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Extinct and extant rove beetles meet in the matrix: Early Cretaceous fossils shed light on the evolution of a hyperdiverse insect lineage (Coleoptera: Staphylinidae: Staphylininae)

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Abstract

Description of the Early Cretaceous (Yixian Formation, China) fauna of Staphylininae and Paederinae rove beetles, and a rigorous (maximum parsimony, maximum likelihood and Bayesian inference) phylogenetic analysis of both extinct and extant taxa resulted in the following discoveries: a stem lineage sister to Staphylininae + Paederinae; a new tribe for Staphylininae, Thayeralinini trib. n.; several extinct species of the extant tribe Arrowinini; extinct basal lineages of the extant tribe Staphylinini; two stem genera of the ''Xantholinine-lineage'' (Staphylininae); and recovery of *Mesostaphylinus* in Paederinae with several new species. It is demonstrated that by the Early Cretaceous, Paederinae and Staphylininae were already diversified into groups, some of which now represent extant tribes but not the branches dominating in the modern biota. While the study of the Early Cretaceous rove beetle fauna pushes the estimated divergence time between Paederinae and Staphylininae down into the Jurassic, it also suggests that presently hyperdiverse groups of Staphylininae originated some time later than the Early Cretaceous. In addition to one new tribe, five new genera (*Paleothius*, *Cretoprosopus*, *Thayeralinus*, *Paleowinus* and *Durothorax*) and 17 new species are described in Staphylininae, and three new species of *Mesostaphylinus* are described in Paederinae. *Mesostaphylinus fraternus* (*incertae sedis*) is moved to the genus *Thayeralinus* (Staphylininae).

With 58 331 described recent and fossil species (A. Newton, pers. comm.), the rove beetles (Staphylinidae, as defined by Grebennikov and Newton, 2009; Bouchard et al., 2011) comprise the largest family of organisms and are abundant or even predominant inhabitants of terrestrial landscapes worldwide. Comprehension of such hyperdiversity in contemporary and historical perspectives requires an ability to trace, in time and space, the rove beetle ''tree of life'' from tens of thousands of its uppermost branches (recent species) down to its root (a hypothetical common ancestor). As old as the Late Triassic (Grimaldi and Engel, 2005; Chatzimanolis et al. 2012), Staphylinidae are the most ancient staphyliniform family of beetles and a rather old lineage of the polyphagan beetles (Meller et al., 2011). Given the very high extinction rate in the course of biological evolution (Nee and May, 1997), and the relatively old age of Staphylinidae, numerous extinct (stem) lineages of rove beetles, and thus their fossils, are expected to be discovered.

Generally, stem lineages that branched off closer to the root of a given phylogenetic clade preserve traits of high evolutionary interest (Huelsenbeck, 1991). This is also true for Staphylinidae, where previous phylogenetic reconstructions struggled with poor resolution of basal relationships (e.g. summary of phylogenies in Thayer,

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2005). To some extent, unresolved basal nodes of the rove beetle phylogeny were caused by a lack of data about stem lineages, primarily because staphylinid fossils have been rather neglected. Recently, however, we are witnessing a spike of interest in the study of Mesozoic rove beetle fossils. For example, several new taxa were described in Clarke and Chatzimanolis (2009), Yue et al. (2009, 2010a,b, 2011), Chatzimanolis et al. (2010b, 2012), Cai et al. (2011), Thayer et al. (2012) and Schomann and Solodovnikov (2012); and even more fossil material of rove beetles in collections is in the process of examination.

In particular, an impressive collection of exceptionally well preserved rove beetle rock fossils from the Yixian Formation has been assembled at the Capital Normal University in Beijing, China. The precise age of the Yixian Formation is subject to continuing debate, but its Early Cretaceous dating of 125–121 Ma (Swisher et al., 1999; Li et al., 2001; Pang et al., 2002), as opposed to Late Jurassic (Ren et al., 1997; Zheng et al., 2003), or Jurassic/Cretaceous boundary (Wang et al., 2004), seems more plausible (Zhou et al., 2003). The Yixian Formation is very well known in paleontology as a source of dinosaur (Chen et al., 1998), mammal (Hu et al., 1997; Luo et al., 2007), angiosperm plant (Sun et al., 1998) and insect (Ren, 1998) taxa that have contributed much to understanding the evolution of their respective groups.

Since several studies implicitly or explicitly suggested that the Jurassic was a period of diversification of Staphylinidae into subfamilies (Tikhomirova, 1968, 1973, 1980; Ryvkin, 1985, 1988; Clarke and Chatzimanolis, 2009; Grebennikov and Newton, 2009; Yue et al., 2011; Schomann and Solodovnikov, 2012; Thayer et al., 2012), it is logical to assume that key diversification events among and within various rove beetle tribes could have happened during the Cretaceous. Therefore Cretaceous fossils from the Yixian formation show great promise for tracing the early evolution of modern subfamilies and tribes of Staphylinidae. Furthermore, unlike other Late Jurassic or Early Cretaceous rock fossils of Staphylinidae, those of the Yixian Formation are promising because of their exceptional preservation due to very fine grains of the rock matrix (Zhou et al., 2003; Fürsich et al., 2007). Some of the earlier examined rove beetle fossils from the Yixian Formation (e.g. *Megolisthaerus chinensis* Solodovnikov and Yue in Yue et al., 2010b) indicate rather peculiar stem lineages that do not fit the traditional classification of the family that has emerged from the study of crown groups only. The limited utility of the existing classification creates difficulties for the placement of Mezosoic fossils and calls for their simultaneous phylogenetic study with recent taxa. Such an approach has been implemented for many animal groups that have a sound fossil record, that are better explored taxonomically, and that are not so species-rich (Cobbett et al., 2007). For phylogenetic studies of Staphylinidae, fossils have been limited to narrative discussion and such combined analyses have not been attempted (except for Scydmaeninae from Baltic Amber (Jaoszyński, 2012).

Given the above, we have begun a rigorous phylogenetic study of the rove beetle fossils from the Yixian Formation, with a focus on subfamily Staphylininae. Over the past decade, phylogenetic analyses of extant taxa (Assing, 2000; Solodovnikov and Newton, 2005; Solodovnikov, 2006; Solodovnikov and Schomann, 2009; Chatzimanolis et al., 2010a; Clarke, 2011; Li and Zhou, 2011; Pietrykowska-Tudruj et al., 2011) have generated detailed character systems and recovered some phylogenetic patterns for this subfamily. They have also posed clear questions that may be answered by fossils. By selecting Staphylininae as the target group of the analysis, we inevitably had to include at least its sister group Paederinae, and the subfamily Pseudopsinae as a sister group to Staphylininae + Paederinae (Grebennikov and Newton, 2009). This broader scope is essential because it is impossible to assign many of the fossils from the Yixian Formation to subfamily even though they resemble Staphylininae, Paederinae, or a similar unknown lineage. To provide a clear formulation of our research questions, goals, methodology, and the context for our results, this paper includes an extended introduction that summarizes all published data on the basal phylogeny and Mezosoic fossil record of the subfamilies Staphylininae, Paederinae and allied groups.

Materials and methods

Examination and deposition of fossils. All rock fossils from the Yixian Formation were examined dry or moistened with 70% alcohol, using Leica MZ12.5 and Leica M205C dissecting microscopes.

Photos of fossils were taken with a Leica DFC 420 camera attached to a Leica MZ16A microscope (lighting by Leica CLS 150XE) with the help of Leica Application Suite (Leica Microsystems, 2003–2007). Original coloured, high-resolution and larger-size photos can be accessed online in the Supporting information. Smaller black-and-white versions of the photos are published here as Figs 9–11, 15–17, 20–22, 26–28, 32–34, 38–40, 44, 45, 47, 49–51 and 55–57.

Drawings in Figs 12–14, 18, 19, 23–25, 29–31, 35–37, 41–43, 46, 48, 52–54, 58 and 59 were made with pencil as follows. Main proportions were sketched by tracing on a sheet of paper placed over a photograph of a specimen. Then details were illustrated freehand by observing a specimen under a dissecting microscope. In most cases only one drawing was made per species, showing the beetle from its best preserved side (dorsal, ventral, lateral, or transitional) and with structures from the opposite side (facing away from the observer) drawn in dotted lines. Rarely, when many structures from the opposite sides were preserved in a specimen, so that a combined drawing would have been too complicated, two opposite views have been drawn (Figs 23, 24; 29, 30; 41, 42; 52, 53).

Measurements of the fossils (mm) were taken with a calibrated ocular micrometer. Unless stated otherwise in the respective descriptions, measurements were taken and abbreviated as follows: ATL, anterior tibia length; AL, antenna length (from apex of segment XI to base of segment I when antenna is outstretched); EL, elytral length (from basal margin usually clear at base of the shoulder to the most distal margin of elytra); EW, elytral width (combined width of both elytra when they are closed along suture); HL, head length (from base of labrum to neck constriction if such is developed, or to the posterior margin of head capsule); HW, head width (maximal, including eyes); MTL, middle tibia length; PL, pronotum length (along its median axis); PTL, posterior tibia length; PW, pronotum width (maximal); TBL, total body length (usually measured from apex of mandibles, or from apical margin of mandibles when they are closed, to the apex of abdomen, as if the beetle body is positioned straight). Because of the variable position of fossilized beetles and incomplete preservation of their body parts, it was impossible to standardize measurements as usually done in descriptions of recent species. For that reason, some measurements have been omitted. For the judgment of some measurements and proportions, users are encouraged to use illustrations provided with the scale bars.

All fossil specimens from the Yixian Formation studied here are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University in Beijing, China (CNUB). All come from two localities in China: most are from Huangbanjigou, Chaomidian Village, Beipiao City in Liaoning Province; but five species (*Thayeralinus glandulifer* sp. n., *T. giganteus* sp. n., *Paleowinus fossilis* sp. n., *P. mirabilis* sp. n. and *P. chinensis* sp. n.) are from Liutiaogou Village of Ningcheng County of Inner Mongolia. Specimens of *Apticax* are kept at the Staatliches Museum für Naturkunde, Stuttgart, Germany.

Examination and deposition of extant taxa. Recent species were examined under the same dissecting microscopes as fossils. They were macerated in 10% KOH, rinsed in distilled water, disarticulated when necessary, and stored/examined in the small Petri dishes with glycerine. All specimens are kept at the Zoological Museum in Copenhagen, Denmark (ZMUC).

Data matrix construction. The character matrix (file Staph_fossils_matrix.nex, Data S1 in Supporting information) was constructed with Mesquite ver. 2.71 (Maddison and Maddison, 2009). Because some phylogenetic software counts characters starting from 0, our character list (Table 1) starts from character 0. This matrix is an extension of the data set in Solodovnikov and Newton (2005). It includes 70 characters (numbered 0–69) scored for 53 taxa.

All recent and most fossil species were scored by examination of actual specimens. When scoring poorly preserved characters from fossils was subject to ambiguous interpretation, we favoured a missing data entry over a potentially incorrect homology assessment. Unknown character states were coded with "?", inapplicable states with "–". Five fossil species (*Cretoquedius oculatus* Ryvkin, 1988; *Thayeralinus fraternus* (Zhang, Wang et Xu, 1992), *Mesostaphylinus laiyangensis* Zhang, 1988; *Sulcelytrinus antiquus* Tikhomirova, 1968 and *Tunicopterus sigara* Tikhomirova, 1968), for which the corresponding specimens were not available for study, were scored from their published descriptions.

Phylogenetic methods. Although the probabalistic methods maximum likelihood (ML) and Bayesian inference (BI) prevail in modern, molecular-based phylogenetic analyses, the maximum parsimony (MP) criterion is still a predominant method for analysis of morphology. Lewis (2001) introduced the one-parameter Mk model for morphological estimation under the likelihood criterion. The Mk model was derived from the JC69 model used in molecular analyses, and unlike previously developed probabalistic models simulating parsimony, it assumes the same branch length for all characters (Lewis, 2001). The likelihood-based methods are fundamentally different from parsimony in implying the amount of change along branches, and thus take into account autapomorphic characters that are uninformative in parsimony. Therefore morphological analysis within a likelihood framework may reveal interesting new phylogenetic patterns. Overall, both parsimony and likelihood phylogenetic methods were shown to yield generally similar topologies in morphological analyses, even when fossils are included (Nylander et al., 2004; Müller and Reisz, 2006). Therefore, to test the robustness of our results, we performed both types of analyses: under parsimony (MP) and likelihood criteria (BI and ML).

Maximum parsimony (MP). All parsimony analyses were conducted in TNT 1.1 (Goloboff et al., 2003) using the "traditional search" option to find most parsimonious trees (MPTs) under the following parameters: memory set to hold 1 000 000 trees; tree bisection–reconnection (TBR) branch-swapping algorithm with 10 000 replications saving 1000 trees per replicate; zero-length branches collapse after the search. All character states were treated as unordered and equally weighted. Separate analyses under implied weights of characters (Goloboff et al., 2003) were also conducted, using concavity factor gradually varying from 1 to 20. Branch support was calculated using Bremer (1994) and bootstrap support values (Felsenstein, 1985).

Maximum likelihood. The analyses were performed using Garli 2.0 (Zwickl, 2006) and raxmlGUI (Silvestro and Michalak, 2011) under the Mk model described above. For the above-mentioned reasons, autapomorphic characters were included in the analyses. Since Garli 2.0 does not implement the gamma distribution option for the Mk model, and raxmlGUI does, but requires a gamma distribution for ML estimation, we used both programs for testing the influence of the gamma distribution on our phylogenetic topology. This was done because previous studies (Nylander et al., 2004; Wiens et al., 2005; Müller and Reisz, 2006) showed that gamma distribution of rate variation across sites can alter topology and the likelihood score in morphological analyses. The ML analyses were applied only to two data sets: recent (R) taxa (ML/R analysis 6) and recent plus fossil (RF) taxa (exluding nine least-stable taxa, the ML/RF analysis 10), both rooted with *Oxytelus*.

The analyses with Garli were run with the following options: 20 independent ML runs for ML/R analysis 6 and 15 runs (to save computational time) for ML/RF analysis 10, using the automatic stopping option that terminates the search when the likelihood score remains constant for 10^6 consecutive generations. The analyses using raxmlGUI were performed with the multigamma option. ML/R analysis 6 was conducted using 500 independent searches, while for the larger data set of ML/RF analysis 10 we performed four different runs with 500 independent searches each. The nodal support was calculated using raxmlGUI via the rapid bootstrap algorithm with 1000 replicates (Stamatakis et al., 2008).

Bayesian inference. Bayesian analyses were conducted in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) using the Mk model and default settings for priors. As explained above, autapomorphic characters were included in the data set, and similarly to the ML, analyses were conducted with and without gamma distribution (six rate categories). All analyses used four chains and two runs of 5 000 000 generations each with a tree sampled every 1000th generation. The number of generations before stationarity was reached constituted 25%, which was disregarded as burn-in.

Character mapping. Character changes were mapped on the most parsimonious tree chosen to demonstrate the phylogenetic relationships using WinClada ver. 1.00.08 (Nixon, 2002) under ambiguous optimization.

Taxonomy versus phylogeny. The principles of phylogenetic systematics imply that, ideally, the composition of taxa must be equivalent to monophyletic clades of a phylogenetic tree, while their rank is fully consistent with the tree topology. In practice, fragmentarily preserved fossils sometimes forced us to depart from those principles in favour of practicality and stability of nomenclature. For example, contrary to the phylogenetic topology in Fig. 5, we did not erect new poorly characterized family-group taxa for some fossil species (e.g. genus *Apticax*, some species of *Mesostaphylinus*, genera *Paleothius*, *Cretoprosopus*, *Durothorax*, and some species of *Cretoquedius*), but left them *incertae sedis*. Also, for the time being, we preferred a seemingly polyphyletic genus *Cretoquedius* instead of erecting a few poorly defined genera. *Cretoquedius* may become a natural group or could be divided into better characterized taxa when additional specimens (or characters) are discovered. Subsequent splitting of potentially composite taxa seems more defensible than creating poorly defined genera and more names than necessary. For similar reasons, but given their peculiar phylogenetic position combined with very insufficient preservation, two species (Gen. 1 sp. and Gen. 2 sp.) are left unnamed. Each case of ambiguous systematic placement is discussed in detail under "Systematic palaeontology".

Phylogeny, evolution, and classification of the Staphylininae–Paederinae lineage: a review of published data

Sister-group relationships of Paederinae and Staphylininae. Sister-group relationships of Paederinae and Staphylininae were implied even in early classification systems (the latest examples being Crowson, 1955; Tikhomirova, 1973) and were sustained in more recent morphological studies and their synopses (Lawrence and Newton, 1995; Beutel and Molenda, 1997; Hansen, 1997; Assing, 2000; Solodovnikov and Newton, 2005). Molecular works, even though rare, are less consistent in this respect. While Ballard et al. (1998) supported morphological views, Caterino et al. (2005) and Hunt et al. (2007) did not place representatives of Paederinae and Staphylininae as sister clades. However, the latter two molecular phylogenies targeted basal relationships of Staphyliniformia or Coleoptera, respectively, and they displayed many other highly controversial groupings within Staphylinidae; most likely their results are artefacts of incomplete data sets.

Table 1
List of characters

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0 *Submentum*: (0) apparently glabrous; (1) with multiple long setae not differentiated into macrosetae and smaller setae; (2) with one-one to few pairs of macrosetae

1 *Antennal insertions*, *base of first antennomere*: (0) exposed; (1) concealed by a frontal projection

2 *Antennal insertions*, *distance between them*: (0) longer than distance from base of antenna to eye; (1) equal to or smaller than distance from base of antenna to eye

3 *Head capsule*, *development of neck constriction*: (0) without distinct neck constriction; at most head capsule slightly constricted at sides only; (1) with distinct neck constriction

4 *Frontoclypeal suture*: (0) present; (1) absent

5 *Nuchal ridge*: (0) absent; (1) present

6 *Ventral basal ridge*: (0) absent; (1) present, along considerable portion of postoccipital suture; (2) present, strongly projecting anteriad; (3) present, extending more or less parallel to ventral portion of postoccipital suture

7 *Postgenal ridge*: (0) absent; (1) present

8 *Postmandibular ridge*: (0) absent; (1) present but more or less short; (2) present, long

9 *Infraorbital ridge*: (0) absent; (1) present, long, extending at least along basal half of head capsule; (2) present but very short, developed only at base of head

10 *Labrum*, *shape*: (0) quadrate, entire; (1) quadrate to moderately transverse, possibly bilobed to some extent; (2) strongly transverse, possibly bilobed to some extent

11 *Labrum*, *transparent apical membrane*: (0) absent; (1) present

12 *Mandible molae*: (0) contiguous, very well developed and broad, with characteristic microstructure; (1) contiguous but consisting of narrow edge with microtrichia; (2) not contiguous, very weakly developed to absent

13 *Mandible prostheca*: (0) present as row of short setae attached to inner margin of mandible, without well developed supporting structure; (1) present with a more or less well developed lanceolate supporting structure

14 *Maxillary palps*, *apical palpomere*: (0) elongate and nearly or quite as wide as penultimate palpomere; (1) aciculate, less than half as wide as penultimate palpomere; (2) conical, sometimes can be maybe with truncate base, about half or less as wide as penultimate palpomere; (3) wide, apically wider than penultimate segment and usually truncate

15 *Maxillary palps*, *shape and setation of penultimate segment*: (0) gradually widened towards apex or cylindrical, with at most few macrosetae; (1) more or less inflated (with convex sides), heavily setose

16 *Ligula*: (0) bilobed, very wide and apically truncate; (1) bilobed, with large rounded lobes; (2) bilobed, with small rounded lobes; (3) small, entire (may be slightly notched at middle); (4) strongly reduced, indistinct

17 *Labial palps*, *apical palpomere*: (0) nearly or quite as wide as penultimate palpomere; (1) about half or less as wide as penultimate palpomere, more or less aciculate; (2) apically wider than penultimate segment

18 *Mentum*, *chaetotaxy*: (0) with one pair of macrosetae; (1) with two pairs of macrosetae; (2) with three pairs of macrosetae; (3) without distinct macrosetae

19 *Antesternal plates*: (0) absent; (1) present

20 *Antesternal plate(s)*, *state of development*: (0) present as pair of small, well separated sclerites; (1) present as pair of large contiguous plates or single large plate

21 *Pronotum*, *superior marginal line of pronotal hypomeron vs anterior angles of pronotum*: (0) marginal line (sometimes indistinct) developed through its whole length, not deflexed under anterior angle of pronotum; (1) marginal line developed through its whole length, deflexed under anterior angle of pronotum; (2) marginal line short, deflexed but not extend to anterior edge of pronotum

22 *Pronotum*, *superior marginal line vs inferior marginal line of hypomeron*: (0) inferior line shorter than superior line and not meeting with the latter (sometimes very obsolete, almost indistinct and tracked by the inferior margin of pronotal hypomeron only); (1) inferior line subcontiguous or fused to superior line posterior to anterior angles of pronotum

23 *Pronotum*, *front angles*: (0) not produced beyond (anterad of) anterior margin of prosternum; (1) produced beyond (anterad of) anterior margin of prosternum.

24 *Pronotal hypomeron*: (0) not inflexed (i.e. visible in lateral view of prothorax); (1) inflexed (i.e. not visible in lateral view of prothorax)

25 *Pronotal postcoxal process of hypomeron*: (0) well developed and sclerotized similarly to rest of hypomeron; (1) variously developed but weakly sclerotized, translucent, somewhat flexible; (2) absent; (3) caudal, postcoxal area of ventral part of prothorax entirely sclerotized

Note. The postcoxal process is often erroneously referred to as the epimere or proepimeron (Smetana and Davies, 2000); it is definitely not of pleural origin as those terms imply, but rather a part of the hypomeron (Hlavac, 1975; Naomi, 1987–1990, part V)

26 *Pronotosternal suture*: (0) well developed, clearly visible; (1) indistinct; prosternum fused with pronotum

Note. This is the “sternonotal suture” of Blackwelder (1936), but the “tergopleural suture” of Naomi (1987–1990)

27 *Prosternum*, *extent of longitudinal carina*: (0) along furcasternum only; (1) along furcasternum and at least part of basisternum; (2) along basisternum only; (3) carina absent

Note. The “basisternum” of Blackwelder (1936) is the “composite ventral plate” (basisternum + preepisternum)” of Naomi (1987–1990, part V)

28 *Prosternum*, *shape of longitudinal carina*: (0) carina, at least in its basal part, sharp, forming a well defined ridge; (1) carina more or less rounded, from obtuse ridge to smooth prominence of prosternum

29 *Prosternum*, *setation of basisternum*: (0) more or less even, without conspicuous macrosetae; (1) with one pair of macrosetae; (2) with two pairs of macrosetae; (3) glabrous

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Table 1
(*Continued*)

30	*Mesoventrite*, *setation*: (0) glabrous or with numerous more or less even setae, no macrosetae; (1) with group of a few macrosetae, sometimes combined with shorter general setation; macrosetae not in V- or U-shaped line; (2) with a few macrosetae in more or less V- or U-shaped line parallel to a carina; (3) with one pair of macrosetae
31	*Mesoventrite*, *medial carina*: (0) present in coxal acetabulum only, not on ventral surface; (1) present in coxal acetabulum and at least posterior (intercoxal) part of ventral surface of metaventrite; (2) absent *Note*. In *Tachinus*, a narrow intercoxal process of themesosternum conceals the knife-like medial acetabular part of the mesosternum, which is contiguous with the metasternum
32	*Mesoventrite*, *medial transverse carina*: (0) absent; (1) present, laterally intersecting or extending beyond mesoventral-pleural suture (when the latter is distinct); (2) present, laterally directed towards sternacostal carina but obsolete before reaching it *Note*. A carina of state 1 has apparently been misinterpreted as the posterior carina of the prepectus (Naomi, 1987–1990, part VI, fig. 4C), but in our examined Paederinae a normally delimited prepectus is also present
33	*Mesoventrite*, *position and shape of mesoventral-pleural suture (or its traces)*: (0) straight, transverse; (1) straight, oblique (i.e. medial end of suture situated anterior to its lateral end); (2) more or less curved so that medial part of suture is more longitudinal and lateral part more transverse; (3) mesoventral-pleural suture absent *Note*. The sutures are only vaguely indicated in *Nudobius*
34	*Mesoventrite*, *posterior carina of prepectus*: (0) straight or very gradually curved, parallel to anterior edge of mesosternum, not angulate; (1) distinctly angulate at middle, forming obtuse to sharp angle
35	*Mesoscutellum*: (0) with one transverse carina; (1) with two transverse carinae *Note*. The single carina, or the more posterior one of those taxa with two carinae, apparently corresponds to the "prescutoscutellar suture" of Blackwelder (1936, fig. 4C), and the more anterior of two carinae to the "prescutal suture" of the same author and figure, but Naomi (1987–1990, part VI) considered the first as a secondary ridge and the second (anterior) as a "prescutoscutal suture". In *Pseudopsis*, the single carina is strongly bicurved and possibly not homologous to the single straight carina of the other taxa
36	*Mesocoxal cavities*: (0) contiguous; (1) more or less widely separated by elevated part of metasternum; (2) narrowly separated by mesosternal intercoxal process
37	*Protibial ventral setae*: (0) denser than on meso- and metatibiae, but not formed into distinct transverse or oblique comblike rows (except a single row near tibial apex); (1) denser than on meso- and metatibiae, and formed into several to many transverse or oblique comblike rows
38	*Anterior tarsi*: (0) not distinctly wider than middle and posterior tarsi, usually without spatulate setae ventrally; (1) distinctly wider than middle and posterior tarsi, usually with spatulate adhesive setae ventrally
39	*Tarsal empodium*: (0) with one pair of setae; (1) glabrous
40	*Tarsal empodial setae*: (0) about as long as, or longer than claws; (1) much shorter (about half or less as long as) claws
41	*Hind coxal shape*: (0) wider than long, with laterodorsal portion widely exposed in ventral view; (1) about as long as wide or elongate, with laterodorsal portion moderately to scarcely exposed in ventral view; (2) about as long as wide or elongate, with wide lateroventral lobe concealing laterodorsal portion in ventral view
42	*Elytra*, *epipleural ridge*: (0) absent; (1) present
43	*Elytral epipleural ridge*: (0) nearly complete, extending from apex past humerus towards base; (1) incomplete, extending from apex towards humerus but not reaching humerus
44	*Elytral sub-basal ridge*: (0) immediately adjacent to elytral articulation, short, not extending laterally to humerus, or absent; (1) long, not adjacent to elytral articulation and extending from level of middle of scutellum to elytral humerus
45	*Wing venation*: (0) including completely separate MP3, MP4 and CuA veins; (1) with separate MP3, but MP4 and CuA largely or completely fused; (2) with single vein in this area probably representing fused MP4 and CuA *Note*. Venation terminology follows that of Kukalová-Peck and Lawrence (1993, fig. 46)
46	*Abdominal tergite III*, *transverse basal carinae*: (0) only anterior; (1) anterior and posterior
47	*Abdominal tergite IV*, *transverse basal carinae*: (0) only anterior; (1) anterior and posterior *Note to characters 47–51*. The presence of one (anterior) transverse basal carina ("transverse basal suture" of Naomi, 1987–1990, part IX) on each tergum seems to be a widespread and perhaps basal condition for staphylinids; this carina is usually closer to the base of the tergum than to the imbedded spiracles, and is usually continued on the adjacent paratergite. The second (posterior) carina, when there are two, is posterior to the above carina and not continued on the adjacent paratergite. When any of these carinae are not fully developed (i.e. interrupted or short, we call them incomplete
48	*Abdominal tergite V*, *transverse basal carinae*: (0) only anterior, complete; (1) anterior and posterior, two complete; (2) only anterior, incomplete
49	*Abdominal tergite VI*, *transverse basal carinae*: (0) only anterior, complete; (1) anterior and posterior, two complete; (2) only anterior, incomplete; (3) anterior complete, posterior incomplete
50	*Abdominal tergite VII*, *transverse basal carinae*: (0) only anterior, complete; (1) anterior and posterior, complete; (2) only anterior, incomplete
51	*Abdominal tergite VIII*, *transverse basal carinae*: (0) only anterior, complete; (1) only anterior, incomplete; (2) absent
52	*Prototergal glands*: (0) absent; (1) present *Note*. "Prototergal glands" is the term suggested for these paired structures on abdominal tergite I in the study by Quennedey et al. (2002). The distinctness and structure of the glands varies among the examined taxa, from vague depressions with different surface sculpture from the rest of the tergite in *Dinothenarus* to deep cavities with associated setae and glands

Table 1
(*Continued*)

53	*Abdominal segments III–VI, number of paratergites*: (0) each segment with one paratergite on each side; (1) each segment with two paratergites on each side
54	*Abdominal segment VII, number of paratergites*: (0) with one paratergite on each side; (1) with two paratergites on each side, meeting obliquely or transversely so that one is more anterior than the other; (2) no paratergites
55	*Abdominal intersegmental membranes*: (0) attached to apical margin of preceding segment; (1) attached somewhat anterad of apical margin of preceding segment so latter projects over base of membrane
56	*Abdominal intersegmental membranes between segments III and VII, pattern of minute sclerites*: (0) irregular or quadrangular, more or less rounded sclerites occupying < 70% of membrane surface; (1) rectangular sclerites occupying > 80% of membrane surface; (2) hexagonal sclerites occupying > 80% of membrane surface; (3) triangular or multiangular sclerites occupying > 70% of membrane surface
57	*Defensive (odoriferous) glands near abdominal apex*: (0) apparently absent; (1) present as paired eversible membranous gland reservoirs in the connecting membrane between terga VIII and IX (Dettner, 1993, fig. 2D1–4); (2) present as paired noneversible gland reservoirs opening at anterior margin of tergum IX (Herman, 1975, fig. 27); (3) present as unpaired noneversible gland reservoir opening near anus (Dettner, 1993, fig. 2A2); (4) present as paired noneversible gland reservoirs opening at lateral tergal sclerites IX *Note*. Problems associated with the detection of this character are discussed in notes to character 56 in Solodovnikov and Newton (2005: 409)
58	*Male sternum VIII, apex*: (0) medially straight to very slightly concave; (1) with single, variably developed median emargination; (2) with a pair of emarginations, medially produced between them; (3) with median process
59	*Male sternum IX, shape*: (0) more or less symmetrical; (1) basally weakly to strongly asymmetrical
60	*Male lateral tergal sclerites IX*: (0) dorsally fused in front of tergum X; (1) dorsally separated, distance between margins more or less gradually increasing posteriorly; (2) dorsally separated, but anteriorly more or less contiguous, margins more or less abruptly diverging posteriorly; (3) dorsally widely separated by tergum X
61	*Female lateral tergal sclerites IX*: (0) dorsally fused in front of tergum X; (1) dorsally separated, distance between margins more or less gradually increasing posteriorly; (2) dorsally separated, but anteriorly more or less contiguous, margins more or less abruptly diverging posteriorly; (3) dorsally widely separated
62	*Male and female tergal sclerites IX, shape*: (0) produced but more or less flat, apically obtuse to sharp, sometimes with spine-like process; (1) produced into more or less inflated, apically sharp process; (2) produced into more or less inflated, apically obtuse or rounded process; (3) not produced into processes
63	*Female sternum IX, development of central sclerite*: (0) absent; (1) present
64	*Ovipositor*: (0) consisting of paired proximal and distal gonocoxites, usually also with styli; (1) consisting of paired gonocoxites only; (2) consisting of paired proximal gonocoxites and single distal gonocoxite (i.e. distal gonocoxites are fused to each other) *Note*. The stylus may be minute and, when apparently absent, may be fused to the distal gonocoxite; it is coded as present if there is a distinct membranous articulation between it and the distal gonocoxite. The coding for *Maorothius* is taken from Assing (2000), who indicates a single pair of gonocoxites (our state 1) for most species, but these are partially or entirely fused in a few species, including *M. brouni* (the species studied here). Similarly, Herman (1975) describes wide variation for *Pseudopsis*—not all have fused distal gonocoxites and some (even with fused distal gonocoxites) have styli (states 0, 3 plus styli)
65	*Aedeagus, parameres*: (0) paired, well separated; (1) paired, contiguous; (2) fused into a single lobe; (3) absent
66	*Aedeagus, sensory peg setae of the paramere(s)*: (0) absent; (1) present *Note*. In the examined species of *Erichsonius* (*E. patella*) the peg setae are sharp-tipped and unpigmented, but more typical peg setae (black, round-tipped) are found in other species of the genus (Coiffait, 1974)
67	*Aedeagus, basal part of median lobe*: (0) bulbus more or less symmetrical; (1) bulbus more or less asymmetrical
68	*Aedeagus, position of parameral side in repose in abdomen*: (0) dorsal; (1) ventral; (2) left lateral; (3) right lateral
69	*Abdominal segment II*: (0) well developed (sternite II similar to sternite III in shape; tergite II not distinctly reduced); (1) reduced (tergite II reduced, its shape different from shape of tergite III; sternite II absent)

Staphylininae. The latest morphology-based study of the subject (Solodovnikov and Newton, 2005) divided the subfamily into two major clades: [Platyprosopini (Diochini (Maorothiini (Othiini + Xantholinini)))] and [Arrowinini + Staphylinini], the "Xantholinine-" and "Staphylinine-" lineages, respectively. Although disagreeing with earlier views (Tikhomirova, 1973; Assing, 2000) regarding placement of the odd tribes Diochini or Platyprosopini, this topology was otherwise largely consistent with them. The only available molecular phylogeny involving these relationships (Chatzimanolis et al., 2010a) displayed stronger disagreements with the morphology-based schemes and with traditional classification. For example, in Chatzimanolis et al. (2010a), the clade (Othiini + Xantholinini) was nested within Staphylinini. However, this study targeted resolution within tribe Staphylinini, and therefore, the basal relationships recovered within the subfamily should be taken with caution.

Within the "Xantholinine-lineage" [Platyprosopini (Diochini (Maorothiini (Othiini + Xantholinini)))], all tribes except Xantholinini are relatively species-poor or at most moderately diverse, and geographically more or less restricted (the New Zealand endemic Maorothiini, the mostly Holarctic Othiinini, the primarily pantropical Diochini). The globally distributed, more diverse and species-rich (120 genera, 1734 species; here and below all numbers of genera and species for various higher taxa are kindly provided by A. Newton) tribe Xantholinini has never been the subject of a phylogenetic study at the intra-tribal level.

The two tribes of the "Staphylinine-lineage" are also very unequal in species diversity and geographical distribution. While Staphylinini (211 genera, 5725 species worldwide) is among the largest tribes of rove beetles, Arrowinini comprises a single genus with only four species confined to South Africa (Solodovnikov and Newton, 2005). The hyperdiverse tribe Staphylinini was phylogenetically explored in some recent papers. Of these, with minor disagreements among each other, the morphology-based (Solodovnikov, 2006; Solodovnikov and Schomann, 2009) and molecular-based (Chatzimanolis et al., 2010a) phylogenies reveal the following pattern. A few genera such as *Afroquedius* Solodovnikov, 2006; *Astrapeus* Gravenhorst, 1802, *Parisanopus* Brèthes, 1900, and *Valdiviodes* Smetana, 1981 form basal lineages of the tribe, all species-poor and narrowly distributed in scattered regions around the globe. After they branched off, the main stock of Staphylinini evolved into two large clades comprising subtribes Quediina and Amblyopinina (both subtribes in the new senses of Solodovnikov, 2012), and a very species-rich clade "Staphylinini propria" (defined in Chatzimanolis et al., 2010a). While Quediina (14 genera, 1094 species) is confined primarily to the northern temperate forests of the world, and Amblyopinina (19 genera, 260 species) to their southern temperate counterparts, both groups are notably lacking in the (sub)tropical latitudes, especially in the entire region of Sub-Saharan Africa (Solodovnikov and Schomann, 2009).

"Staphylinini propria", the most species-rich and ecologically diverse lineage of Staphylinini, consists of the subtribes Anisolinina, Staphylinina, Philonthina and Xanthopygina. "Staphylinini propria"as a whole is a globally distributed lineage that is, however, markedly depauperate in the temperate part of South America and in Australia, and nearly absent from New Zealand.

The monobasic subtribe Hyptiomina includes the primarily Neotropical, morphologically highly specialized subcortical genus *Holisus*. Morphology- and DNA-based phylogenetic analyses yield strongly conflicting results regarding its sister-group relationships within Staphylinini. Solodovnikov and Schomann (2009) and Li and Zhou (2011) placed it nested within the subtribe Philonthina, while Chatzimanolis et al. (2010a) grouped it with the subtribe Tanygnathinina.

Paederinae. In contrast to Staphylininae, a subfamily-wide phylogenetic analysis of Paederinae has never been conducted. Conventionally, Paederinae is divided into two tribes, Paederini and Pinophilini (Newton and Thayer, 2005). Pinophilini is a rather specialized, species-rich (27 genera, 1122 species), more or less homogeneous and mostly pan(sub)tropical group that is divided into two subtribes, while Paederini is a larger, globally distributed and phylogenetically much more diverse lineage (195 genera, 5365 species), that is conventionally divided into several subtribes (Newton and Thayer, 2005; Bouchard et al., 2011). Some authors (Crowson, 1955) suggested that ancestral Paederinae looked somewhat like Pinophilini or the genus *Achenium* (now in the subtribe Lathrobiina). Coiffait (1972), on the contrary, considered Pinophilini as a more derived lineage within Paederinae. According to Newton (1985), a group of genera (*Dicax* group) placed in Cryptobiina (as defined in Herman, 1981) could be a rather basal lineage of Paederinae. Although there are phylogenies for some subtribes of Paederinae (Herman, 1970, 1981, 1991, 2010), the subfamily as a whole requires modern phylogenetic study.

Mesozoic fossil record of the Staphylininae–Paederinae lineage: a review of published data

The described fossil record of Staphylinidae summarized in Herman (2001), EDNA database (EDNA, 2011), Ponomarenko and Kirejtshuk (2011), Chatzimanolis and Engel (2011, Baltic Amber only) and Chatzimanolis et al. (2012) includes 87 genera and 302 species. Here, without attempting a detailed overview of the entire staphylinid fossil record, we survey all published data on Mesozoic rove beetle fossils with particular focus on species that were (or could be) identified as Staphylininae, Paederinae, or allied lineages. The review covers the period from 230 to 65 Mya, i.e. from the Late Triassic (where the putative earliest rove beetle belongs) to the end of the Cretaceous. The Cenozoic fossil record of Staphylininae and Paederinae is not considered in this review because it has a more modern aspect and is less relevant for the study of fossils of the Yixian Formation.

The oldest rove beetle is *Leehermania prorova* Chatzimanolis, Grimaldi et Engel, 2012 from the Late Triassic of Virginia, dated approximately 230–220 Ma (Grimaldi and Engel, 2005; Chatzimanolis et al. 2012). That species has no resemblance to either Staphylininae or Paederinae and, as hypothesized by Chatzimanolis et al. (2012) is affiliated with the tachyporine group of subfamilies. After a period without any fossil record, the mid- to late-Jurassic period (*ca.* 180–150 Ma) has yielded a diverse assemblage of more than two dozen named extinct genera of Staphylinidae, almost all of them placed in, or resembling, members of the subfamilies Omaliinae, Tachyporinae, Oxytelinae, Trigonurinae, Olisthaerinae and Piestinae (Tikhomirova, 1968; Ryvkin, 1985). Only two of these can be associated with the Staphylininae–Paederinae lineage: *Sulcelytrinus antiquus* Tichomirova, 1968 and *Tunicopterus sigara* Tichomirova, 1968, both described from the Upper Jurassic locality at Karatau, Kazakhstan (Tikhomirova, 1968). Although neither *Sulcelytrinus* nor *Tunicopterus* was placed into any of the subfamilies of Staphylinidae, Tikhomirova (1968) noted some resemblance of *Sulcelytrinus antiquus* to recent members of Staphylininae, while she suggested *Tunicopterus sigara* was somewhat similar to modern members of the subfamilies Paederinae and Staphylininae.

From the Cretaceous period, we know five described species that were, or can be, assigned to the Staphylininae–Paederinae lineage with varying levels of confidence. Two species, *Mesostaphylinus laiyangensis* Zhang, 1988 and *M. fraternus* Zhang, Wang et Xu, 1992, were described from the Laiyang Formation of Shandong Province in China (Zhang, 1988; Zhang et al., 1992). Age estimates for the Laiyang Formation range from the Late Jurassic (Zhang, 1988) to the Early Cretaceous (Liu, 1990; Yu, 1990; Grimaldi and Engel, 2005), the latter now accepted as more plausible (Jarzembowski and Mostovski, 2000). The original descriptions of *Mesostaphylinus laiyangensis* and *M. fraternus* are of very poor quality, and their authors did not express any hypotheses about the systematic position of these taxa. Based on the habitus and some characters extracted from the mentioned publications (Zhang, 1988; Zhang et al., 1992), it can be suggested that *M. laiyangensis* belongs to Paederinae and *M. fraternus* to Staphylininae.

Recently, Schomann and Solodovnikov (2012) described the new genus *Apticax* with two species from the Early Cretaceous Crato Formation in Brazil that, although resembling Paederinae in some characters, were classified as *incertae sedis* within Staphylinidae due to a lack of convincing data for a more exact placement.

After no fossil record for our target lineages through much of the Cretaceous, *Cretoquedius oculatus* Ryvkin, 1988 was described from a locality in north-eastern Russia dated as Cenomanian (Upper Cretaceous) and placed in the subtribe Quediina of the tribe Staphylinini (Ryvkin, 1988). *Cretoquedius oculatus* is until now the earliest and the only definitive member of the subfamily Staphylininae among Cretaceous fossils.

Two species of the genus *Laostaphylinus* Zhang, 1988 described from the Laiyang Formation of Shandong Province in China (Zhang, 1988) without assignment to a subfamily, as judged from their descriptions, do not belong to the "Staphylininae–Paederinae lineage". Some undescribed rove beetle specimens (or misidentified as such) from the Early Cretaceous Crato Formation in Brazil were discussed by Schomann and Solodovnikov (2012).

In summary, the hitherto described Mesozoic fossil record of our target lineage of Staphylinidae is very poor and hardly informative for phylogenetic purposes. Most of the known fossil species are from Asia, two from South America. With the exception of *Cretoquedius oculatus*, they were not assigned to subfamilies. However, a wealth of previously undescribed material promises to provide new insights into the evolution of the Staphylininae–Paederinae lineage.

Interestingly, the oldest fossils clearly identified as Paederinae were described from Baltic amber (Paśnik and Kubisz, 2002; Eocene, mid-Tertiary) and are much younger than the oldest definitive Staphylininae from the Upper Cretaceous. Assuming these are sister subfamilies, such an age discrepancy in known fossils is noteworthy.

Finally, other useful reviews of the Mesozoic fossil record of different lineages of Staphylinidae were recently published by Clarke and Chatzimanolis (2009), Grebennikov and Newton (2009), Chatzimanolis et al. (2010a), Cai et al. (2011), Schomann and Solodovnikov (2012), Thayer et al. (2012) and Chatzimanolis et al. (2012).

Evolution of the Staphylininae–Paederinae lineage: hypotheses to test with fossils

Our primary goal in the analysis of fossil species from the Yixian Formation is to resolve their systematic position. However, reciprocally, we also aim to improve the phylogeny of our entire target group as previously inferred from the study of extant taxa only. To clarify this reciprocal aspect, we summarize some current open questions within the phylogenetics of the Staphylininae–Paederinae lineage in the form of predictions that should be either corroborated or rejected by the Early Cretaceous fossils. Also, we explain the ways in which the study of fossils can test and improve a phylogeny.

Firstly, a simultaneous phylogenetic analysis of recent and fossil taxa is a direct test of a given phylogenetic topology obtained from the study of recent taxa only. The latter, if correct, should hold with the addition of fossils. Secondly, in the case of several alternative topologies, we may expect that those with older fossils branching off from more basal nodes and younger fossils stemming from more terminal nodes are most plausible. Finally, since evolutionary events are certainly largely triggered by global environmental processes such as plate tectonics, climate change, catastrophic impacts, co-evolution with other radiations, etc., a plausible phylogeny should be consistent with the timing of those events when placed on a time scale using fossils. For an old, diverse, and global group such as Staphylinidae, and for its Staphylininae–Paederinae lineage, possible congruence with several paleoenvironmental events could be explored.

Data on the ages of other rove beetle subfamilies more or less related to Staphylininae and Paederinae (Clarke and Chatzimanolis, 2009; Grebennikov and Newton, 2009; Yue et al., 2011; Schomann and Solodovnikov, 2012) suggest that by the Early Cretaceous, the Staphylininae–Paederinae lineage could have existed already. Therefore it is likely that both subfamilies would be present in the sample from the Yixian

Formation. Assuming that basal relationships within the subfamily Staphylininae inferred from the study of recent lineages are correct, the tribes Arrowinini and Platyprosopini must be older than some terminal lineages of the tribe Staphylinini, while the tribes Maorothiini and Diochini must be older than the tribe Xantholinini. Similarly, assuming that the currently hypothesized phylogeny of Staphylinini is accurate, the isolated basal genera of that tribe must be older than lineages within the more terminal clade ''Staphylinini propria''. Therefore taxa of these older clades are more likely to be found in our sample of fossils.

Additional hypotheses to test derive from biogeographical patterns of the phylogeny of Staphylinini (Solodovnikov and Schomann, 2009; Chatzimanolis et al., 2010a). The narrow distributions of basal Staphylinini genera that are scattered around the world are simplest to explain as relicts from a formerly broad Pangean distribution of their common ancestor. The fact that the north temperate Quediina are confined almost exclusively to the Holarctic region, while the south temperate Amblyopinina are restricted mostly to southern South America, Australia and the adjacent part of New Guinea, as well as New Zealand and New Caledonia, is noteworthy. Whether Quediina and Amblyopinina are sister groups, or are separated from each other by some nodes, remains unclear. However, their distributions and more or less close affiliation to each other allow an assumption that divergence of these north (Quediina) and south (Amblyopinina) temperate clades could be associated with the fragmentation of Pangea into Laurasia and Gondwana. Based on sister-group relationships and distribution of the ''Staphylinini propria'' that are predominant in Eurasia, North, Central and tropical South America, abundant in Africa, but extremely poorly represented in the south temperate areas, one can suggest that the lineage originated in Laurasia sometime when it was already well separated from Gondwana. If the phylogeny of Staphylinini as we know it now is an accurate hypothesis of evolution, and the above assumptions about divergence times of clades within Staphylinini are correct, fossils of the Yixian Formation may contain basal Pangean ''Quediina-like'' genera and basal Laurasian Quediina, but not Gondwanan Amblyopinina. Also, it is unlikely that these fossils will represent terminal clades of the ''Staphylinini propria''. Therefore fossils from the Yixian Formation are of such an age that they have potential to test these these predictions.

Phylogenetic analysis

Characters. The character list for the data set is presented in Table 1.

Taxon sample and outgroup. By visual examination of all rove beetle specimens from the Yixian Formation, we selected those that looked similar to modern Staphylininae, Paederinae, or closely related lineages. Specimens identified as, or resembling, any lineage far outside the core of the Staphylininae group of subfamilies (the clade (Pseudopsinae (Staphylininae + Paederinae)) after Grebennikov and Newton, 2009) were excluded from further consideration within this study. After identification of the selected fossils with varying degrees of confidence as members of Staphylininae, Paederinae, either of those, or some undetected related lineage, we sampled all main extant lineages of these two subfamilies for the data matrix. Only one extant member of Pseudopsinae (sister group to Staphylininae + Paederinae) was added since none of the fossils resembled that subfamily.

The genera *Tachinus* (Tachyporinae) and *Oxytelus* (Oxytelinae) were chosen as candidates for outgroup taxa, as both are outside the Staphylininae-group of subfamilies. To define which of these would perform better in the more complex analyses with fossils (RF analyses; and thus missing data), we first ran two parsimony analyses with the subsets of our data matrix comprising only recent taxa (R analyses, specifically MP/R analyses 1 and 2; Table 2). Analysis MP/R 1 included both *Tachinus* (root) and *Oxytelus*. Analysis 2 excluded *Tachinus* and was rooted with *Oxytelus*. Analysis MP/R 1 yielded nine MPTs ($L = 265$), while analysis MP/R 2 yielded one MPT ($L = 249$; Fig. 6). The strict consensus of the MPTs of analysis MP/R 1 and the MPT from analysis MP/R 2 had fully congruent topologies. Next, we performed MP analyses of our entire matrix (recent + fossil taxa, MP/RF) with the same alternative outgroup/rooting options: MP/RF analyses 3 (rooted with *Tachinus*) and 4 (without *Tachinus*, rooted with *Oxytelus*), which resulted in 385 500 shortest trees ($L = 288$) and 3890 shortest trees ($L = 272$), respectively. As the analyses that included *Tachinus* as an outgroup (MP/R analysis 1 and MP/RF analysis 3) found far more MPTs compared with those that excluded it (MP/R analysis 2 and MP/RF analysis 4), *Oxytelus* was selected as the outgroup and *Tachinus* was omitted from further analyses.

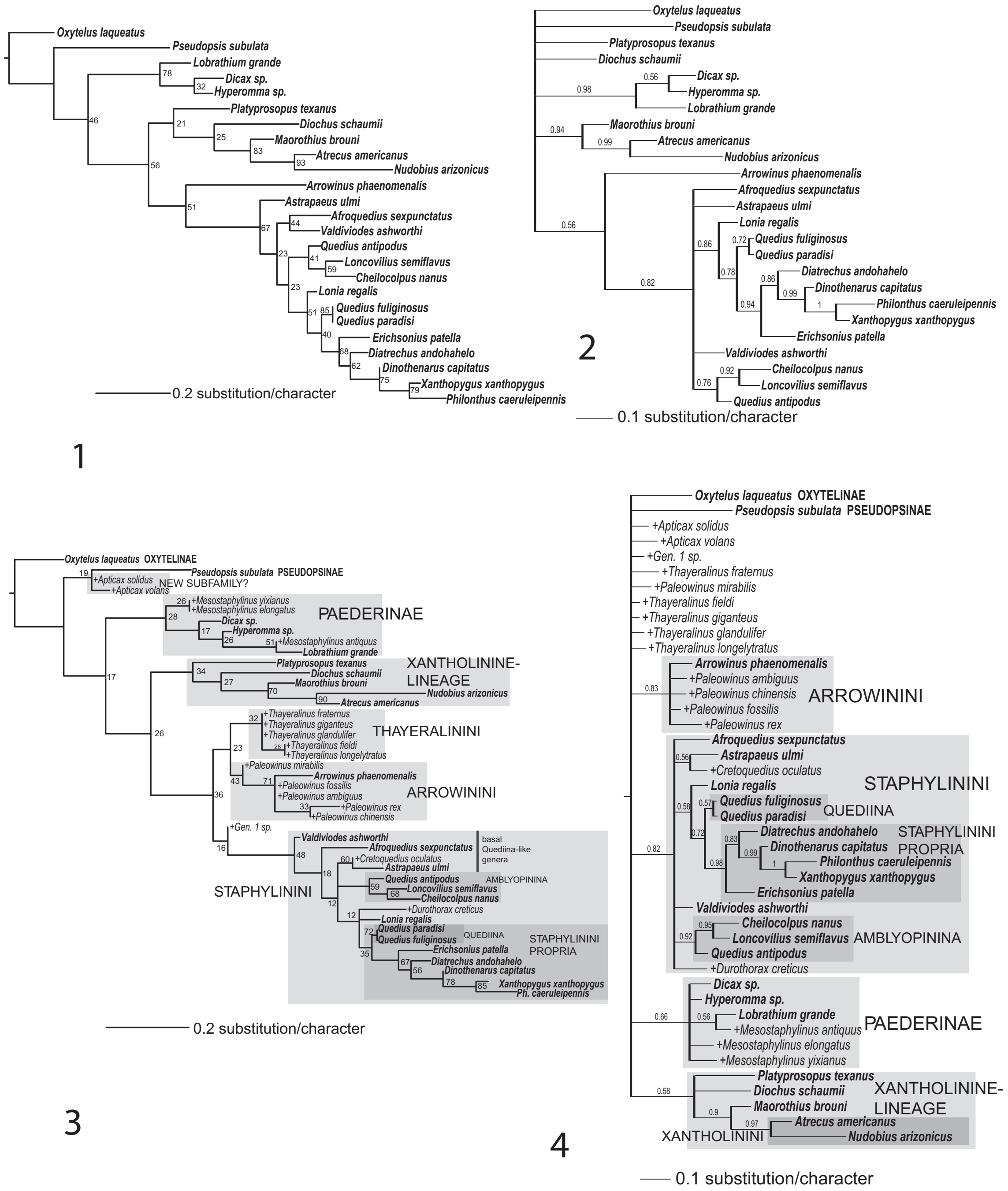
Taxa with missing characters: leaf stability index. The datamatrix (file Staph_fossils_matrix.nex, Data S1) includes 37% missing data, non-uniformly distributed among fossil taxa because of varying degrees of specimen completeness. Although missing data are not considered a direct threat to phylogenetic accuracy (Wiens, 1998, 2003a,b, 2005, 2006; Kearney, 2002; Kearney and Clark, 2003; Cobbett et al., 2007), their impact depends on their distribution and quality of other data with which they interact, obscuring the phylogenetic signal of a data set in some situations

(Gauthier et al., 1988). For example, although MP/RF analysis 4 (−*Tachinus*, +*Oxytelus* as outgroup) gave fewer MPTs than MP/RF analysis 3 (+*Tachinus* as outgroup), the number of trees was still rather high and led to a very poorly resolved consensus. We assumed that this was largely a result of missing entries ("?") in the data set, because MP/R analyses 1 and 2 (only recent taxa, naturally without missing data) yielded either one or only a few MPTs, respectively. Therefore we excluded the three least-preserved fossil taxa (*Sulcelytrinus antiquus*, *Tunicopterus sigara* and *Mesostaphylinus laiyangensis*, each having only two to six characters available from their descriptions, out of 70 in the data matrix) and performed a parsimony analysis of the remaining fossil and recent taxa (MP/RF analysis 5). It resulted in 300 MPTs ($L = 270$; the majority rule consensus shown in Fig. 5) and indicated that the elimination of taxa with particularly large numbers of missing characters significantly improved resolution of the phylogenetic search.

However, the number of MPTs was still high in MP/RF analysis five relative to the analysis of recent taxa only, with a poorly resolved strict consensus as a result. Since not only the relative amount of missing data, but also (if not mostly) their combination with the existing characters, may cause undesired impact, the further arbitrary elimination of any taxon based on the next greatest number of missing characters alone was not a solution. We applied the leaf stability index (Thorley and Wilkinson, 1999; Thorley and Page, 2000) to determine which of the taxa were phylogenetically most unstable and thus could be excluded from the target analysis. We calculated the leaf stability indexes for all taxa across 300 trees from MP/RF analysis five using Phyutility 2.2 (Smith and Dunn, 2008). The obtained indices (Table S1 in Supporting information) varied from 0.62606383 in *Cretoprosopus problematicus* indicating the lowest stability, to 0.999113475 in seven taxa (including some fossils) indicating the highest stability. Within that gradient, *Cretoprosopus problematicus* sp.n., *Paleothius gracilis* sp.n., Gen. 2 sp., *C. dorsalis* sp.n., *C. distinctus* sp.n. and *C. infractus* sp.n. (all fossils) had an index lower than the lowest index displayed by an extant taxon (*Astrapaeus ulmi* (Rossi, 1790), naturally without missing data, index 0.95) and were excluded from the final taxon sample. The parsimony analysis of this truncated data set (MP/RF analysis 8) resulted in eight MPTs ($L = 265$). The analysis of this data set under implied weighting parsimony (MPi/RF analysis 9) yielded four MPTs of the same length as the MPTs of the unweighted analysis, when k varied from 6 to 20. This improved resolution indicated that an optimal matrix was reached, at least as far as maximum parsimony analyses were concerned. To make the results of the ML and BI analyses fully comparable with MP, we used the same optimal taxon sampling for analyses 10–11 (Table 2) as for analyses 8–9.

Alternative analytical methods and phylogenetic signal. The results of the MP analyses of recent taxa alone (MP/R analysis 2, Fig. 6), as well as recent and fossils together (MP/RF analyses 5, 8 and 9; Figs 5, 7 and 8) are fully consistent with previously published morphology-based phylogenetic work on Staphylininae (Solodovnikov and Newton, 2005; Solodovnikov, 2006; Solodovnikov and Schomann, 2009; Li and Zhou, 2011). This is not surprising, at least for the MP/R analyses, since the character systems and taxa used here are largely similar to those in previous work. However, the plausibility of our MP/RF results is further supported by congruence with model-based ML (Figs 1 and 3) and BI (Figs 2 and 4) analyses conducted here as exploratory. These analyses are considered in more detail below.

The ML analysis of recent taxa (ML/R analysis 6) using a gamma distribution parameter (in raxmlGUI, Fig. 1) resulted in the same topology as the corresponding MP tree (MP/R analysis 2, Fig. 6). The ML analysis of fossils and recent taxa (ML/RF analysis 10, Fig. 3) yielded a topology almost identical to the corresponding MP tree (MP/RF analysis 9; Figs 7 and 8). ML/RF analysis 10 differs from MP/RF analysis 9 only in the position of Gen. 1 sp. and *Durothorax creticus*. The same ML analyses without a gamma distribution parameter (in Garli) yielded trees that were generally congruent with the corresponding MP and ML with gamma distribution parameter (raxmlGUI) trees, but strongly conflicted concerning the rather terminal position of the Paederinae and Pseudopsinae, nested within the Staphylininae (Figs S1 and S2 in Supporting information, branches marked in red). Not only is this result inconsistent with earlier, well supported hypotheses, it places the Early Cretaceous fossil genus *Apticax* rather terminally on the phylogenetic tree. Although a terminal position of *Apticax* is not a decisive argument alone to favour the topology recovered under a gamma distribution, the combined evidence of previous studies recovering (1) the clade Pseudopsinae (Paederinae + Staphylininae), and (2) the basal position of *Apticax* within the Staphylininae and Paederinae complex (Schomann and Solodovnikov, 2012), makes a nested position of Pseudopsinae, Paederinae and *Apticax* within Staphylininae (Fig. S2) seem implausible. In accordance with previous studies (Nylander et al., 2004; Wiens et al., 2005; Müller and Reisz, 2006), this result indicates that a gamma distribution in morphological analyses alters tree topology and, at least in this case, improves it. However, we cannot directly compare the likelihood scores for the Mk and Mk + Γ models due to the fact that the calculation of phylogenies with and

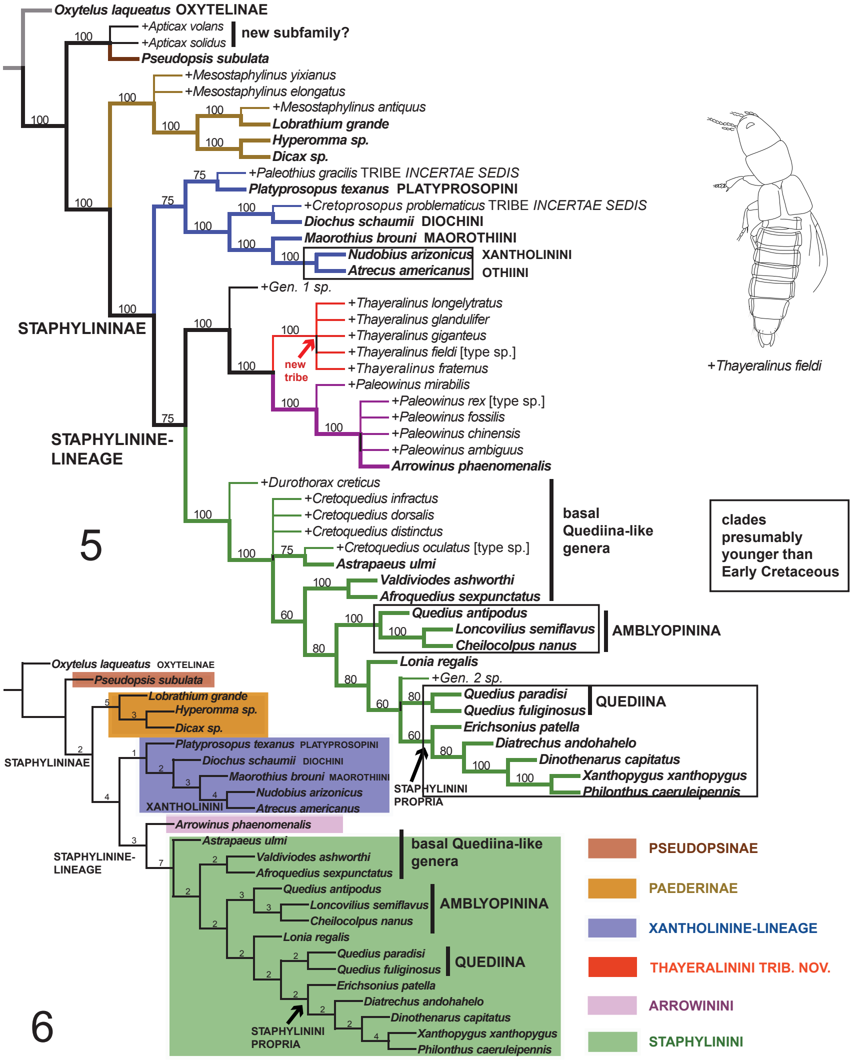


Figs 1–4. Results of model-based phylogenetic analyses: 1, analysis 1 [maximum likelihood (ML), performed in raxmlGUI, recent taxa only]; 2, analysis 7 [Bayesian inference (BI), recent taxa only]; 3, analysis 10 (ML, performed in raxmlGUI, recent and fossil taxa); 4, analysis 11 (BI, recent and fossil taxa). Numbers at nodes in Figs 2 and 4 indicate posterior probabilities. Numbers at nodes in Figs 1 and 3 indicate bootstrap support. Clades congruent among model-based (Figs 3 and 4) and parsimony (Fig. 5) analyses are marked by grey boxes in Figs 3 and 4 and annotated. In analyses 10 and 11 (Figs 3 and 4, respectively) only fossils with leaf stability index > 0.95 (Table S1) are included. In all figures, names of recent species are in bold font, names of fossil species in regular font, marked +.

without a gamma parameter was perfomed in different programs (Stamatakis, the RAxML manual).

The BI results are congruent with those of MP and ML; however, they are less resolved overall (Figs 2 and 4). The inclusion and exclusion of a gamma parameter did not alter topologies obtained by means of BI.

Phylogenetic results and systematics. The fact that all phylogenetic methods generated congruent results from



Figs 5 and 6. Results of maximum parsimony (MP) analyses: 5, majority rule consensus tree of analysis 5 (MP, recent and fossil taxa together); type species of non-monotypic newly described fossil genera are marked with "[type sp.]"; 6, single most parsimonious tree of analysis 2 (MP, only recent taxa). Names of recent species are in bold font; names of fossil species in regular font, marked +. Numbers at nodes in Fig. 5 indicate percentage of clade recovery, numbers at nodes in Fig. 6 indicate Bremer support. Analysis 5 (Fig. 5) includes all fossil taxa from the data matrix (Table S1) except three very data-poor species (*Sulcelytrinus antiquus*, *Tunicopterus sigara* and *Mesostaphylinus laiyangensis*) scored from their original descriptions.

our data set indicates a strong phylogenetic signal and supports the plausibility of our tree topology. For simplicity, hereafter we refer only to the MP results (Figs 5, 7 and 8), especially to the tree resulting from the most inclusive analysis (MP/RF analysis 5; Fig. 5). The first divergence divided the ingroup into a small clade comprising a polytomy of species of *Apticax* (described in Schomann and Solodovnikov, 2012 as Staphylinidae *incertae sedis*) and Pseudopsinae, as well as the large clade corresponding to the subfamilies Paederinae and Staphylininae. Phylogenetic study of fossils from the Yixian Formation corroborated the hitherto well established sister-group relationships of Pseudopsinae with the clade Paederinae + Staphylininae. Although poor preservation of the available specimens of *Apticax* and their partial resemblance to modern Paederinae did not allow unambiguous classification of this genus in Schomann and Solodovnikov (2012), the analysis here suggests that *Apticax* may represent a stem lineage of subfamilial rank. Based on the resolution of *Mesostaphylinus antiquus* within the Paederinae clade, it is considered a definitive fossil representative of the subfamily Paederinae, while *M. elongatus* and *M. yixianus* could also be interpreted as stem groups representing extinct lineages sister to the modern Paederinae. However, based on their morphology, and the stronger synapomorphy support for clade 1 than clade 2 (Fig. 7), it seems more reasonable for now to expand the concept of Paederinae to include *M. elongatus* and *M. yixianus*.

The subfamily Staphylininae (labelled as such in Fig. 5) is well supported as monophyletic in its current sense by several synapomorphies (clade 3 in Fig. 7), and includes most of the fossils studied here. It is divided into the previously recognized Xantholinine- (blue clade in Fig. 5) and Staphylinine- (labelled as such in Fig. 5) lineages. Two fossil species from the Yixian Formation, *Paleothius gracilis* and *Cretoprosopus problematicus*, are recovered as extinct members of the Xantholinine-lineage. Despite their sister relationships, which suggest a separate tribal rank for each, both new genera are classified as "*incertae sedis*" within Staphylininae because of the insufficient material available for their proper diagnosis.

The Staphylinine-lineage is divided into two clades: the tribe Staphylinini (green clade in Fig. 5) and its sister clade comprising Gen. 1 sp., together with tribes Thayeralinini (trib. n., red clade in Fig. 5) and Arrowinini (violet clade in Fig. 5). This sister clade to Staphylinini is the most exciting and satisfying discovery of this paper. The tribe Arrowinini includes its extant type genus *Arrowinus* and five extinct species from the Yixian Formation, all placed in the new genus *Paleowinus*. It is noteworthy that this broader concept of Arrowinini (*Arrowinus* + *Paleowinus*) was recovered by all three analytical approaches (ML, BI and MP, Figs 3–5, respectively). The new tribe Thayeralinini includes five species united in the new genus *Thayeralinus* (four new species and one, *T. fraternus*, transferred from the genus *Mesostaphylinus*; for details see "Systematic palaeontology"). Morphologically, *Thayeralinus* are very peculiar and bear two features unique among Staphylininae: 42-1, epipleural ridge present on elytra; and 69-0, well developed abdominal segment II. Both characters are optimized as ambiguous synapomorphies in Fig. 7 (clade 5). Based on these synapomorphies and the sister-group relationship with the tribe Arrowinini, we erect a new tribe Thayeralinini for *Thayeralinus*.

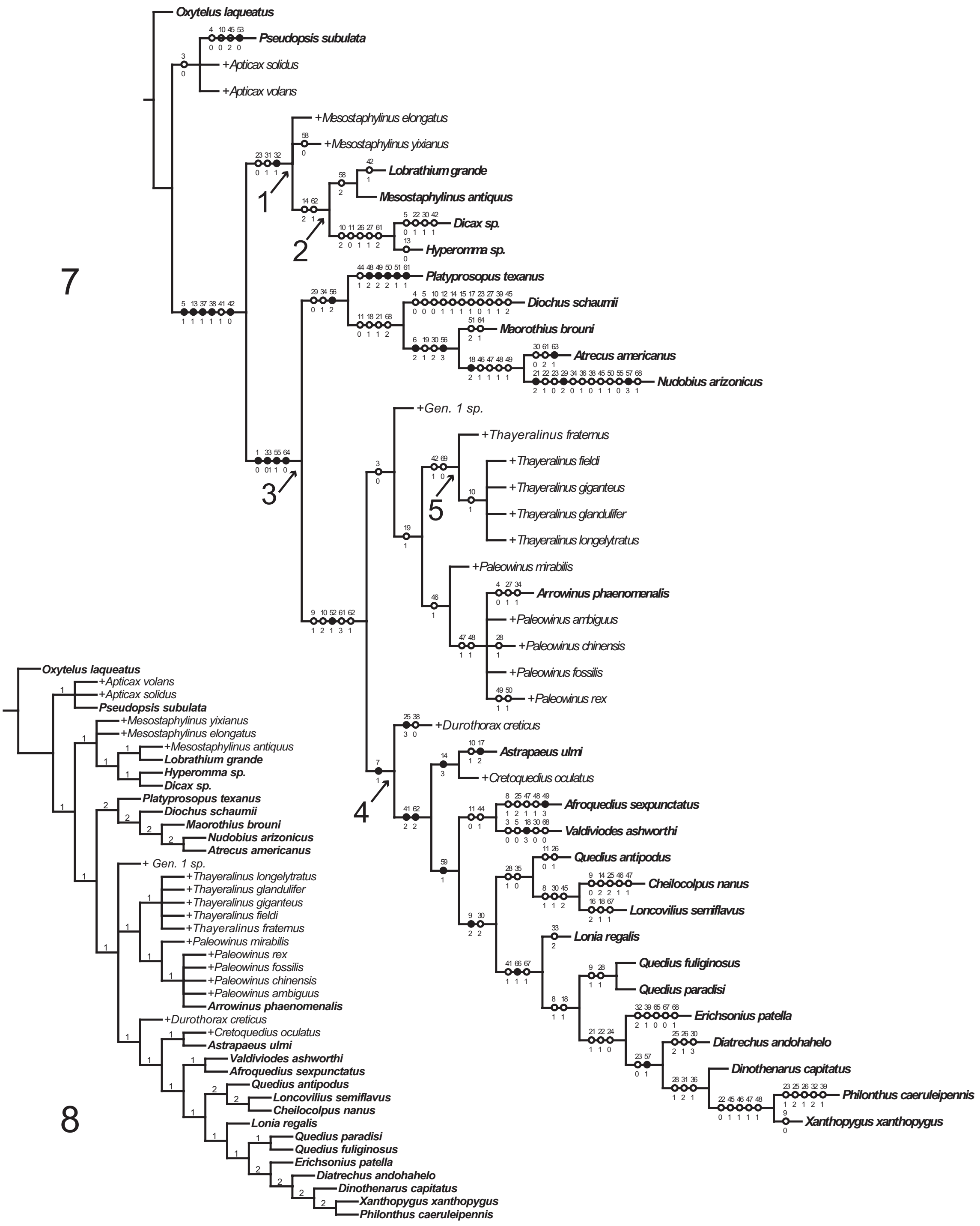
The species Gen. 1 sp. is a sister group to the clade Thayeralinini + Arrowinini. Cladistically it should be placed in a new genus and possibly a new tribe. However, poor preservation of the respective specimen casts doubt on the robustness of such phylogenetic result, and does not allow an informative diagnosis of a potential new family-group taxon. Therefore Gen. 1 sp. is left unnamed here, calling attention for a future evaluation of that potentially peculiar taxon when new material is available for study.

The remaining five fossil species are resolved as more or less basal lineages in the tribe Staphylinini (green clade in Fig. 5). The most isolated is *Durothorax creticus*, a lineage sister to all other members of this tribe. Next follows a polytomy formed by three species of *Cretoquedius: C. distinctus*, *C. dorsalis*, *C. infractus*, and a clade including all extant Staphylinini plus two extinct species, *C. oculatus* from Upper Cretaceous and the unnamed species Gen. 2 sp. from the Yixian Formation. Species of *Cretoquedius* may actually represent diverse lineages that eventually should be classified in different genera but, as discussed above, we prefer not to erect these until they can be better characterized by study of more material. Also, we have refrained from the formal description of the species Gen. 2 sp. because of its poor preservation combined

Table 2
Summary of the analysis

N	Type of analysis	Number of most parsimonious trees (MPTs)	Tree length (TL)/ln *L*	Illustration in this paper	Illustration in Supporting information
1	MP/R (Tach)	9	265		Figure S1
2	MP/R (Ox)	1	249	Figure 6	
3	MP/RF (Tach)	385 500	288		
4	MP/RF (Ox)	3890	272		
5	MP/RF (–3; Ox)	300	270	Figure 5	
6	ML/R (Ox)		942.6550 (Mk) 1229.672461 (Mk + Γ)	Figure 1	
7	BI/R (Ox)			Figure 2	
8	MP/RF (–9; Ox)	8	265		Figure S2
9	MPi/RF (–9; Ox)	4	265	Figures 7 and 8	
10	ML/RF (–9; Ox)		1035.6570 (Mk) 1332.441026 (Mk + Γ)	Figure 3	
11	BI/RF (–9; Ox)			Figure 4	

BI, Bayesian inference; ML, maximum likelihood; MP, maximum parsimony (unweighted); MPi, maximum parsimony (with implied weights, k = 6–20); F, fossil taxa included in the analysis; R, recent taxa included in the analysis; MPT, most parsimonious tree; *N*, analysis number; TL, tree length for MP analyses; ln *L*, likelihood score for ML analyses; (Ox), *Oxytelus* as an outgroup/root (*Tachinus* excluded from analysis); (Tach), *Tachinus* as an outgroup/root, with *Oxytelus* included as part of ingroup; (–3), three least preserved taxa excluded from the analysis (*Sulcelytrinus antiquus*, *Tunicopterus sigara* and *Mesostaphylinus laiyangensis*, scored from their very fragmentary published descriptions); (–9), nine least preserved taxa excluded from the analysis (three preceding and *Paleothius problematicus*, *P. gracilis*, Gen. 2 sp., *C. dorsalis*, *C. distinctus* and *C. infractus*, selected for exclusion based on the leaf stability index, Table S1).



Figs 7 and 8. Results of maximum parsimony (MP) analyses: 7, one of the four most parsimonious trees of analysis 9 (Table 2) with mapped character evolution; 8, strict consensus of the four most parsimonious trees resulting from analysis 9. Circles with numbers along branches indicate synapomorphies (autapomorphies for terminal branches): black, unambiguous; white, ambiguous; character numbers above synapomorphy circles, synapomorphous character state numbers below circles. Small numbers at nodes in Fig. 8 indicate Bremer support. Large numbers with arrows in Fig. 7 indicate clades of interest mentioned in the paper. Names of recent species are in bold font; names of fossil species in regular font are marked +.

with a rather terminal phylogenetic position inside the clade of recent Staphylinini. Such sister relationships of Gen. 2 sp. require proper assessment of certain characters to segregate a new taxon from its relatives. Unfortunately, such characters are not preserved in that fossil specimen.

Since *Durothorax creticus*, all new species of *Cretoquedius*, and Gen. 2 sp. fit the diagnosis of the tribe Staphylinini, we accept the placement of these stem groups in Staphylinini. In the analysis, the tribe Staphylinini in this sense is well supported by one unambiguous synapomorphy (7-1, presence of postgenal ridge, clade 4 in Fig. 7).

Discussion and conclusions

The analysis of Early Cretaceous fossils confirmed the sister relationships of Paederinae and Staphylininae and the monophyly of both subfamilies, and revealed expected but hitherto unknown stem lineages of Paederinae (represented by fossils such as *Mesostaphylinus elongatus* and *M. yixianus*) that existed at the earlier stages of Paederinae evolution. Placement of *Apticax* outside the clade Paederinae + Staphylininae suggests a former higher diversity of lineages stemming from the node that gave rise to modern Paederinae and Staphylininae. This, in turn, suggests that by the Early Cretaceous, Staphylininae, Paederinae, and their possible sister stem groups were already rather diversified, pushing the time of their origin and initial divergence significantly deeper in time, possibly down into the Jurassic period. This estimated Jurassic origin is consistent with the latest ideas of Jurassic ages for other related lineages of the Staphylininae group of subfamilies (Clarke and Chatzimanolis, 2009; Grebennikov and Newton, 2009; Yue et al., 2011).

Within the subfamily Staphylininae, examination of fossils corroborated earlier defined sister-group relationships of the xantholinine- and staphylinine-lineages and their internal topologies. It also revealed a number of stem groups for both, and contradicted the molecular-based hypothesis (Chatzimanolis et al., 2010a) that the clade Xantholinini + Othiini was nested within the current tribe Staphylinini.

Discovery of abundant fossil representatives of the hitherto monobasic Arrowinini (the only recent genus *Arrowinus* is endemic to South Africa) in China is direct evidence of a greater diversity and much broader distribution of that tribe historically, confirming an earlier hypothesis about the relictual nature of Arrowinini within Staphylininae (Solodovnikov and Newton, 2005). The inferred past distribution of Arrowinini across an area that was a single Pangean landmass in the Jurassic suggests a pre-Cretaceous origin and diversification, before the gradual Pangean fragmentation during the Late Jurassic and Cretaceous periods, and the subsequent high rate of extinction. The new tribe Thayeralinini, morphologically very peculiar compared with the recent fauna, apparently was also a well diversified species-rich group by the Early Cretaceous that eventually became extinct. Its morphology brings new insight about the morphospace of Staphylininae that has existed over the course of evolution of this subfamily.

Our simultaneous analysis of extant and fossil taxa corroborates the monophyly of the tribe Staphylinini, and reveals stem lineages at or near the base of that clade (Fig. 5). The ''Quediina-like'' appearance of these stem lineages corroborates the relict nature of extant basal monotypic or species-poor genera such as *Astrapaeus*, *Valdiviodes* and *Afroquedius*, and suggests a ''Quediina-like'' hypothetical common ancestor of Staphylinini.

The fact that none of the Early Cretaceous fossils analysed here was placed in the clades (*Dicax* + *Hyperomma*), (Maorothiini (Othiini + Xantholinini)), Amblyopinina, or (Quediina + ''Staphylinini propria'') does not necessary imply a younger than Early Cretaceous age for these groups, since fossils from the Early Cretaceous were placed in or near their sister clades. However, this at least suggests that diversifications within these mentioned clades could have taken place later than the Early Cretaceous.

These presumably younger clades that did not include any Early Cretaceous fossils in our analysis are groups of rove beetles that are particularly species-rich, common, or even predominant in the modern biota (clades outlined in Fig. 5). For example: Amblyopinina dominate forest floor habitats in southern temperate forests, Quediina do so in their northern temperate analogs; Philonthina are abundant and species-rich in the tropics of Africa and Asia as well as the Holarctic; Xanthopygina are a dominant group of Staphylinini in the Neotropical region; and Xantholinini are noticable everywhere except at high latitudes and in other extreme environments. In many ways, the faunal compositions of Staphylininae in the modern biota are very different from that of the Early Cretaceous. Groups dominant in our sample of fossils from the Yixian Formation either are entirely extinct now (e.g. Thayeralinini trib. n.), or are represented very poorly in the modern biota (e.g. Arrowinini or ''Quediina-like'' basal genera of Staphylinini). Apparently, the sister and oldest internal lineages of Paederinae and Staphylininae witnessed full evolutionary cycles from birth, through peak of diversification, to decline and extinction—over a rather long time span (well over 100 Myr). The modern fauna of these subfamilies, therefore, is a mix of old relict groups and younger lineages that are species-rich, abundant and often widespread, and are currently experiencing their own evolutionary peak.

Prospects for future research

Ideally, morphology of fossils could be integrated with morphology and DNA sequences of extant taxa to perform a ''dated total evidence'' analysis, as recently pioneered by Pyron (2011) and Ronquist *et al.* (2012).

However, DNA sequences that would be representative for such a study have not yet been generated in Staphylinidae, with the exception of some groups in Aleocharinae (Elven et al., 2010, 2012) and the tribe Staphylinini (Chatzimanolis et al., 2010a). With the examination of more fossils from various geographical locations and periods, and the acquisition of more molecular sequence data, a rigorous time-calibrated phylogenetic analysis could be implemented for the Staphylininae–Paederinae lineage or even for a more inclusive clade of Staphylinidae. Such an analysis should allow for the generation of quantitative hypotheses, presented only narratively here. The present integration of extant and stem rove beetle lineages in one phylogeny reconstruction is a step towards such a study for this hyperdiverse and landscape-dominating lineage of life on Earth.

Systematic palaeontology

Key to genera of Mezosoic Staphylininae, Paederinae, and allied lineages

1. Elytra with well defined posterior and sutural angles, forming a clear posterior margin; at suture, elytra equal to or shorter than at lateral margins. Body size varies .... 2.

–. Elytra with distinct sutural angle but broadly rounded posterior angle, therefore limits of posterior elytral margin unclear laterally; elytra at suture longer than at lateral margins. Body length 5.3 mm………………*Tunicopterus sigara* Tikhomirova (fig. 16 in Tikhomirova, 1968); Upper Jurassic, Karatau, Kazakhstan (subfamily unknown).

2. Elytra smooth or punctate, but never distinctly striate .... 3.

–. Elytra distinctly striate .... 10.

3. Head widest posteriorly where, without any neck constriction, it is tightly inserted into prothorax; contours of pronotum continuous with contours of head so that they are hardly delineated from each other and form a ‘‘bulldozer-like’’ forebody .... 4.

–. Head with or without neck, but always wider in front of attachment to prothorax; contours of head and pronotum always distinctly delineated from each other by more or less developed constriction .... 6.

4. Abdomen as in all recent Staphylininae or Paederinae: with segment II strongly reduced, fully hidden under elytra, so that segment III is the first visible behind apical margin of elytra, and only six free abdominal segments (III–VIII) are easily seen. Body size varies, but rarely longer than 12 mm .... 5.

–. Abdomen with well developed free segment II that is the first visible behind apical margin of elytra, so seven free abdominal segments (II–VIII) are usually easily seen. Large, body length 14–27 mm…….*Thayeralinus* Solodovnikov et Yue, gen. n. (Figs 20–31); Early Cretaceous, Yixian Formation (Staphylininae).

5. Antennae shorter: antennomeres 7–10 each as long as wide or slightly transverse. Smaller and more gracile (body length ca. 9.0 mm)……………*Cretoprosopus problematicus* Solodovnikov et Yue, gen. et sp. n. (Figs 15, 18); Early Cretaceous, Yixian Formation, China (Staphylininae).

–. Antennae longer: antennomeres 7–10 each distinctly to slightly longer than wide, not transverse. Larger and more robust (body length ca. 11.0 mm)…………………*Apticax solidus* Schomann et Solodovnikov (Schomann and Solodovnikov, 2012, fig. 2); Early Cretaceous, Crato Formation, Brazil (subfamily unknown).

6. Pronotum always distinctly longer than wide; head without infraorbital ridges extending through most of head length; prothorax with membanous postcoxal area or with heavily sclerotized postcoxal processes of pronotum, but never with large sclerites embedding spiracles separated from pronotum .... 7.

–. Pronotum of various shapes but never distinctly elongate, at most about as long as wide; head with infraorbital ridges extending through most of head length; if prothorax somewhat elongate, postcoxal area of prothorax with large sclerite (or pair of sclerites) embedding spiracles and separated from pronotum .... 8.

7. Pronotum with well sclerotized postcoxal processes; neck very distinct. ……………………..*Mesostaphylinus* Zhang, 1988 (Figs 9–14; Zhang, 1988, photo 1); Early Cretaceous, Laiyang and Yixian Formations, China (Paederinae).

–. Pronotum without postcoxal processes; head somewhat constricted posteriad but neck poorly developed………………*Paleothius gracilis* Solodovnikov et Yue, gen. et sp. n. (Figs 16, 17, 19); Early Cretaceous, Yixian Formation, China (Staphylininae).

8. Ventral prothorax behind coxae with large sclerite (sometimes paired) embedding spiracles and separated from pronotum……………*Durothorax creticus* Solodovnikov et Yue, gen. et sp. n. (Figs 47, 48); Early Cretaceous, Yixian Formation, China (Staphylininae).

–. Ventral prothorax behind coxae membranous, without large sclerite(s) embedding spiracles and separated from pronotum .... 9.

9. Eyes rather small, in dorsal view usually distinctly shorter than, or at most as long as tempora; first two or three visible abdominal tergites with two basal carinae each; neck poorly developed. Usually large (body length 11–37 mm, mostly > 17 mm)………………………. *Paleowinus* Solodovnikov et Yue, gen. n. (Figs 32–46); Early Cretaceous, Yixian Formation, China (Staphylininae).

–. Eyes more or less large, at least as long as tempora in dorsal view; first two visible abdominal tergites with one basal carina each; neck well developed. Usually smaller beetles (body length 8–13 mm)………………………..*Cretoquedius* Ryvkin, 1988 (Figs 49–59; Ryvkin, 1988, fig. 2); Early Cretaceous, Yixian Formation, China; Upper Cretaceous, NE Russia (Staphylininae).

10. Head with distinct neck. Abdomen with well developed free segment II that is the first visible behind apical margin of elytra, soseven free abdominal segments (II–VIII) are easily seen. Larger (body length 10.5 mm)………………………*Sulcelytrinus antiquus* Tikhomirova (Tikhomirova, 1968, fig. 15); Upper Jurassic, Karatau, Kazakhstan; subfamily unknown.

–. Head without neck. Abdomen as in all recent Staphylininae and Paederinae: with segment II strongly reduced, fully hidden under elytra, so that segment III is the first visible behind apical margin of elytra, and usually six free abdominal segments (III-VIII) are easily seen. Smaller (body length ca. 7.0 mm…………………..*Apticax volans* Schomann et Solodovnikov (fig. 1 in Schomann and Solodovnikov, 2012); Early Cretaceous, Crato Formation, Brazil; subfamily unknown.

Order Coleoptera Linnaeus, 1758
Family Staphylinidae Latreille, 1802

Incertae sedis

Genus *Sulcelytrinus* Tikhomirova, 1968 (monobasic)

Sulcelytrinus antiquus Tikhomirova, 1968

In the original description of this genus and species from the Upper Jurassic of Karatau (Kazakhstan) Tikhomirova (1968) mentioned that "in habitus it somewhat resembles extant members of the subfamily Staphylininae, but differs from those in sculpture of the elytra that are with deep stria of punctures". Exploratory phylogenetic analyses here, conducted for the entire sample of taxa (e.g. analyses 3 and 4, Table 2), where *Sulcelytrinus antiquus* was scored from its published description, were not informative about sister relationships of that taxon. Therefore, together with some other fossil taxa with low leaf stability index (Table S1), *S. antiquus* was excluded from the final analysis and thus remains as *incertae sedis* within Staphylinidae. Based on the illustration in Tikhomirova (1968), *S. antiquus* has a well developed abdominal segment II, a feature not mentioned in the original description but important considering the character state discovered here as diagnostic for the new tribe Thayeralinini (see below). Also, similar to Thayeralinini, *S. antiquus* is relatively large (length of body 10.5 mm) and has a broad neck. However, none of the species of Thayeralinini has striate elytra. This character state of *S. antiquus* is shared with *Apticax volans* Schomann et Solodovnikov, 2012; one of the extinct species from the Crato Formation with uncertain systematic position within the Staphylinine-group of subfamilies (Schomann and Solodovnikov, 2012, and see below).

Genus *Tunicopterus* Tikhomirova, 1968 (monobasic)

Tunicopterus sigara Tikhomirova, 1968

Like *Sulcelytrinus*, *Tunicopterus sigara* is known from a single specimen from the Upper Jurassic of Karatau (Kazakhstan). In the original description, Tikhomirova (1968) mentioned that "it is somewhat similar to the modern genera of the subfamilies Staphylininae and Paederinae, but differs from those in long egg-shaped elytra with entirely rounded posterior angles, and the elytra of *Tunicopterus* are longer at suture than along lateral margins". Our exploratory phylogenetic analyses (3 and 4, Table 2) conducted for the entire sample of taxa were not informative about the position of *T. sigara*. They vaguely suggested that it might represent a lineage that is a member of, or a sister to, the subfamily Pseudopsinae. However, the low leaf stability index (Table 3) led to the exclusion of this fossil from the final analysis. For the time being it remains *incertae sedis* within the family Staphylinidae.

Genus *Apticax* Schomann et Solodovnikov, 2012

Type species. *Apticax volans* Schomann et Solodovnikov, 2012.

The recently described genus *Apticax* (Schomann and Solodovnikov, 2012) from the Early Cretaceous Crato Formation in Brazil includes two species, *A. volans* Schomann et Solodovnikov, 2012 and *A. solidus* Schomann et Solodovnikov, 2012. According to the analysis here, these species form a polytomy with the recent subfamily Pseudopsinae (Figs 5 and 7). The present analysis supports one of the hypotheses in Schomann and Solodovnikov (2012) that *Apticax* is a hitherto unknown stem lineage of Staphylinidae related to the Staphylininae + Paederinae clade. If that is true, a new subfamily should be erected for *Apticax*. However, until more characters can be examined through the study of more material, any formal taxonomic decision regarding this genus is premature. Some resemblance of *Apticax* with Paederinae, and of *A. solidus* with *Paleowinus* and *Thayeralinus* (see below), as well as the shared striate elytra between *A. volans* and *Sulcelytrinus antiquus*, are noteworthy.

Subfamily Paederinae Fleming, 1821

Incertae sedis

Genus *Mesostaphylinus* Zhang, 1988 (Figs 9–14, S3–5)

Type species. *Mesostaphylinus laiyangensis* Zhang, 1988.

Redescription. Head capsule rounded to slightly elongate with distinct neck constriction and elongate neck; without fronto-clypeal suture, with gular sutures fused along most of their length (visible only in *M. antiquus*), and with dorsal basal ridge near occipital foramen (visible only in *M. antiquus*); eyes moderately large (visible only in *M. elongatus*), about as long as tempora. Antennae 11-segmented, inserted anterior to eyes, mode of insertion not clear in any of the available specimens; antennomere 1 moderately elongate, roughly as long as next two antennomeres (2 and 3) combined, antennomeres 6–10 gradually becoming shorter towards apex of antenna (from about as wide as long to transverse), last antennomere about as long as wide or slightly elongate, apically more or less dome-shaped. Details of mandibles not clearly visible in any examined specimens, but seemingly rather short and robust. Labrum (seen only in *M. antiquus*) moderately transverse. Maxillary palps (seen only in *M. yixianus*) with apical segment conical, about 2.5 times as long as wide, and longer than penultimate segment. Labial palps not preserved. In all specimens pronotum visible from lateral side only, its shape not entirely clear, apparently pronotum slightly oblong, with broad pronotal hypomeron extending into distinct postcoxal process (clearly seen in *M. elongatus* and *M. yixianus*, traces in *M. antiquus*); structure of prosternum poorly preserved. Mesothorax relatively long, with longitudinal median carina (seen in *M. yixianus* and *M. elongatus*) and medial transverse carina (seen only in *M. yixianus*) laterally intersecting with mesoventral-pleural sutures; mesoscutellum not preserved. Elytra relatively short, as long as pronotum, at least in *M. elongatus* with a structure that can be interpreted as epipleural ridge extending from humerus to about middle of elytral length. Metathorax relatively short. At least in *M. yixianus*, hind wings well developed, with venation not preserved. All legs moderately long, with large contiguous anterior coxae, rather broad anterior femora, and more or less dilated tarsomeres I–IV of anterior tarsi; middle coxae poorly preserved but seemingly contiguous; shape of posterior coxae not seen in detail, but about as long as wide; only anterior tarsi fully preserved (in *M. yixianus*), with five tarsomeres. Abdomen with two pairs of paratergites at least on tergites III–VI (paratergites poorly preserved in *M. elongatus*); paratergites of each pair well separated from each other; lateral tergal sclerites IX dorsally contiguous or fused (exact condition not clear due to poor preservation and (or) concealment under tergite VIII), apically produced into sharp processes; sexual dimorphism is not known because of poor preservation of relevant structures; in *M. antiquus* sternite VIII with two apical emarginations separated by obtuse median process; abdominal tergites III–VII with one basal carina each (in *M. elongatus* not all carinae are seen, but assumed).

Comparison. Among the Cretaceous fossil species that can be assigned either to Staphylininae or Paederinae, *Mesostaphylinus* can be distinguished by the rather narrow, medium-sized body, elongate head and pronotum, and the very distinct neck constriction of the head.

Notes on the systematic position. Due to the very poor description of the genus *Mesostaphylinus* and its type species *M. laiyangensis* (Zhang, 1988), the identity and systematic position of *Mesostaphylinus* will remain unclear until the specimen of *M. laiyangensis* becomes available for a revision. New species described below are placed in *Mesostaphylinus* based largely on their habitus similarity with *M. laiyangensis*. *Mesostaphylinus fraternus* Zhang, Wang et Xu, 1992 is here transferred to the genus *Thayeralinus* based on the present phylogenetic analysis (for details see below). Based on the analyses (Figs 5 and 7) conducted without *M. laiyangensis* because of its low leaf stability index (Table S1), at least *M. antiquus* is clearly identified as a member of the extant subfamily Paederinae, while *Mesostaphylinus* as a whole remains a genus of convenience for several morphologically similar species from a similar time horizon. Following the character optimization (Fig. 7) that indicates at least one unambiguous synapomorphy (32-1, transverse carina of the mesothorax extending laterally beyond mesoventral-pleural sutures) for clade 1, and presence of the postcoxal process (one of the diagnostic characters of modern Paederinae, visible in *M. yixianus* and *M. elongatus*), we consider *M. elongatus* and *M. yixianus* as members of the subfamily Paederinae, rather than as a separate, unknown lineage(s) of subfamilar rank. Additionally, both species are similar in habitus to *M. antiquus* and *M. laiyangensis* (characters of the habitus were not scored for the cladistic analysis). Placement of *Mesostaphylinus* in the subfamily Paederinae is supported by the combination of the following characters: hypomera of prothorax with sclerotized postcoxal processes, elytra possibly with epipleural ridge, mesothorax elongate with median transverse carina intersecting with mesoventral-pleural sutures; and lateral tergal sclerites IX dorsally contiguous or fused.

Finally, we infer that at least all three newly described species of *Mesostaphylinus* (*M. elongatus*, *M. yixianus* and *M. antiquus*) have an apical attachment of the intersegmental abdominal membrane, which is characteristic of the majority of recent Paederinae. This can be inferred because the abdomen is largely extended with the intersegmental membranes fully exposed in the studied specimens of *Mesostaphylinus*. Apparently, extension of the abdomen was triggered when the specimens fell in the water and remained there for an extended period of time, the deduced fossilization condition at this locality (Zhou et al., 2003). The apical attachment of the intersegmental membrane facilitates a stronger extension of the abdomen compared with the subapical attachment found in most Staphylininae. In the fossil Staphylininae described here from the same formation, the abdomens are less extended than in *Mesostaphylinus* despite the same fossilization conditions.

The apparent frontal attachment of antennae in *M. yixianus* and *M. elongatus*, as well as traces of frontal furrows in *M. elongatus*, may suggest that these two species are instead related to the “Xantholinine-lineage” of Staphylininae. Apical attachment of the intersegmental membrane of the abdomen and frontal furrows are characteristic for some recent genera of the tribe Xantholinini. Nevertheless, the present phylogenetic analyses favor the position of *Mesostaphylinus* as a member of Paederinae.

Finally, it should be stressed that until the present study, the oldest known Paederinae were from Baltic Amber, 54.8–23.8 Ma (Paśnik and Kubisz, 2002). Discovery of *Mesostaphylinus* in Paederinae pushes back the known age of this subfamily significantly and makes the age of sister groups Paederinae and Staphylininae phylogenetically compatible.

Mesostaphylinus laiyangensis Zhang, 1988
Mesostaphylinus laiyangensis: Zhang, 1988: 79.

The original description of this species (Zhang, 1988), based on the holotype, is very poor and does not list enough character states for its reliable taxonomic assignment. As can be seen in Zhang (1988, photo 1 of Plate I and the respective line drawing), the attachment of the middle legs to the mesothorax in *M. laiyangensis* indicates the same elongate mesothorax characteristic of *M. elongatus*, *M. yixianus*, *M. antiquus*, and many extant Paederinae. Although vaguely illustrated, the abdominal apex in *M. laiyangensis* shows basally contiguous lateral tergal sclerites of segment IX, a condition characteristic of many extant Paederinae (but also some Staphylininae from the "Xantholinine-lineage"). Re-examination of this specimen is badly needed.

Mesostaphylinus elongatus Solodovnikov et Yue sp. n.
(Figs 9 and 12, S3)

Material examined. Holotype, sex unknown, CNU-COL-LB2008786 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 9.0 mm, AL 1.4, HL 1.2, PL 1.2, EL 1.2, ATL 0.5, MTL 0.6.

Description. Head capsule poorly preserved, but characteristic for the genus, seemingly elongate, with large eyes about as long as tempora, and faint frontal furrows. Antennae as described for the genus, with antennomeres 4–10 distinctly widening towards apex. Mouthparts not preserved. Pronotum with distinct postcoxal process. Meso- and metathorax poorly preserved, but median longitudinal carina of mesothorax clearly visible. Elytra about as long as pronotum, with distinct line interpreted as epipleural ridge extending from humerus to about middle of elytral length. Only anterior and middle legs preserved, their structure as described for the genus; middle legs slightly longer than anterior legs. Abdomen as described for the genus, but structure of paratergites poorly visible, and basal carinae visible only on tergites III and IV. Segments III–IV with one pair of paratergites, paratergites of other segments not preserved; dorsally contiguous or fused lateral tergal sclerites IX very distinct.

Comparison. *Mesostaphylinus elongatus* is very similar to *M. yixianus* (Figs 10 and 13), but differs from it by the slightly longer antennae and pronotum and, as far as can be judged from the partial preservation, in having dilated anterior tarsi. It differs from *M. antiquus* in the distinctly more oblong head.

Etymology. The species name is the Latin adjective meaning "elongate" that refers to the body shape.

Mesostaphylinus yixianus Solodovnikov et Yue sp. n.
(Figs 10 and 13, S4)

Material examined. Holotype, male, CNU-COL-LB2008767 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 8.5 mm, AL 1.1, HL 1.1, PL 1.0, EL 1.2, ATL 0.4, MTL 0.6.

Description. Shape of head capsule unclear, but generally fitting generic description; eyes not preserved. Antennal insertions unclear; antennae as described for the genus; antennomere 1 slightly shorter than antennomeres 2 and 3 combined; antennomere 2 slightly longer than wide, antennomeres 3 and 4 about as long as wide; following antennomeres relatively broader. Maxillary palps as described for the genus, last segment conical. Shape of pronotum not very clear, but apparently as in *M. elongatus*. Elytra relatively short, with apparently obtuse sutural angles. Legs as in the genus description (posterior legs not preserved); anterior tarsi only slightly dilated; anterior femora moderately wide, with apical spur; anterior and middle legs of about same length. Abdomen as described for the genus; male sternite IX with slightly concave apex.

Comparison. *Mesostaphylinus yixianus* is most similar to *M. elongatus* (Figs 9 and 12), but differs by the slightly shorter antennae and pronotum, and, as far as can be judged from the partial preservation, in the non-dilated tarsomeres of the anterior tarsi. It differs from *M. antiquus* by its distinctly more oblong head.

Etymology. The species name is the Latin adjective derived from the name of the Yixian Formation, where this species originated.

Mesostaphylinus antiquus Solodovnikov et Yue sp. n. (Figs 11 and 14, S5)

Material examined. Holotype, male, CNU-COL-LB2008783 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 8.5 mm, AL 1.2, HL 0.9, PL 1.2, EL 1.1, ATL 0.5,.

Description. Head about as long as wide with broadly rounded tempora, with well developed neck constriction, nuchal ridge and dorsal basal ridge; eyes not preserved. Gular sutures fused along most of head capsule length, abruptly diverging anteriad near submentum. Antennal insertions poorly preserved, but seemingly intact base of left antenna suggesting their position near latero-anterior margin of frons; antennomere 1 about as long as 2 and 3 combined; 2 and 3 each longer than wide; following antennomeres gradually becoming shorter and wider towards apex of antenna. Shape of mandibles poorly preserved, but seemingly robust, with broad base and sharp apex. Labrum transverse. Prothorax not well preserved, distinctly longer than head (measured from apex of closed mandibles to neck constriction); pronotum with traces of postcoxal processes (their presence ambiguous). Elytra relatively short, slightly shorter than pronotum, their epipleural part not seen. Legs as described for the genus, with dilated anterior tarsi, with anterior legs distinctly shorter than middle and posterior; tarsal formula unclear (tarsi of anterior and posterior legs only partially preserved, those of middle legs not at all); anterior and posterior coxae as for genus, middle coxae not preserved. Abdomen as described for the genus, but distinctly wider in posterior part than at base; number of parategites on segments III and VII unclear; male sternite VIII apically with two emarginations and rounded medial process between them.

Comparison. *Mesostaphylinus antiquus* differs from both *M. elongatus* (Figs 9 and 12) and *M. yixianus* (Figs 10 and 13) by its rounded (not elongate) head and relatively shorter elytra.

Etymology. The species name is the Latin adjective meaning “ancient”.

Subfamily Staphylininae Latreille, 1802

Incertae sedis

Genus *Cretoprosopus* Solodovnikov et Yue gen. n. (Figs 15 and 18, S6)

Type species. *Cretoprosopus problematicus* Solodovnikov et Yue sp. n.

Description. Head capsule not well preserved, but distinctly either with broad neck or without neck constriction; eyes not preserved. Fronto-clypeal suture present. Antennae 11-segmented, their mode of insertion unclear, but as seen in left antenna, apparently attached near antero-lateral margins of frons; antennomere 1 slightly shorter than antennomeres 2 and 3 combined; antennomere 3 distinctly longer than antennomere 2; the following antennomeres gradually becoming shorter and wider towards antennal apex; antennomeres 9 and 10 distinctly transverse; last (11) antennomere about as wide as long, with subapical incision. Details of mandibles not seen. Labrum seemingly bilobed, strongly transverse. Maxillary palps with apical segment fusiform, about 2.5 times as long as wide, and longer than penultimate segment. Labial palps not well preserved, but visible traces suggest they are similar to maxillary palps. Prothorax poorly preserved, with apparently slightly oblong pronotum. Elytra relatively short, about as long as pronotum, covered with short setae, seemingly without epipleural ridge. All legs moderately long, tarsal formula 5-5-5: anterior legs slightly shorter than middle legs, middle legs slightly shorter than posterior legs; anterior legs robust, with broad femora and tibia, anterior tarsi with strongly dilated tarsomeres I–IV; femora and tibia of middle legs more slender than those of anterior legs, the latter with pronounced spines; shape of posterior coxae not seen in detail, but about as long as wide, otherwise shape of posterior legs similar to middle legs; middle and posterior tarsi not expanded. Abdomen with two pairs of paratergites at least on tergites III–VI, paratergites of each pair well separated from each other.

Comparison and notes on the systematic position. Among the Cretaceous species of Staphylininae *Cretoprosopus* can be distinguished by the combination of a broad neck (no visible neck constriction) and the poorly developed abdominal segment II (only six abdominal segments visible ventrally, as in most Staphylininae). From *Mesostaphylinus*, it also differs by the broad neck and presence of a fronto-clypeal suture. Unlike *Apticax volans*, *Cretoprosopus* has non-striate elytra, and unlike *A. solidus*, it has a smaller body, transverse antennomeres 5-10, and a distinct fronto-clypeal suture. Unfortunately, *C. problematicus* is a poorly preserved specimen with important characters of the thorax not visible. For example, the shape of the prothorax, as far as it can be seen, suggests that its pronotal hypomera may in fact have postcoxal processes. If so, this species may represent a lineage of Paederinae, or some basal lineage similar to *Apticax*. Because of a low leaf stability index (Table S1) *Cretoprosopus* had to be excluded from the more informative phylogenetic analyses 8–11. Given such uncertainity, we refrain from erecting a tribe for this genus as implied by the tree topology (Fig. 5).

Etymology. The genus name is derived from the combination of the Latin word "creta" and part of the genus name *Platyprosopus*, referring to the Cretaceous age of this new genus and its loose habitus resemblance to Platyprosopini; like *Platyprosopus*, it is masculine in gender.

Cretoprosopus problematicus Solodovnikov et Yue sp. n.
(Figs 15 and 18, S6)

Material examined. Holotype, sex unknown, CNU-COL-LB2007502 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 9.3 mm, AL 1.7, HL 1.5, PL 1.5, EL 1.7, ATL 0.7, MTL 1.0.

Description. In addition to the characters indicated in the description of the genus, the species is characterized by the proportions of its body parts, and in particular: antennomere 1 slightly shorter than antennomeres 2 and 3 combined; antennomere 3 distinctly longer than antennomere 2; the following antennomeres gradually becoming shorter and wider towards antennal apex; antennomeres 9 and 10 distinctly transverse; last (antennomere 11) about as wide as long, with subapical incision. Pronotum seems longer than wide. Middle and posterior legs slightly longer than anterior legs. *Comparison*. See comparison for *Cretoprosopus*.

Etymology. The species name is the Latin adjective meaning "problematic". It refers to the difficulty surrounding the placement of this species, because of its poor preservation.

Genus *Paleothius* Solodovnikov et Yue gen. n.
(Figs 16, 17 and 19, S7 and S8)

Type species. *Paleothius gracilis* Solodovnikov et Yue sp. n.

Description. Head with broad but distinct neck. Eyes not preserved. Gula distinct, diverging anteriad, but gular sutures poorly visible at base, probably fused behind middle of head; ventral side of head with traces resembling infraorbital ridges that also may be grooves. Antennae inserted at anterior margin of frons rather close to each other, details of their insertions not clearly seen. Mandibles broad in basal two-thirds of their length, apically curved, narrow and sharp, rather symmetrical, longer than wide; right mandible with two teeth internally, one sharp and another stout; left mandible with one visible stout tooth. Maxillary palp with apical segment oblong, fusiform, slightly longer than preceding segment. Pronotum with a faint trace of pronotal hypomeron preserved on right side of beetle lacking postcoxal process. Prosternum with straight apical margin and sharp intercoxal process. Anterior coxae not preserved, but based on the position of anterior femora and sharp mesocoxal process, probably contiguous. Elytra seemingly without epipleural ridge, with sub-basal ridge long, not adjacent to elytral articulation and extending from level of middle of scutellum to elytral humerus. Mesoscutellum with one transverse carina. Mesosternum with sharp intercoxal process; mesocoxae contiguous. Metathorax relatively long; posterior coxae slightly wider than long. Legs relatively short, all about same length, with broad femora and slender tibiae. Anterior tarsi not preserved; middle and posterior tarsi not dilated, 5-segmented. Abdomen parallel-sided along most of its length; segments III–VI each with two pairs of paratergites, segment VII with one pair of short paratergites; segments IX and X not visible, except protruding bunches of setae at apex of lateral tergal sclerites IX; abdominal tergites III–VII with one basal carina each.

Comparison. Although *Paleothius gracilis* resembles species of *Mesostaphylinus*, it has a larger body size and lacks a distinct neck constriction. *Paleothius* is significantly smaller than any of the species of *Thayeralinus* or *Paleowinus*, and additionally differs from both of those by its more gracile body, especially the distinctly elongate pronotum. *Paleothius* differs from *Cretoquedius* by its less developed neck constriction and only one (contrary to two) transverse carina at the base of the scutellum. Unlike *Durothorax*, *Paleothius* has basally confluent (as opposed to separate) gular sutures and has no large sclerite at the base of the prothorax behind the anterior coxae.

Etymology. The name of this new extinct genus is a fusion of the Latinized prefix *paleo*- (old) with the name of the extant genus *Othius*, to which it has some resemblance and affinity within the subfamily Staphylininae; like *Othius*, it is masculine in gender.

Notes on the systematic position. The phylogenetic position of *P. gracilis* was revealed in the less robust but more inclusive analysis 5 (Table 2), but was excluded from the more robust but less inclusive analysis 8, because of its low leaf stability index (Table S1). Placement of *Paleothius* within Staphylininae is the best justified hypothesis until more specimens are discovered. Its placement within Staphylininae is also consistent with its habitus, the presumably non-concealed articulation of antennae to the frons, and the pronotal hypomera without a postcoxal process. With so many uncertain character states, we refrain from erecting a tribe for this genus as implied by the tree topology (Fig. 5).

Paleothius gracilis Solodovnikov et Yue sp. n. (Figs 16, 17 and 19, S8 and S9)

Material examined. Holotype, sex unknown, CNU-COL-LB2008172P (part) and CNU-COL-LB2008172C (counterpart; CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 10 mm, AL 1.5, HL (from tips of mandibles to anterior margin of pronotum) 1.5, HW 1.0, PL 1.3, PW 1.1, EL 1.5, EW 1.3, ATL 0.6, MTL 0.7,

Description. In addition to the characters indicated in the description of the genus, the species is characterized by the proportions of its body parts, and in particular: antennomere 1 slightly shorter than antennomeres 2 and 3 together, antennomere 1 longer than 2, antennomere 4 shorter than 3; antennomere 5 longer than 4, antennomeres 6–10 each about as long as 4 and slightly wider than long, similar to each other in shape and size.

Comparison. See this section for *Paleothius* above.

Etymology. The name of the new species is the Latin adjective meaning "slender".

Gen. 1 sp. (Figs 40 and 43, S19)

Material examined. male, CNU-COL-LB2008174 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 17.5 mm, HW 2.7, EL 3.0, EW 3.8, PL 2.2, PW 3.0.

Description. Head capsule roundish, with small eyes (tempora *ca*. 3 times as long as eye diameter); gular sutures running very close to each other at base and along middle of head capsule length, diverging anterad at submentum; infraorbital ridges extending from base of head capsule to about middle of its length. Antenna poorly preserved with only three rather slender antennomeres (probably 1–3) visible. Mandibles elongate and strong, with broad basal part and narrower, sharply pointed apical part; a large and sharp tooth visible on internal side of left mandible. Pronotum wider than long, with distinct anterior angles, with slightly rounded sides and broadly rounded hind corners; anterior angles of pronotum strongly protruding over anterior margin of prosternum; pronotal hypomera not well preserved, not seen in detail. Prosternum seemingly (see "Remarks" below) with two pairs of antesternal plates; sternacostal ridge well developed, longitudinal carina of prosternum sharp, developed through furcasternum and basisternum; notosternal suture very distinct. Elytra relatively short, only slightly longer than pronotum, on sides slightly diverging posterad, their epipleural part poorly preserved. Metathorax relatively short. Legs not preserved; based on traces of anterior and posterior coxae and shape of mesocoxal cavities, coxae typical for genus. Abdomen as described for genus, with well preserved long, erect and stout setae along apical margins of abdominal sternites. Male sternite VIII apically with slight medial emargination; male sternite IX entire; lateral tergal sclerites IX as described for the genus.

Comparison. Due to robust habitus and poorly developed neck constriction, Gen. 1 sp. strongly resembles *Paleowinus*, and somewhat resembles *Thayeralinus* and *Apticax*. Similarly to *Paleowinus mirabilis* and *P. ambiguus*, the pronotum of Gen. 1 sp. is not narrowed anteriad, but Gen. 1 sp. is significantly smaller than *P. mirabilis* and significantly larger than *P. ambiguus*. Gen. 1 sp. differs from *Thayeralinus* in poorly developed, not visible as such, abdominal segment II. It differs from *Apticax* in marked neck constriction.

Remarks. Our cladistic analysis places this species as a sister group to the clade comprising Arrowinini and Thayeralinini (Figs 5 and 7), which would imply the creation of a separate genus and tribe for it. However, unlike the well represented and thus well characterized Arrowinini and Thayeralinini, Gen. 1 sp. is known from only one rather poorly preserved specimen in which many characters important for higher classification within Staphylininae are not visible. For example, the neck region is poorly preserved and it is not clear whether observed fragments are large antesternal plates or broken (distorted) parts of the head capsule. Therefore, instead of erecting a highly ambiguous new genus placed *incertae sedis*, we leave the species undescribed pending discovery of new material that may shed light on the identity of that lineage.

Tribe Thayeralinini Solodovnikov et Yue trib. n. (Figs 20–31 and 60, S9–13)

Type genus. *Thayeralinus* Solodovnikov et Yue gen. n.

This new tribe (red clade in Fig. 5 and clade 5 in Fig. 7) is erected for five species of the new extinct genus *Thayeralinus*, which is a sister group to the tribe Arrowinini in the new sense (extant genus *Arrowinus* plus the new extinct genus *Paleowinus*). Due to the unique combination of characters in *Thayeralinus* (two of which were optimized as ambiguous synapomorphies: 42-1: epipleural ridge of elytra; 69-0: well developed abdominal segment II, Fig. 7), it is a more practical solution to erect a new tribe for this genus rather than radically expand the existing diagnosis of the tribe Arrowinini. Moreover, a separate tribal rank for both sister clades (Thayeralinini and Arrowinini) better reflects the very deep divergence time between them suggested by the present analysis of Staphylininae.

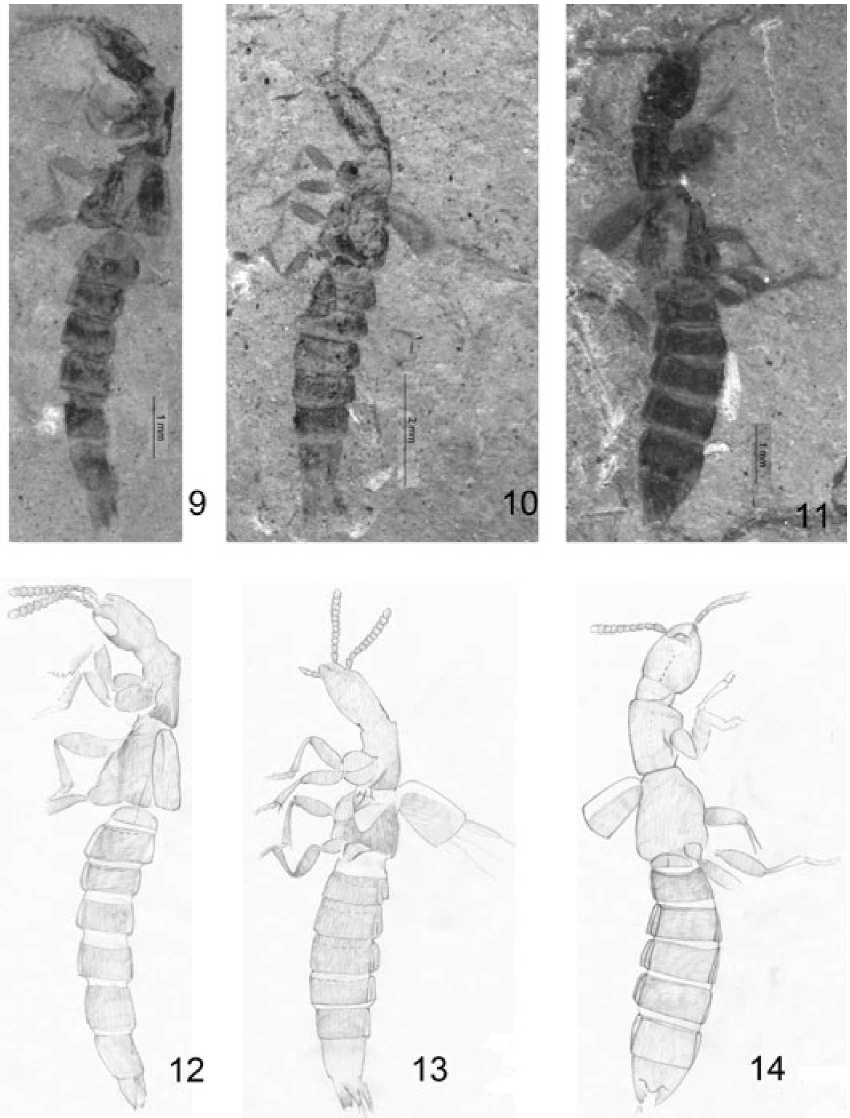
Diagnosis. Within the entire family Staphylinidae, the new tribe is characterized by the following unique combination of characters: head without neck constriction, seemingly without fronto-clypeal suture, with infraorbital ridges; antennae inserted laterally at frons, with distance between antennal insertions longer than distance from antennal insertion to inner margin of eye; probably (as can be seen only in *Thayeralinus giganteus*) antennal insertions concealed (or nearly so) by slight frontal projections (similarly to extant Paederinae); prothorax with two pairs of (possibly soft) antesternal sclerites, and with translucent apparently weakly sclerotized postcoxal processes separated from the pronotal hypomeron by a suture; elytra with an epipleural ridge; abdominal tergite I with prototergal glands; abdominal segment II well developed as a separate segment; abdominal tergites III–VI with two pairs of rather broad paratergites that possibly are nearly fused with each other; tergite VII with at least one pair of paratergites (number of paratergites is unclear due to insufficient preservation).

Genus *Thayeralinus* Solodovnikov et Yue gen. n. (Figs 20–31 and 60, S9–13)

Type species. *Thayeralinus fieldi* Solodovnikov et Yue sp. n.

Description. Beetles of large to moderate size, with robust "bulldozer-like" forebody, at least some species with bi-colored elytra. Head without neck constriction, with infraorbital ridges, and with curved gular sutures connected or nearly connected at around middle part of head. Possible traces of a fronto-clypeal suture seen only in *T. longelytratus*. Eyes small to moderate size, their diameter always significantly shorter than length of tempora. Eleven-segmented antennae inserted laterally at frons, with distance between antennal insertions longer than distance from antennal insertion to inner margin of eye; antennal insertions (visible only in *T. giganteus*) probably concealed by slight frontal projections (similarly to extant Paederinae); antennomere 1 elongate, next antennomeres gradually becoming shorter towards apex, antennomeres 2–3 (combined) longer than 1. Mandibles moderately elongate, broad at base, robust, with sharp apex and 1–2 strong teeth internally. Labrum (clearly seen only in *T. fieldi*) moderately broad. Maxillary palps with very elongate apical segment about as wide as, and as long as, penultimate segment, apically pointed. Labial palps much shorter than maxillary palps, with last segment only slightly longer than wide, apically truncate. Pronotum transverse, somewhat trapezoidal; pronotal hypomera apparently more or less inflexed under pronotum, with more weakly sclerotized large postcoxal process separated from hypomeron by a suture (visible in *T. fieldi* and *T. giganteus*); prosternum with straight anterior margin to which two pairs of apparently flexible antesternal sclerites are attached (best visible in *T. fieldi*), separated from pronotum by distinct notosternal suture, with more or less developed middle longitudinal carina between anterior coxae and well developed sternacostal ridge. Elytra from relatively short to moderately elongate, without distinct punctation or striae, with distinct epipleura separated by epipleural ridge (visible in *T. fieldi* and *T. giganteus*). Mesothorax with contiguous to subcontiguous coxal cavities. Metathorax variously developed (relatively longest in *T. giganteus*, shorter in all other species). Hind wings well developed in at least some species. All legs moderately long, with robust tibiae armed externally with thick setae and spines, and with large apical spurs; all tarsi 5-segmented, anterior tarsi with widened tarsomeres I–IV; anterior and middle coxae elongate, more or less conical; posterior coxae about as wide as long, with slightly exposed laterodorsal portion. Abdomen elongate, with well developed segment II, two pairs of paratergites on tergites III–VI, and possibly one pair on tergite VII (paratergites are tightly contiguous or maybe partly fused to each other in each pair, an unambigous judgement is impossible because of suboptimal preservation of the available specimens); tergite I (hidden under elytra) with prototergal glands (cuticular manifestations of those glands are visible in *T. glandulifer*); male sternite VIII with slight medial concavity, female sternite VIII simple, with smoothly rounded apical margin; male and female lateral tergal sclerites IX produced into apically inflated and sharp processes, with bunches of long setae; male sternite IX entire, female with ovipositor consisting of paired proximal and distal gonocoxites (presence or absence of styli cannot be established because of inadequate preservation of ovipositor parts); at least abdominal tergites III–VI with one basal carina each; often abdominal segments, especially apical one, laterally and apically fringed with long stout setae.

Comparison. The combination of characters diagnostic for *Thayeralinus* (and thus for the monobasic Thayeralinini) is unique and not known in any other recent or extinct genera of Staphylinidae. Among the fauna of the same geological time, *Thayeralinus* resembles *Paleowinus* and *Apticax*. It differs strongly from both of them in the well developed abdominal segment II. Additionally, *Thayeralinus* can be distinguished from *Paleowinus* by the head and pronotum, which fit tightly together to form a bulldozer-like forebody.



Figs 9–14. New species of Paederinae from Yixian Formation: 9, 12, *Mesostaphylinus elongatus*; 10, 13, *M. yixianus*; 11, 14, *M. antiquus*; 9–11, photos; 12–14, drawings (in Fig. 14, structures of gula located on side facing away from the viewer shown in dotted lines).

Etymology. It is our pleasure to dedicate this new, phylogenetically important genus to our friends and colleagues Drs Margaret Thayer and Alfred Newton (Field Museum, Chicago, IL, USA). Alfred and Margaret are among the few people attempting large-scale studies of rove beetle evolution, crucial for a stable higher-level classification of this enormously diverse beetle family. The genus name is a combination of Margaret's surname "Thayer" and the first syllable of Alfred Newton's first name, and is masculine in gender.

Thayeralinus fieldi Solodovnikov et Yue sp. n.
(Figs 20, 21, 23, 24 and 60, S9 and S10)

Material examined. Holotype, female, CNU-COL-LB2008173P (part) and CNU-COL-LB2008173C (counterpart; CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 14 mm, HL (from distal marginal contour of mandibles to anterior margin of pronotum) 2.3, HW 2.5, PL 2.0, PW 2.5, EL 2.5, ATL 1.1, MTL 1.1.,

Description. Head capsule somewhat trapezoidal; gular sutures converging close to each other along middle part of head capsule; gula diverging anterad and posterad; eyes not visible; infraorbital ridges extended from base of head nearly to base of mandibles. Mandibles closed and not clearly visible, but obviously stout, curved, apically sharp. Antennae moderately long, their insertions unclear; antennomere 1 only partly preserved, 3 longer than 2, 4 shorter than 3; antennomeres 5–10 gradually becoming wider and shorter towards apex of antenna; last antennomere with obtuse apex. Labrum transverse, its shape poorly preserved. Maxillary and labial palps as in the genus description. Pronotum slightly wider than long, trapezoidal, with distinct anterior and posterior angles, anteriorly as wide as head, with sides gradually converging posterad; more weakly sclerotized postcoxal processes large, broad at base and elongate. Sternacostal ridge of prosternum very well developed; longitudinal carina of prosternum sharp, extended along furcasternum only. Both pairs of antesternal sclerites distinct: medial pair wider than lateral pair. Elytra relatively short, with traces of some color pattern combining dark and pale colors. Wings well developed. Legs and abdomen as in the genus description, but neither tergite I nor its prototergal glands can be seen. Ovipositor with gonocoxites without clear division into proximal and distal sclerites, possibly because of poor preservation.

Comparison. *Thayeralinus fieldi* differs from all other species of the genus by the distinctly smaller size of the body, the bicolored elytra, the relatively thicker, more robust legs, and some proportions of the body.

Etymology. The species name is dedicated to the Field Museum, a world class research institution housing an outstanding collection of rove beetles. It is a patronymic noun in the genitive case. By naming a species within the genus *Thayeralinus* after the Field Museum, we link Alfred and Margaret, colleagues to whom this genus is dedicated, to their work place.

Thayeralinus longelytratus Solodovnikov et Yue sp. n.
(Figs 22 and 25, S11)

Material examined. Holotype, male, CNU-COL-LB2008181 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 22 mm, HL (from anterior margin of labrum to anterior margin of pronotum) 4.5, HW 4.2, PL 4.2, PW 5.7, EL 6.0.,

Description. Head capsule oblong, with very small round eyes. Antennal base not well preserved, but antennae apparently inserted latero-anteriorly near anterior margin of eyes, distance between antennal insertions much longer than distance from either insertion to margin of eye; only first three segments of antennae preserved, rather slender. Mandibles longer than wide, with broad basal part, and much narrower, strongly curved, more or less acute apical portion, each mandible with one strong tooth internally. Traces of possible fronto-clypeal suture visible on left side of head. Labrum poorly visible, apparently strongly transverse. Maxillary and labial palps as described for the genus. Pronotum wider than long and distinctly wider than head, widest behind its middle, with distinct anterior angles and broadly rounded posterior angles. Elytra relatively long, significantly longer than pronotum, sides slightly diverging posterad. With traces of well developed hind wing. Legs not preserved. Abdomen as described for the genus, its ventral side not preserved. Aedeagus with sharply pointed apex.

Comparison. *Thayeralinus longelytratus* differs from all other species of the genus by the distinctly elongate elytra and shape of the pronotum that is widest behind its middle (all other species of *Thayeralinus* have the pronotum widest at or very near the anterior margin).

Etymology. The species name is an adjective derived from the Latin adjective "longus" (long) and Latinized Greek word "elytron" and refers to the relatively long elytra of this species.

Thayeralinus glandulifer Solodovnikov et Yue sp. n.
(Figs 28 and 31, S13)

Material examined. Holotype, sex unknown, CNU-COL-NN2008241 (CNUB).

Locality and horizon. Liutiaogou Village, Ningcheng County, Inner Mongolia, China, Yixian Formation, Early Cretaceous.

Measurements. TBL 27 mm, HL (from distal marginal contour of mandibles to anterior margin of pronotum) 2.3, HW 2.5, PL 2.0, PW 2.5, EL 2.5, ATL 1.1, MTL 1.1.

Description. Head capsule about as long as wide, with eyes of moderate size (tempora *ca*. 2.5 times as long as eye diameter); gular sutures arcuate, nearly fused in middle part of head. Neither antennae nor antennal insertions preserved. Mandibles, as far as can be seen, of typical structure for the genus, but apparently with relatively smaller internal teeth. Shape of pronotum poorly preserved, but seeming to have somewhat rounded lateral margins. Elytra relatively short, with poorly preserved epipleural part, with apparently obtuse sutural angle. Legs as described for the genus; anterior legs slightly shorter than middle and posterior legs; visible anterior coxae characteristic for the genus. Abdomen as described for the genus, but segments VIII–X only partially preserved; tergite I with trace of an ovoid cuticular manifestation of prototergal gland.

Comparison. *Thayeralinus glandulifer* differs from all other congeners in its distinctly short elytra.

Etymology. The species name is a Latin adjective meaning "bearing gland". It refers to a well preserved trace of the prototergal gland in the holotype.

Thayeralinus giganteus Solodovnikov et Yue sp. n.
(Figs 26, 27, 29, 30, S12)

Material examined. Holotype, female, CNU-COL-NN2009253P (part) and CNU-COL-NN2009253C (counterpart; CNUB).

Locality and horizon. Liutiaogou Village, Ningcheng County, Inner Mongolia, China, Yixian Formation, Early Cretaceous.

Measurements. TBL 26 mm, HL (from visible base of mandibles along their internal sides to anterior margin of pronotum) 3.0, HW 3.5, PL 3.0, PW 4.4, EL (from apex of mesoscutellum to sutural angle) 3.5, ATL 1.6, MTL 1.9.

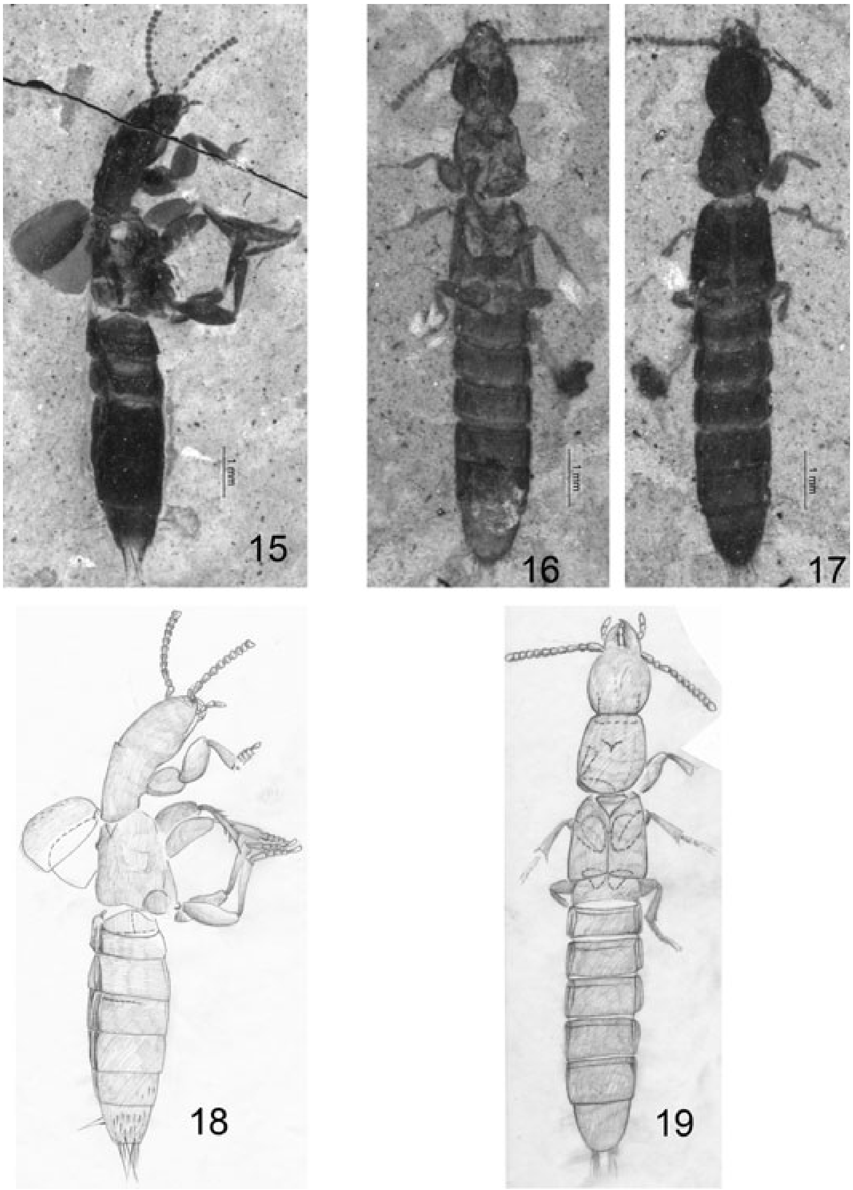
Description. Head capsule about as long as wide with tempora gradually converging anterad; eyes not visible, if present probably rather small; gular sutures fused along median part of head capsule, so gula is distinct only anteriorly; infraorbital ridges very distinct, extending from base of head capsule to base of mandible. Antennae and their insertions only partially preserved, but antennae seemingly inserted latero-anteriorly, with insertions concealed under frontal projections; few visible antennomeres (2–7 of one antenna, apparently detached from the basal antennomere) each longer than wide, gradually becoming shorter towards antennal apex. Mandibles characteristic for the genus. Maxillary palps as described for the genus, rather slender. Pronotum transverse, widest at anterior margin, with sides broadly rounded posteriorly; prosternum with sharp intercoxal process, probably with median longitudinal carina (poorly visible, most likely very short); pronotal hypomera rather wide, with small but distinct triangle-shaped semi-sclerotized postcoxal processes; notosternal suture distinct. Elytra relatively oblong, with poorly imprinted epipleural part, however long epipleura separated by epipleural ridge visible. Metathorax much longer than short mesothorax; well preserved middle and posterior coxae of typical structure for genus; mesocoxae contiguous. Legs as for genus (middle and posterior tarsi not preserved). Abdomen as for genus, but suture between paratergites not visible (perhaps with only one pair of paratergites per segment). Proximal and distal gonocoxites of ovipositor clearly visible.

Comparison. *Thayeralinus giganteus* is distinctly larger than *T. fieldi*, and it has distinctly more elongate elytra than *T. glandulifer*. In contrast to the similar *T. longelytratus*, *T. giganteus* has the pronotum widest at the anterior margin (in *T. longelytratus* it is widest posterior to the middle).

Etymology. The species name is the Latin adjective meaning "gigantic". It refers to the distinctly large body size.

Thayeralinus fraternus (Zhang, Wang et Xu, 1992) new combination
Mesostaphylinus fraternus: Zhang, Wang et Xu 1992: 277

This apparently rather well preserved species was very inadequately described and illustrated. Although



Figs 15–19. New species of the Staphylinine-lineage of the subfamily Staphylininae from Yixian Formation: 15, 18, *Cretoprosopus problematicus*; 16, 17, 19, *Paleothius gracilis* (16, part; 17, counterpart of the holotype); 15–17, photos; 18, 19, drawings (in Fig. 19 structures of legs, ventral side of thorax and head located on the side facing away from the viewer shown in dotted lines).

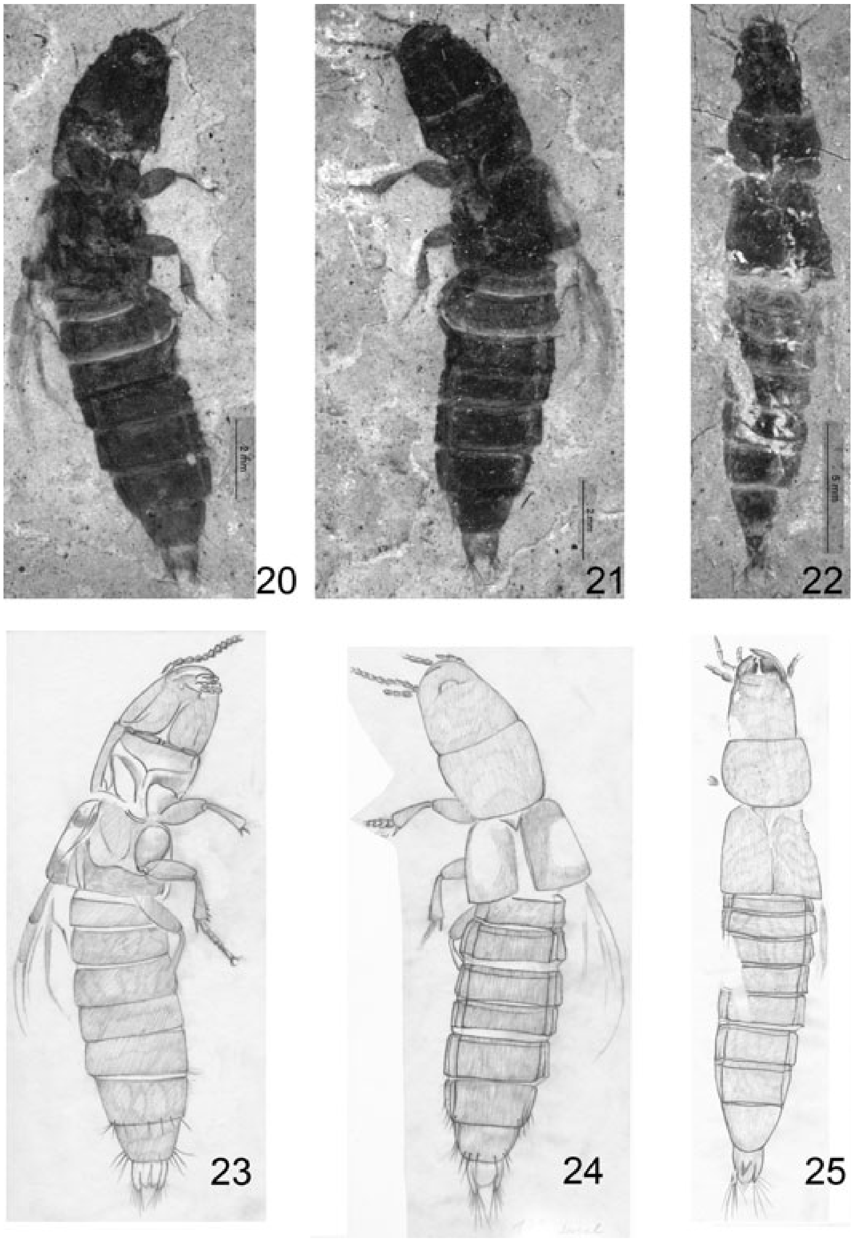
it was placed in *Mesostaphylinus*, it differs from the type species *M. laiyangensis* by the following: a relatively short mesothorax; seven (versus six in *M. laiyangensis*) ventrally visible abdominal segments; and a very different shape of abdominal tergite X and lateral tergal sclerites IX. These characters, observed from the photo and line drawing in the original description of *M. fraternus*, clearly indicate that this species is not congeneric with *M. laiyangensis*. Since our phylogenetic analysis places *M. fraternus* in *Thayeralinus* (Figs 5 and 7), this new combination is proposed here.

Tribe Arrowinini Solodovnikov et Newton, 2005 (Figs 32–46, S14–18, S20, S21)

Paleowinus Solodovnikov et Yue gen. n. (Figs 32–46, S14–18, S20, S21)

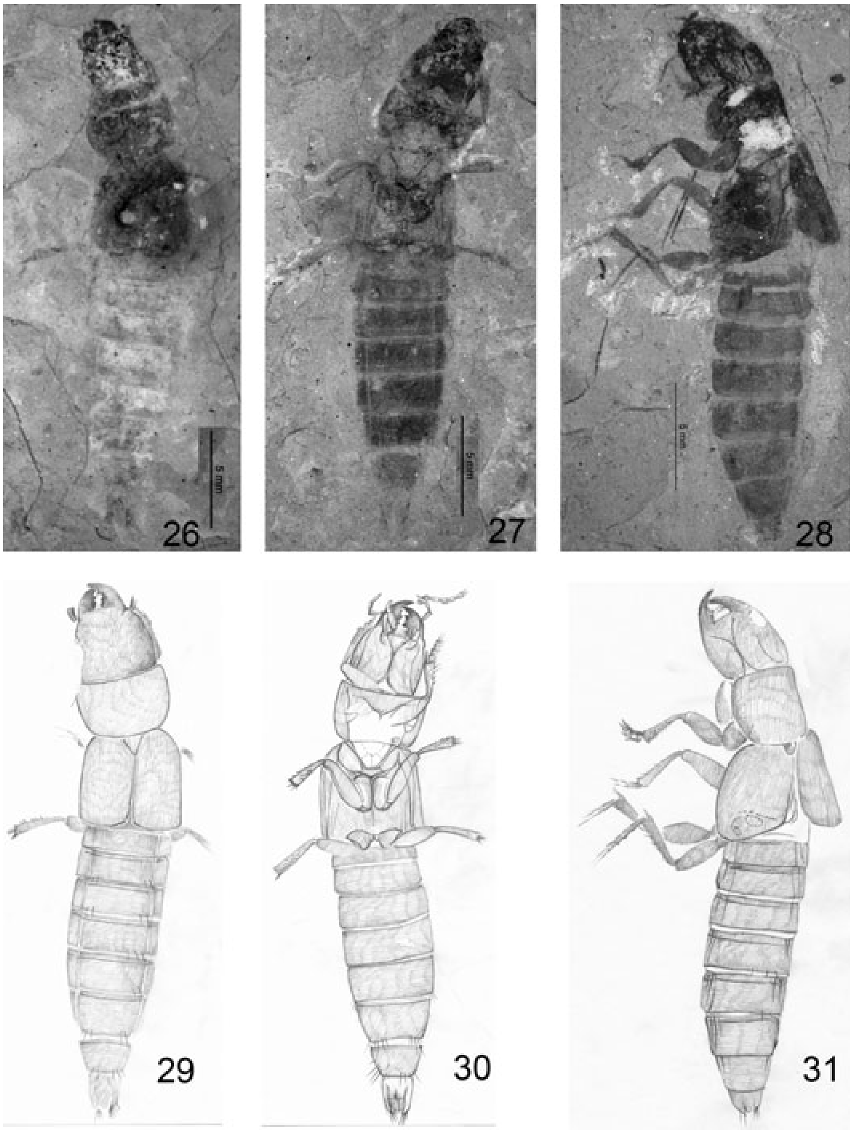
Type species. *Paleowinus rex* Solodovnikov et Yue sp. n.

Description. Rove beetles of large to moderate size, at least some species bi- or multicolored. Head without neck constriction, without fronto-clypeal suture, with



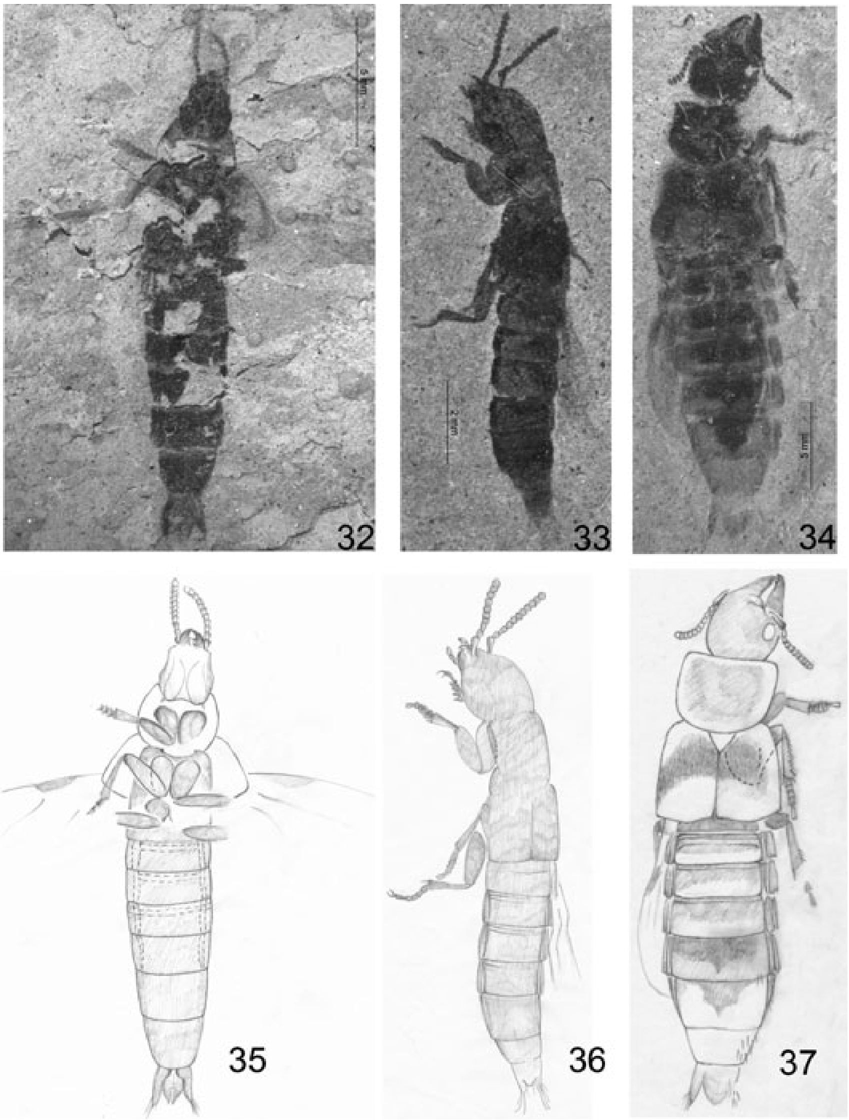
Figs 20–25. New species of the tribe Thayeralinini from Yixian Formation: 20, 21, 23, 24, *Thayeralinus fieldi* (20, part; 21, counterpart of the holotype); 22, 25, *T. longelytratus;* 20–22, photos; 23–25, drawings (23, *T. fieldi*, reconstruction of the ventral side of the holotype; 24, same species but reconstruction of the dorsal side of the holotype).

infraorbital ridges and arcuate gular sutures (infraorbital ridges and gula preserved only in the type species). Eyes of moderate size, their longitudinal diameter from slightly to much shorter than tempora. Eleven-segmented antennae inserted at frons, anteromedially from eyes, with distance between antennal insertions distinctly longer than distance from antennal insertion to inner margin of eye; antennal insertions not concealed; antennomere 1 moderately elongate, roughly as long as antennomeres 2 and 3 combined, antennomeres 4–10 relatively short, transverse, last (antennomere 11) about as long as wide, apically dome-shaped. Mandibles moderately elongate, broad at base, robust, with sharp apex and 1–2 teeth internally. Labrum (clearly seen only in *P. mirabilis*) transverse. Maxillary palps with fusiform apical segment about 2 times as long as wide, and as long as penultimate segment. Labial palps (seen only in *P. chinensis*) much shorter than maxillary palps, with last segment only slightly longer than wide, apparently



Figs 26–31. New species of the tribe Thayeralinini from Yixian Formation: 26, 27, 29, 30, *Thayeralinus giganteus* (26, part; 27, counterpart of the holotype); 28, 31, *T. glandulifer*; 26-28, photos; 29-31, drawings (29, *T. giganteus*, reconstruction of the dorsal side of the holotype; 30, same but ventral).

apically truncate. Shape of pronotum variable, but pronotal hypomera apparently more or less strongly inflexed under pronotum (postcoxal area poorly preserved in all specimens, presence of semi-sclerotized postcoxal process uncertain); anterior angles of pronotum produced over straight anterior margin of prosternum, seemingly without antesternal sclerites, prosternum with distinct sternacostal ridge but without longitudinal carina (at least along basisternum; prosternal area visible only in *P. chinensis*); notosternal suture well developed (visible only in *P. fossilis*). Elytra moderately elongate, without distinct punctation or striae, seemingly without epipleural ridge; with long subbasal ridge not adjacent to elytral articulation but extending from the level of about middle of mesoscutellum length to elytral humerus. Mesothorax, at least where visible (*P. rex*, *P. mirabilis*, *P. chinensis*), with subcontiguous coxal cavities; mesoscutellum with one transverse carina. Metathorax moderately elongate. Hind wings well developed (visible in all except *P. ambiguus*), with completely separate MP3, MP4 and CuA veins (as seen in *P. rex*). All legs moderately long; tibiae, where seen, externally armed with strong setae and spines, with large apical spurs; all tarsi 5-segmented, anterior tarsi with widened tarsomeres I–IV; anterior and middle coxae elongate, more or less



Figs 32–37. New species of the tribe Arrowinini from Yixian Formation: 32, 35, *Paleowinus fossilis*; 33, 36, *P. ambiguus*; 34, 37, *P. mirabilis*; 32–34, photos; 35–37, drawings (in Fig. 35, structures of right middle coxa, paratergites and basal carinae of abdominal tergites located on the side facing away from the viewer shown in dotted lines; in Fig. 37, same applies for basal part of right middle leg).

conical, contiguous; posterior coxae about as long as wide. Abdomen elongate, with two pairs of paratergites on segments III–VII; paratergites on each side well separated from each other; tergite I (hidden under elytra) with prototergal glands (cuticular manifestation of those glands visible in *P. rex*); male sternite VIII simple, without medial concavity, male and female lateral tergal sclerites IX produced into apically inflated and sharp processes, with bunches of long setae; male and female sternite IX entire; in females ovipositor consisting of paired structures, subdivision into distal and proximal gonocoxites uncertain because of poor preservation; abdominal tergite III always with two basal carinae, tergites IV–VII with one or two basal carinae each (bases of abdominal tergites VI and VII not visible in some species); apical abdominal segments with long stout setae.

Comparison and systematic notes. The genus *Paleowinus* is placed in the tribe Arrowinini based on our cladistic analysis and the following combination of characters: only slightly distinct neck constriction; well developed infraorbital ridges; prothorax with straight anterior margin of prosternum and anterior angles of pronotum protruding over prosternum; long elytral subbasal ridge not adjacent to elytral articulation but extending from the level of about middle of mesoscutellum length to elytral humerus; and well developed prototergal glands on abdominal segment I.

As far as can be observed, *Paleowinus* differs from *Arrowinus* in the absence of the frontoclypeal suture and antesternal sclerites. Among the related extinct taxa of the same geological time, *Paleowinus* resembles *Thayeralinus* and *Apticax*. From *Thayeralinus*, it differs in the strongly reduced abdominal segment II and the shape of the forebody, where the base of the head is narrower than the apical margin of the pronotum, not forming a "bulldozer-like" forebody. *Paleowinus* additionally differs from *Thayeralinus* by having: more transverse antennomeres 4-9; relatively shorter apical and subapical segments of maxillary palps; two (cf. one in *Thayeralinus*) basal carinae on abdominal tergites; no antesternal plates; no epipleural ridge; no fringes of stout setae on the abdominal segments; and well separated paratergites on each side. From *Apticax*, *Paleowinus* differs clearly by the shape of the head and pronotum, which do not form a bulldozer-like forebody.

From *Cretoquedius*, *Paleowinus* differs by the poorly developed neck constriction and smaller eyes. Unlike *Durothorax*, *Paleowinus* has a poorly developed neck constriction and an unsclerotized area of the prothorax behind the anterior coxae.

As in *Mesostaphylinus* and *Apticax*, the composition of *Paleowinus* does not entirely correspond with the tree topology (Fig. 5). Strictly following the topology, all species sharing the same clade with the genus *Arrowinus* could be assigned to that genus, while *P. mirabilis*, could be placed in a separate genus, as it is sister to the *Arrowinus*-clade. However, we avoided this for two reasons. First, the clade that includes *Arrowinus* and four species of *Paleowinus* is a polytomy. Second, the genus *Arrowinus* is a well characterized recent taxon, while the extinct genus *Paleowinus* is known from only fragmentary material. Its diagnosis and composition are likely to change when more specimens and/or extinct species become available for study. Therefore we place all extinct species of the violet clade in Fig. 5 in the genus *Paleowinus*.

Etymology. The name of the new genus is composed from the Latin prefix *paleo*- and part of the extant genus name *Arrowinus*, with which it has an affinity; it is masculine in gender.

Paleowinus rex Solodovnikov et Yue, sp. n. (Figs 44–46, S20, S21)

Material examined. Holotype, sex unknown, CNU-COL-LB2008212PC (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 37 mm, HL (from base of labrum to posterior margin of head capsule) 4.0, PL: 4.2.

Description. Head capsule slightly elongate, with relatively small eyes (tempora *ca*. 3 times as long as their diameter). Antennae not preserved, except antennomere 1, which looks typical for the genus; antennal insertions apparently typical for the genus. Mandibles robust, as in other species of the genus, but rather elongate, other details of their structure not preserved. Pronotum very poorly preserved, seemingly about the same length as head. Mesoscutellum with one basal carina. Elytra (based on partially preserved right elytron) relatively elongate, with clear sub-basal ridge extending from near middle of scutellum to humerus; preserved elytron bears traces of colour pattern combining dark and pale colours. Mesocoxal cavities large, apparently subcontiguous. Metathorax rather long; hind wings well developed, with completely separate MP3, MP4 and CuA veins. Legs not preserved, except large elongate anterior coxae and traces of anterior and posterior femora. Abdomen as described for genus, with well preserved large, ovoid cavities (cuticular manifestations of prototergal glands) on tergite I; tergites III–VII with two basal carinae each, with relatively large, clearly visible spiracles; surface of tergites covered with dense and short setation; apex of abdomen poorly preserved.

Comparison. *Paleowinus rex* is the largest species in the genus. From *P. mirabilis*, a large congener, it differs by its uniform coloration (well preserved at least on the abdomen) and by the head, which appears to be slightly more elongate.

Etymology. The name of the new species is a Latin adjective that means "king". It refers to the very large size and predatory, powerful appearance of this species, which must have been a king among the smaller creatures in Cretaceous leaf litter. Although at a smaller spatial sclae, *Paleowinus rex* was "ruling" much earlier than the iconic dinosaur *Tyrannosarus rex*.

Paleowinus fossilis Solodovnikov et Yue sp. n. (Figs 32 and 35, S14)

Material examined. Holotype, female, CNU-COL-NN2008175 (CNUB).

Locality and horizon. Liutiaogou Village, Ningcheng County, Inner Mongolia, China, Yixian Formation, Early Cretaceous.

Measurements. TBL 18 mm, AL 2.3, HL (from tips of mandibles to basal margin of head capsule) 2.7, PL 2.3, PW 2.1, ATL 1.0, MTL 1.8.

Description. Head capsule slightly oval, with well developed, relatively large eyes (their diameter about as long tempora); infraorbital ridges extending from base of head nearly to base of mandibles; gular sutures arcuate, separated from each other, diverging anteriad and posteriad before reaching submentum and basal margin of head, respectively. Antennal bases not very clearly seen, but seemingly antennae inserted at anterior margin of frons, anterior to eyes; distance between them longer than distance from either insertion to margin of eye; antennomere 1 about as long as antennomeres 2 and 3, the following antennomeres from about as long as wide to becoming slightly transverse towards antennal apex, last segment dome-like. Mandibles rather short, with sharp apex and large internal teeth (two teeth on left mandible, one broad tooth—on right). Pronotum slightly wider than long, wider than head, widest behind its middle, with very distinct anterior angles and broadly rounded sides with indistinct posterior angles; anterior angles of pronotum strongly projecting anteriad over apical margin of prosternum; pronotal hypomera wide, but too poorly preserved to see details of their structure. Mesosternum very short, with poorly visible but seemingly sharp mesosternal process. Elytra relatively short. Metathorax rather long; hind wings well developed. Legs and abdomen as described for genus, but prototergal glands not seen because of poor preservation of dorsal side. Ovipositor without distinct division of valvifers into distal and proximal gonocoxites, possibly due to poor preservation.

Comparison. *Paleowinus fossilis* differs from all other congeners by its relatively large eyes that are as long as the tempora.

Etymology. The species name is a Latin adjective that means "fossil".

Paleowinus ambiguus Solodovnikov et Yue, sp. n.
(Figs 33 and 36, S15)

Material examined. Holotype, sex unknown, CNU-COL-LB2008211 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 11 mm, AL 1.6, HL (from visible apex of right mandible to anterior margin of pronotum) 1.6, PL 1.6, ATL 0.7, MTL 1.0.

Description. Head capsule round, but its details, poorly preserved, eyes not preserved. Antennae inserted at anterior margin of frons, obviously anterior to eyes and presumably distance between them longer than distance from either insertion to margin of eye, antennomere 1 about as long as antennomeres 2 and 3 together, antennomere 3 distinctly longer than antennomere 2, other antennomeres as described for the genus. Mandibles typical for the genus. Apical and subapical segments of maxillary palp as described for the genus. Pronotum about as long as head, but its shape not well preserved. Legs as described for genus, except apical spurs, setae, and spines not seen on tibiae. Anterior legs slightly shorter than middle and posterior legs, with anterior tibia thicker than middle and posterior. Abdomen typical for the genus, its apex poorly preserved.

Comparison. *Paleowinus ambiguus* is distinctly smaller than other species of the genus. It differs from *P. chinensis*, the next smallest species of the genus, in the relatively broader head.

Etymology. The name of this species is a Latin adjective that means "ambiguous". It refers to the poor preservation, which makes the precise identification of this species somewhat difficult.

Paleowinus mirabilis Solodovnikov et Yue sp. n.
(Figs 34 and 37, S16)

Material examined. Holotype, sex unknown, CNU-COL-NN2008069 (CNUB).

Locality and horizon. Liutiaogou Village, Ningcheng County, Inner Mongolia, China, Yixian Formation, Early Cretaceous.

Measurements. TBL 30 mm, AL 5.3, HL (from base of labrum to anterior margin of pronotum) 3.2, PL 4.2, PW 5.4, EL (from apex of mesoscutellum to sutural angle) 3.5, EW 7.1, ATL 2.0, MTL 3.0.

Description. Large species, bi- or multicoloured, with darker transverse band across elytra and darker basal areas of abdominal tergites III–VII. Head darkened, pronotum darkened with wide pale margins; abdominal tergites III to V mostly dark but with pale apical margin, abdominal tergites VI and VII mostly pale with broad dark area basally and in the middle, abdominal apex pale. Head capsule broadly rounded, about as long as wide, eyes rather small (tempora *ca*. 3 times as long as eye diameter), situated dorso-laterally on head. Antennae inserted at latero-anterior margins of frons, anterior to eyes, distance between antennal insertions longer than distance from either insertion to margin of eye; antennae as described for the genus, except antennomere 1 longer, *ca*. as long as antennomeres 2–4 together; antennomeres 5–10 distinctly transverse. Mandible strong, rather elongate, internal teeth situated close to mandibular apex. Labrum only partly preserved, but obviously transverse. Pronotum 1.3 times as wide as long, wider than head, with distinct anterior angles, and broadly rounded posterior angles. Elytra, legs and abdomen as described for the genus, but only middle coxae can be traced; prototergal glands not visible, and only tergite III with two basal carinae, tergites IV and V with one, bases of other tergites not visible. Wings present.

Comparison. This species differs from all other congeners in the remarkable body coloration. Additionally, it is significantly larger than *P. ambiguus*, *P. chinensis* and *P. fossilis*.

Etymology. The name of the new species is a Latin adjective that means "wonderful". It refers to the very attractive color pattern of this species.

Paleowinus chinensis Solodovnikov et Yue, sp. n.
(Figs 38, 39, 41 and 42, S17 and S18)

Material examined. Holotype, male, CNU-COL-NN2008240P (part) and CNU-COL-NN2008240C (counterpart; CNUB).

Locality and horizon. Liutiaogou Village, Ningcheng County, Inner Mongolia, China, Yixian Formation, Early Cretaceous.

Measurements. TBL 14 mm, AL 2.3, HL (from base of right antenna to posterior margin of head capsule) 1.8, PL 2.2, PW 5.4, EL 2.6.

Description. Head capsule slightly elongate, but shape not very clear; antennae inserted at anterior margin of frons, anterior to eyes; distance between antennal insertions unclear but seemingly larger than distance from antenna to internal margin of eye; antennomere 1 *ca.* as long antennomeres 2 and 3 combined, other antennomeres also as described for the genus. Mandibles poorly preserved, but seemingly of similar shape to other species of the genus. Maxillary and labial palps as described for the genus. Pronotum apparently slightly longer than wide, with distinct anterior angles and broadly obtuse posterior angles. Elytra, meso- and metathorax, as well as legs as described for the genus, these parts overall not well preserved; in particular, anterior tarsi not preserved. Hind wings well developed. Abdomen as described for the genus: tergites III and V each with two basal carinae, apparently tergite IV also; bases of other tergites not visible.

Comparison. *Paleowinus chinensis* is distinctly smaller than *P. mirabilis* and *P. rex* and larger than *P. ambiguus*. It also has a narrower head capsule than *P. ambiguus* and smaller eyes than *P. fossilis*.

Etymology. The name of the new species is a Latinized adjective that means "Chinese". It refers to the country where the specimen was collected and where research on fossil Staphylinidae is currently very active.

Tribe Staphylinini Latreille, 1802

Incertae sedis

Genus *Durothorax* Solodovnikov et Yue gen. n.
(Figs 47 and 48, S22)

Type species. *Durothorax creticus* Solodovnikov et Yue sp. n.

Description. Head capsule slightly elongate, with distinct neck constriction, with infraorbital ridges extending from base of head to base of mandible and with clear postgenal ridges; gular sutures slightly arcuate, forming wide gula. Eyes small, tempora nearly 4 times as long as eyes. Eleven-segmented antennae inserted at frons, anteromedially from eyes, antennal insertions not visible but obviously not concealed under frontal projections; antennomere 1 moderately elongate, roughly as long as antennomeres 2 and 3 combined, the latter two subequal in length; antennomere 4 longer than wide, and as long as antennomere 3; antennomeres 5–10 relatively short, becoming transverse towards antennal apex, last (antennomere 11) slightly longer than wide, ovoid in shape. Mandibles poorly preserved. Labrum and labium not preserved. Maxillary palps with fusiform apical segment *ca.* 2.5 times as long as wide, longer than penultimate segment. Shape of pronotum not clear, but pronotal hypomera apparently inflexed under pronotum; anterior angles of pronotum strongly produced over anterior margin of prosternum, latter with slightly concave anterior margin; prothorax without antesternal sclerites; notosternal suture well developed; prosternum poorly preserved, but seemingly with distinct sternacostal ridge and, at least along basisternum, without longitudinal median carina; caudal area of ventral aspect of prothorax behind anterior coxae seemingly fully sclerotized (spiracles not visible). Elytra about as long as pronotum, their shape unclear; their poorly preserved epipleural area with a likely epipleural ridge. Mesothorax short, with sharp mesocoxal process; mesocoxae contiguous. Metathorax elongate. All legs moderately long with coxae typical for the tribe Staphylinini; posterior coxae with moderately exposed latero-dorsal portion; tibiae, where seen externally, without strong setae and spines; only anterior tarsi with fully preserved segmentation, 5-segmented. Abdomen elongate, with two pairs of paratergites on tergites III–VI; paratergites on each side of abdominal segment well separated from each other; paratergites of segment VII obscured by state of preservation; apical margin of sternite VIII simple, without medial concavity; lateral tergal sclerites IX produced into apically inflated and sharp processes; male and female abdominal features unknown; abdominal tergites III–VII each with one basal carina.

Comparison and systematic notes. Based on our cladistic analysis, *Durothorax* is sister lineage to all other Staphylinini. Because of an unresolved polytomy at the base of Staphylinini consisting of the extinct species *Cretoquedius distinctus*, *C. dorsalis* and *C. infractus*, and the rest of the tribe (Fig. 5); the incomplete morphologies of fossils; and the overall agreement of *Durothorax creticus* with the diagnosis of Staphylinini, we place all of these extinct lineages in that tribe. Furthermore, the tribe Staphylinini in this new expanded sense is supported by one unambiguous synapomorphy (clade 4 in Fig. 7: 7-1, presence of the postgenal ridge).

Among the early fossil fauna of Staphylininae, *Durothorax* can be distinguished by its head, which has a well developed neck constriction, and the postgenal ridges. *Durothorax* is distinguished from the genus *Cretoquedius* by the fully sclerotized postcoxal part of the prothorax. Among recent Staphylinini, the genus *Indoquedius* has a similarly sclerotized postcoxal area of prothorax, but *Durothorax* differs from *Indoquedius* by the very small eyes and narrow (not expanded) anterior tarsi.

Etymology. The name of the new genus is derived from the Latin "durus" (hard) and "thorax" (thorax), and refers to the strongly sclerotized postcoxal area of the genus; it is masculine in gender.

Durothorax creticus Solodovnikov et Yue sp. n.
(Figs 47 and 48, S22)

Material examined. Holotype, sex unknown, CNU-COL-LB2008235 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 8 mm, AL 1.3, HL (from distal visible margin formed by closed mandibles to neck constriction) 1.0, PL 1.5, EL 1.5, ATL 0.5..

Description. The species description coincides with the above genus description.

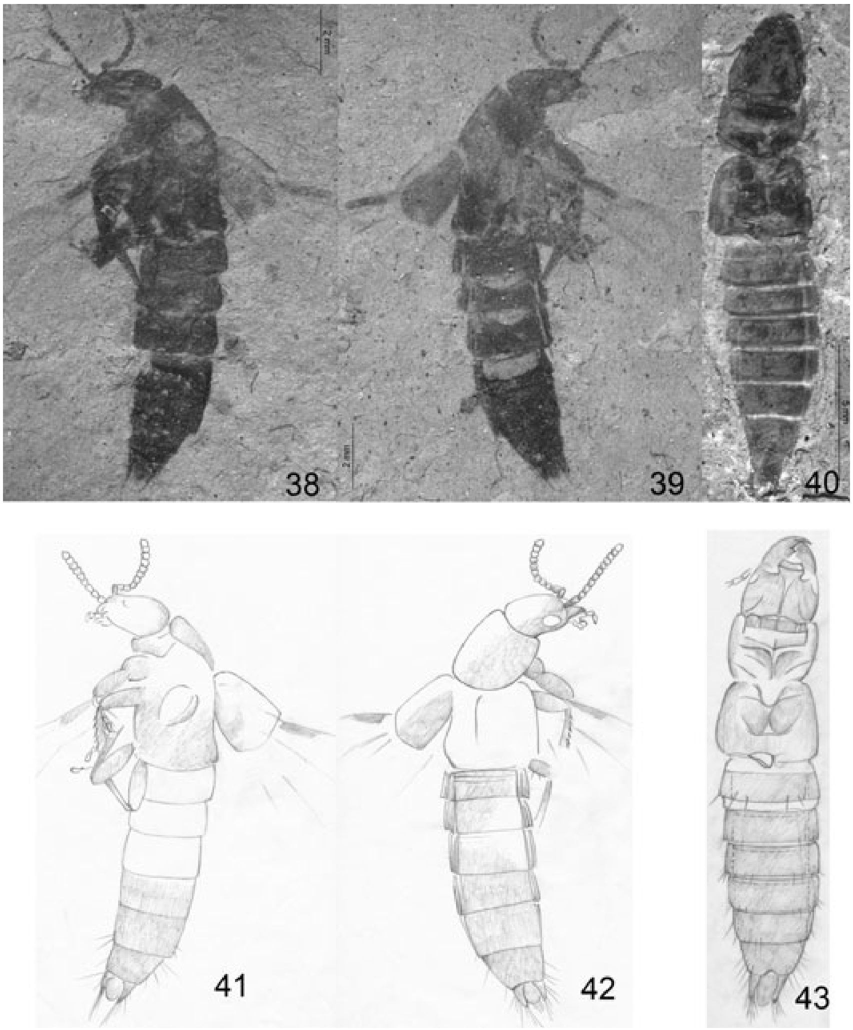
Comparison. See above under *Durothorax*.

Etymology. The species name is a Latinized adjective referring to the Cretaceous period, when the species lived.

Genus *Cretoquedius* Ryvkin, 1988 (Figs 49–59, S23–27)

Type species. *Cretoquedius oculatus* Ryvkin, 1988.

Redescription. Head with distinct neck constriction, without fronto-clypeal suture, with infraorbital ridges and distinct postgenal and ventral basal ridges (all ridges visible only in *C. distinctus*); gular sutures strongly arcuate, leaving very narrow gula in middle of head capsule; eyes very large to moderate in size, their longitudinal diameter equal to shorter than tempora. Eleven-segmented antennae inserted at frons, antero-medially from eyes, with distance between antennal insertions distinctly longer than distance from antennal insertion to inner margin of eye; antennal insertions not concealed; antennomere 1 moderately elongate, roughly as long as antennomeres 2 and 3 combined, antennomeres 4–10 relatively short, from about as long as wide to distinctly transverse, last (antennomere 11) about as long as wide or slightly elongate, dome-shaped. Mandibles poorly preserved in most examined specimens, but seemingly moderately elongate, broad at base, robust, with sharp apex and at least one tooth internally (as seen in *C. distinctus*). Labrum poorly preserved but distinctly strongly transverse. Maxillary palps with fusiform apical segment about 3 times as long as wide and longer than penultimate segment. Labial palps not preserved. Pronotum distinctly transverse to about as long as wide, but always with distinct anterior angles, broadly rounded, indistinct posterior angles, and sides broadly rounded; pronotal hypomera poorly visible, unclear if postcoxal process present; pronotosternal sutures well developed; prosternum with sharp longitudinal carina along furcasternum. Mesothorax short; mesosternum with sharp intercoxal process; mesocoxae almost contiguous; mesoscutellum with two basal carinae. Elytra moderately elongate, without distinct punctation or striae, seemingly without epipleural ridge. Metathorax moderately elongate. Hind wings well developed. All legs moderately long; all coxae of structure typical for tribe Staphylinini; posterior coxae about as long as wide, with laterodorsal portion moderately exposed in ventral view; anterior and middle tibiae (where visible) with setae and spines along external sides; tarsal formula 5–5–5, anterior tarsi with dilated tarsomeres I–IV. Abdomen elongate, with two pairs of paratergites on tergites III–VII; paratergites on each side of a segment well separated from each other; male sternite VIII simple, without medial concavity, male lateral tergal sclerites IX produced into apically inflated and

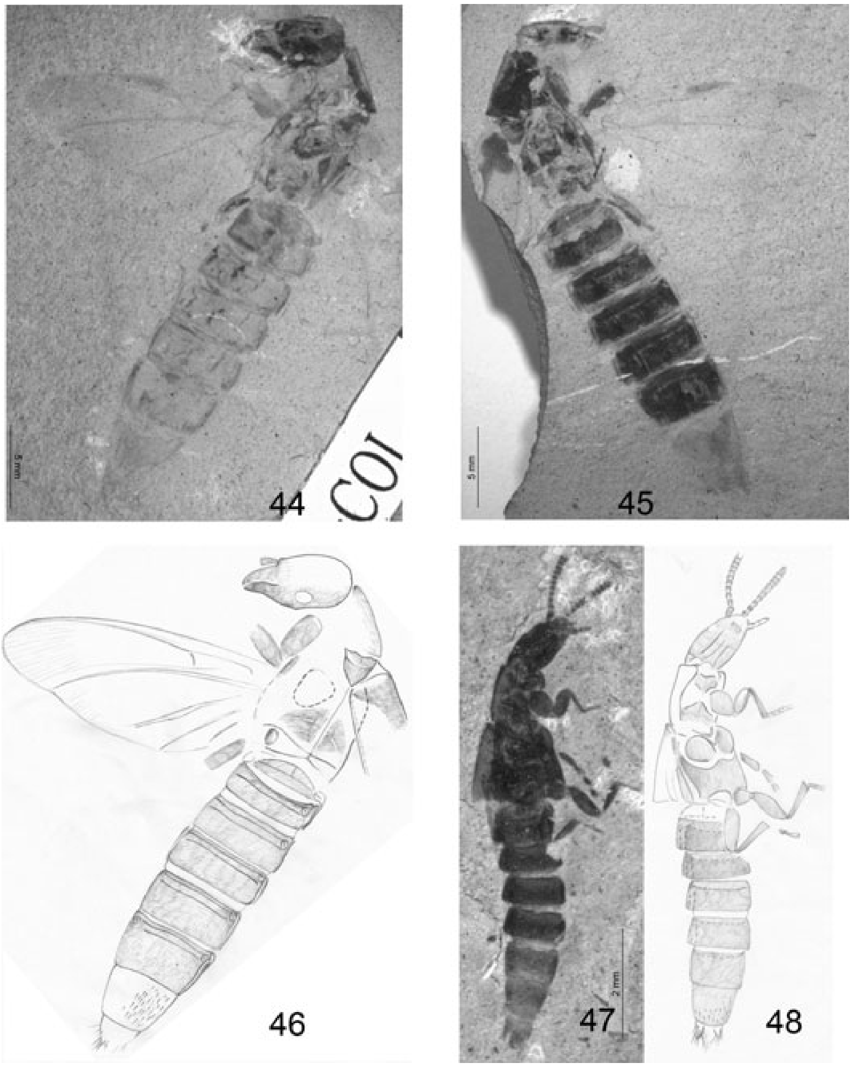


Figs 38–43. New species of the tribe Arrowinini and similar unnamed genus from Yixian Formation: 38, 39, 41, 42, *Paleowinus chinensis*; 40, 43, Gen. 1 sp.; 38–40, photos; 41–43, drawings (in Fig. 41, *P. chinensis* is reconstructed fom left ventro-lateral view, in Fig. 42, same species but reconstructed from right dorso-lateral view; in Fig. 43, paratergites and basal carinae of abdominal tergites located on the side facing away from the viewer shown in dotted lines).

obtuse processes, with bunches of long setae; male sternite IX usually entire; female secondary sexual structures unknown (all available specimens are either males or have poorly preserved abdominal apices); abdominal tergites III–VII with one basal carina each; abdominal segments without fringes of long stout setae, but covered with more or less dense short setation.

Comparison. *Cretoquedius* differs from *Durothorax* in the non-sclerotized postcoxal area of the prothorax, the medially very narrow gula, and the apically obtuse processes of lateral tergal sclerites IX. *Cretoquedius* differs from *Thayeralinus* in having a distinct neck constriction and more transverse antennomeres 4–9, well separated paratergites at each side, a weakly developed abdominal segment II, no antesternal plates, and no epipleural ridge. *Cretoquedius* differs from *Paleowinus* by the distinct neck, well developed postgenal and ventral basal ridges, abdominal tergites with only one basal carina (two in *Paleowinus*), and mesoscutellum with two basal carinae (one in *Paleowinus*).

Remarks. As follows from the phylogenetic analysis, the placement of the new fossil species *Cretoquedius distinctus*, *C. dorsalis*, and *C. infractus* to *Cretoquedius*, the genus whose hitherto only known species is a sister group to *Astrapeus* (Figs 5 and 7), makes *Cretoquedius* a genus of convenience. However, since all new species share the incomplete diagnosis of *Cretoquedius* and their phylogenetic position remains largely unresolved (Fig. 5), a composite extinct genus *Cretoquedius* is the most practical solution.



Figs 44–48. New species of Staphylininae from Yixian Formation: 44–46, *Paleowinus rex* (tribe Arrowinini); (44, holotype, counterpart; 45, holotype, part); 47, 48, *Durothorax creticus* (tribe Staphylinini); 44, 45, 47, photos; 46, 48, drawings (in Fig. 46, *P. rex* is reconstructed fom left dorsolateral view, left middle coxal cavity facing away from the viewer and contours of thorax hidden under right elytron and left wing shown in dotted lines. In Fig. 48, *D. creticus* reconstructed from right ventro-lateral view; paratergites and carinae on abdominal tergites facing away from the viewer shown in dotted lines).

Cretoquedius distinctus Solodovnikov et Yue sp. n.
(Figs 49, 50, 52 and 53, S23 and S24)

Material examined. Holotype, male, CNU-COL-LB2008673P (part) and CNU-COL-LB2008673C (counterpart; CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 8 mm, AL 1.9, HL (from base of labrum to anterior margin of pronotum) 1.0, HW 1.2, PL 1.1, PW 1.3, EL (from the level of posterior margin of pronotum to the most distal part of elytral posterior margin) 1.8, EW 1.9, ATL 0.9, MTL 1.0.

Description. Head as described for the genus, with relatively large eyes (eye diameter *ca.* as long as temple); gular sutures arcuate, running very close to each other in middle part of head capsule, strongly diverging anterad, and slightly diverging near occipital foramen. Antennae characteristic for genus, with antennomere 3 distinctly longer than 2. Mouthparts as in the the genus description. Pronotum slightly wider than long, with blunt but distinct anterior angles, and broadly rounded posterior angles, with relatively narrow hypomera; in other details thorax as for genus; pronotal hypomera wide; basisternum of prosternum strongly transverse; furcasternum longer than basisternum, with distinct sharp longitudinal carina. Elytra relatively oblong, slightly diverging posterad. Meso- and metathorax as for genus. Legs as in the genus description; anterior and middle tibiae with distinct spines or spine-like strong setae externally; anterior legs slightly shorter than middle and posterior legs. Abdomen as described for the genus, except male sternite IX slightly emarginate apically.

Comparison. *Cretoquedius distinctus* differs from *C. oculatus* (Ryvkin, 1988, fig. 2) by the much smaller eyes. The smaller body size and slightly transverse pronotum distinguish *C. distinctus* from *C. dorsalis*. From *C. infractus*, *C. distinctus* also differs in the smaller body size, much larger eyes, and the less pronounced anterior angles of the pronotum.

Etymology. The species name is the Latin adjective meaning "distinct". It refers to the exceptionally high quality of preservation of the holotype.

Cretoquedius infractus Solodovnikov et Yue sp. n.
(Figs 55, 56 and 58, S26 and S27)

Material examined. Holotype, female, CNU-COL-LB200951P (part) and CNU-COL-LB200951C (counterpart; CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 12.5 mm, AL 2.0, HL 1.3, HW 1.5, PL 1.4, PW 1.6, EL 2.3, EW 1.6, ATL 0.7.

Description. Head with distinct neck constriction and infraorbital ridges; neck relatively broad; traces of gular sutures indicate gula as described for the genus. Antennal insertions poorly preserved but antennae seemingly inserted at anterior margin of frons; eyes very small, tempora 3.5 times as long as longitudinal diameter of eye; antennae as described for the genus. Pronotum slightly wider than long, about as wide as head, widest around middle, with distinct anterior angles and broadly rounded posterior angles. Elytra distinctly longer than pronotum. Mesoscutellum seemingly with one transverse carina. Hind wings seemingly well developed, but venation poorly preserved. Middle and posterior legs poorly preserved; anterior legs with dilated tarsi. Abdomen as described for the genus, covered by short, dense setae. Ovipositor with distinct proximal and distal gonocoxites.

Comparison. *Cretoquedius infractus* differs from its congeners by its much smaller eyes. Unlike *C. dorsalis*, in which the eyes were not preserved, *C. infractus* has a distinctly transverse pronotum.

Etymology. The species name is the Latin adjective that means "broken". It refers to the detached forebody of the holotype.

Cretoquedius dorsalis Solodovnikov et Yue sp. n.
(Figs 51 and 54, S25)

Material examined. Holotype, sex unknown, CNU-COL-LB2008058 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

Measurements. TBL 11.5 mm, HL (from distal contour of closed mandibles to anterior margin of pronotum) 1.6, HW 1.5, PL 1.7, PW 1.8, EL 1.8.

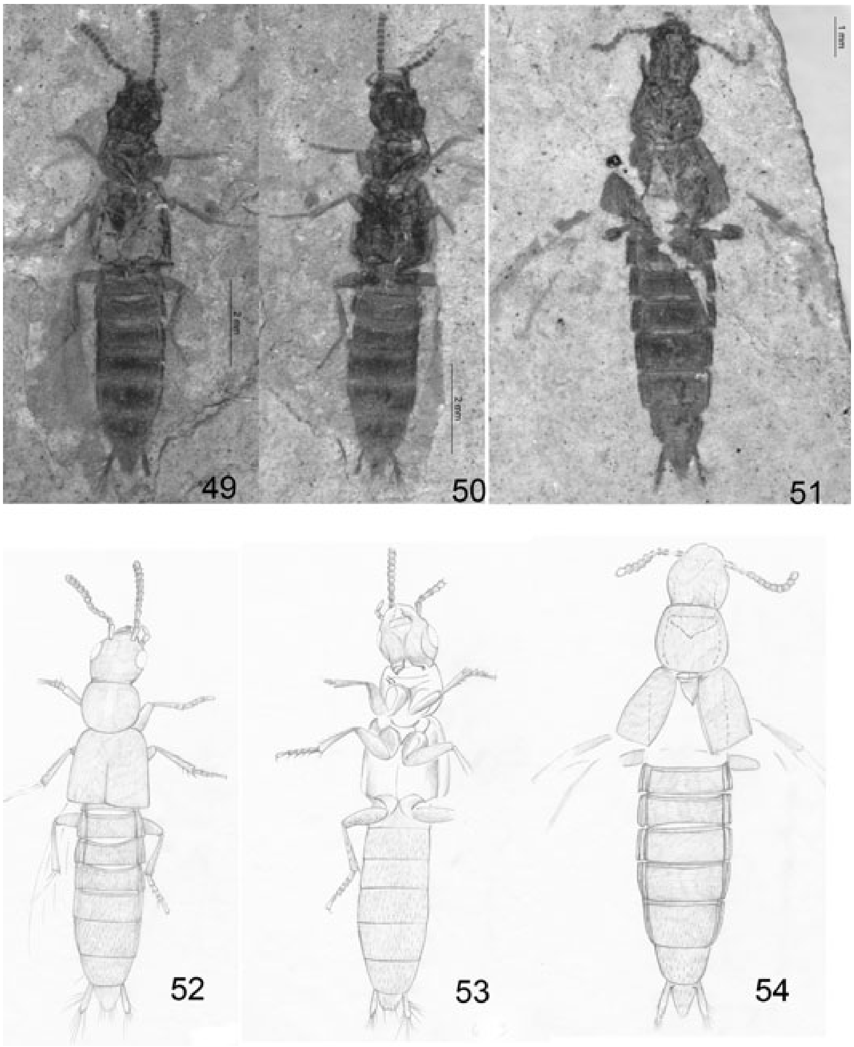
Description. Head capsule round, with distinct traces of infraorbital ridges; neck constriction distinct, but neck relatively broad; traces of gular sutures indicate gula as described for the genus. Antennae poorly preserved but seemingly at anterior margin of frons; eyes not preserved; antennomeres as described for the genus, with traces of antennomere 1, longer than antennomeres 2 and 3 together; antennomere 3 longer than 2, antennomere 2 longer than 4. Pronotum about as wide as long, wider than head, widest behind middle, with smooth but distinct anterior angles and broadly rounded posterior angles. Elytra slightly longer than pronotum. Mesoscutellum with two transverse carinae. Hind wings well developed, but venation poorly preserved. Legs, except posterior femora, not preserved. Abdomen as described for the genus, covered by short, dense setae.

Comparison. *Cretoquedius dorsalis* is the large species in the genus, much larger than *C. oculatus* (Ryvkin, 1988, fig. 2). It can be distinguished from *C. distinctus* and *C. infractus* by the relatively longer pronotum.

Etymology. The species name is the Latin adjective that means "dorsal". It refers to the dorsal side of the body that is better preserved than the ventral side in the holotype.
Gen. 2 sp. (Figs 57 and 59)

Material examined. sex unknown, CNU-COL-LB2008107 (CNUB).

Locality and horizon. Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, Yixian Formation, Early Cretaceous.

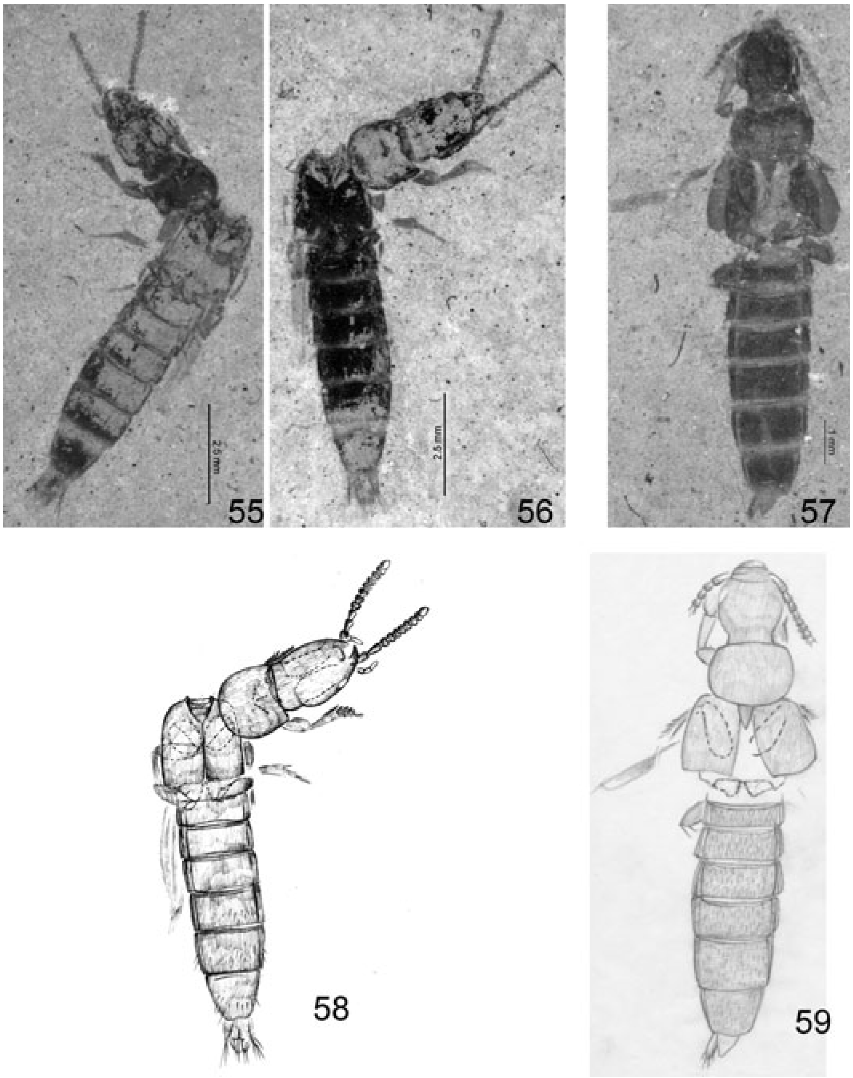


Figs 49–54. New species of *Cretoquedius* (tribe Staphylinini) from Yixian Formation: 49, 50, 52, 53, *C. distinctus* (49, holotype, part; 50, holotype, counterpart); 51, 54, *C. dorsalis*; 49-51, photos; 52-54, drawings (in Fig. 52, *C. distinctus* is reconstructed from dorsal side; in Fig. 53, same species reconstructed from ventral side; in Fig. 54, some ventral structures of head and thorax facing away from the viewer shown in dotted lines).

Measurements. TBL 11 mm, HL 1.6, PL 1.4, PW 1.8, EL 1.7, EW 1.5, ATL 0.7.

Description. Head capsule broadly rounded, with gradual but distinct neck constriction; eyes relatively small, tempora nearly 3 times as long as eyes. Labrum strongly transverse. Antennae inserted at anterior margin of frons, anterior to eyes, distance between them longer than distance from either insertion to margin of eye; antennomere 1 slightly longer than antenomeres 2 and 3; antennomere 4 only slightly shorter than 3, the following antennomeres (only 5–9 are preserved) about as long as wide. Mouthparts not preserved. Pronotum distinctly transverse, with slightly distinct anterior angles, broadly rounded sides, and indistinct posterior angles. Elytra distinctly longer than pronotum. Metathorax moderately long. Hind wings present, but very poorly preserved. Shape of legs generally as described for the genus, but anterior tarsi very strongly dilated and anterior tibiae robust and rather broad; middle tibae with distinct lateral spines; posterior coxae slightly wider than long, details of their structure poorly preserved. Abdomen oblong, its structure as described for the genus; only dorsal side of abdomen preserved.

Comparison. Gen. 2 sp. resembles *Cretoquedius* and the recent genus *Quedius*. Poor preservation of Gen. 2 sp. makes a proper comparison impossible. It differs from from all species of *Cretoquedius* by its relatively narrower neck and strongly transverse pronotum.



Figs 55–59. New species of *Cretoquedius* and similar unnamed genus (tribe Staphylinini) from Yixian Formation: 55, 56, 58, *C. infractus* (55, holotype, part; 56, holotype, counterpart); 57, 59, Gen. 2 sp.; 55–57, photos; 58, 59, drawings (in these figs., *C. infractus* and Gen. 2 sp. reconstructed from dorsal side, some ventral structures of head and thorax facing away from the viewer shown in dotted lines).

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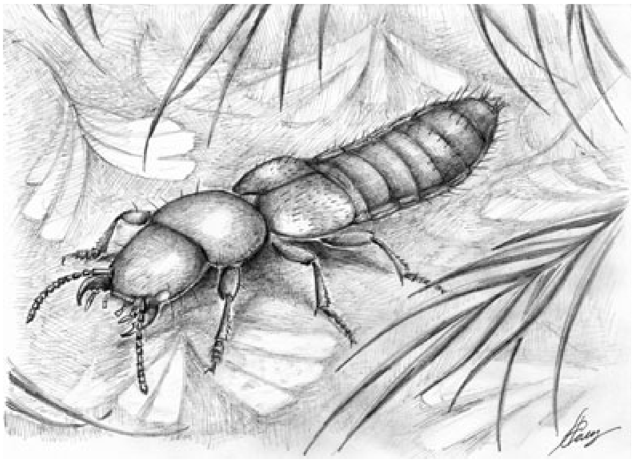

Fig. 60. *Thayeralinus fieldi* hunting in Early Cretaceous leaf litter. Artistic reconstruction by A. Solodovnikov, based on the holotype.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. File Staph_fossils_matrix.nex. Data matrix in Nexus format. "?", missing data; "–", inapplicable character states.

Table S1. Leaf stability index of taxa calculated across 300 most parsimonious trees of the maximum parsimony analysis 5 using Phyutility 2.2 (Smith and Dunn, 2008). The higher the index, the more stable is the phylogenetic position of a taxon aross the explored tree space.

Fig. S1. Result of analysis 1 (maximum likelihood, performed in Garli, recent taxa only). Controversial, rather terminal position of Paederinae and Pseudopsinae marked in red.

Fig. S2. Result of analysis 10 (maximum likelihood, performed in Garli, recent and fossil taxa). Only fossils with leaf stability index > 0.95 (Table S1) are included. Names of recent species in bold font, names of fossil species in regular font, marked +. Controversial, rather terminal position of Paederinae, *Apticax* and Pseudopsinae marked in red.

Fig. S3. *Mesostaphylinus elongatus*, holotype.

Fig. S4. *M. yixianus*, holotype.

Fig. S5. *M. antiquus*, holotype .

Fig. S6. *Cretoprosopus problematicus*, holotype .

Fig. S7. *Paleothius gracilis,* holotype, part.

Fig. S8. *Paleothius gracilis,* holotype, counterpart.

Fig. S9. *Thayeralinus fieldi,* holotype, part.

Fig. S10. *Thayeralinus fieldi*, holotype, counterpart.

Fig. S11. *Thayeralinus longelytratus*, holotype.

Fig. S12. *Thayeralinus giganteus,* holotype, counterpart.

Fig. S13. *Thayeralinus glandulifer*, holotype .

Fig. S14. *Paleowinus fossilis*, holotype .

Fig. S15. *Paleowinus ambiguus*, holotype.

Fig. S16. *Paleowinus mirabilis*, holotype .

Fig. S17. *Paleowinus chinensis*, holotype, part .

Fig. S18. *Paleowinus chinensis*, holotype, counterpart.

Fig. S19. *Genus 1 sp.,* specimen CNU-COL-LB2008174.

Fig. S20. *Paleowinus rex,* holotype, part.

Fig. S21. *Paleowinus rex,* holotype, counterpart.

Fig. S22. *Durothorax creticus*, holotype.

Fig. S23. *Cretoquedius distinctus*, holotype, part.

Fig. S24. *Cretoquedius distinctus,* holotype, counterpart.

Fig. S25. *Cretoquedius dorsalis*, holotype .

Fig. S26. *Cretoquedius infractus,* holotype, part .

Fig. S27. *Cretoquedius infractus,* holotype, counterpart .

Fig. S28. *Genus 2 sp.,* specimen CNU-COL-LB2008107.