1	0	0	
<i>R. raffrayi</i>	1	0	0	0	0	?	2	1	4	?	3	0	1	0	0	1	1	1	0	?	5	1	2	1	0	0	0	1	0	0	
<i>S. zhiltzovae</i>	?	?	?	?	?	?	2	0	3	?	1	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	?	?	?	
<i>T. anguliscutis</i>	?	0	0	0	?	?	2	1	3	?	2	0	0	0	0	1	1	1	0	2	?	0	1	0	0	0	0	1	0	1	
<i>T. cinerea</i>	1	0	0	0	0	1	2	1	?	?	2	0	0	0	0	1	1	1	0	3	4	0	1	0	0	0	1	0	1	0	
<i>T. favella</i>	1	0	0	0	?	?	2	1	?	?	4	0	0	0	0	1	1	1	0	2	?	0	1	0	0	0	0	1	0	0	
<i>T. japonica</i>	1	0	0	0	?	?	2	1	3	?	2	0	0	0	0	1	1	1	1	1	?	0	1	0	0	0	0	1	0	1	
<i>T. kapnodes</i>	1	0	0	0	?	?	2	1	3	?	4	0	0	0	0	1	1	1	0	2	?	0	1	0	0	0	1	1	0	1	
<i>T. kurosawai</i>	1	0	0	0	?	?	?	?	?	?	?	0	0	0	0	1	1	1	1	1	?	0	1	0	0	0	0	1	0	1	
<i>T. leucophaea</i>	1	0	0	0	0	1	2	1	?	?	2	2	0	1	0	0	1	1	1	0	2	2	0	1	0	0	0	0	1	0	0
<i>T. moultoni</i>	1	0	0	0	?	?	2	1	4	?	4	0	0	0	0	1	1	1	0	2	1	0	1	0	0	0	1	1	?	?	
<i>T. mucida</i>	1	0	0	0	?	?	2	1	3	?	4	0	0	0	0	1	1	1	0	4	4	0	1	0	0	0	0	1	0	1	
<i>T. sibyllae</i>	1	0	0	0	?	?	2	1	?	?	4	0	0	0	0	1	1	1	0	4	?	0	1	0	0	0	0	1	?	?	
<i>T. trabecula</i>	1	0	0	0	?	?	2	1	?	?	4	0	0	0	0	1	1	1	1	1	?	0	1	0	0	0	0	1	0	1	
<i>T. yamato</i>	1	0	0	0	?	?	?	1	?	?	?	0	0	0	0	1	1	1	1	1	?	0	1	0	0	0	0	?	?	?	
<i>Tet. bruchi</i>	1	0	1	0	0	0	8	1	2	1	4	1	0	0	0	0	0	1	1	2	1	0	1	0	0	0	0	0	0	0	
<i>Tet. wagneri</i>	1	0	1	0	0	?	8	1	2	1	4	1	0	0	0	0	0	1	1	2	1	0	1	0	0	0	0	0	0	0	
<i>Trachypachus</i>	1	1	0	0	?	0	?	0	?	?	?	1	0	0	0	1	0	2	0	0	0	0	1	0	0	0	0	0	0	0	
<i>E. dermestoides</i>	1	1	0	0	?	0	3	0	0	1	1	1	0	0	0	0	?	2	0	0	0	0	1	0	0	0	0	0	0	0	

Data matrix (Continued).

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
<i>B. germanica</i>	?	?	0	?	?	?	?	?	0	0	0	0	0	0	0	?	?	?	?	?	0	0	?	?	?	?	?	?	?	
<i>S. lutaria</i>	?	?	0	?	?	?	?	?	0	0	0	0	0	0	0	?	?	?	?	?	0	0	?	0	0	0	0	0	0	
<i>A. apodema</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>A. eumana</i>	0	2	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	2	0	0	1	?	?	?	?	?	
<i>A. mathesonae</i>	0	2	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	2	0	0	1	?	?	?	?	?	
<i>A. youanga</i>	0	2	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	?	?	?	?	?	
<i>Asc. mimeta</i>	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	?	?	?	?	?	
<i>Asc. sciasma</i>	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	?	?	?	?	?	
<i>Asc. scalena</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>C. relict</i>	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	0	?	0	0	0	?	?	?	?	?	
<i>Cup. capitatus</i>	0	0	0	1	1	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	?	?	?	?	?	
<i>D. varians</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	
<i>M. debilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	1	?	0	0	0	1	1	1	1	1	1	
<i>O. mastersii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	2	0	0	0	0	1	2	1	0	?	
<i>O. rutherfordi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	1	0	0	?	?	?	?	?	?	?	
<i>O. sagitta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>O. stanleyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	?	0	0	0	?	?	?	?	?	?	
<i>P. ascius</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>P. brasiliensis</i>	?	?	?	?	?	?	?	?	1	0	0	0	0	0	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pri. serrata</i>	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	0	0	?	?	?	?	?	?	?	1	1	?	1	?
<i>Pro. latreillei</i>	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	3	0	0	0	?	?	?	?	?	
<i>Pro. lobiceps</i>	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	3	0	0	0	?	?	?	?	?	
<i>R. adjuncta</i>	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	0	0	0	2	1	0	0	?	?	?	?	?	
<i>R. anosibense</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	2	0	0	0	2	1	1	0	?	?	?	?	?
<i>R. cretaceotincta</i>	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	0	0	0	0	1	0	0	?	?	?	?	?	
<i>R. lugubris</i>	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	0	0	0	2	1	1	0	?	?	?	?	?	
<i>R. raffrayi</i>	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	0	0	0	0	1	0	0	1	1	1	1	1	
<i>S. zhiltzovae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. anguliscutis</i>	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	0	2	0	1	0	0	0	?	?	?	?	?	
<i>T. cinerea</i>	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	2	0	1	0	0	0	1	1	1	1	?	
<i>T. favella</i>	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	2	0	1	0	0	0	?	?	?	?	?	
<i>T. japonica</i>	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	2	0	1	0	0	0	?	?	?	?	?	
<i>T. kapnodes</i>	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	1	0	0	2	0	1	0	0	0	?	?	?	?	?	
<i>T. kurosawai</i>	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	2	0	1	0	0	0	?	?	?	?	?	
<i>T. leucophaea</i>	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	?	?	?	?	?	
<i>T. moultoni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. mucida</i>	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	1	0	0	2	0	1	0	0	0	?	?	?	?	?	
<i>T. sibyllae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. trabecula</i>	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0	?	?	?	?	?	
<i>T. yamato</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Tet. bruchi</i>	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	?	?	?	?	?	
<i>Tet. wagneri</i>	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	?	?	?	?	?	
<i>Trachypachus</i>	?	?	0	?	?	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	0	0	?	0	0	0	0	0	
<i>E. dermestoides</i>	?	?	0	?	?	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	0	0	?	0	0	1	1	1	0

Data matrix (Continued).

	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110
<i>B. germanica</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>S. lutaria</i>	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. apodema</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>A. eumana</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>A. mathesonae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>A. youanga</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Asc. mimeta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Asc. sciasma</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Asc. scalena</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>C. relicta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cup. capitatus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>D. varians</i>	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	0	?
<i>M. debilis</i>	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1
<i>O. mastersii</i>	0	?	1	0	1	1	1	?	?	?	0	0	1	1	0	0	0	0	0	1
<i>O. rutherfordi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>O. sagitta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>O. stanleyi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>P. ascius</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>P. brasiliensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pri. serrata</i>	1	?	1	1	1	?	?	?	?	?	0	?	?	?	?	0	0	?	0	1
<i>Pro. latreillei</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pro. lobiceps</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>R. adjuncta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>R. anosibense</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>R. cretaceotincta</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>R. lugubris</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>R. raffrayi</i>	1	0	1	1	1	1	1	1	?	1	1	1	1	1	1	0	1	1	0	1
<i>S. zhiltzovae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. anguliscutis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. cinerea</i>	1	?	1	1	1	1	1	?	?	?	1	1	1	1	1	0	1	1	0	1
<i>T. favella</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. japonica</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. kapnodes</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. kurosawai</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. leucophaea</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. moultoni</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. mucida</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. sibyllae</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. trabecula</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>T. yamato</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Tet. bruchi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Tet. wagneri</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Trachypachus</i>	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>E. dermestoides</i>	1	0	0	0	0	0	0	0	0	?	0	0	1	0	0	1	0	0	0	0