



# On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera

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## Abstract

Internal and external features of *Tetraphalerus bruchi* were studied using X-ray microtomography ( $\mu$ -CT) and other techniques, and head structures were described in detail.  $\mu$ -Ct is highly efficient for the assessment of anatomical data. A data matrix with 90 morphological characters of recent and fossil beetles was analyzed with different approaches (parsimony, Bayesian analysis). The results of the parsimony analysis resulted in the following branching pattern: ( $\dagger$ Tshekardocoleidae + ( $\dagger$ Permocupedidae,  $\dagger$ Rhombocoleidae + ( $\dagger$ Triadocupedidae + ((Adephaga + (Myxophaga + Polyphaga)))) + Archostemata s.str. [including Jurodidae])). *Sikhotealinia* is placed as sister group of  $\dagger$ Jurodes (Jurodidae), and Jurodidae as sister group of the remaining Archostemata (Bayesian analysis) or of a clade comprising Micromalthidae, Crowsoniellidae,  $\dagger$ Ademosynidae,  $\dagger$ Schizophoridae and  $\dagger$ Catiniidae. The monophyly of Ommatidae and Cupedidae is well supported and *Priacma* is placed as the sister group of all other Cupedidae. Important events in the early evolution of Coleoptera are the shortening of the elytra and the transformation of the elytral venation (Coleoptera excluding  $\dagger$ Tshekardocoleidae), the formation of a closed subelytral space (Coleoptera excluding  $\dagger$ Tshekardocoleidae and  $\dagger$ Permocupedidae), the reduction of two apical antennomeres, and the loss of the broad prothoracic postcoxal bridge (Coleoptera excluding  $\dagger$ Tshekardocoleidae,  $\dagger$ Permocupedidae and  $\dagger$ Rhombocoleidae). Plesiomorphic features preserved in extant Archostemata are the tuberculate cuticle, the elytral pattern with parallel longitudinal ribs and window punctures, a mesoventrite with a transverse ridge, triangular mesocoxae with a distinct meron, and the exposed metatrochantin. The fossils included in the analyses do not only contribute to the reconstruction of character evolution but also influence the branching pattern. An understanding of the major evolutionary events in Coleoptera would not be possible without considering the rich fossil record of Permian and Mesozoic beetles.

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With  $\approx$  350 000 described extant species and many millions more that have ever existed (Ponomarenko, 2002) Coleoptera are by far the most successful order of insects. In contrast to this extreme total diversity, the “archaic” suborder Archostemata (Crowson, 1962) comprises only 40 extant species. Nevertheless it is a fascinating group containing some of the most obscure and enigmatic representatives of Coleoptera.  $\dagger$ Tshekardocoleidae, the earliest known beetle fossils from Lower Permian (Artinskian) deposits (Kukalová, 1969;

Ponomarenko, 1969; Crowson, 1975a; Kukalová and Willmann, 1990; Carpenter, 1992) have been classified in Archostemata as defined in the traditional sense (e.g., Ponomarenko, 1969). This group was widespread and apparently more successful than the other beetle suborders in the first half of the Mesozoic (e.g., Madygen Formation [Triassic], Hetangian and Sinemurian [Jurassic]; Ponomarenko, 1969, 1995). Later, diversity dropped dramatically and the suborder became extinct in Europe (with the exception of *Crowsoniella relictata* Pace, 1975) and in most other parts of the Palearctic (e.g., Hörnschemeyer, 2005). Today it is represented only by 13 or 14 species-poor genera and four or five families.

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Extant archostematan beetles display a remarkable mixture of “primitive” and highly specialized features. Thoracic features are clearly plesiomorphic compared with what is found in all other extant beetles (Baehr, 1975; Beutel and Haas, 2000), whereas head structures and genitalia appear highly derived, at least in the majority of the known species (e.g., Edwards, 1953a,b; Hörschemeyer et al., 2002; Hörschemeyer 2005). The known larvae of Archostemata are by no means “primitive” but highly specialized wood boring forms (Beutel and Hörschemeyer, 2002a,b), superficially similar to the wood boring larvae of Cerambycidae.

All species of Archostemata are considered rare or extremely rare (e.g., Crowson, 1962). *Micromalthus debilis* LeConte, 1878, the only genus of Micromalthidae, is only sporadically collected. Larval specimens of *Micromalthus* were found in Eocene Baltic amber, in Oligocene amber from Mexico and in Early Cretaceous Lebanese amber (Grimaldi and Engel, 2005). The original area of distribution of the extant species is the eastern part of North America, but today, due to transportation with timber, it is recorded from many parts of the world (e.g., Hawaii, South Africa, Austria). *Micromalthus debilis* has arguably the most complicated life cycle of all beetles, with hypermetamorphosis, different kinds of parthenogenesis, pedogenetic larvae and vivipary (Pollock and Normark, 2002). *Crowsoniella relictata* is the only extant European species of Archostemata and the only species of Crowsoniellidae (Crowson, 1975b; Pace, 1975). A series of this strongly miniaturized and strongly flattened beetle was collected in northern Italy (Lazio) in 1974. Since then, despite of considerable efforts, no additional specimens have been found. The larvae are yet unknown and virtually nothing is known about the life habits of the species.

The most obscure species assigned to Archostemata is *Sikhotealinia zhiltsovae* Lafer, 1996. The only known specimen was found dead at a river edge in the Russian Far East (Sikhotealin Mountains). The species was adequately described by Lafer (1996). However, the available morphological data are limited and the internal features, the immature stages, and the natural history are completely unknown. Similarities of *Sikhotealinia* with Jurodidae, which were considered as extinct by that time, were pointed out by A.G. Ponomarenko to A.G. Kirejtshuk, and the latter author placed the genus in this family (Kirejtshuk, 1999/2000). Jurodidae including *Sikhotealinia* was tentatively placed in Archostemata (Kirejtshuk, 1999/2000; Hörschemeyer, 2005), but affinities with Polyphaga and other beetle subgroups were discussed by both authors.

With 31 species and nine genera Cupedidae is the most species-rich extant family of Archostemata (e.g., Neboiss, 1984; Hörschemeyer, 2005). Ommatidae comprises the genera *Omma* (Australia) and *Tetraphalerus* (South America) and a total of six extant species.

*Tetraphalerus bruchi* (Fig. 1), one of two tetraphalerid species, plays a central role in the present investigation. Like the other extant species, it occurs in very arid areas of northern Argentina. The larvae are unknown and the adults lead a cryptic life and were only rarely collected on light traps under very specific weather conditions. The fossil history of *Tetraphalerus* reaches back to the Jurassic. In contrast to the very limited range of the genus today, the recorded distribution in the Mesozoic was remarkably wide. At least 13 extinct species are known from Jurassic and Cretaceous Lagerstätten in China, Russia, Great Britain and Spain (Crowson, 1962; Ponomarenko, 1969, 2000; Tan et al., 2005).

Until now, the morphology of *Tetraphalerus* was very insufficiently known. Only brief descriptions of external features and of the male genitalia were available (Monrós and Monrós, 1952; Vidal Sarmiento, 1969; Vulcano and Pereira, 1975), and information about habits and natural history is still extremely scarce. In the framework of the Beetle Tree of Life project (<http://insects.oeb.harvard.edu/ATOL>) a series of adults was collected by Dra. Adriana Marvaldi. Some specimens will be used to obtain molecular data and others were donated to us for morphological investigations in the framework of BToL. We decided to examine and describe the head in detail, as this tagma is highly complex and often provides valuable phylogenetic information (e.g., Hörschemeyer et al., 2002, 2006). However, we also made a survey of characters of other body parts, especially of the thoracic segments. This was made possible in an unusually efficient way using X-ray microtomography ( $\mu$ -CT). One purpose of the present study is to explore and further establish this innovative technology.

The morphological data we obtained were combined with characters of other groups of Archostemata and other beetle taxa and analyzed cladistically with different approaches. The main aims were the assessment of the relationships of the archostematan families and genera, the clarification of the placement of the enigmatic *Sikhotealinia*, and finally the reconstruction of the basal branching events in Coleoptera.

Despite the considerable lack of information on some of the extinct and extant groups (e.g., *Sikhotealinia*, *Crowsoniella*), we decided to include them in the analysis. It was pointed out by Donoghue et al. (1989) that there are other sources of missing data than non-preservation in fossils (or lack of morphological observations) (e.g., inapplicable characters), and that fossil taxa can play a vital part in reconstructing phylogeny, even though it may be impossible to reconstruct a considerable portion of the features accessible in extant species. Moreover, it was emphasized by Ponomarenko (1995) that an understanding of the evolution of Coleoptera is not possible without considering the species from the rich fossil record.



Fig. 1. *Tetraphalerus bruchi*, habitus lateral view.

## Materials and methods

### Specimens preserved in fluid

Archostemata: *Tetraphalerus bruchi* Heller, 1913 (Argentina, Provincia de Mendoza, collected by Dra. Adriana Marvaldi).

*Priacma serrata* LeConte, 1861 (Montana, USA, collected by one of the authors [T.H.]).

*Micromalthus debilis* LeConte, 1878 (adults and larvae from laboratory colony, M. A. Perotti, Bangor, UK).

*Cupes capitatus* Fabricius, 1801 (USA, collected by W. E. Steiner, Smithsonian).

*Tenomerga cinerea* (Say, 1831) (USA, collected by W. E. Steiner, Smithsonian).

*Distocupes varians* (Lea, 1902) (Australia, collected by John F. Lawrence).

*Rhipsideigma raffrayi* (Fairmaire, 1884) [larvae, Madagascar, Petr Svácha (Institute of Entomology; České Budějovice)].

Adephaga: *Trachypachus holmbergi* Mannerheim [adults and larvae, Edmonton, Canada, collected by R. E. Roughley (University of Manitoba)].

Myxophaga: *Torridincola rhodesica* Steffan, 1964 (adults and larvae), *Iapir bristkii* (Reichardt & Costa, 1967) (larvae).

Polyphaga: *Helophorus* spp. (adults and larvae).

### Dried specimens

*Omma stanleyi* Newman, 1839 (Australia, from the Australian National Insect Collection, CSIRO, Australia).

*Crowsoniella relictata* Pace 1975 (type and paratypes at the Museo Civico di Storia Naturale, Verona, Italy).

*Rhipsideigma cretaceotincta* (Kolbe, 1897) [Natural History Museum, London, UK (BMNH); Museum für Naturkunde, Berlin, Germany (ZMHB)].

*Paracupes brasiliensis* Kolbe, 1898 [dried specimens from the collections at the Natural History Museum, London, UK (BMNH); Zoologische Staatssammlung München, Germany (ZSMC); Museum für Naturkunde, Berlin, Germany (ZMHB)].

## Fossils

Ommatidae incertae sedis (three specimens, Upper Jurassic or Lower Cretaceous, Yixian Formation of western Liaoning, China).

The holotype of *Sikhotealinia zhiltsovae* Lafer 1996 was examined at the Museum für Naturkunde Berlin during a visit of Prof. Dr A.G. Kirejtshuk. The drawing of the mesothorax was made using photographs of the holotype made available on the internet (<http://www.zin.ru/Animalia/Coleoptera/rus/sikhot06.htm>).

Data on fossil taxa were mainly extracted from the literature, with Ponomarenko's comprehensive and detailed treatment (Ponomarenko, 1969) as the most important source. Additionally, electronic images of fossils were made available by Prof. Dr A.G. Ponomarenko. Fossil groups only known from detached elytra (e.g., †Schizocoleidae, †Asiocoleidae) were not included in the analyses.

The specimens of *Tetraphalerus bruchi* were collected with light traps and preserved in 90% ethanol. For the reconstruction of musculature, digestive tract, endoskeleton and brain serial cross-sections were made. One specimen was studied with high-resolution  $\mu$ -CT. The specimen used for serial sectioning was embedded in Araldit<sup>®</sup>, cut at 1  $\mu$ m with a Microm microtome (HM 360) and stained with Azan. The specimen for the  $\mu$ -CT investigation was treated with Dubosque-Brazil for 2 days, then gradually transferred to 100% ethanol and critical point dried (Balzers CPD 030 Critical Point Dryer). The  $\mu$ -CT data were obtained by Dr J. Goebbels and J. Nötel at the Federal Institute for Materials Research and Testing (BAM), Berlin, Germany. The data set has a spatial resolution of 2.5  $\mu$ m in three dimensions. Another specimen was cleaned with ultrasonic sound and sputter-coated with gold for scanning electron microscopy. Pictures were taken with an FEI scanning electron microscope (XL 30 ESEM). Anatomical drawings of the head were made using  $\mu$ -CT image stacks and three-dimensional reconstructions obtained with the automatic volume-rendering option in Imaris 4.5. AnalySIS<sup>®</sup> software was used for the documentation of serial microtome sections. The terminology for muscles of the head follows von Kéler (1963).

Character analysis was carried out with NONA (Goloboff, 1995), PAUP\* 4.0b10 (Swofford, 2001) and MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Bremer-support values were calculated with AutoDecay 5.0 (Eriksson, 2003). *Sialis* sp. and *Chauliodes* sp. were used as outgroup taxa and treated as all other groups in the analysis (simultaneous analysis; Nixon and Carpenter, 1993).

## Results

### *Tetraphalerus bruchi*

*Surface structure (Figs 2 and 3).* Almost all parts of the head capsule covered with tubercles. Only the ventrolateral antennal furrows and the small area close to the secondary mandibular articulation are smooth. Tubercles are roughly pentagonal, closely adjacent, on

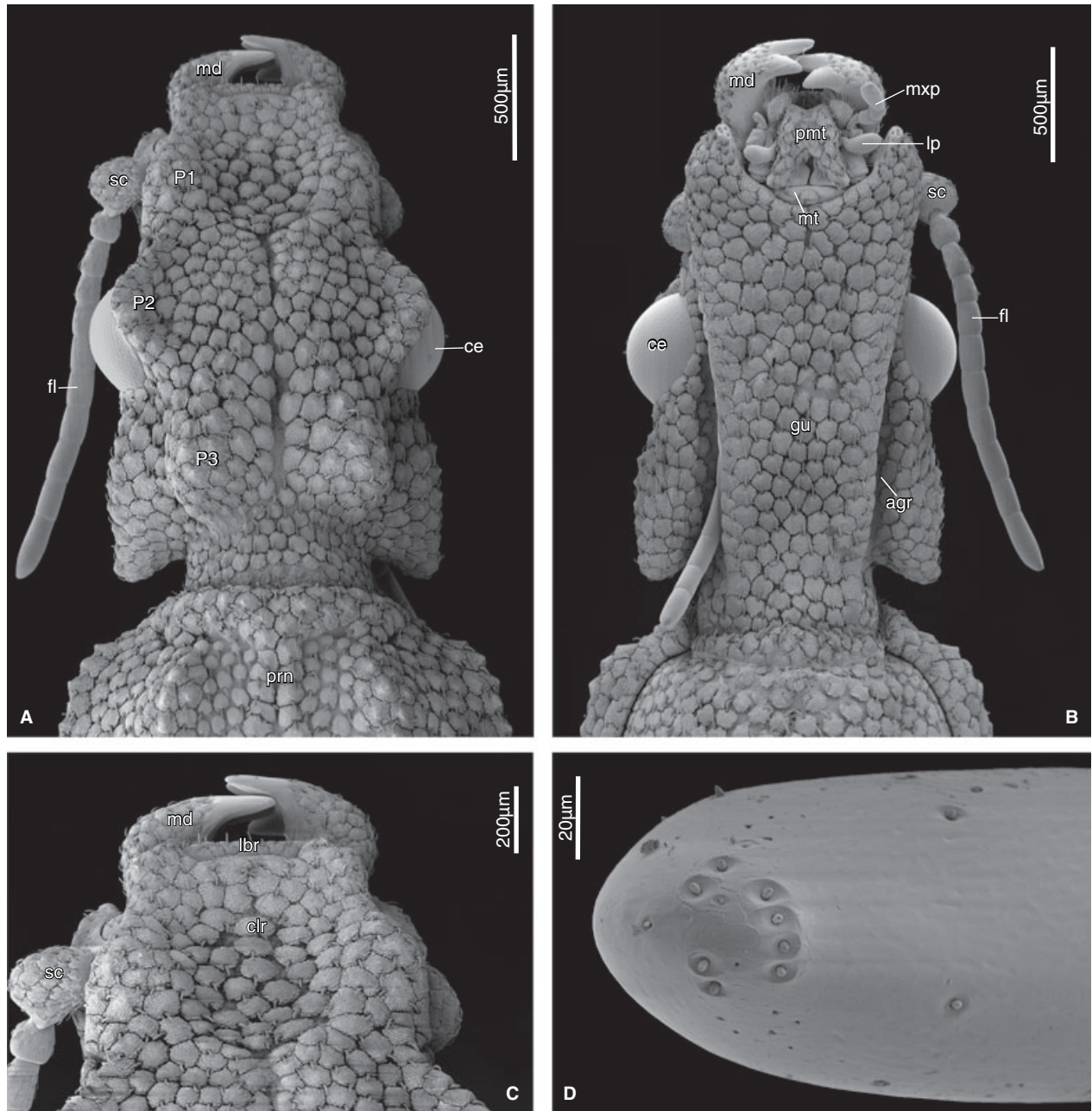


Fig. 2. (A–D) *T. bruchi*, head, SEM micrographs. (A) Dorsal view; (B) ventral view; (C) anterior head region, dorsal view; (D) apex of antennomere 11. Abbreviations: agr, antennal groove; ce, compound eye; clr, clypeal region; fl, antennal flagellum; gu, gular region; lbr, labrum; lp, labial palp; md, mandible; mxp, maxillary palp; P1, supraantennal protuberance; P2, supraocular protuberance; P3, posteromesal protuberance; sc, scapus.

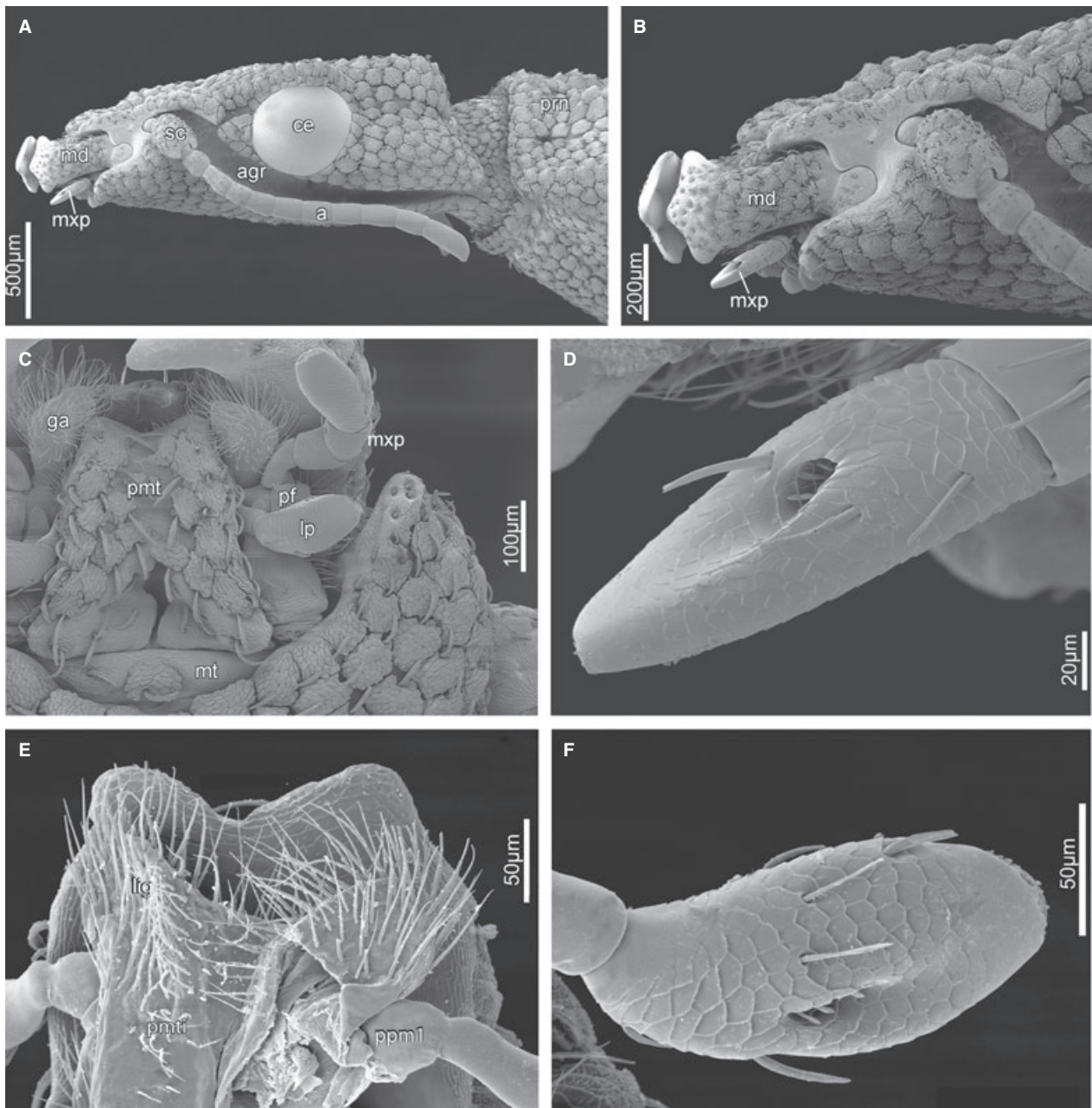


Fig. 3. (A–F) *T. bruchi*, head, SEM micrographs. (A) Lateral view; (B) lateral view, mouthparts; (C) ventral view, ventral mouthparts view; (D) apical maxillary palomere with sensorial groove; (E) prementum, dorsal view; (F) apical labial palomere with sensorial groove. Abbreviations: a, antenna; agr, antennal groove; ce, compound eye; ga, galea; lp, labial palp; md, mandible; mxp, maxillary palp; pf, palpifer; pmt, prementum; ppm1, labial palpomere; sc, scapus.

average  $\approx 80 \mu\text{m}$  wide. Each have a fairly short, slightly flattened seta. Scale-like setae are absent. The surface of the tubercles is distinctly sculptured, with minute scale-like structures of  $\approx 10 \mu\text{m}$  width.

**External head capsule** (Figs 2 and 3). Head is strongly elongate, distinctly flattened dorsoventrally, wedge-shaped, pronouncedly prognathous,  $\approx 2.4$ – $2.45$  mm long in females (1.7 mm in males), maximum width

1.7 mm (1.2 mm in males) at ocular region. Color light gray to gray–brown on surface formed by tubercles. Ocelli absent. Compound eyes nearly round, well developed; surface smooth; ommatidia very small; moderately protruding laterally in middle region of head; internally enclosed by extensive circumocular ridge. Y-shaped line on dorsal side of head results from narrow gap between tubercles; median part elongate

and paired anterior branches short. Coronal, frontal and frontoclypeal sutures absent; zones of weakness or internal ridge not recognizable on microtome sections or  $\mu$ -CT images. Clypeal area fairly long and rounded laterally; anterior part largely covers labrum; moderately distinct bulges formed by lateral margins above antennal insertions (P1) enclose shallow dorsomedian clypeal concavity (Figs 1A,C and 10D–F). Lateral margin of frontal area forms moderately developed rounded projection above compound eyes (P2). Conspicuous genal projection present between posterior ocular margin and narrow neck region. Posterolateral edge of projection rounded. Angle between lateral and posterior margins  $\approx 70^\circ$ . Pair of moderately convex swellings (P3) present above genal ridges (Figs 1A and 10D–F); separated by median furrow; almost vertical posterior edge meets dorsal side of narrow neck region. Ventral wall of head capsule evenly rounded anterolaterally. Deep, rounded emargination present anteromedially. Deep, smooth, slightly curved longitudinal furrows between antennal articulation and neck region serve for reception of antennae in resting position (Figs 2B and 3A); sharp ventrolateral edges forming mesal margin slightly converging posteriorly; dorsally delimited by lateral edge of posterior clypeal area, triangular area anterior to compound eye delimited by gap between tubercles, row of tubercles below compound eyes, and sharply pronounced lateral edge of genal projection. Posterior tentorial grooves not recognizable externally, covered by lateral expansions of cuticular tubercles. Gula forming ventromedian part of head capsule elongate, laterally not delimited by gular sutures (Fig. 2B).

*Cephalic endoskeleton* (Figs 6A, 7 and 8A,C,D). Postoccipital ridge moderately developed, slightly broader laterally than dorsally. Gular ridges absent. Tentorium partly reduced. Posterior tentorial arms arise from central region of head capsule; distinctly separated from each other; strongly developed, almost parallel and fairly short. Tentorial bridge connecting posterior arms well developed. Dorsal arms flattened and weakly sclerotized, fairly wide; dorsally attached to head capsule by fibrillae. Anterior tentorial grooves not recognizable externally. Anterior arms reduced.

*Labrum* (Figs 2C and 6B). Small and largely covered by clypeus but not fused with it. Inserted in shallow transverse emargination of anterior clypeal margin. Setae on tubercles covering narrow exposed part of labrum directed anteriorly. Ventral side as strongly sclerotized as dorsal side.

Musculature (nomenclature follows von K  ler, 1963): *Musculus* (= M) *labroepipharyngalis* (7), absent; *M. frontoepipharyngalis* (8), absent; *M. frontoepipharyngalis* (9), absent.

*Antenna* (Figs 2, 3A,B and 9D). Filiform, 11-segmented, short, reaching anterior margin of prothorax posteriorly. Inserted at anterior end of antennal groove,

slightly caudad of mandibular articulation. Scapus divided into smaller, smooth, globular basal part articulating with head capsule, and larger, barrel-shaped distal portion with tuberculate cuticle; apical part of distal portion rounded anteriorly and angular posteriorly, with incision allowing backward movement of antenna. Surface of antennomeres 2–11 devoid of tubercles, largely smooth; few short and thin setae present on scapus and antennomeres 3 and 4. Pedicel short, with globular basal part articulating with the scapus. Flagellomeres cylindrical, distinctly longer than wide, increasing in length towards antennal apex; apex of antennomere 11 with group of minute sensorial papillae ( $\approx 3 \mu\text{m}$  length) inserted in small, shallow concavities; similar sensilla not arranged in clusters also present on proximal part of segment 11 and on antennomeres 5–10.

Musculature (Figs 5B, 6B and 8A,C,D): strongly developed, *M. tentorioscapalis anterior* (1), O (= origin): with wide, fan-shaped base on dorsal tentorial arm, I (= insertion): anteriorly on scapal base; *M. tentorioscapalis posterior* (2), O: frons mediad of *M. tentorioscapalis anterior*, I: posteriorly on scapal base; *M. tentorioscapalis lateralis* (3) and *medialis* (4), absent or merged with previous two muscles; *M. scapopedicellaris lateralis/medialis* (5/6), O: anterior and posterior wall of scapus, I: base of pedicellus.

*Mandible* (Fig. 4). Anteriorly directed, elongate, distinctly protruding; strongly curved. Lateral surface covered with tubercles. Three strongly developed apical teeth arranged in vertical row. Mola and prostheca absent. Mandibular bases widely separated and asymmetrical. Mesal surface partly covered with stiff hairs; concave on one mandible and convex on the other. Minute rounded cuticular teeth on dorsomesal mandibular base interact with sclerotized ventral wall of labrum. Dorsal, secondary mandibular joint normally developed, with socket on mandibular base and condyle on corresponding part of head capsule; condyle-like lateral process of lateral mandibular base fits into recess of head capsule below and anterior to antennal insertion. Adductor tendon extensive, anterior part V-shaped in cross-section, posterior part Y-shaped; abductor tendon round in cross-section anteriorly, flat and moderately broad posteriorly.

Musculature (Figs 5–7 and 9C–F): *M. craniomandibularis internus* (11) largest muscle of head, composed of numerous thin bundles, O: large parts of posterior head capsule, including the ventromesal and dorsal wall of genal extension, dorsal protuberance, the dorsal and lateral walls of the neck region and lateral postoccipital ridge, I: large forked adductor tendon; *M. craniomandibularis externus* (12), composed of many thin bundles, O: anteroventral wall of head capsule and ventral wall of genal extension, I: abductor tendon; *M. tentoriomandibularis* (13), not identified, probably absent.

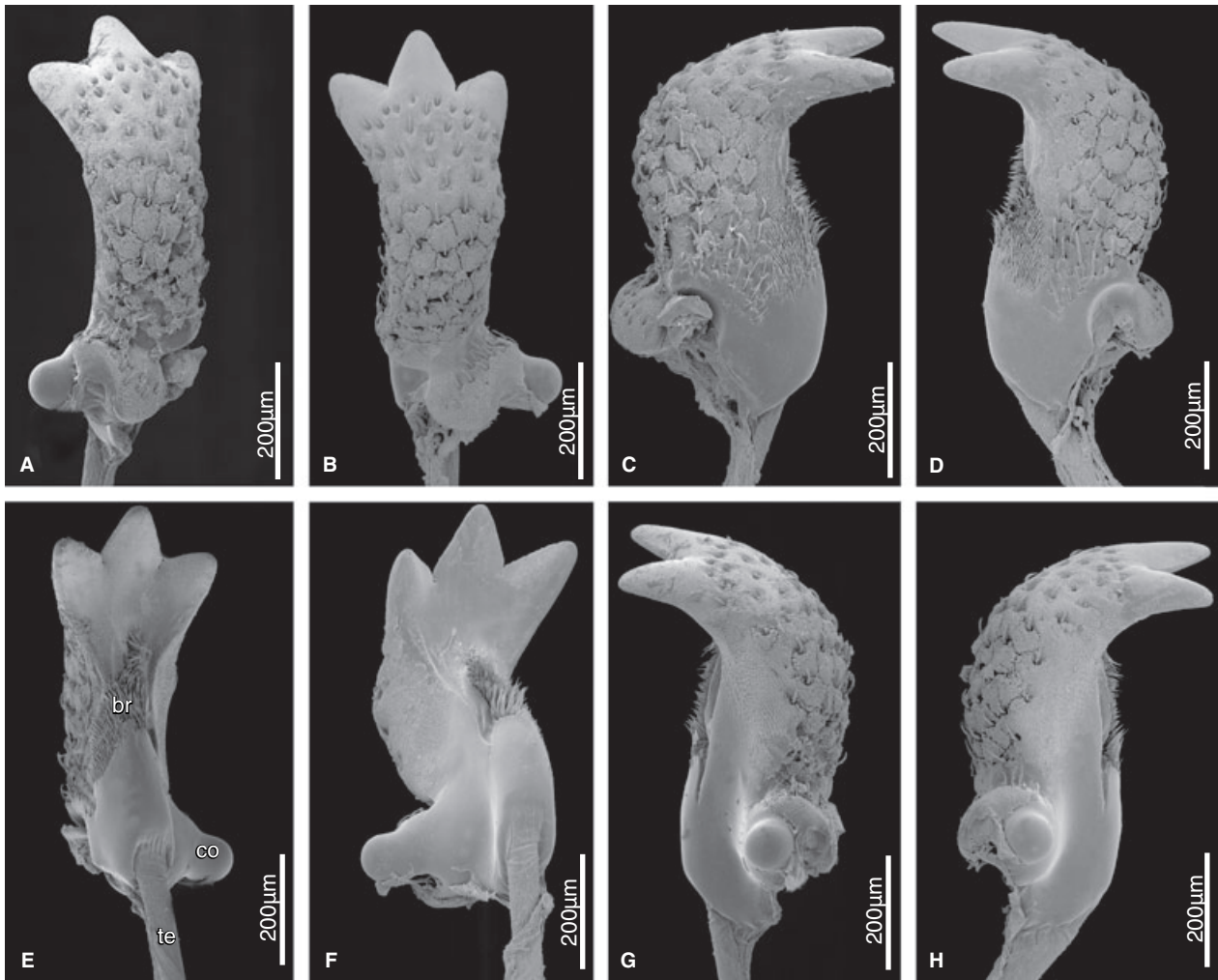


Fig. 4. (A–F) *T. bruchi*, mandibles, SEM micrographs. (A,B) Left and right mandible, lateral view; (C,D) left and right mandible, dorsal view; (E,F) left and right mandible, mesal view; (G,H) left and right mandible, ventral view. Abbreviation: br, bristles; co, condyle; te, tendon.

**Maxilla** (Figs 2B, 3C,D and 9A,B). Small, inserted between premental plate and rounded projection of head capsule below mandibular articulation. Cardo small, nearly quadrangular; transverse sclerotized bar at mesal base serves for attachment of extrinsic cardinal muscles. Subdivision of stipes not recognizable. Well developed palpifer laterally attached to stipes, set with fine setae along lateral margin. Galea flattened, moderately narrowed basally, broad and rounded apically; marginal area densely covered with long fine setulae. Lacinia (Fig. 9B) broadly attached to mesal margin of stipes; covered by prementum; sclerotized narrow apical part densely set with mesally directed bristles; large semi-membranous lobe-like part of lacinia with less dense vestiture of hairs. Palp four-segmented, slightly longer than premental sclerite; palpomere 1 fairly slender and curved; palpomeres 2 and 3 about as long as wide, slightly widening towards apex; palpomere 4 larger than other segment; mesal and lateral margins evenly

rounded; basal part with honeycomb-like surface structure; slender,  $\approx 20 \mu\text{m}$  long sensilla inserted in deep cavity on dorsal side (Fig. 3C).

**Musculature** (Figs 5, 6A, 7 and 9C–E): M. craniocardinalis externus (15), strongly developed, O: ventral wall of head capsule, central submental region, I: strong tendon inserted on lateral base of cardo; M. tentoriocardinalis (17), a slender muscle, O: lateral side of posterior tentorial arm, I: mesally on base of cardo; M. tentoriostipitalis (18), strongly developed muscle, O: lateral side of posterior tentorial arm, together with M. 17, I: mesally on stipital base; M. craniolacinalis (19), O: ventral wall of head capsule, posteriad of origin of anterior subcomponent of M. 12, I: tendon attached to base of lacinia; M. stipitolacinalis (20), possibly represented by muscle connecting ventral stipital wall with mesal maxillary base; M. stipitogalealis (21), slender transverse muscle, O: dorsal side of stipes, posteriad of M. stipitopalpalis (22/23), I: short apodeme



Fig. 5. (A,B) *T. bruchi*, automatic volume-renderings. Abbreviations: an, antennal nerve; ce, cerebrum; de, deutocerebrum; fl, flagellum; md, mandible; mxp, maxillary palp; olo, optical lobe; p, protocerebrum; ph, pharynx; sc, scapus; sevc, connectives; soeg, subesophageal complex; tm, transverse muscle; (1) *M. tentorioscapalis anterior*; (2) *M. tentorioscapalis posterior*; (11/12) *Mm. craniomandibularis internus/externus*; (15) *M. craniocardinalis*; (17) *M. tentoriocardinalis*; (28) *M. submentopraementalis*; (29) *M. tentoriopraementalis inferior*; (44) *M. clypeobuccalis anterior*; (45) *M. frontobuccalis anterior*; (46) *M. frontobuccalis posterior*; (50) *M. tentoriobuccalis posterior*; (52) *M. tentoriopharyngalis posterior*.

on base of galea; *M. stipitopalpalis externus/internus* (22/23), not distinctly divided into two bundles, O: broad attachment area on dorsal side of stipes, I: tendon inserted on base of proximal palpomere; *M. palpopalpalis primus* (23), slender muscle composed of two parallel bundles, O: base of palpomere 1, I: base of palpomere 2; *M. p. secundus-quartus* (24–27), not identified on available sections.

**Labium** (Figs 2B and 3C,E,F). Submentum completely integrated into ventral wall of head capsule. Posterior margin marked by posterior tentorial pits. Mentum represented by short transverse sclerite with slightly convex posterior margin and straight anterior margin; surface devoid of tubercles. Prementum composed of large, strongly sclerotized external plate-like structure (Figs 3C, 7 and 9B) and largely internalized and unsclerotized part (Figs 3E and 9B); tubercles absent from posterolateral parts of plate, but present on other areas; long, strong apodeme arises from deep posteromedian pit; internalized part of prementum largely unsclerotized, composed of lateral horizontal folds and paired, paramedian vertical folds; anteriorly

extended as flat, bilobed ligula; ligula densely set with long hairs like vertical premental folds. Palp three-segmented; fairly short, slender basal palpomere completely hidden under premental plate, articulating with moderately sclerotized palpigers on ventral side of internalized premental part; palpomere 2 fairly slender, slightly widening apically; palpomere 3 larger than other segments; shape and surface structure similar to apical maxillary palpomere, with similar cavity with sensilla and apical recess with minute sensilla (Fig. 3F).

**Musculature** (Figs 5A, 6A and 7): *M. submentopraementalis* (28), closely connected with *M. tentoriopraementalis inferior* and superior, O: ventral wall of head capsule between posterior tentorial arms, I: tendon attached to median premental apodeme; *M. tentoriopraementalis inferior* (29), well developed, O: mesally on posterior tentorial arms, I: laterally on basal sclerotizations of concealed upper part of prementum; *M. tentoriopraementalis superior* (30), well developed, very closely connected with *M. 29*, O: posterior tentorial arm, together with *M. 29*, I: dorsally on upper part of prementum, close to median line; *M. praementopara-*



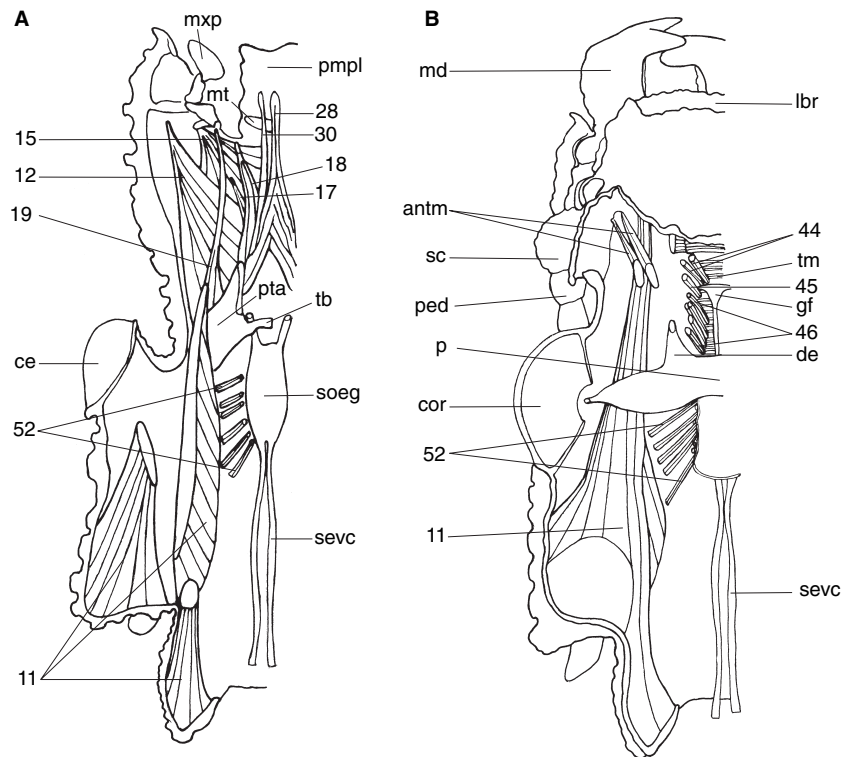


Fig. 6. (A,B) *T. bruchi*, horizontal section. (A) Lower level; (B) higher level. Abbreviations: antm, antennal muscles; ce, compound eye; cor, circumocular ridge; gf, frontal ganglion; lbr, labrum; md, mandible; mt, mentum; mxp, maxillary palp; p, protocerebrum; pmpl, premental plate; ped, pedicellus; sc, scapus; sevc, second ventral connective; soeg, subesophageal complex; t11, tendon of *M. craniomandibularis internus*; tb, tentorial bridge; tm, transverse muscle; (11/12) *Mm. craniomandibularis internus/externus*; (15) *M. craniocardinalis*; (17) *M. tentoriocardinalis*; (18) *M. tentoriostipitalis*; (19) *M. craniolacinalis*; (28) *M. submentopraementalis*; (30) *M. tentoriopraementalis superior*; (44) *M. clypeobuccalis anterior*; (45) *M. frontobuccalis anterior*; (46) *M. frontobuccalis posterior*; (52) *M. tentoriopharyngalis posterior*.

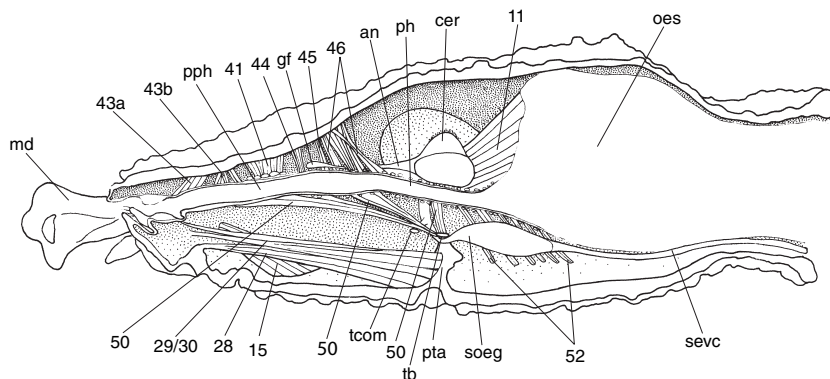


Fig. 7. *T. bruchi*, head, sagittal section. Abbreviations: an, antennal nerve; cer, brain; gf, ganglion frontale; oes, esophagus; ph, pharynx; pph, prepharynx; pta, posterior tentorial arms; sevc, second ventral connective; soeg, subesophageal complex; tb, tentorial bridge; tcom, tritocerebral commissure; (11) *M. craniomandibularis internus*; (15) *M. craniocardinalis*; (28) *M. submentopraementalis*; (29/30) *M. tentoriopraementalis inferior/superior*; (41) *M. frontohypopharyngalis*; (43a/b) *M. clypeopalatalis*; (44) *M. clypeobuccalis anterior*; (45) *M. frontobuccalis anterior*; (46) *M. frontobuccalis posterior*; (50) *M. tentoriobuccalis posterior*; (52) *M. tentoriopharyngalis posterior*.

glossalis/praementoglossalis (31/32), absent; *M. prae-mentopalpalis externus* (34), well developed, O: base of palpifer, I: base of proximal palpomere; *M. palpopalpalis labii primus-secundus* (35, 36), not identified on available sections and  $\mu$ -CT images, probably absent.

*Epipharynx and anterior part of digestive tract* (Figs 5B, 7 and 8). Semimembranous anterior epipharyngeal roof of cibarium with median longitudinal bulge, but without distinct fold covered with microtrichia. Open cibarium followed by preoral chamber



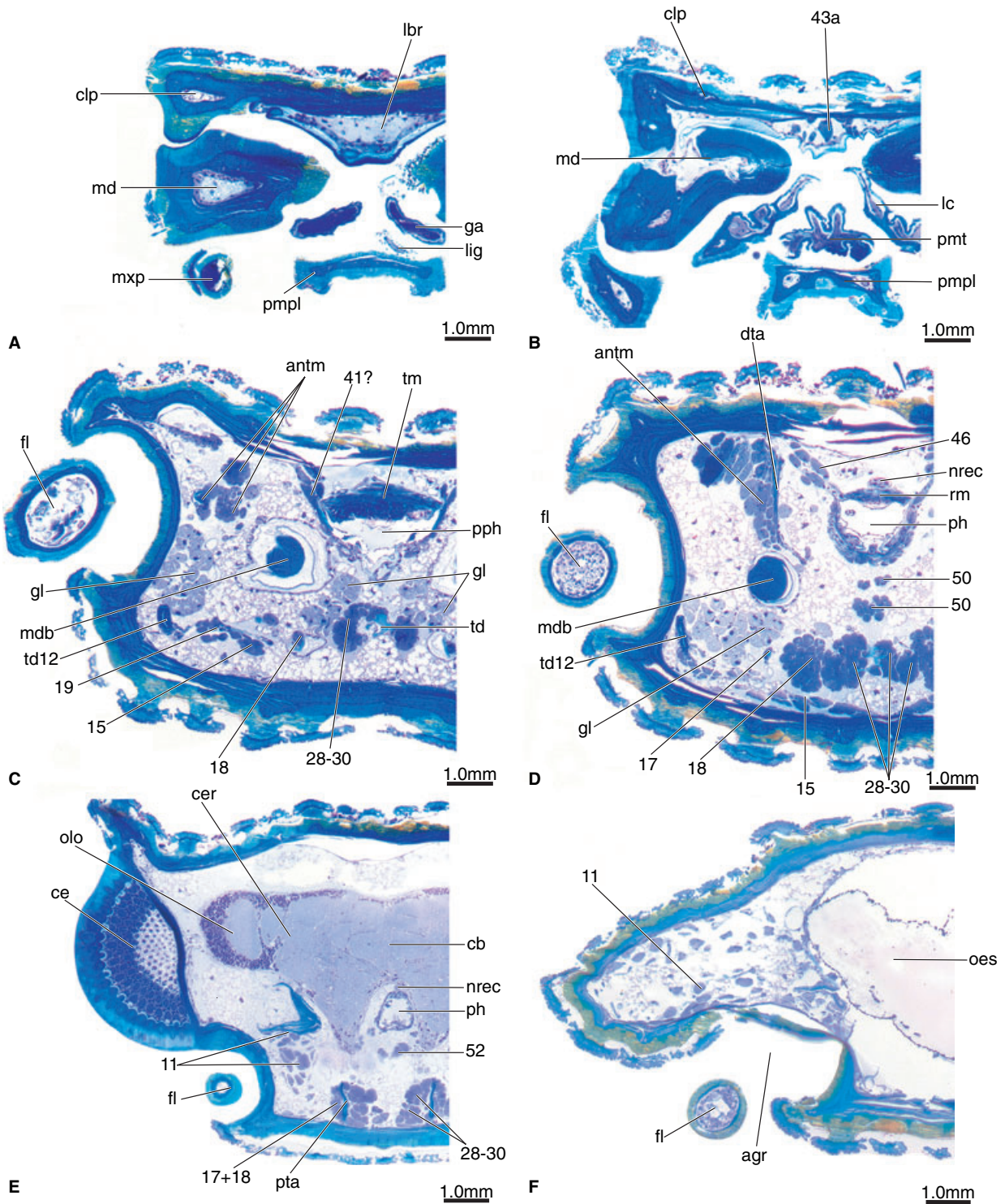


Fig. 9. (A–F) *T. bruchi*, head, cross-sections. (A) Anterior labral region. (B) anterior clypeal region. (C) prepharyngeal region. (D) anterior pharyngeal region. (E) ocular region. (F) posterior head region. Abbreviations: agr, antennal groove; antm, antennal muscles; cer, brain; clp, clypeus; dta, dorsal tentorial arm; fl, antennal flagellum; ga, galea; gl, gland; lbr, labrum; lc, lacinia; lig, ligula; md, mandible; mdb, mandibular base; mxp, maxillary palp; nrec, nervus recurrens; ph, pharynx; pmp, premental plate; pph, prepharynx; pta, posterior tentorial arms; rm, ring muscle; td, tendon; tm, transverse muscle; (11) *M. craniomandibularis internus*; td12, tendon of *M. craniomandibularis externus*; (15) *M. craniocardinalis*; (17) *M. tentoriocardinalis*; (18) *M. tentoriostipitalis*; (19) *M. craniolacinalis*; (28–30) *M. submentopraementalis*, *Mm. tentoriopraementalis inferior/superior*; (41) *M. frontohypopharyngalis*; (43a) *M. clypeopalatalis anterior*; (46) *M. frontobuccalis posterior*; (50) *M. tentoriobuccalis posterior*; (52) *M. tentoriopharyngalis posterior*.

broad tendons serving as insertion areas broadly attached to upper edges of sclerotized lateral walls of prepharyngeal tube (i.e., hypopharyngeal suspensoria); *M. tentoriohypopharyngalis* (42) absent.

The muscle interpreted as *M. 41* here inserts anteriorly of the frontal connective, which is not the case in other insects (see e.g., von K eler, 1963). It cannot be fully excluded that it is a subcomponent of *M. 43*, with an unusual insertion.

*Pharynx* (Figs 6–8, 7 and 9). Precerebral part moderately wide. Distinct dorsolateral, ventrolateral and ventral folds serve as attachment areas of dilators. Postcerebral pharynx and esophagus extremely widened (Figs 7 and 9F), with very thin wall and completely lacking ring muscles and longitudinal muscles.

Musculature (Figs 7, 8 and 9D–F): *M. clypeobuccalis* (44), two well developed bundles immediately anteriorly of frontal ganglion, O: posterior clypeofrontal region, I: immediately anteriorly of anatomical mouth; *M. frontobuccalis anterior* (45), one slender bundle, O: posteriorly of *M. 44*, I: laterally on anterior precerebral pharynx; *M. frontobuccalis posterior* (46), strongly developed series of bundles, O: posteriorly of *M. 45*, I: successively on dorsal folds of posterior precerebral pharynx; *M. tentoriobuccalis anterior* (48) absent; *M. tentoriobuccalis posterior* (50), three well developed subcomponents, O: tentorial bridge, I: ventrally on posterior hypopharynx and ventrolaterally on anterior pharynx; *M. verticopharyngalis* (51), absent; *M. tentoriopharyngalis* (52), two complex series of thin muscles, O: laterally on gular region, mesad of lower edge of antennal grooves, I: ventrally on posterior hypopharynx and ventrolaterally on posterior pharynx.

An unusual pair of strong longitudinal muscles runs along the posterior pharynx dorsolaterally. It is posteriorly attached to the thin wall of the anterior part of the esophagus. Gland-like tissue is present above and below it.

It cannot be fully excluded that the muscle interpreted as *M. 45* here is in fact *M. frontohypopharyngalis*, given the very unusual shape and insertion (see above). In that case it would be likely that *M. frontobuccalis anterior* is represented by a bundle assigned to *M. 46* here.

*Brain and subesophageal complex* (Figs 5, 7 and 9E). Brain small in relation to head size, dumbbell-shaped, connecting compound eyes; optic neuropiles and central body well developed; tritocerebral commissure thin. Slender subesophageal complex located in central head region below posterior pharynx and anterior esophagus, connected with brain by thin circumesophageal connectives; connectives linking subesophageal complex with prothoracic ganglion thin and very long. Frontal ganglion elongated; frontal connectives very thin.

*Glands* (Fig. 9C,D). Large paired glands arranged as loose aggregates present in anterior head region between

mandibular adductor and abductor tendons. Salivary glands and salivarium absent.

*Cavities* (Fig. 9C). Cavities below lateral clypeal bulges separated from rest of head myxocoel by oblique diaphragma formed by connective tissue.

#### List of characters (see also Table 1)

##### Adults.

1. Externally visible membranes: (0) present; (1) absent. Externally visible membranes are largely or completely absent in fossil and extant beetles (Figs 11 and 12) with very few exceptions. The body is almost always unusually strongly sclerotized compared with other insects.

2. Tubercles: (0) absent or very indistinct; (1) present. Distinctly developed rounded or pentagonal cuticular tubercles are present in Cupedidae and Ommatidae (Figs 1–3 and 9–11), and also in most fossil taxa traditionally assigned to Archostemata (Ponomarenko, 1969: e.g., †*Tshekardocoleidae*, †*Permocupedidae*, †*Rhombocoleidae*, †*Triadocupedinae*). They are absent in all extant non-archostematan beetles, in the small species *Micromalthus debilis* and *Crowsoniella relictata*, in *Sikhotealinia* (Lafer, 1996) and †*Jurodes* (Kirejtshuk, 1999/2000), in †*Ademosynidae* and †*Catiniidae* (Ponomarenko, 1969), in some representatives of †*Schizophoridae* (present in †*Triassocoleus* and †*Salebroferus*; Ponomarenko, 1969, figs 93 and 96), and probably also in †*Permosynidae* (Ponomarenko, 2003).

3. Scale-like setae: (0) absent; (1) present. Setae modified as scales are inserted on the cuticular tubercles in Cupedidae and *Omma* (H ornschemeyer et al., 2002). They are absent in *Micromalthus*, *Crowsoniella* (Pace, 1975) and *Sikhotealinia*, and in all outgroup taxa. Usually, the presence or absence in fossils with cuticular tubercles cannot be verified. However, they are distinctly recognizable in a fossil species of *Paracupes* from New Jersey (Cretaceous) (Lubkin, 2003). The setae on the pentagonal tubercles of *Tetraphalerus* (Figs 1 and 2) are flattened (coded as 0) but distinctly different from the scales of *Omma* or Cupedidae. Longitudinal ridges are present on the scales in *Ascioplaga*.

4. Ocelli: (0) three; (1) absent. Three ocelli are present in Corydalidae and *Sikhotealinia* (Lafer, 1996). Two ocelli or one occasionally occur in Polyphaga (see Leschen and Beutel, 2004). They are absent from the other taxa under consideration (coded as [?] for fossil taxa).

5. Constricted neck and postocular extensions: (0) absent or indistinct; (1) present. A strongly constricted neck region and conspicuous postocular extensions are present in *Tetraphalerus* (Figs 2A and 3A) and all other adults of Archostemata (including *Sikhotealinia*) (Lafer, 1996; H ornschemeyer et al., 2002; H ornschemeyer, 2005) except for the miniaturized species *Micromalthus debilis*. The constriction and extensions are absent or indistinct

in the outgroup taxa and in the fossil taxa under consideration (Fig. 12; Ponomarenko, 1969, figs 29, 30, 37, 44 and 87; indistinct in *Triassocoleus*, fig. 94) with the exception of †*Jurodes* (Kirejtshuk, 1999/2000, fig. 1).

Characters 6–9 (Fig. 10): Conspicuous protuberances on the dorsal surface of the head are a characteristic feature of Archostemata. They occur in four positions, above the antennal insertions (P1), above the compound

Table 1  
Character state matrix for phylogenetic analysis. For explanation of characters see text

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
<i>Sialidae</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Chauliodinae</i>	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1
<i>Trachypachus</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0
<i>Helophorus</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Torrindicola</i>	1	0	0	1	0	0	0	0	0	0	2	–	0	0	0	0	0	0	1	1	0	1	0
<i>Micromalthus</i>	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	2	?	1	?	?	0	1	0
<i>Priacma</i>	1	1	1	1	1	2	1	1	1	0	0	0	1	0	1	1	0	0	1	1	1	1	0
<i>Paracupes</i>	1	1	1	1	1	2	0	0	0	0	0	1	?	?	?	1	0	?	?	?	1	1	1
<i>Ascioplaga</i>	1	1	1	1	1	2	2	1	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1
<i>Cupes</i>	1	1	1	1	1	2	2	2	1	0	0	0	1	1	0	1	1	0	?	1	?	1	1
<i>Tenomerga</i>	1	1	1	1	1	2	2	2	1	0	0	1	1	0	1	1	0	?	?	?	1	1	1
<i>Rhipsideigma</i>	1	1	1	1	1	2	2	2	1	0	0	1	?	0	?	1	0	?	?	?	1	1	1
<i>Distocupes</i>	1	1	1	1	1	2	2	1	0	0	0	1	1	0	1	1	0	?	?	?	1	1	1
<i>Omma</i>	1	1	1	1	1	1	2	0	0	0	1	0	?	0	?	1	2	?	?	?	0	1	0
<i>Tetraphalerus</i>	1	1	0	1	1	1	1	1	0	1	2	–	0	1	1	1	1	1	1	1	0	1	0
<i>Crowsoniella</i>	1	0	0	1	1	0	1	0	0	2	2	–	?	?	?	1	2	?	?	?	0	1	0
<i>Sikhotealinia</i>	1	0	0	0	1	0	0	1	0	2	0	0	?	0	?	0	0	?	?	?	0	1	1
† <i>Jurodes</i>	1	0	0	?	1	0	0	1	0	2	0	0	?	?	?	0	0	?	?	?	0	1	0
†Tshekardocoleidae	1	1	?	?	0	0	0	0	0	0	0	?	?	?	?	0	0	?	?	?	0	0	0
†Permocupedidae	1	1	?	?	0	0	0	0	0	0	?	?	?	?	?	0	0	?	?	?	0	0	0
†Rhombocoleidae	1	1	?	?	0	?	?	?	0	?	0	0	?	?	?	?	?	?	?	?	0	0	0
†Triadocupedinae	1	1	?	?	0	0	0&1&2	0	0	0	0	0	?	?	?	0	0	?	?	?	0	1	0
†Ademosynidae	1	0	0	?	0	0	?	?	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0
†Schizophoridae	1	0	0	?	0	0	?	?	0	0	0	0	?	?	?	?	?	?	?	?	0	1	0
†Catiniidae	1	0	0	?	0	0	1	0	0	0	0	0	?	?	?	?	?	?	?	?	0	1	0

	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4
	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	4	5	
<i>Sialidae</i>	1	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	
<i>Chauliodinae</i>	1	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Trachypachus</i>	1	0	–	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	1	0	0	1	
<i>Helophorus</i>	1	0	–	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	2	1	0	1	1	
<i>Torrindicola</i>	?	0	–	0	0	?	2	0	–	–	–	0	0	0	2	0	0	1	1	1	1	0	1	
<i>Micromalthus</i>	2	0	1	1	0	0	2	1	1	0	0	0	0	0	2	2	?	1	0	?	0	0	0	
<i>Priacma</i>	1	1	0	0	0	0	1	0	1	0	0	1	1	0	0	2	1	1	1	1	0	0	1	
<i>Paracupes</i>	?	1	0	0	0	0	1	0	1	0	0	1	1	0	0	2	?	1	1	0	0	1	1	
<i>Ascioplaga</i>	0	0	0	0	1	1	1	0	1	0	0	1	1	1	1	2	1	1	1	0	1	1	1	
<i>Cupes</i>	?	0	0	0	1	0	1	0	1	0	0	1	1	1	1	2	1	1	1	1	0	1	1	
<i>Tenomerga</i>	?	0	0	0	1	0	1	0	1	0	0	1	1	0	1	2	?	1	1	0	1	1	1	
<i>Rhipsideigma</i>	?	0	0	0	1	0	1	0	1	0	0	1	1	1	1	2	?	1	1	0	1	1	1	
<i>Distocupes</i>	?	0	0	0	1	1	1	0	1	0	0	1	1	1	1	2	?	1	1	0	1	1	1	
<i>Omma</i>	?	0	1	1	0	0	0	1	0	1	1	1	0	0	2	?	1	0	?	0	0	0	0	
<i>Tetraphalerus</i>	2	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0	
<i>Crowsoniella</i>	?	2	–	–	–	?	2	2	1	0	0	0	0	0	2	1	?	1	0	?	1	0	0	
<i>Sikhotealinia</i>	?	0	–	0	?	?	0	0	?	?	?	0	?	?	?	?	?	1	1	?	0	0	0	
† <i>Jurodes</i>	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	
†Tshekardocoleidae	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	1	
†Permocupedidae	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	1	
†Rhombocoleidae	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	0	1
†Triadocupedinae	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	0	1
†Ademosynidae	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	1
†Schizophoridae	?	0&1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	1
†Catiniidae	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	0

Table 1  
Continued

	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6
	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	6
<i>Sialidae</i>	–	0	0	0	0	0	0	0	?	0	1	0	0	–	0	0	0	0	0	0	0	0
<i>Chauliodinae</i>	–	0	0	0	0	0	0	0	?	0	0	0	0	–	0	0	0	0	0	0	0	0
<i>Trachypachus</i>	0	0	0	2	0	1	1	1	1	1	0	1	2	1	2	1	1	1	1	0	1	0
<i>Helophorus</i>	0	0	0	0	0	2	1	1	1	1	0	1	2	1	2	1	2	1	0	1	0	0
<i>Torridincola</i>	1	0	1	0	0	2	1	1	1	1	1	1	2	1	2	1	1	1	0	2	0	0
<i>Micromalthus</i>	–	0	1	0	0	0	1	1	?	1	0	1	2	1	2	1	2	1	?	1	0	0
<i>Priacma</i>	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1	1	2	1	1
<i>Paracupes</i>	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1	1	2	1	1
<i>Ascioplaga</i>	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1	1	2	1	1
<i>Cupes</i>	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1	1	2	1	1
<i>Tenomergera</i>	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1	1	2	1	1
<i>Rhipsideigma</i>	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1	1	2	1	1
<i>Distocupes</i>	0	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	1	1	1	2	1	1
<i>Omma</i>	0	0	1	1	2	0	0	0	0	0	0	1	1	0	2	1	1	1	?	2	0	0
<i>Tetraphalerus</i>	–	0	1	0	2	0	0	0	0	0	0	1	1	0	2	1	1	1	1	2	0	0
<i>Crowsoniella</i>	–	0	1	0	?	0	1	1	0	1	0	1	2	1	2	–	–	1	?	2	0	0
<i>Sikhotealinia</i>	–	0	1	0	?	0	0	0	?	0	1	1	1	1	2	1	2	1	1	1	0	0
† <i>Jurodes</i>	0	0	1	?	?	?	?	?	?	?	1	1	1	?	2	?	?	?	1	2	0	0
† Tshekardocoleidae	1	1	1	0	?	?	?	?	?	0	0	1	0	0	0	0	0	1	?	2	0	0
† Permocupedidae	0	1	1	0	?	?	0	?	?	0	0	1	1	0	1	?	?	?	?	2	0	0
† Rhombocoleidae	0	1	1	0	?	?	0	0	?	0	0	1	1	0&1	2	?	?	?	?	2	0	0
† Triadocupedinae	0	0	1	0	?	?	0	0	?	0	0	1	1	0	2	1	?	?	?	2	0	0
† Ademosynidae	0	0	1	0	?	?	0	?	?	0	0	1	2	1	2	?	?	?	?	2	0	0
† Schizophoridae	0	0	1	0	?	?	0	?	?	0	0	1	2	1	2	?	?	?	?	2	0	0
† Catiniidae	0	0	1	0	?	?	?	?	?	1	0	1	2	1	2	?	?	?	?	2	0	0

	6	6	6	7	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	9	
	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
<i>Sialidae</i>	0	0	0	0	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chauliodinae</i>	0	0	0	0	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trachypachus</i>	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Helophorus</i>	0	0	0	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	0	0	0	1	0	0
<i>Torridincola</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0
<i>Micromalthus</i>	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	1	0	1	1	0	1
<i>Priacma</i>	?	1	1	1	1	1	1	1	1	1	1	1	0	0	1	?	?	?	0	1	?	0	1	1
<i>Paracupes</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ascioplaga</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cupes</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	1
<i>Tenomergera</i>	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1
<i>Rhipsideigma</i>	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1
<i>Distocupes</i>	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	0	1	1	0	1	1
<i>Omma</i>	0	1	2	1	0	0	0	1	0	0	1	1	0	0	0	1	1	0	0	0	0	1	?	?
<i>Tetraphalerus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Crowsoniella</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Sikhotealinia</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† <i>Jurodes</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† Tshekardocoleidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† Permocupedidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† Rhombocoleidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† Triadocupedinae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† Ademosynidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† Schizophoridae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
† Catiniidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

eyes (P2), laterad of the median line near the posterior margin of the head (P3) and laterally on the posterior head region (P4). Size and shape of the protuberances vary considerably between taxa. All protuberances are absent in the non-archostematan taxa.

6. Supraantennal protuberance (Fig. 10: P1): (0) absent; (1) present as moderately distinct bulge; (2) present as strongly pronounced protuberance. Present as moderately distinct bulge above the antennal base in *Omma* and *Tetraphalerus* (Figs 2C and 3B). Developed



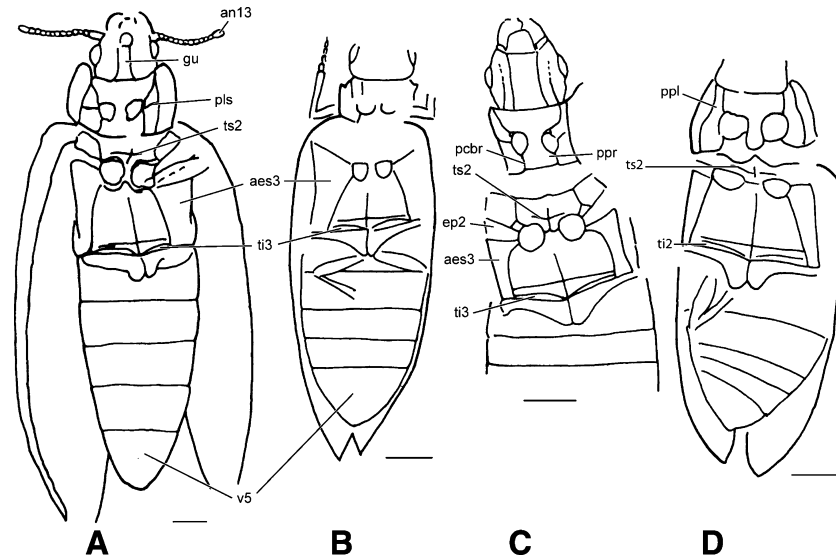


Fig. 12. (A–D) Fossil taxa assigned to Archostemata. (A) †*Tshekardocoleus* (†Tshekardocoleidae) (redrawn from Ponomarenko, 2000, fig. 2a); (B) †*Stegocupes* (†Permocupedidae); (C) †*Rhombocoleites* (†Rhombocoleidae); (D) †*Dolychosyne* (†Ademosynidae), abdomen presumably shrunken (B–D redrawn from Ponomarenko, 1969, figs 42, 71 and 87).

head region in some genera of Cupedidae (e.g., *Priacma*, *Cupes*, *Tenomerga*; Fig. 10A–C). Absent in *Tetrphalerus* (Figs 2A and 3A) and the other archostematan genera (e.g., Pace, 1975, fig. 1) including *Sikhotealinia*. Also absent in the fossil taxa (Ponomarenko, 1969).

10. Antennal groove on head; (0) absent; (1) below compound eye; (2) above compound eye. Deep antennal grooves are present below the compound eyes in *Tetrphalerus* (Figs 2B and 3A), and above it in *Crowsoniella* (Pace, 1975), *Sikhotealinia* (Lafer, 1996, fig. 137.1) and †*Jurodes* (Kirejtshuk, 1999/2000, fig. 1). An antennal groove is absent in *Omma*, Cupedidae and *Micromalthus*, and it is also missing in fossil taxa with the possible exception of †Rhombocoleidae (Ponomarenko, 1969, fig. 87).

11. Gular sutures: (0) complete, reaching hind margin of head capsule; (1) incomplete, not reaching hind margin of head capsule; (2) absent. The gular sutures do not reach the hind margin of the head capsule in *Omma*, and they are not recognizable in *Tetrphalerus* (Fig. 2B) and *Torridincola* (Beutel and Vanin, 2005, fig. 6.3A).

12. Shape of gula: (0) not converging posteriorly; (1) converging posteriorly. The gular sutures are usually converging posteriorly in Cupedidae. They are diverging in *Priacma*, *Omma*, *Sikhotealinia* (Lafer, 1996, fig. 2), †Tshekardocoleidae, †Rhombocoleidae, †Triadocupedinae, †Schizophoridae and †Catiniidae (Ponomarenko, 1969, figs 29, 43, 87, 89, 91 and 111).

13. Tentorial bridge: (0) present; (1) absent. Present in *Tetrphalerus* (Figs 6A and 8C,D), but missing in other adults of Archostemata examined. The condition in *Omma*, *Crowsoniella* and *Sikhotealinia* is unknown.

14. Posterior tentorial grooves: (0) externally visible; (1) not visible externally. Generally visible in Archoste-

mata, but not recognizable externally in *Micromalthus* and *Tetrphalerus* (Fig. 2B).

15. Anterior tentorial arms: (0) well developed; (1) strongly reduced or absent, not connected with posterior tentorium. Distinctly or completely reduced in *Tetrphalerus* (Fig. 8A,C,D) and in other adults of Archostemata examined (Hörschemeyer et al., 2002).

16. Frontoclypeal suture: (0) present; (1) absent. Usually absent in extant Archostemata (Figs 2A,C and 7) and also in some fossil taxa (e.g., †*Dolychosyne*, †*Hadeocoleus*; Ponomarenko, 1969, figs 71 and 88), but present in *Sikhotealinia* (Lafer, 1996, fig. 137.1), †*Jurodes* (Kirejtshuk, 1999/2000, fig. 1), †*Sylvacoleus* (Tshekardocoleidae) and †*Permocupes* (Ponomarenko, 1969, figs 29 and 37).

17. Labrum: (0) free, connected with clypeus by membrane; (1) indistinctly separated from clypeus, largely or completely immobilized; (2) fused with head capsule. Free in Cupedidae, †Tshekardocoleidae, †Permocupidae (Ponomarenko, 1969, figs 29, 37 and 45) and †Triadocupedinae, and also free and large in *Sikhotealinia* (Lafer, 1996) and †*Jurodes* (Kirejtshuk, 1999/2000, fig. 1). Not fused with head capsule but immobilized in *Tetrphalerus* (Figs 1C and 6B). Fused in *Micromalthus*, *Crowsoniella* and *Omma*.

18. *M. labroepipharyngalis* (M. 7): (0) present; (1) absent. Absent in *Tetrphalerus* (Fig. 7), but present in *Priacma* and *Ascioplaga* (Hörschemeyer et al., 2002, 2006), and also in *Sialis* (Röber, 1942).

19. *M. frontolabralis* (M. 8): (0) present; (1) absent. Absent in *Tetrphalerus* (Fig. 7) like in all other beetles (e.g., Dorsey, 1943; Hörschemeyer et al., 2002, 2006; Anton and Beutel, 2006; Dressler, 2006). Present in *Sialis* (Röber, 1942).



20. *M. frontoepipharyngalis* (M. 9): (0) present; (1) absent. Absent in *Tetraphalerus* (Fig. 7) like in *Priacma* (Hörschemeyer et al., 2002) and many other beetles (e.g., Dorsey, 1943; Dressler, 2006). Present as a very thin bundle in *Ascioplaga* (Hörschemeyer et al., 2006). Well developed in *Helophorus* (Anton and Beutel, 2004) and Megaloptera (Maki, 1936; Röber, 1942).

21. Length of antenna: (0) not reaching mesothorax posteriorly; (1) very elongate, reaching middle region of body. The antennae are very elongate in Cupedidae (e.g., Hörschemeyer, 2005) but moderately long or even short in other members of Archostemata (Figs 2A and 3A) including *Sikhotealinia* and the fossils and non-archostematan taxa considered here.

22. Number of antennomeres: (0) 13 or more; (1) 11 or less. Thirteen antennomeres are present in †Tshecardocoleidae, †Permocupedidae and †Rhombocoleidae (Ponomarenko, 1969), but 11 in the other fossil taxa considered here (Ponomarenko, 1969) and 11 or less in extant beetles.

23. Location of antennal insertion on head capsule: (0) laterally; (1) dorsally. Laterally in *Priacma*, Ommatidae (Fig. 3a,b), *Micromalthus* and *Crowsoniella*, and also in the fossil taxa including †*Jurodes* (Ponomarenko, 1969; Kirejtshuk, 1999/2000, fig. 1). On dorsal side of head capsule in Cupedidae excluding *Priacma* (Hörschemeyer et al., 2002, 2006) and in *Sikhotealinia* (Lafer, 1996).

24. Extrinsic antennal muscles: (0) four; (1) three; (2) two. Two are present in *Tetraphalerus* (Figs 6B and 8A,C,D), three in *Priacma*, *Trachypachus* (Dressler, 2006) and Megaloptera (Maki, 1936; Röber, 1942), and four in *Ascioplaga* (Hörschemeyer et al., 2006).

25. Shape of mandible: (0) short or moderately long, largely covered by labrum in repose (1) very elongate and protruding in resting position (3) vestigial. Moderately long or short and largely covered by the labrum in the resting position in most extant Archostemata and most of the fossil taxa under consideration (with the exception of †*Catabrycus* [coded as 0 for †Schizophoridae] and the possible exception of †*Rhombocoleites*; Ponomarenko, 1969, figs 87 and 108). Exceptionally long and distinctly protruding in *Priacma*, *Paracupes* and *Tetraphalerus* (Figs 2B, 6B and 7). Vestigial in *Crowsoniella* (Pace, 1975).

26. Ventromesal margin of sculptured mandibular surface: (0) not reaching position of mandibular condyle; (1) reaching mandibular condyle. The sculptured lateral surface of the mandibles of Ommatidae (Fig. 4) and *Micromalthus* reaches the position of the posterior condyle (primary mandibular joint) or even beyond it.

27. Cutting edge of mandible: (0) horizontal (1) with three vertically arranged teeth. Three teeth are arranged in a vertical row in Ommatidae (Fig. 4) and *Micromalthus* (Hörschemeyer et al., 2002). The cutting edge is horizontal in Cupedidae as in most other beetles (e.g., *Sikhotealinia*).

28. Separate areas with different surfaces on ventral side of mandible: (0) absent; (1) present. The ventral surface of the mandible is subdivided by ridges or grooves into two or three areas with different surface structures in *Cupes*, *Ascioplaga*, *Tenomerga* and *Distocupes*.

29. Deep pit in cranio-lateral area of ventral surface of mandible: (0) absent; (1) present. In *Ascioplaga* and *Distocupes* a deep, rounded groove is present on the ventral surface of the mandible. Comparable structures are unknown in other groups of Coleoptera.

30. Galea: (0) without globular distal galeomere and basal galeomere not slender and stalk-like; (1) stalk-like basal galeomere and globular distal galeomere; (2) absent. The galea is usually present in extant Archostemata (Figs 3C and 9A) but completely reduced in *Crowsoniella* (Pace, 1975, fig. 6; Hörschemeyer, 2005) and *Micromalthus* (Hörschemeyer, 2005), and also in Myxophaga (Lawrence, 1982; Beutel, 2005). The galea of Cupedidae is characterized by a slender, rod-like basal part and a globular pubescent distal part (Hörschemeyer et al., 2002, 2006). The galea is usually two-segmented and palp-like in Adephaga and the basal part is usually broad in Polyphaga.

31. Lacinia: (0) present; (1) absent. Usually present (Fig. 9B) but absent in *Crowsoniella* (Pace, 1975, fig. 6; Hörschemeyer, 2005) and *Micromalthus* (Hörschemeyer, 2005).

32. Apical segment of maxillary palp: (0) with only one apical field of sensilla (campaniform sensilla) (1) with an apical and a dorsolateral field of sensilla. An apical field of sensilla, usually of the campaniform type, is present on the apical maxillary and labial palpomeres of nearly all insects. In Coleoptera, an additional field is present. It is located in the dorsolateral area of the apical palpomeres and contains long, strongly developed sensilla with blunt, rounded tips (Guse and Honomichl, 1980; Honomichl, 1980; Honomichl and Guse, 1981; Mann and Crowson, 1984; Hörschemeyer et al., 2002). Similar fields of sensilla are also known from some basal Hymenoptera (Vilhelmsen, 1996). The character is scored as (–) for *Torridincola* as the apical palpomere is highly reduced in Myxophaga excluding Lepiceridae (e.g., Anton and Beutel, 2006).

33. Digitiform sensilla on apical maxillary palpomere: (0) absent; (1) present. The dorsolateral field of sensilla of the apical maxillary palpomere contains recessed digitiform sensilla in all extant Coleoptera with the exception of Archostemata (Honomichl, 1980).

34. Pit containing sensilla on dorsolateral field of apical maxillary palpomere: (0) absent; (1) present. The sensilla of the dorsolateral field are usually exposed or inserted in a shallow concavity, but placed in a deep pit in *Tetraphalerus* (Fig. 3D) and *Omma*. In *Tetraphalerus* the opening of the pit is as wide as the pit at its base. In *Omma* the opening of the pit is less than half

the diameter of the base of the pit (not coded as separate character states) (Hörschemeyer et al., 2002, 2006).

35. Deep basal cavity of prementum: (0) absent; (1) present. The pit and the corresponding very strongly developed internal apodeme for attachment of the median premental retractor (M. 28) are present in *Tetraphalerus* (Figs 3C and 7), *Omma* and Cupedidae. It is absent in *Micromalthus* and *Crowsoniella* (Pace, 1975, fig. 6) and also in *Sikhotealinia* (Lafer, 1996, fig. 2, pers. obs., Beutel).

36. Lid-like ventral premental plate: (0) absent; (1) present. A large lid-like premental plate is characteristic for Cupedidae and Ommatidae (Figs 3C, 7 and 9B). It covers the unsclerotized dorsal parts of the prementum. It is also present in *Crowsoniella*, with a fairly short transverse part and a median spoon-shaped process. It is attached to the narrow transverse mentum (Pace, 1975, fig. 6). The plate is absent in *Micromalthus* (Hörschemeyer, 2005). It cannot be excluded that the plate-like structure visible in specimens of *Sikhotealinia* (and †*Jurodes*; Kirejtshuk, 1999/2000, fig. 2) is possibly an enlarged mentum, similar to the condition in Helophoridae (Anton and Beutel, 2004). Therefore we coded the character as (?).

37. Transverse ridge of prementum: (0) absent; (1) present. Present in the caudal third of the premental plate in *Ascioplaga*, *Cupes* and *Distocupes*.

38. Anterior appendages of prementum: (0) paired ligula; (1) ligula subdivided into many digitiform appendages; (2) absent. Subdivided into many digitiform appendages in representatives of *Cupes*, *Ascioplaga*, *Distocupes* and *Tenomerga*. Absent in *Micromalthus* and *Crowsoniella*. The paired ligula of Megaloptera (Maki, 1936, fig. 2; Röber, 1942, fig. 15) and Coleoptera is likely formed by fusion of the glossae and paraglossae.

39. Mentum: (0) distinctly developed; (1) vestigial but recognizable as a transverse sclerite between the submentum and the premental plate; (2) absent. A separate mentum is not recognizable in most representatives of Archostemata (e.g., *Priacma*; Hörschemeyer et al., 2002). However, a distinct transverse structure is present in *Tetraphalerus* (Figs 3C and 6A) and *Crowsoniella* (Pace, 1975, fig. 6).

40. M. tentoriopharyngalis posterior (M. 52): (0) moderately sized, not distinctly subdivided into individual bundles; (1) complex, composed of series of bundles, origin from the gular ridges or lateral gular region. Originating from the lateral gular region or gular ridges and composed of one or two series of bundles in *Tetraphalerus* (Figs 6B and 7) and the members of Cupedidae examined (Hörschemeyer et al., 2002, 2006). Not distinctly subdivided into individual bundles in Megaloptera (Maki, 1936, fig. 11 [51]; Röber, 1942, fig. 23) and moderately sized and compact in *Trachypa-*

*chus* and *Helophorus* (Anton and Beutel, 2004; Dressler, 2006).

41. Propleural suture (0) present; (1) absent. Present in Chauliodinae (Maki, 1936, fig. 14), †Tshekardocoleidae, †Permocupedidae (Fig. 12), and †Triaplidae (Ponomarenko, 1969, figs 29, 43, 45 and 87). The condition in †Rhombocoleidae is unclear.

42. Exposure of propleura: (0) fully exposed, propleura reaches anterior margin of prothorax; (1) exposed, not reaching anterior margin of prothorax; (2) internalized. The propleura is exposed in Coleoptera excluding Polyphaga and reaches the anterior prothoracic margin in extant Archostemata excluding Cupedidae (Fig. 11; propleuron fused with the sternum and notum in *Micromalthus* and with the notum in *Crowsoniella*; Lawrence, 1982; Lawrence et al., 1999). The same condition is found in †Tshekardocoleidae, †Permocupedidae, †Rhombocoleidae, †Ademosynidae (Fig. 12), †Schizophoridae and †Catiniidae (Ponomarenko, 1969, figs 71, 87, 88 and 109; not in †Triadocupedinae).

43. Fusion of propleura and protrochantinus: (0) absent; (1) present. Fused in Myxophaga and Polyphaga (e.g., Lawrence, 1982).

44. Prosternal grooves for tarsomeres: (0) absent; (1) present. Present in Cupedidae excluding *Priacma* and *Paracupes*, and also in *Crowsoniella* (Hörschemeyer et al., 2006). Absent in Ommatidae (Fig. 11), *Sikhotealinia* (Lafer, 1996, fig. 136.3) and in the fossil taxa under consideration (Ponomarenko, 1969).

45. Length of prosternal process: (0) not reaching beyond hind margin of procoxae, very short or absent; (1) reaching hind margin of procoxae (see Hörschemeyer et al., 2002, 2006). Very short or absent in *Micromalthus*, *Crowsoniella*, Ommatidae (Fig. 11), *Sikhotealinia* and †Catiniidae (Ponomarenko, 1969). Apparently well developed in †*Jurodes* (Kirejtshuk, 1999/2000, fig. 2).

46. Shape of prosternal process: (0) not broadened apically; (1) apically broadened and truncate. Broadened and apically truncate in †Tshekardocoleidae, †Permocupedidae, †Rhombocoleidae (Fig. 12), †Triadocupedinae (Ponomarenko, 1969), Torridincolidae (Beutel and Vanin, 2005) and some other groups of beetles (e.g., Rhysodidae).

47. Broad prothoracic postcoxal bridge: (0) absent; (1) present. Present in †Tshekardocoleidae (Fig. 12A), †Permocupedidae and in contrast to Beutel (1997) also in †Rhombocoleidae (Fig. 12C; Ponomarenko, 1969, fig. 87). Absent in the other taxa under consideration.

48. Mesocoxal cavities: (0) not bordered by metanepisternum; (1) bordered by metanepisternum (complex type; Bell, 1967). The metanepisternum forms a part of the lateral border of the mesocoxal cavities in Cupedidae, Ommatidae (Fig. 11), *Sikhotealinia* (Fig. 13), †*Jurodes*, Myxophaga, Derodontidae and in the fossil taxa under consideration (Fig. 12) (Lawrence, 1982;

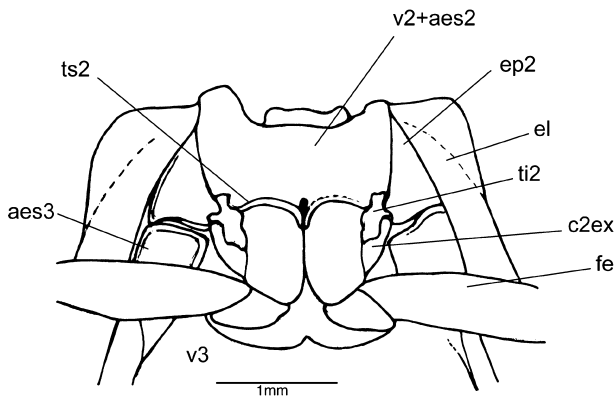


Fig. 13. *Sikhotealinia zhiltsovae*, mesothorax, ventral view. Abbreviations: aes3, metanepisternum; c2ex, mesocoxal extension; el, elytra; ep2, mesepimeron; fe, femur; ti2, mesotrochantinus; ts2, transverse suture of mesothorax; v2 + aes2, mesoventrite and mesanepisternum; v3, metaventrite. Drawn from a photograph made available on the internet (<http://www.zin.ru/Animalia/Coleoptera/rus/sikhote06.htm>).

Lafer, 1996, fig. 3; Kirejtshuk, 1999/2000, fig. 3; Hörnschemeyer, 2005).

49. Mesoventrite with anteromedian pit for reception of prosternal process: (0) absent or only very shallow concavity; (1) distinct, rounded groove; (2) large hexagonal groove. A small but distinct pit is present in Cupedidae (see Hörnschemeyer et al., 2006). A large pentagonal groove occurs in Trachypachidae and other groups of Adephega (Beutel, 1992).

50. Propleuro-mesepisternal locking mechanism: (0) absent; (1) propleural condyle and mesepisternal socket; (2) mesepisternal condyle and propleural socket. With a propleural condyle and mesepisternal socket in Cupedidae and with a mesepisternal condyle and propleural socket in Ommatidae (Lawrence, 1999; Hörnschemeyer et al., 2006).

51. Connection of meso- and metaventrite: (0) sclerites distinctly separated, connected by a membrane; (1) articulated but not firmly connected; (2) firmly connected between and within mesocoxal cavities. Loosely connected by the intersegmental membrane in extant Archostemata (Fig. 13). Interlocked but not firmly connected in Adephega (Beutel and Haas, 2000). Rigidly connected in Myxophaga and in Polyphaga with very few exceptions (Leiodidae partim, Scirtoidea, Derodontidae; Lawrence, 1999; Friedrich and Beutel, 2006).

52. Transverse suture of mesoventrite: (0) present; (1) absent. Present in Cupedidae and Ommatidae. Indistinct in  $\mu$ -CT images of *Tetraphalerus* (Fig. 11B), but clearly recognizable externally with the light microscope and as a low internal ridge. Also present in the fossil taxa under consideration (Fig. 12; Ponomarenko, 1969, figs 43, 46, 71, 92 and 96) with the exception of †Catiniidae. A transverse line separates a very narrow stripe anterior of the mesocoxa from the rest of the ventrite in *Sikhote-*

*alinia* (Fig. 13; Lafer, 1996, fig. 3). We consider this as the transverse suture of the mesoventrite (coded as [0]).

53. Mesal coxal joints of mesoventrite: (0) present; (1) absent. Present in Ommatidae (Fig. 11B) and Cupedidae (Baehr, 1975, fig. 3: pl-cx), and apparently also in *Sikhotealinia* (Fig. 13) and †*Jurodes* (Kirejtshuk, 1999/2000, fig. 2). Also recognizable in †Triadocupedinae (Ponomarenko, 1969, figs 45 and 46) and †Rhombocoleidae (Fig. 12C). Absent in *Crowsoniella* (Pace, 1975), all non-archostematan beetles (Beutel and Haas, 2000), and probably also in Catiniidae (Ponomarenko, 1969).

54. Shape of mesocoxae: (0) globular or conical; (1) with deep lateral excavation and triangular lateral extension. Mesocoxae with a deep lateral excavation and a triangular extension articulating with a fairly large exposed trochantin are characteristic for Cupedidae (e.g., Baehr, 1975, fig. 3), Ommatidae (Fig. 11B), *Sikhotealinia* (Fig. 13), and †*Jurodes* (Kirejtshuk, 1999/2000, fig. 3). The coxae are more or less conical or globular in the other fossil and extant taxa under consideration. The lateral extension is likely homologous with the mesocoxal meron (see Maki, 1936, fig. 14 [m]).

55. Exposed metatrochantin: (0) present, distinctly developed; (1) indistinct or absent. Distinctly developed in Cupedidae and Ommatidae (Fig. 11B), and in the fossil taxa under consideration with the exception of †Catiniidae and †Schizophoridae (very narrow element possibly exposed in †*Catinius*; Ponomarenko, 1969, fig. 111). An exposed metatrochantin is probably also present in *Sikhotealinia* (Lafer, 1996). However, as the condition is not entirely clear, we preferred to code the character as (?).

56. Shape of penultimate tarsomere: (0) not distinctly bilobed; (1) distinctly bilobed. Bilobed in Cupedidae (Lawrence, 1999; Hörnschemeyer et al., 2002, 2006) and Sialidae.

57. Forewings: (0) membranous; (1) transformed into sclerotized elytra. Elytra with epipleura are present in all beetles (Figs 1 and 11) with the exception of neotenous forms (e.g., Beutel and Haas, 2000).

58. Venation of forewings: (0) distinct, not arranged in parallel rows; (1) parallel arrangement of distinct longitudinal veins; (2) longitudinal veins very indistinct or absent. A parallel arrangement of the longitudinal veins or ridges is characteristic for Cupedidae, Ommatidae (Fig. 11), †Permocupedidae, †Rhombocoleidae and †Triadocupedinae (Crowson, 1962; Ponomarenko, 1969, 2003, 2004). Distinctly curved veins not arranged in a parallel pattern are still present in †Tshekardocoleidae (Kukalová, 1969, figs 1–5; Ponomarenko, 2002, 2004, fig. 1a). The longitudinal veins are absent in †Ademosynidae, †Schizophoridae and †Catiniidae, and also in *Crowsoniella*, *Sikhotealinia* and non-archostematan beetles. They are very faint in *Micromalthus* (coded as 2). There is more variation in this character than

represented by the states listed here (see e.g., Ponomarenko, 1969). However, as our taxon sampling of early fossils is restricted by the exclusion of groups only represented by detached elytra (e.g., †Schizocoleidae, †Asiocoleidae), we decided to code only the major types of the elytral venation.

59. Elytral sclerotization pattern: (0) with a pattern of unsclerotized window punctures; (1) entirely sclerotized. The pattern with window punctures (Lawrence, 1982) is present in Cupedidae and Ommatidae (Fig. 11A), and in the fossil families under consideration with the exception of †Jurodidae, †Ademosynidae, †Catiniidae and †Schizophoridae (Ponomarenko, 1969, 2003, 2004; Kirejtshuk, 1999/2000). It is scarcely recognizable in most members of †Rhombocoleidae, but distinct in †*Schizotaldycupes* (Ponomarenko, 1969) (coded as 0 & 1 for the family).

60. Elytral apex: (0) distinctly reaching beyond abdominal apex posteriorly; (1) slightly reaching beyond abdominal apex posteriorly; (2) reaching abdominal apex or shorter. The elytra of beetles are usually precisely adapted to the shape of the abdomen, thus forming a closed subelytral space (e.g., Beutel, 1997). This is not the case in †Tshekardocoleidae (Fig. 12A) and †Permocupedidae (Ponomarenko, 1969, figs 30, 41 and 42; Ponomarenko, 2004, fig. 1a; Kukulová, 1969, fig. 1). The elytra distinctly reach beyond the abdominal apex posteriorly in the former taxon and are also distinctly broader. The elytra are only slightly longer than the abdomen in †Permocupedidae (Fig. 12B).

61. Transverse folding mechanism of hind wings: (0) absent; (1) present. Absent in †Tshekardocoleidae (Kukulová, 1969) but present in extant beetles (e.g., Beutel and Haas, 2000), in †Triadocupedinae [Ponomarenko, 1969, fig. 44b, and probably also in other fossil taxa under consideration (coded as?)].

62. Oblongum cell of hind wing: (0) closed cell not differentiated as oblongum cell; (1) oblongum present; (2) open or absent. Absent in *Micromalthus* and *Sikhotealinia* (Lafer, 1996; Hörnschemeyer, 2005) and also in polyphagan beetles.

63. Abdominal sternite I: exposed; (1) concealed under metacoxae, largely or completely reduced. Reduced in all extant and fossil beetles (e.g., Beutel and Haas, 2000).

64. Median ridge on ventrite 1: (0) absent; (1) present. Present in *Sikhotealinia*, †*Jurodes* (Kirejtshuk, 1999/2000), Cupedidae and Ommatidae. The condition in *Crowsoniella* is unclear.

65. Number of exposed abdominal sternites (excluding sternite I): (0) more than six; (1) six; (2) five. Five sternites are usually exposed in Archostemata (including fossil taxa; Fig. 12; Ponomarenko, 1969), but six are visible in *Micromalthus*, *Sikhotealinia* (Lafer, 1996, fig. 3) and †*Jurodes* (Kirejtshuk, 1999/2000).

66. Arrangement of abdominal sterna: (0) abutting, not overlapping; (1) tegular or overlapping (Lawrence, 1999; Hörnschemeyer et al., 2002, 2006). Overlapping in Cupedidae.

*Larvae.* All larval stages of *Ascioplaga*, *Paracupes*, *Tetraphalerus*, *Crowsoniella*, *Sikhotealinia* and fossil taxa and later instars of *Priacma* are unknown. See Lawrence (1999), Beutel and Haas (2000), Beutel and Hörnschemeyer (2002a,b) and Grebennikov (2004) for explanation of characters:

67. Head shape of later instars: (0) parallel-sided, slightly narrowing anteriorly, or evenly rounded; (1) transverse, strongly rounded laterally, greatest width near hind margin. Transverse in larvae of Cupedidae and *Micromalthus* (Beutel and Hörnschemeyer, 2002a,b).

68. Posteromedian emargination of head capsule: (0) absent; (1) present. Present in all known archostematan larvae (Beutel and Hörnschemeyer, 2002a,b).

69. Endocarina: (0) absent; (1) present, undivided; (2) present, forked. Undivided in Cupedidae and *Micromalthus* and forked in *Omma* (Lawrence, 1999; Beutel and Hörnschemeyer, 2002a).

70. Frontal suture of second and third instars: (0) distinct; (1) indistinct or absent. Absent in the known archostematan larva (Beutel and Hörnschemeyer, 2002a,b).

71. Stemmata: (0) more than one pair of stemmata; (1) one pair of stemmata or eyeless. One pair or absent in Cupedidae and *Micromalthus* (Lawrence, 1999; Beutel and Hörnschemeyer, 2002a).

72. Length of antenna: (0) at least 20% of greatest width of head capsule; (1) less than 20% of greatest width of head capsule. Strongly shortened in Cupedidae and *Micromalthus* (Beutel and Hörnschemeyer, 2002a).

73. Antennal segments: (0) four or more; (1) three or less. Three or less in Myxophaga and Polyphaga (with very few exceptions; e.g., Lawrence, 1982).

74. Shape of distal part of mandible: (0) less than three apices; (1) three apices. Three apices in the known archostematan larvae (Lawrence, 1999; Beutel and Hörnschemeyer, 2002a).

75. Retinaculum: (0) present; (1) absent. Present in *Omma* and different non-archostematan groups (Lawrence, 1999; Beutel and Hörnschemeyer, 2002a).

76. Shape of mola: (0) not quadrangular, not delimited by a distinct margin; (1) quadrangular and delimited by a distinct margin; (2) missing. Quadrangular in larvae of Cupedidae and *Micromalthus* (Beutel and Hörnschemeyer, 2002a).

77. Ligula: (0) unsclerotized; (1) sclerotized, enlarged and wedge-shaped. Sclerotized and wedge-shaped in all known archostematan larvae (Lawrence, 1999; Beutel and Hörnschemeyer, 2002a,b).

78. Mentum and submentum: (0) not fused; (1) fused and narrowed between maxillary grooves. Fused in the

known archostematan larvae (Beutel and Hörnschemeyer, 2002a).

79. Prothorax: (0) as broad as following segments; (1) broader than following segments. Broader in *Rhipsideigma* and *Tenomerga* (Beutel and Hörnschemeyer, 2002b).

80. Leg segments: (0) six; (1) five. Five in Myxophaga and Polyphaga (e.g., Lawrence, 1982).

81. Claws: (0) paired; (1) unpaired. Unpaired in Myxophaga, Polyphaga and most groups of Cupedidae (Ross and Potheary, 1970; Lawrence, 1982; paired in *Tenomerga*; Böving, 1929).

82. Abdominal segments I–III of later instars: (0) shorter than thorax; (1) longer than thorax. Longer in the known archostematan larvae (Lawrence, 1999; Beutel and Hörnschemeyer, 2002a,b).

83. Tergal ampullae: (0) absent; (1) present. Present in the known larvae of Cupedidae and *Micromalthus*. Absent in *Omma* (Lawrence, 1999).

84. Ventral asperities: (0) absent; (1) present. Present in Cupedidae and *Micromalthus* (Beutel and Hörnschemeyer, 2002a).

85. Lateral longitudinal bulge of abdominal segments I–VII: (0) absent; (1) present. Present in *Rhipsideigma*, *Cupes* and *Tenomerga* (Beutel and Hörnschemeyer, 2002b).

86. Sclerotized process of tergum IX: (0) absent; (1) present. Present in Cupedidae and *Micromalthus* (Beutel and Hörnschemeyer, 2002a).

87. Eversible lobes of segment IX: (0) absent; (1) present. Present in Cupedidae and *Micromalthus* (Beutel and Hörnschemeyer, 2002a).

88. Urogomphi: (0) absent; (1) present. Absent in Archostemata (Lawrence, 1982, 1999).

89. Segment X: (0) exposed; (1) not visible externally. Not visible in the known archostematan larvae (Lawrence, 1999; Beutel and Hörnschemeyer, 2002a,b).

90. Larval habitat: (0) not associated with wood; (1) associated with wood. Larvae of Cupedidae and *Micromalthus* are associated with wood. Unknown for other archostematan taxa.

#### *Phylogenetic analyses (Figs 14–17)*

The data were analyzed with NONA (Ratchet, 1000 replicates) (Goloboff, 1995) and the branch and bound algorithm of PAUP\* 4.0b10 (Swofford, 2001) with all options set to default values. All characters were coded as unordered and had equal weights.

The parsimony analysis (NONA) of the complete data set produced four minimal length trees with 175 steps and a consistency index (CI) of 0.64 (Fig. 14). The unambiguous apomorphies are mapped on the tree in Fig. 14 (tree with collapsed unsupported branches, identical with strict consensus tree). The Bremer support values were calculated with AutoDecay 5.0 in PAUP

(Eriksson, 2003). The bootstrap values were calculated with the bootstrap algorithm of NONA (1000 replicates).

For the analysis with MrBayes polymorphous character representations were replaced by “?” to represent uncertain character states. The analysis was run twice with fossil taxa included and twice with fossil taxa excluded. For all analyses we used the standard model for morphological characters as implemented in MrBayes 3.1.2 and proposed by Lewis (2001) and Nylander et al. (2004). We employed the simplest version of the model with all state frequencies (change rates) set equal and fixed to symmetrical Dirichlet of –1, all topologies with equal probabilities and unconstrained branch length (exponential 10.0). In all analyses multiple chains were calculated with a ratio of one cold to three heated chains and the temperature parameter set to 0.20.

For the data set with fossils included two independent analyses were run, one with 5 million generations (ngen), four simultaneous runs (nrun), six chains (nchains) and with every 200th generation sampled (samplefreq). The second run was calculated with 10 million generations, two simultaneous runs, four chains, and with every 100th generation sampled. Other parameters were set to default values.

For the evaluation of the results a quarter of the samples from each run was discarded as “burn in”. From the remaining data 50%-majority rule cladograms were constructed (sumt) with the option to display all compatible groups in the cladograms. The results of the two different runs are nearly identical with average likelihoods of –663.96 for both runs and average standard deviations for the split frequencies at 0.006211 and 0.006602, respectively. Both runs produced the same topology.

For the data set without fossils the same double analysis was done. The results were also very similar with average likelihoods of –585.70 and 585.67 and average standard deviations of split frequencies at 0.002211 and 0.001273, respectively. The cladograms for both runs were again identical.

All cladograms of the Bayesian analysis are largely compatible with the cladograms obtained from the parsimony analysis, but differ in the arrangement of the stem lineage of Coleoptera, and also in the arrangement of the extant archostematan groups (see below).

#### **Discussion**

The  $\mu$ -CT applied in this study is very useful for the documentation of external features (Figs 10 and 11), but especially for internal structures including soft parts such as muscles and elements of the central nervous system (Fig. 5). The technique is largely artifact free and non-destructive and can be applied for very rare species

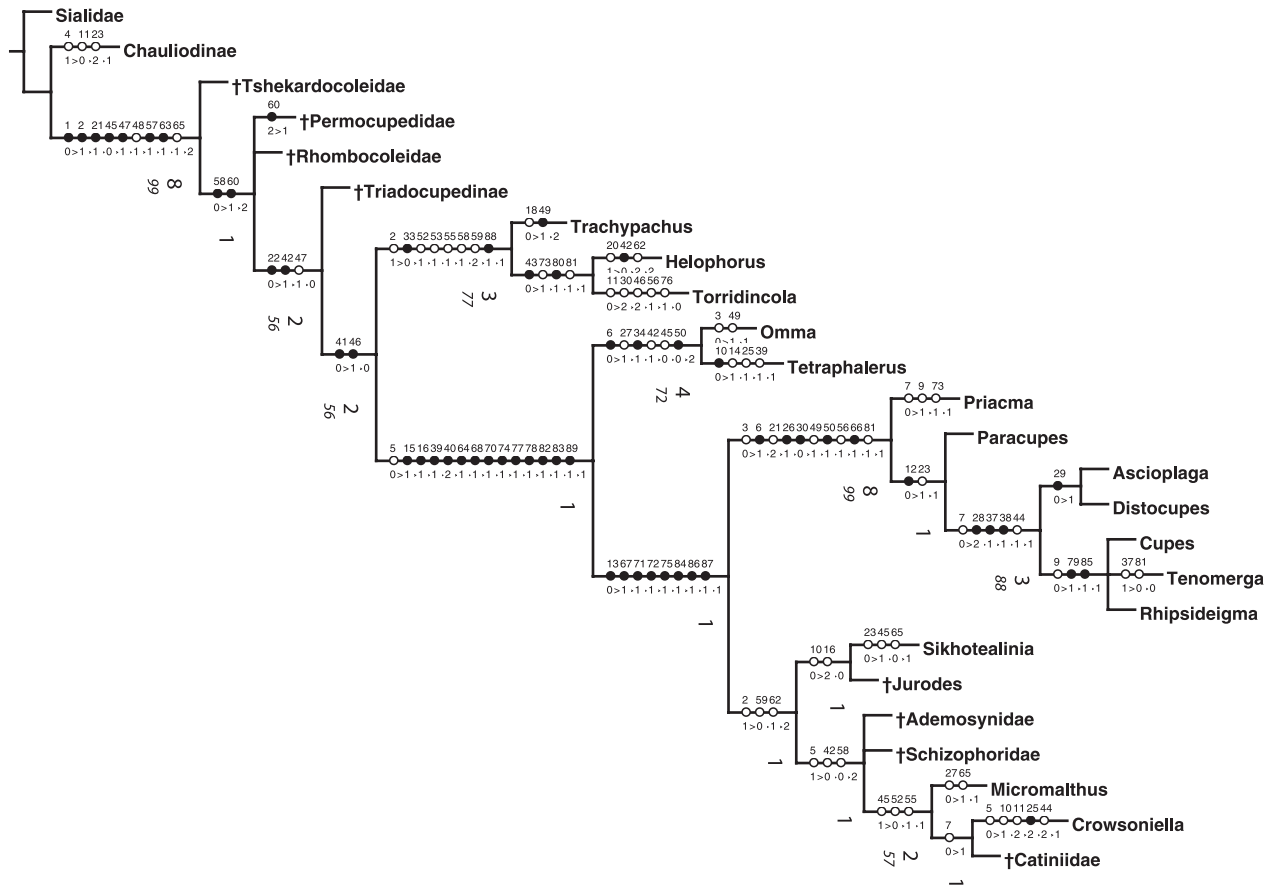


Fig. 14. Cladogram, parsimony analysis (NONA), ratchet, 1000 replicates. Tree with unsupported branches collapsed (identical with strict consensus of four minimal length trees) with a length of 176 steps and a consistency index (CI) of 0.63. The unambiguous apomorphies are mapped on the tree (see text for explanation). Bremer support values right to branches, bootstrap values (in italics) below.

or even type material (see also Hörnschemeyer et al., 2002). Based on the obtained image stacks, three-dimensional reconstructions using the automatic volume-rendering option in Imaris can be obtained within minutes (Fig. 5). Three-dimensional reconstructions using digitalized selected structures and Maya software (Fig. 8) are more time consuming, but still highly efficient compared with earlier approaches (e.g., Beutel and Haas, 1998). The  $\mu$ -CT technique has the potential to revolutionize insect internal anatomy and may turn out as extremely useful in the morphological part of the Beetle Tree of Life (BTOL) project. Its use will strongly accelerate the acquisition and documentation of high-quality anatomical data.

*Tetraphalerus bruchi* is apparently a highly specialized species, mainly adapted to a cryptic life in subcortical habitats. In contrast to plesiomorphic features of the thorax, such as the large exposed propleuron, the loosely connected meso- and metaventrites, and the exposed metatrochantin (Fig. 11), features of the head are mostly derived. The strongly elongated shape, peculiar mushroom-shaped tubercles (also present in other subcortical insects, e.g., Aradidae), a sharply

delimited ventral antennal groove with a smooth surface, and the presence of only two extrinsic antennal muscles are possible autapomorphies of the genus (Figs 2 and 3). A plesiomorphic feature of *Archostemata* compared with other representatives of *Archostemata* is the presence of a well developed tentorial bridge (Figs 7 and 8D). The position of *Tetraphalerus* as sister group of *Omma* is clearly confirmed by the results of our study. Synapomorphies are the presence of a deep pit with sensilla on the apical maxillary palpomere (Fig. 3D) and possibly the specific propleural–mesepisternal locking mechanism with a condyle on the latter part (Lawrence, 1999). Another potential synapomorphy of the genera is the unusual shape of the mandibles with three apical teeth arranged in a vertical row (Fig. 4). This derived feature has apparently evolved independently in *Micromalthus*.

The monophyly of *Archostemata* including *Sikhotealinia* (as the sister group of †*Jurodes*) and the extinct families †*Ademosynidae*, †*Schizophoridae* and †*Catiniidae* is suggested by 14 unambiguous changes in the parsimony analysis including the fossil taxa. Autapomorphies are the reduction of the anterior tentorial arms

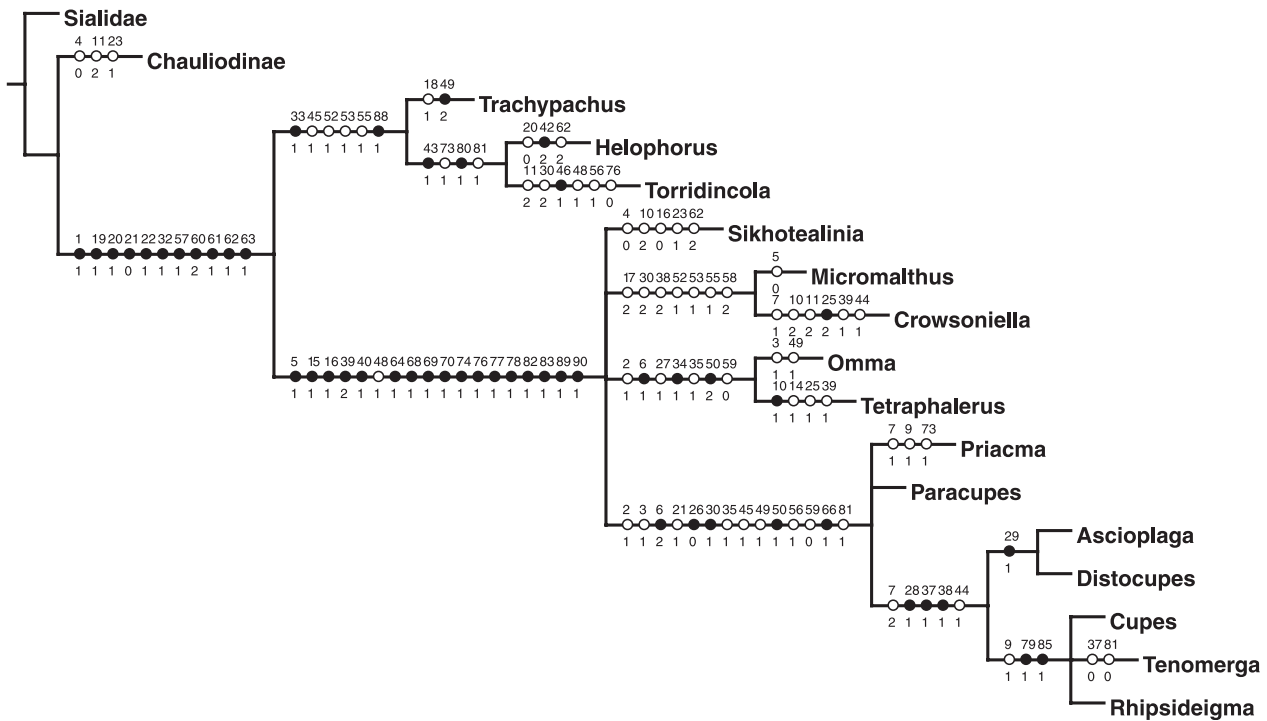


Fig. 15. Cladogram, parsimony analysis (NONA), ratchet, 1000 replicates, fossil taxa excluded. Strict consensus tree of three most parsimonious trees with a length of 165 steps and a CI of 0.85. The unambiguous apomorphies are mapped on the tree (see text for explanation) (tree with collapsed unsupported branches, identical with strict consensus tree). Bremer support values right to branches, bootstrap values (in italics) below.

(Fig. 8), the reduction of the frontoclypeal suture (reversal in Jurodidae), the distinctly reduced mentum (Fig. 3C), a posterior tentoriopharyngeal muscle composed of a series of bundles (Fig. 7), a median ridge on the first abdominal ventrite, and several larval features. This appears to be a very strong support for this lineage containing some of the extinct and all extant taxa assigned to Archostemata. However, it has to be noted that most of these characters are (and will likely remain) unconfirmed for several extant and all fossil taxa under consideration.

Ommatidae is placed as the sister group of the remaining Archostemata, including the extinct families †Ademosynidae, †Schizophoridae and †Catiniidae. The monophyly of this clade is supported by one apomorphy of adults, the absence of the tentorial bridge, and by seven apomorphies of larvae. The larval features strongly support a clade comprising Micromalthidae and Cupedidae, but not Ommatidae (see Figs 14 and 17B; Beutel and Hörnschemeyer, 2002a). However, as it is the case with the presumptive archostematan autapomorphies, all eight characters are unconfirmed for the fossil taxa, and also for *Crowsoniella* and *Sikhotealinia*. Unfortunately the larvae of both extant genera are unknown and their discovery in the near future is very unlikely.

The loss of cuticular tubercles and of elytral window punctures and the absence of a closed oblongum cell are potential synapomorphies of Jurodidae, †Ademosyn-

idae, †Schizophoridae, †Catiniidae, Micromalthidae and Crowsoniellidae. All three features are reductions, with parallel evolution in the other beetle suborders, and the placement of the three extinct families appears very uncertain considering the amount of missing data. The unambiguous apomorphies in support of a clade comprising Micromalthidae and Crowsoniellidae (and †Catiniidae) are also reductions, which are also found in non-archostematan beetles (loss of the transverse suture of the mesoventrite and absence of an exposed metatrochantin). The loss of the galea and lacinia are further potential synapomorphies of both taxa. However, it cannot be excluded that all reductions shared by the two taxa have evolved independently in correlation with a distinct size reduction and possibly also with non-feeding in adults. All species of Ommatidae and Cupedidae are distinctly larger than 10 mm, whereas adults of *Micromalthus* range between 1.6 and 2.2 mm in size and *Crowsoniella* between 1.32 and 1.74 mm (Pace, 1975; Hörnschemeyer, 2005). The condition of the mouthparts (e.g., vestigial mandibles; Pace, 1975) of *Crowsoniella* suggests that feeding in the adult stage plays a very minor part if at all, and feeding is not recorded for the short-lived adults of *Micromalthus*.

Adults of Micromalthidae differ strongly from the typical archostematan morphology, as it is represented by Cupedidae and Ommatidae. In addition to the features mentioned above, they also lack the plate-like

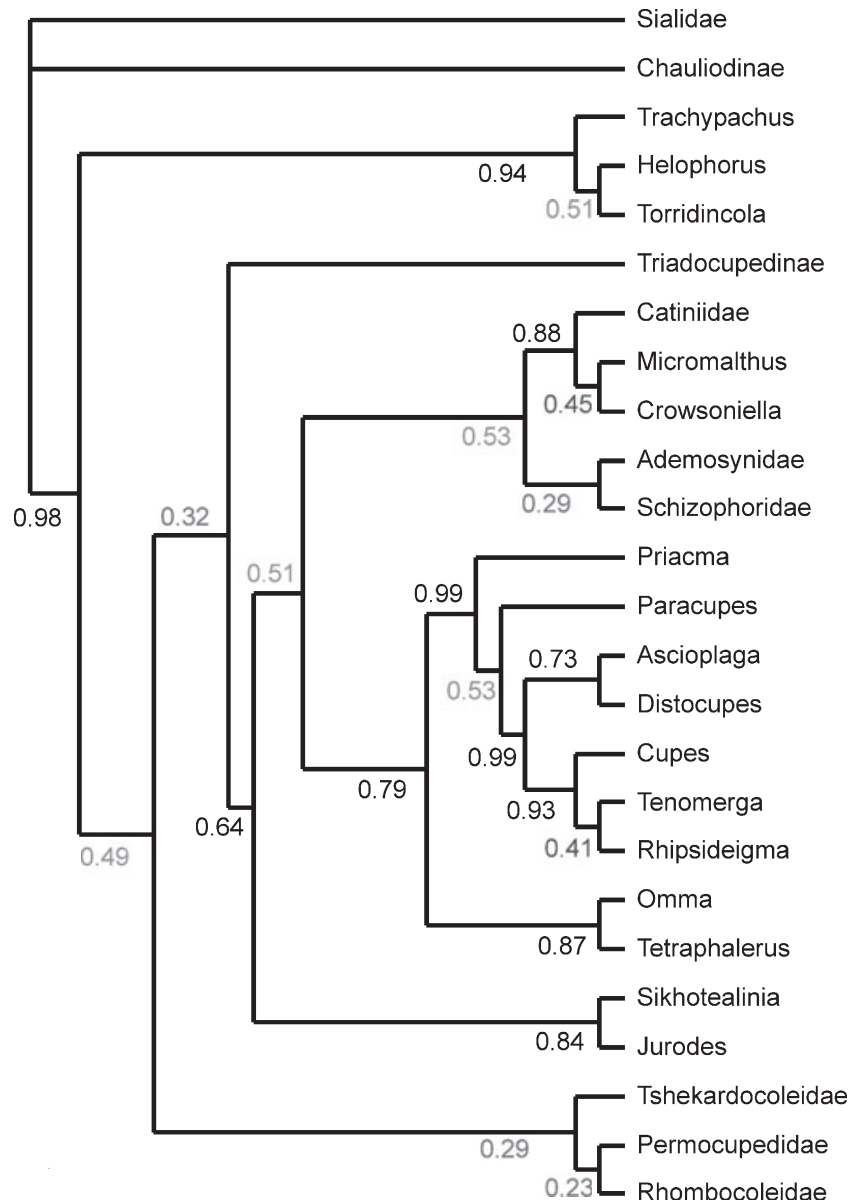


Fig. 16. Cladogram based on Bayesian analysis. All taxa included.

prementum, the characteristic head shape with a constricted neck region, and any protuberances on the dorsal side of the head. The body is weakly sclerotized, the elytra are shortened, all prothoracic sclerites are fused, and six or seven abdominal sternites are exposed. The placement of *Micromalthus* was often challenged (e.g., Barlet, 1996; see Beutel and Hörnschemeyer, 2002a). However, as pointed out above, larval features very clearly indicate, that they belong to Archostemata (Fig. 17B) as it has already been suggested by Forbes (1922) and Böving and Craighead (1931).

The placement of *Sikhotealinia shiltzovae* in Jurodidae (Kirejtshuk, 1999/2000) is confirmed and the family is unambiguously placed as sister taxon of the micromalt-

hid-crowsoniellid lineage in the parsimony analysis with the full data set (Fig. 14), but as the sister taxon of the remaining Archostemata in the Bayesian analyses (Fig. 17). The similarity between *Sikhotealinia* and †*Jurodes* was already pointed out by Kirejtshuk (1999/2000) and the presence of antennal grooves on the dorsal side of the head is a potential synapomorphy, with parallel evolution in *Crowsoniella*. Considering the amount of missing data, the precise position of Jurodidae should be regarded as an open question. However, the placement of the family within Archostemata is clearly supported by our results (see above). Like *Micromalthus* and *Crowsoniella*, *Sikhotealinia* differs distinctly from “typical” archostematan beetles. It lacks



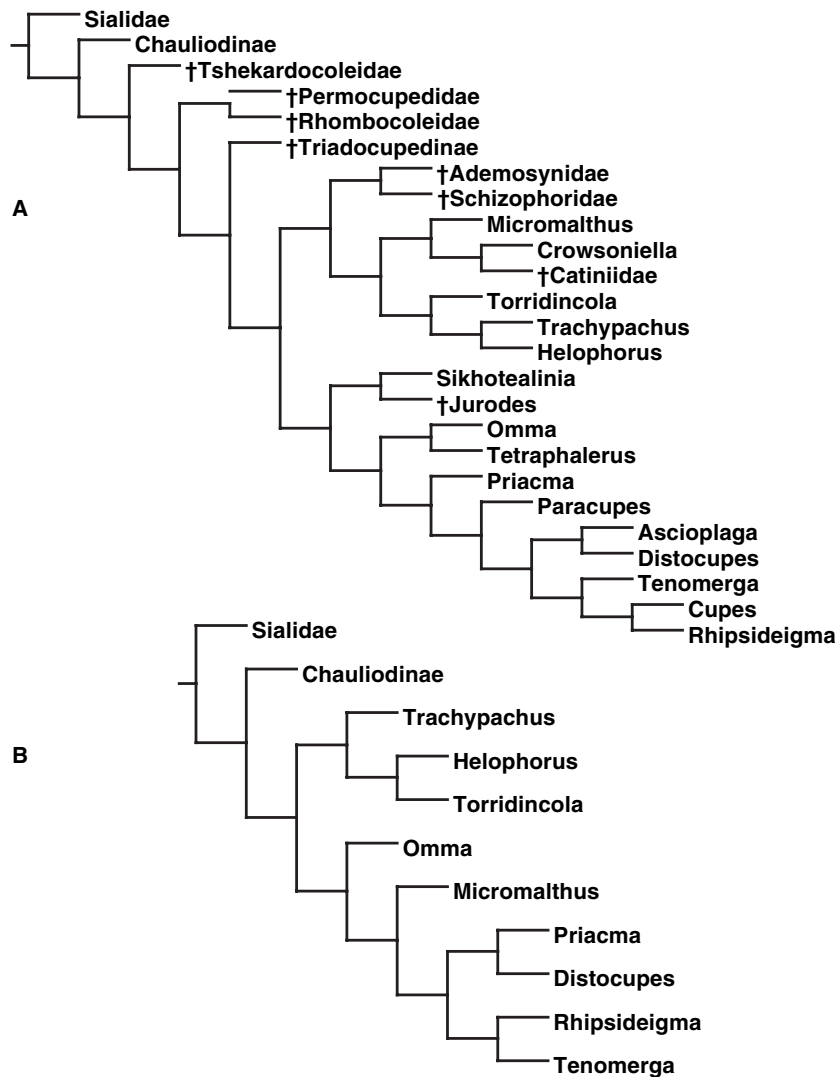


Fig. 17. (A,B) Cladograms, parsimony analysis (NONA), ratchet, 1000 replicates. (A) Larval features excluded, one of two minimal length trees; (B) adult characters and taxa with unknown larvae excluded, single minimal length tree.

cuticular tubercles and window punctures on the elytra, six abdominal segments are exposed, and the wings lack an oblongum. However, the constricted neck and the dorsomesal protuberances (P3) of the head are derived archostematan characters, and *Sikhotealinia* has preserved an array of presumably plesiomorphic archostematan features such as the presence of a transverse ridge of the mesoventrite, the loose connection of the meso- and metaventrite, mesocoxal cavities bordered by the metanepisternum (Fig. 13), broad metacoxae completely separating the metaventrite from the abdomen (Lafer, 1996), and the absence of well developed metacoxal plates. An exposed metatrochantin is also present according to Lafer (1996). However, a more detailed examination would be desirable to confirm this, like in the case of the anterior labial plate (see character 36). In any case, polyphygan affinities of the genus

appear unlikely. An inclusion in Polyphaga would require five additional steps with our data set and a rather unlikely series of character reversals. More detailed morphological information about *Sikhotealinia* should have high priority. Even though only the holotype is available, the examination with the non-destructive  $\mu$ -CT technology should be considered, even though internal structures such as muscles or parts of the nervous system are likely not preserved well. The search for more specimens of the enigmatic beetle species should also have high priority, but is impeded by the lack of information on the exact area of distribution and the completely unknown habits and natural history.

Cupedidae is strongly supported as a clade in all analyses (Figs 14–17). The branching pattern we obtained is largely in agreement with Hörnschemeyer

et al. (2002, 2006). The monophyly of Cupedidae excluding *Priacma* is supported in most (Figs 14, 16 and 17) and the monophyly of Cupedidae excluding *Priacma* and *Paracupes* in all analyses (Figs 14–17). Clades are formed by the genera from Australia (*Distocupes*) and New Caledonia (*Ascioplaga*), and by *Rhipsideigma*, *Cupes* and *Tenomerga*, respectively.

Archostemata as defined here form the sister group of a clade comprising the non-archostematan outgroup taxa (i.e., *Trachypachus* [Adephaga], *Torridincola* [Myxophaga] and *Helophorus* [Polyphaga] in all analyses (Figs 14–17), in agreement with the results of a comprehensive cladistic analysis presented by Beutel and Haas (2000). We refer to the entire clade (including Archostemata) as Coleoptera s.str. The extinct families †Tshekardocoleidae, †Permocupedidae and †Rhombocoleidae, and †Triadocupedinae belong to the stem lineage of Coleoptera, as already suggested by Beutel (1997) based on a non-numerical character analysis. Coleoptera s.l. are strongly supported as a monophyletic group. A strongly sclerotized body without external membranes (Fig. 11), forewings transformed into elytra, a reduced abdominal sternite I, only five exposed abdominal sternites, mesocoxal cavities bordered by the metanepisternum, the tuberculate cuticular surface, a broad and apically truncate prosternal process, a broad prothoracic postcoxal bridge, and mesocoxal cavities bordered by the metanepisternum are derived groundplan features of Coleoptera s.l. (see Fig. 12). With their wedge-shaped prognathous head, a feature shared with the potential sister group Neuropterida (e.g., Maki, 1936; Röber, 1942; not in Coniopterygidae; D. Grimaldi, pers. comm.), the depressed body, forewings covered by sclerotized elytra, and the strongly sclerotized body reinforced by a broad prothoracic postcoxal bridge, the earliest beetles were perfectly adapted for penetrating narrow crevices under bark. Whether the tuberculate surface structure, which is usually maintained in the xylobiontic extant Archostemata, plays a part in this functional context is not entirely clear. Cuticular tubercles occur in other subcortical insects such as Aradidae (Heteroptera), Zopheridae and Colydiidae (both Tenebrionoidea) (D. Grimaldi, pers. comm.; see above), but are absent in other xylobiontic groups such as for instance Buprestidae and Cerambycidae.

The placement of the Lower Permian †Tshekardocoleidae as the sister group of the remaining Coleoptera is well supported in the parsimony analyses (Figs 14 and 17A). It is in agreement with Beutel (1997) and Ponomarenko (2002, fig. 216), and also with the early appearance of the group in the fossil record. Important evolutionary innovations linked with the earliest splitting event in the Lower Permian were shortened elytra better fitting with the shape of the abdomen (Fig. 12), hind wings with a transverse folding mechanism (Beutel

and Haas, 2000), and a distinct modification of the elytral venation (Beutel, 1997; Ponomarenko, 2002). †Tshekardocoleidae were the only beetles in the Lower Permian deposits apart from the recently described †*Permocoleus* (Wellington Formation; Lubkin and Engel, 2005). Apparently they were very rare compared with other insect lineages (Ponomarenko, 2002).

†Permocupedidae and †Rhombocoleidae are the next two branches in the stem lineage of Coleoptera in the parsimony based trees (Figs 14 and 17A). Apomorphies of Coleoptera excluding †Tshekardocoleidae, †Permocupedidae and †Rhombocoleidae are the loss of two terminal antennomeres and of the prothoracic postcoxal bridge. Together with †Asiocoleidae and †Schizocoleidae (only known from detached elytra) they belong to the four families represented in the Upper Permian (Ponomarenko, 2002). The majority of preserved beetles from the Kuznetsk Basin belong to †Permocupedidae. However, Coleoptera were still rare compared with other groups of insects in this period ( $\approx 1\%$ ; Ponomarenko, 2002).

As suggested by Beutel (1997) †Triadocupedinae also belong to the stem lineage and are the sister group of Coleoptera s.str. The loss of the propleural suture and a distinctly narrowed prosternal process are autapomorphies of Coleoptera s.str. A broad prosternal process (and a broad postcoxal bridge) has evolved secondarily in xylobiontic and non-xylobiontic extant groups such as for instance Rhysodidae and Cicindelinae (Beutel, 1992).

The results of the analyses using parsimony (PAUP, NONA) and the Bayesian approach are largely compatible. The monophyly of Coleoptera s.l. and Archostemata (as defined above), the clade comprising the other suborders, the clade comprising †Ademosynidae, †Schizophoridae, †Catiniidae, Micromalthidae and Crowsoniellidae, the monophyly of Ommatidae and Cupedidae, and the branching pattern within the latter family were confirmed with both approaches. However, the Permian lineages †Tshekardocoleidae, †Permocupedidae and †Rhombocoleidae form a clade in the Bayesian tree, and are placed as the sister group of Archostemata + †Triadocupedinae. This appears unlikely considering the fossil record (see above) and the proposed character evolution. Jurodidae (or *Sikhotealinia*) are placed as the sister group of the remaining Archostemata in the Bayesian analyses (including or excluding fossils) and Ommatidae are the sister group of Cupedidae (Fig. 16).

In contrast to the Bayesian analyses (Fig. 16), the exclusion of fossils had an effect on the branching pattern in the parsimony analyses, and the resolution was distinctly reduced (Figs 14 and 15; see above). Ommatidae, Micromalthidae + Crowsoniellidae, *Sikhotealinia* and Cupedidae form an unresolved polytomy in the strict consensus tree, and the relationships between *Priacma*, *Paracupes* and the clade comprising

the remaining Cupedidae are also unresolved (Fig. 15). The results of our analyses clearly show that the fossils play an important part in the reconstruction of the character evolution. When the extinct taxa are excluded, the tuberculate cuticular surface structure, which obviously belongs to the groundplan of beetles, is interpreted as an autapomorphy of Ommatidae and Cupedidae, respectively, and the clearly ancestral mesocoxal cavities of the complex type as an autapomorphy of Archostemata.

The exclusion of larval features has a drastic effect on the results of the analysis as †Ademosynidae and †Schizophoridae and the micromalthid–crowsoniellid–†catiniid clade cluster with the non-archostematan taxa (Fig. 17A). We consider this result as highly unlikely considering the well documented and clearly archostematan morphology of micromalthid larvae (Beutel and Hörnschemeyer, 2002a). An analysis carried out after exclusion of adult characters and all taxa with unknown larvae yielded a branching pattern compatible with the results of the parsimony analysis with the complete data set (Fig. 17B).

Our study fully confirms Ponomarenko's (1995) view, that an understanding of the early evolution of beetles is not possible when the diverse early fossils are ignored. It does not support Patterson's claim that "instances of fossils overturning theories of relationship based on Recent organisms are very rare, and may be nonexistent" (Patterson, 1981). In our analyses, the branching pattern is clearly affected by the fossil taxa, and they contribute significantly to the reconstruction of character evolution, in addition to valuable information about the timing of divergences and extinctions. In agreement with Gauthier et al. (1988), Donoghue et al. (1989) and Eernisse and Kluge (1993) we conclude that despite missing entries in data matrices, it is better to include extinct taxa, than to analyze Recent taxa first and add fossils into appropriate stem lineages ("if at all") as suggested by Ax (1987) (see also Donoghue et al., 1989). The procedure suggested by Ax (1987) is a non-numerical approach in both steps of the character evaluation (or at least in the second). It perpetuates wrong interpretations of character evolution and wrong branching patterns, which may result from the exclusion of fossils.

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