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Description of a new species of Glaresidae (Coleoptera: Scarabaeoidea) from the Jehol Biota of China with a geometric morphometric evaluation

Ming Bai[1,2], Rolf G. Beutel[2], Wangang Liu[1,3], Sha Li[1,3], Mengna Zhang[1,3], Yuanyuan Lu[1,3], Keqing Song[1,3], Dong Ren[*,4] & Xingke Yang[*,1]

[1] Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Box 92, Beichen West Road, Chaoyang District, Beijing, 100101, China; Ming Bai [baim@ioz.ac.cn]; Wanggang Liu [liuwg@ioz.ac.cn]; Sha Li [lisha1988cc@163.com]; Mengna Zhang [ldhp22@163.com]; Yuanyuan Lu [luyuanyuan442@163.com]; Keqing Song [songkq@ioz.ac.cn]; Xingke Yang * [yangxk@ioz.ac.cn] — [2] Institut für Spezielle Zoologie und Evolutionsbiologie, FSU Jena, Jena, 07743, Germany; Rolf G. Beutel [Rolf.Beutel@uni-jena.de] — [3] University of Chinese Academy of Sciences, Yuquan Road, Shijingshan, Beijing, 100039, P.R. China — [4] College of Life Sciences, Capital Normal University, Beijing, 100037, China; Dong Ren* [rendong@cnu.edu.cn] — * Corresponding authors

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Abstract

Glaresis tridentata Bai, Beutel & Ren **sp. nov.** (Scarabaeoidea: Glaresidae) from the Yixian Formation of western Liaoning Province, NE China is described and illustrated. A geometric morphometric analysis of three character systems (head, metatibia and aedeagus) was carried out including 136 specimens from 44 species of three genera of extant and extinct Glaresidae. The variation in these features between *Glaresis tridentata* Bai, Beutel & Ren **sp. nov.** and the other species was estimated based on Principal Component Analysis (PCA), Canonical Variate Analysis (CVA), Discriminant function analysis (DFA) and Minimum Spanning Tree (MST) approaches. The results suggest that Glaresidae, likely the sister group of all other extant Scarabaeoidea, had been established in the Early Cretaceous and contained larger species than today. The assignement of the new species to the genus *Glaresis* is supported. The validity of the genera *Lithoglaresis* and *Cretoglaresis* is questionable.

Key words

Fossil, Glaresidae, Yixian Formation, new species, geometric morphometrics.

1. Introduction

Glaresidae is a small and uniform family of Scarabaeoidea occurring on all continents except for Australia and Antarctica. About fifty extant species are assigned to the genus *Glaresis* and six extinct species are placed in three genera (Scholtz 1982; Scholtz et al. 1987, 1994; Bai et al. 2010). An additional extinct species is described in the present study. Glaresidae was considered as the "most primitive living scarabaeoid group" and as "the sister group of the rest of the Scarabaeoidea" by Scholtz et al. (1994). It has apparently preserved a considerable number of ground plan character states of the superfamily (Scholtz et al. 1994). In a phylogenetic analysis based on morphology, *Glaresis* was indeed placed as the sister taxon of the remaining Scarabaeoidea (Browne & Scholtz 1999).

Until 2007, Glaresidae were not known from the fossil record (Krell 2006). Three extinct species in two new genera of Glaresidae were described by Nikolajev (2007) based on relatively poorly preserved material. The description of *Glaresis cretacea* Nikolajev, for example, was based on a single hind leg. *Cretoglaresis nana* Nikolajev and *Lithoglaresis ponomarenkoi* Nikolajev were described based on incomplete specimens, whereas a second species of *Cretoglaresis*, *C. ovalis*, was represented by a fairly complete body fossil (Nikolajev 2009). An almost complete and well-preserved fossil, *Glaresis orthochilus*, was published by Bai et al. (2010). It confirmed the presence of Glaresidae in the Mesozoic. The new extinct species, *Glaresis tridentata* Bai, Beutel & Ren **sp. nov.** (Figs. 1–2), is the second almost complete and well-preserved glaresid fossil. It provides further evidence on the early evolutionary history of the family.

Head, legs and the aedeagus are the most commonly used body parts in studies on the taxonomy and phylogeny of Glaresidae (Fall 1907; Brown 1928; Petrovitz 1968a,b; Gordon 1970, 1974; Paulian 1981; Scholtz 1983; Warner 1995; Bai et al. 2010; Verdu & Galante 2011; Anton & Beutel 2012). A deep incision between the genal canthus and clypeus is a diagnostic character for the family. The morphology of the hind leg and aedeagus are also crucial for species identification. However, the variability of these characters is still largely unexplored. Consequently we present a geometric morphometric analysis of the head, metatibia and aedeagus, body parts which are preserved in *Glaresis tridentata* **sp. nov.** We applied Principal Component Analysis (PCA), Canonical Variate Analysis (CVA), Discriminant function analysis (DFA) and the Minimum Spanning Tree (MST) approach. The results are evaluated with respect to the validity of the new species and the character quantitative comparison in extinct and extant members of the family. A cladistic evaluation of the relationships within the family with a representative sampling of extinct and extant species would be clearly beyond the scope of this contribution. Moreover, this is greatly impeded by the inaccessibility of many characters in the fossil specimens.

2. Material and methods

2.1. Taxa included in the geometric morphometric analysis

This study is based on 44 species of three genera of extant and extinct Glaresidae. Thirty-eight extant and six extinct species of three genera of Glaresidae were included in the geometric morphometric analysis (Table 1). More than one specimen was used for 12 species and 136 specimens in total. The samples of extant species cover all zoogeographic regions where glaresids occur and represent ~80% of the species known worldwide. Three body parts (head, metatibia and aedeagus) were examined and analysed. Images of the head were extracted from 117 specimens (4 extinct), (Table 1; Fig. 3), metatibial images from 114 (3 extinct) (Table 1; Fig. 4), and images of the aedeagus from 26 (2 extinct) (Table 1; Fig. 5). Intra-specific variation was inferred and discussed based on 12 species, which were all represented by more than one specimen. Complete information for the full taxon sampling of 44 species was not available.

The fossil specimen studied was collected near Chaomidian village, Beipiao City, from the Yixian Formation of western Liaoning, China. Recent studies have confirmed that the Yixian Formation belongs to the Early Cretaceous. The precise range is probably 129.7–122.1 million years ago (Barremian to early Aptian) (Yang et al. 2007; Chang et al. 2009). The strata of Yixian Formation, which are mainly lacustrine sediments intercalated with volcaniclastics (Ren et al. 1995, 2010), are rich in insect fossils (Zhang et al. 2006; Chang & Ren 2008; Zhang et al. 2010; Bai et al. 2010, 2011a, 2012a, 2013; Gao et al. 2012, 2013; Yan et al. 2013). The specimen was examined with a LEICA MZ 12.5 dissecting microscope equipped with a drawing tube. It is deposited in the fossil insect collection of the Key Lab of Insect Evolution & Environmental Changes, The College of Life Science, Capital Normal University, Beijing, China (CNUB; REN Dong, Curator). Extant glaresid specimens are deposited in the Institute of Zoology, Chinese Academy of Sciences (Beijing), Museum of Comparative Zoology (MCZ) at Harvard University (Boston), Museum für Naturkunde (Berlin), Muséum National d'Histoire Naturelle (Paris), The National Museum of Natural History (Prague).

2.2. Geometric morphometric protocols

Geometric morphometrics can be used to determine shape differences, and the resulting phenograms from Procrustes distances can effectively indicate phenetic affinities between the samples, summarizing overall patterns of similarity (Bai & Yang 2007; Bai et al. 2011b, 2012b, 2013; Friedrich et al. 2013). The morphology of the three body parts (head, metatibia and aedeagus) accessible in the specimen of *Glaresis tridentata* Bai, Beutel & Ren **sp. nov.** was represented by curves. Each curve was based on homologous or corresponding criteria in geometric morphometrics of the head (see example in Fig. 3A), metatibia (see example in Fig. 4A) and aedeagus (see example in Fig. 5A), respectively. The curve obtained from the head was resampled into 100 semi-landmarks by equal length, the curve obtained from the metatibia was resampled into 60 semi-landmarks by equal length and the curve obtained from the aedeagus was resampled into 30 semi-landmarks by equal length. All semi-landmarks were converted to landmarks for subsequent analyses.

All images of three characters were extracted from the original references, except for *Glaresis tridentata* Bai, Beutel & Ren **sp. nov.** Due to the strong deformation of the head of *Glaresis tridentata* **sp. nov.** and *Glaresis orthochilus*, new images were reconstructed from

Table 1. List of species examined from Glaresidae for geometric morphometric analysis.

	Species	**Head**	**Metatibia**	**Aedeagus**
1	†*Cretoglaresis nana* Nikolajev, 2007		**1**	
2	†*Cretoglaresis ovalis* Nikolajev, 2009	**1**		**1**
3	†*Glaresis cretacea* Nikolajev, 2007		**1**	
4	†*Glaresis orthochilus* Bai, Krell & Ren, 2010	**1**	**1**	
5	†*Glaresis tridentata* **sp. nov.**	**1**	**1**	**1**
6	†*Lithoglaresis ponomarenkoi* Nikolajev, 2007	**1**		
7	*Glaresis arenata* Gordon, 1974	**1**		**1**
8	*Glaresis beckeri* Solsky, 1870	**11**	**5**	
9	*Glaresis canadensis* Brown, 1928	**1**	**1**	**1**
10	*Glaresis cartwrighti* Gordon, 1970	**1**	**1**	**1**
11	*Glaresis celiae* Scholtz, 1983		**1**	
12	*Glaresis clypeata* Van Dyke, 1928	**1**	**1**	**1**
13	*Glaresis confusa* Brown, 1928	**1**	**1**	**1**
14	*Glaresis dakotensis* Gordon, 1970	**1**	**1**	**1**
15	*Glaresis desperata* Scholtz, 1983		**1**	
16	*Glaresis ecostata* Fall, 1907	**5**	**7**	**1**
17	*Glaresis exasperata* Scholtz, 1983		**1**	
18	*Glaresis foveolata* Scholtz, 1983		**1**	
19	*Glaresis franzi* Paulian, 1981	**1**	**1**	
20	*Glaresis frivaldszkyi* Westwood, 1852 (syn. of *Glaresis rufa* Erichson, 1848)	**13**	**11**	
21	*Glaresis frustrata* Scholtz, 1983		**1**	
22	*Glaresis gordoni* Warner, 1995	**1**	**1**	**1**
23	*Glaresis handlirschi* Reitter, 1893	**8**	**6**	
24	*Glaresis hispana* (Baguena, 1959)	**1**	**1**	**1**
25	*Glaresis holmi* Scholtz, 1983		**1**	
26	*Glaresis holzschuhi* Petrovitz, 1968		**1**	
27	*Glaresis howdeni* Gordon, 1970	**1**	**1**	**1**
28	*Glaresis impressicollis* Petrovitz, 1965	**8**	**10**	**6**
29	*Glaresis inducta* Horn, 1885	**5**	**6**	**1**
30	*Glaresis knausi* Brown, 1928 (syn. of *Glaresis inducta* Horn, 1885)	**4**	**4**	
31	*Glaresis koenigsbaueri* Petrovitz, 1968	**1**	**1**	
32	*Glaresis longisternum* Scholtz, 1983		**1**	
33	*Glaresis medialis* Gordon, 1969	**1**	**1**	**1**
34	*Glaresis mendica* Horn, 1885	**5**	**4**	**1**
35	*Glaresis methneri* Petrovitz, 1965	**7**	**7**	**1**
36	*Glaresis minuta* Scholtz, 1983		**1**	
37	*Glaresis namibensis* Scholtz, 1983		**1**	
38	*Glaresis oxiana* Semenov, 1892	**2**	**2**	
39	*Glaresis penrithae* Scholtz, 1983		**1**	
40	*Glaresis phoenicis* Fall, 1907	**10**	**10**	**1**
41	*Glaresis rufa* Erichson, 1848	**18**	**11**	
42	*Glaresis texana* Gordon, 1970	**1**	**1**	**1**
43	*Glaresis thiniensis* Verdu & Galante, 2001	**1**	**1**	**1**
44	*Glaresis tripolitana* Petrovitz, 1968	**1**	**1**	
45	*Glaresis walzlae* Scholtz, 1983	**1**	**1**	
46	*Glaresis zvirgzdinsi* Warner, 1995	**1**	**1**	**1**

the left and right part before the analysis (Fig. 3B–G). Images were entered in tps-UTILS 1.38 (Rohlf 2006a) and Cartesian coordinates of curves were digitized with tps-DIG 2.05 (Rohlf 2006b). Landmark configurations were scaled, translated and rotated against the consensus configuration using the GLS Procrustes superimposition method (Bookstein 1991). The coordinates were analyzed using tps-RELW 1.44 (Rohlf 2006c) to calculate eigenvalues for each relative warp (Figs. 6A, 7A, 8A). The Canonical Variate Analysis (CVA) and Discriminant function analysis (DFA) analysis of the original landmark data and combined landmark data were based on

MorphoJ 1.06a (Klingenberg 2011) (Figs. 6B, 7B, 8B; Tables 2, 3). Minimum spanning trees (MST) were computed in PAST 3.01 (Hammer 2001). They have a weight less than or equal to the weight of every other spanning tree. Minimum spanning trees have direct applications in the design of networks, including computer networks, telecommunications networks, transportation networks, water supply networks, electrical grids, etc. (Graham & Hell 1985), and they were also applied in taxonomy (Sneath 1957).

3. Results

3.1. Taxonomy

Order Coleoptera Linnaeus, 1758
Family Glaresidae Semenov-Tian-Shanskij & Medvedev, 1932
Genus *Glaresis* Erichson, 1848 (type species: *Glaresis rufa* Erichson, 1848)

Glaresis tridentata **Bai, Beutel & Ren sp. nov.**
(Figs. 1, 2)

Description. Body length: 8.0 mm; width: 3.5 mm. Body shape: broadly oval. ***Head***: Slightly wider than long, broadest at very prominent and evenly rounded region including ocular epicanthus and compound eyes; incision between epicanthus and clypeus not recognizable, apparently absent. Clypeus large; anterior margin straight, slightly shorter than base of the head; anterolateral corners strongly rounded; lateral sides almost parallel. ***Pronotum***: Shape roughly trapezoid, with strongly rounded anterior and posterior edges; at least 1.9 × wider at posterior margin than long (possibly incompletely preserved); wider than head at anterior margin, widest at base; anterior pronotal margin very slightly concave; lateral edges straight, converging towards anterior margin. ***Elytra***: Shape roughly ovoid, with oblique shoulder region and rounded posteromesal edge; appearing short and broad, 1.9 × longer than wide in middle region, together almost twice as broad as pronotum; striae with eight regular rows of very distinct, large punctures; punctures not visible on anterior region of elytra. ***Scutellum***: Triangular, very large, 1.5 × wider than long. ***Legs****:* Protibia with 3 teeth on outer margin, widening towards apex, with the 2nd and 3rd teeth distinctly larger than the proximal one and the 2nd very slightly larger than the apical tooth; mesotibia moderately wide; metafemur moderately wide, very slightly widening distally; metatibia strongly dilated apically, outer margin lacking projection. ***Abdomen***: with five visible sternites; hind margin of last exposed sternite slightly rounded. ***Aedeagus****:* Relatively slender, spindle-shaped, gradually narrowing towards base, apex acuminate; border between parameres and median lobe not clearly recognisable.

Material examined. Holotype: male, well preserved body with elytra, registration No. CNU-COL-LB2010645, collected from Yixian Formation, near Chaomidian village, Beipiao City, Liaoning Province, China; specimen housed in the Key Lab of Insect Evolution & Environmental Changes, the College of Life Science, Capital Normal University, Beijing, China (CNUB).

Diagnosis. This species is distinct from the other glaresid fossils based on the combination of the following characters: large size (8.0 mm long); pronotum shape parabolic: at least 1.9 × wider than long (pronotum not complete), anterior margin of pronotum straight; lateral sides straight and gradually converging anteriorly; protibia with 3 teeth on outer margin.

Etymology. The Latin name refers to the 3 teeth on the external protibial margin.

3.2. Morphological variations of three character systems of Glaresidae

Morphological variations of the three character systems (head, metatibia and aedeagus) were analyzed using tpsSMALL (Rohlf 2003) based on 100, 60 or 30 semi-landmarks, respectively (Figs. 3–5).

Inter-specific comparisons. Even though the morphological variation within Glaresidae was the main goal of this study, we carried out an initial comparison of the head shape between Glaresidae and Aphodiinae. The result of this test showed that Aphodiinae was distant from the cluster formed by the included species of Glaresidae, whereas the head shape of *Glaresis tridentata* **sp. nov.** was placed within the morphological variations of the family.

Morphometric analyses found a strong correlation between the tangent shape and shape space. The correlation between the tangent space (Y) regressed onto Procrustes distance for head, metatibia and aedeagus were 0.999991, 0.999984 and 0.999999, respectively.

The first two relative warps of the curve for head, metatibia and aedeagus accounted for 54.521%, 66.923% and 83.268% of the variation among the species, respectively. These were computed by a singular-value decomposition of the weight matrix (Rohlf 1993). The first two relative warps were plotted to indicate variation along the two axes (Figs. 6A, 7A, 8A; fossil species indicated by black triangles, extant ones by black dots). The shape changes among different species implied by variation along the first two relative warp axes and shape changes are shown as deformations of the GLS (generalized least squares) reference, using thin-plate splines. The splines, which show the deformation of the curve in comparison to that of the reference, indicate the most significant de-

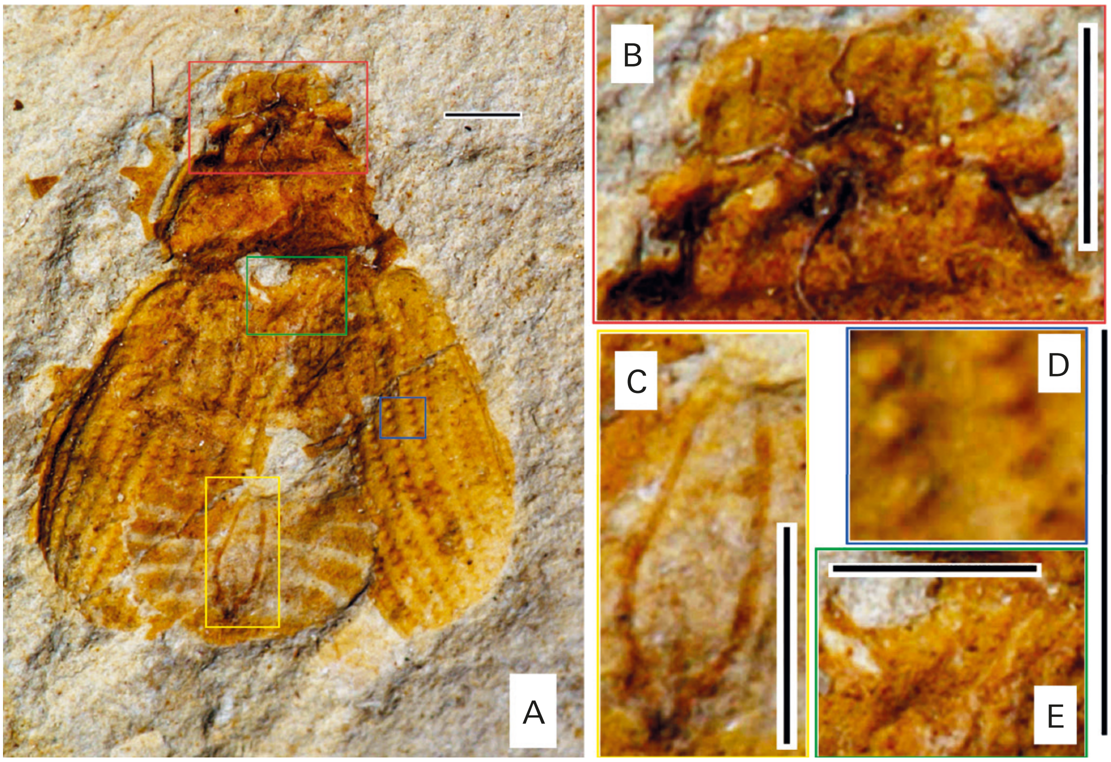

Fig. 1. A: *Glaresis tridentata* Bai, Beutel & Ren sp. nov., holotype, No. CNU-COL-LB2010645. **B**: Head. **C**: Aedeagus. **D**: Elytra (part). **E**: Scutellum. Scale bars represent 1 mm.

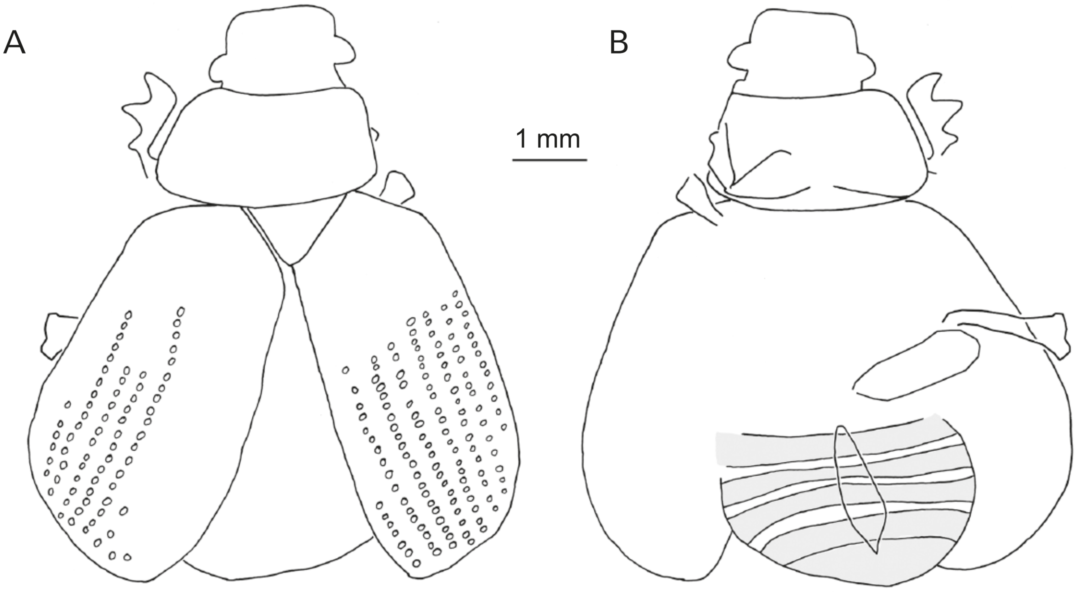

Fig. 2. *Glaresis tridentata* Bai, Beutel & Ren sp. nov., holotype, No. CNU-COL-LB2010645. **A**: Dorsal view. **B**: Ventral view (reconstruction).

formation, as it is situated furthest from the origin. The splines of all fossil species are also presented, except the reconstructed head of two fossil species, which are connected with original head of the fossils (Fig. 6A). The head morphology of *Glaresis tridentata* **sp. nov.** is very close to the origin of the plot from the first two PCA components, which represent the average shape of all samples (Fig. 6A). Minimum spanning trees (MST) shown the possible relationships among extinct and extant glaresid species for three characters were computed and mapped into the PCA plots (Figs. 6C, 7C, 8C).

Based on the above-mentioned differences from Principal Component Analysis (PCA), a Canonical Variate Analysis (CVA) and Discriminant function analysis (DFA) were carried out to test if *Glaresis tridentata* **sp. nov.** is significantly different from modern species or ex-

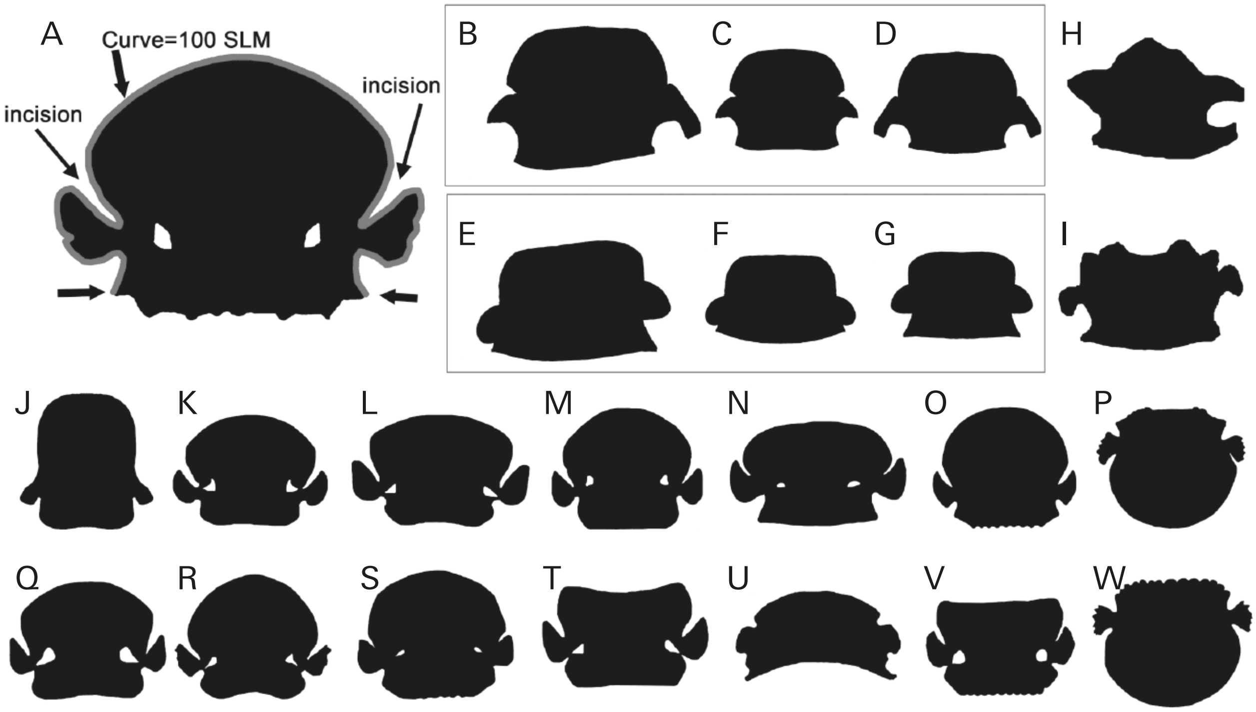

Fig. 3. Head morphology of extant and extinct Glaresidae. **A**: *Glaresis clypeata*, one curve was resampled into 100 semi-landmarks. **B**: *Glaresis orthochilus*, fossil, original. **C**: *Glaresis orthochilus*, fossil, reconstructed from left side. **D**: *Glaresis orthochilus*, fossil, reconstructed from right side. **E**: *Glaresis tridentata* **sp. nov.**, fossil, original. **F**: *Glaresis tridentata* **sp. nov.**, fossil, reconstructed from left side. **G**: *Glaresis tridentata* **sp. nov.**, fossil, reconstructed from right side. **H**: *Cretoglaresis ovalis*, fossil. **I**: *Lithoglaresis ponomarenkoi*, fossil. **J**: *Glaresis arenata*. **K**: *Glaresis canadensis*. **L**: *Glaresis cartwrighti*. **M**: *Glaresis confusa*. **N**: *Glaresis ecostata*. **O**: *Glaresis gordoni*. **P**: *Glaresis hispana*. **Q**: *Glaresis howdeni*. **R**: *Glaresis inducta*. **S**: *Glaresis koenigsbaueri*. **T**: *Glaresis mendica*. **U**: *Glaresis oxiana*. **V**: *Glaresis texana*. **W**: *Glaresis thiniensis*.

tinct glaresids in the three character systems (Figs. 6B, 7B, 8B). Mahalanobis distances and Procrustes distances among groups were computed (Table 2). All obtained *p*-values from permutation tests (10000 permutation rounds) for Mahalanobis distances or Procrustes distances between *Glaresis tridentata* **sp. nov.** and modern species were smaller than 0.05, except the *p*-values for Procrustes distances of the aedeagus. All obtained *p*-values from permutation tests (10000 permutation rounds) for Mahalanobis distances or Procrustes distances between *Glaresis tridentata* **sp. nov.** and glaresid fossils were higher than 0.05, except the *p*-values for Mahalanobis distances of the head and aedeagus. Almost all modern and extinct glaresid species were correctly assigned to their own groups, but not to the group represented by *Glaresis tridentata* **sp. nov.** based on the three characters using the DFA analysis (permutation test=1000) (Figs. 6B, 7B, 8B; Table 3). These results confirm that *Glaresis tridentata* **sp. nov.** is indeed statistically significantly different from all other species examined in this study. But it is closer to the other extinct species investigated here.

Intra-specific comparisons. All specimens belonging to same species were very close to each other in the PCA plots (Figs. 6C, 7C, 8C). The intra-specific variations are smaller than inter-specific variation based on the specimens in this study. In this case, these three characters are suitable to be used in Glaresidae taxonomy.

4. Discussion

For a reliable assignment of a specimen to Scarabaeoidea, it has to show at least one autapomorphy of this taxon, that in the ideal case should not be reduced in any terminal subordinated group at any period (Bai et al. 2013). In extinct members of Scarabaeoidea only characters of adults are available. Krell (2000) gave a list of autapomorphies for the group which are accessible in scarab fossils. *Glaresis tridentata* Bai, Beutel & Ren **sp. nov.** can be classified as a representative of Scarabaeoidea by the presence of distinct fixed teeth on the outer margin of the protibiae.

Reductions in the wing venation (Scholtz et al. 1994) and only five exposed abdominal sternites were suggested as autapomorphies of Glaresidae by Browne & Scholtz (1999). In a recent study five potential cephalic autapomorphies of the family were proposed (Anton & Beutel 2012): a deep incision between the lateral parts of the clypeus and frons allowing dorsal movements of the antennae, a transverse ridge posterior to the anterior clypeal margin, peg-like olfacory sensilla on the distal surface of the first two club segments (IX and X), a maxillary body with a deep dorsal longitudinal furrow bordered by the lacinia and pseudopalpifer, and a strongly convex mentum.

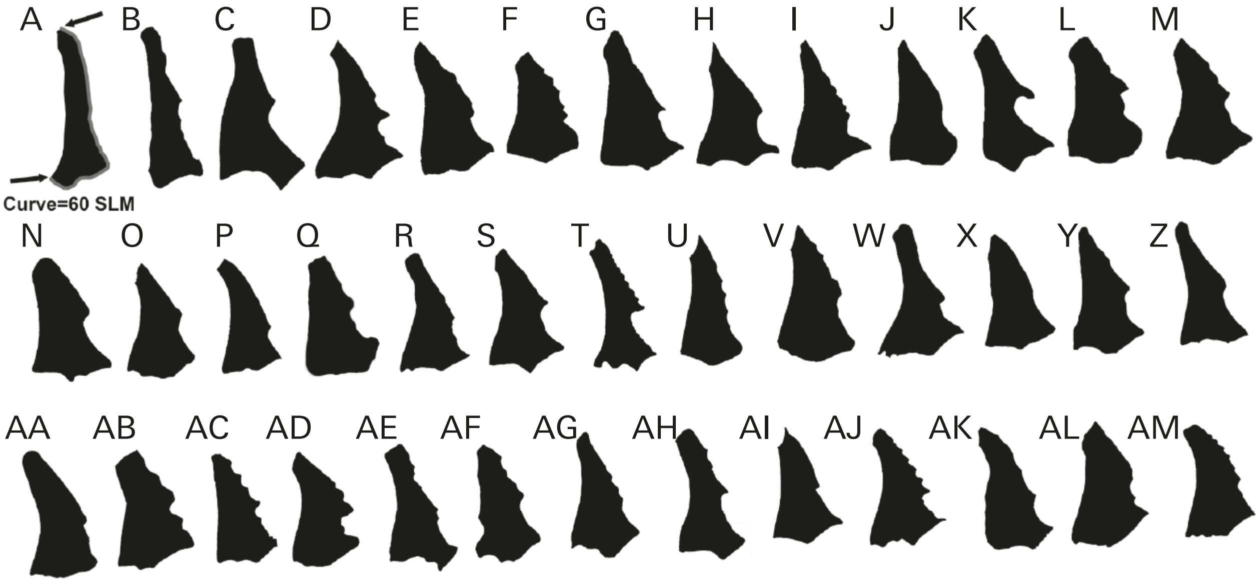

Fig. 4. Metatibial shape of extant and extinct Glaresidae. **A**: *Glaresis tridentata* **sp. nov.**, fossil, one curve was resampled into 60 semi-landmarks. **B**: *Cretoglaresis nana*, fossil. **C**: *Glaresis cretacea*, fossil. **D**: *Glaresis canadensis*. **E**: *Glaresis cartwrighti*. **F**: *Glaresis celiae*. **G**: *Glaresis clypeata*. **H**: *Glaresis confusa*. **I**: *Glaresis dakotensis*. **J**: *Glaresis desperata*. **K**: *Glaresis ecostata*. **L**: *Glaresis exasperata*. **M**: *Glaresis foveolata*. **N**: *Glaresis franzi*. **O**: *Glaresis frustrata*. **P**: *Glaresis gordoni*. **Q**: *Glaresis handlirschi*. **R**: *Glaresis hispana*. **S**: *Glaresis holmi*. **T**: *Glaresis holzschuhi*. **U**: *Glaresis howdeni*. **V**: *Glaresis impressicollis*. **W**: *Glaresis inducta*. **X**: *Glaresis koenigsbaueri*. **Y**: *Glaresis longisternum*. **Z**: *Glaresis medialis*. **AA**: *Glaresis mendica*. **AB**: *Glaresis methneri*. **AC**: *Glaresis minuta*. **AD**: *Glaresis namibensis*. **AE**: *Glaresis oxiana*. **AF**: *Glaresis penrithae*. **AG**: *Glaresis phoenicis*. **AH**: *Glaresis rufa*. **AI**: *Glaresis texana*. **AJ**: *Glaresis thiniensis*. **AK**: *Glaresis tripolitana*. **AL**: *Glaresis walzlae*. **AM**: *Glaresis zvirgzdinsi*.

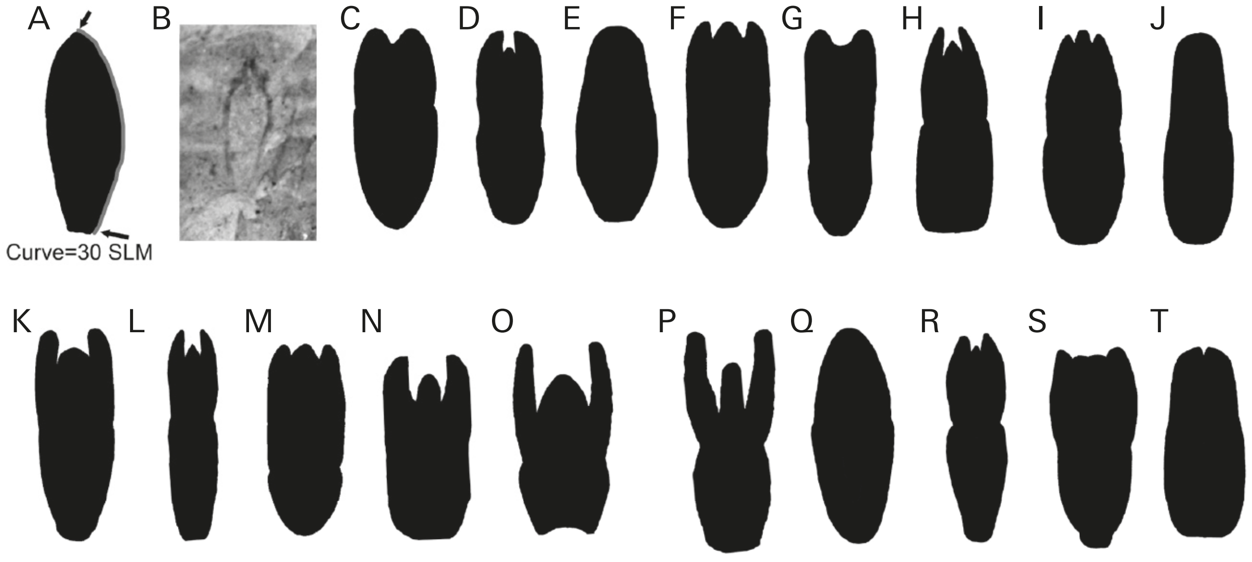

Fig. 5. Aedeagus shape of extant and extinct Glaresidae. **A**: *Cretoglaresis ovalis*, fossil, one curve was resampled into 30 semi-landmarks. **B**: *Glaresis tridentata* **sp. nov.**, fossil. **C**: *Glaresis arenata*. **D**: *Glaresis canadensis*. **E**: *Glaresis cartwrighti*. **F**: *Glaresis clypeata*. **G**: *Glaresis confusa*. **H**: *Glaresis dakotensis*. **I**: *Glaresis ecostata*. **J**: *Glaresis gordoni*. **K**: *Glaresis hispana*. **L**: *Glaresis howdeni*. **M**: *Glaresis impressicollis*. **N**: *Glaresis inducta*. **O**: *Glaresis medialis*. **P**: *Glaresis mendica*. **Q**: *Glaresis phoenicis*. **R**: *Glaresis texana*. **S**: *Glaresis thiniensis*. **T**: *Glaresis zvirgzdinsi*.

The previously identified apomorphic features are of limited use in the context of fossils. Hind wings are neither preserved in the specimen described here nor in the other fossil glaresids described by Nikolayev (2007, 2009) and Bai et al. (2010). Internal characters are almost always completely inaccessible in fossil beetles. The only features visible in all extant and extinct glaresid species are the presence of only five visible abdominal

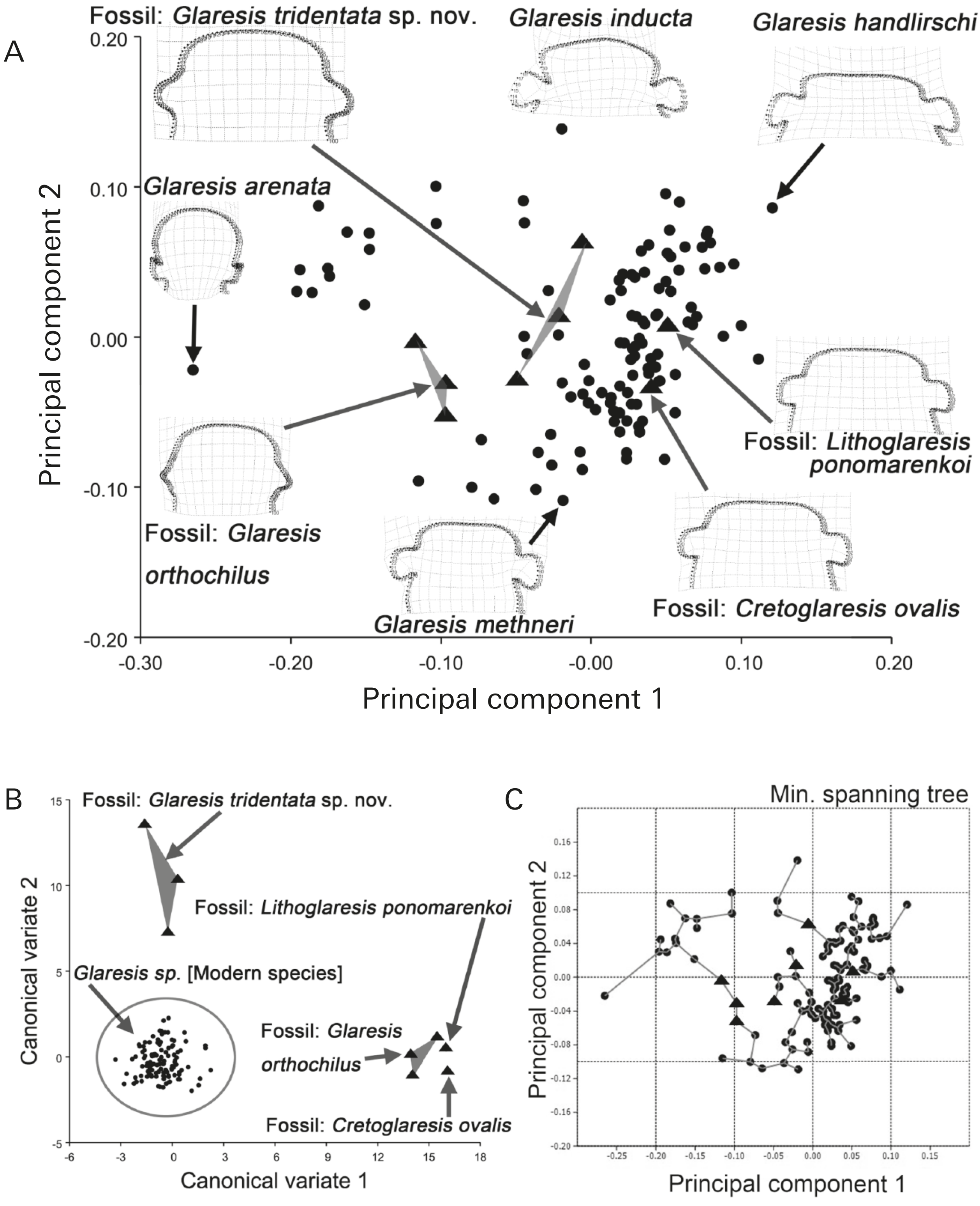

Fig. 6. Head morphological variations of extant and extinct Glaresidae. **A**: Relative warps computed from the data set of 100 semi-landmarks, plotted against one another to indicate positions of the relationships among species relative to one another and to the reference configuration (situated at the origin). **B**: Head morphological difference of extant and extinct Glaresidae based on CVA. **C**: Minimum spanning tree mapped onto a PCA plot.

sternites and the region between the genal canthus and clypeus which is usually deeply incised (Fig. 3A) (SEMENOV-TIAN-SHANSKIJ & MEDVEDEV 1932; MARTINEZ et al. 1961; GORDON 1970).

During the fossilization, all organic chemicals were replaced by other elements in the specimen. What is visible is simply the impression of well sclerotized structures from both sides. In most cases, tergites are not or

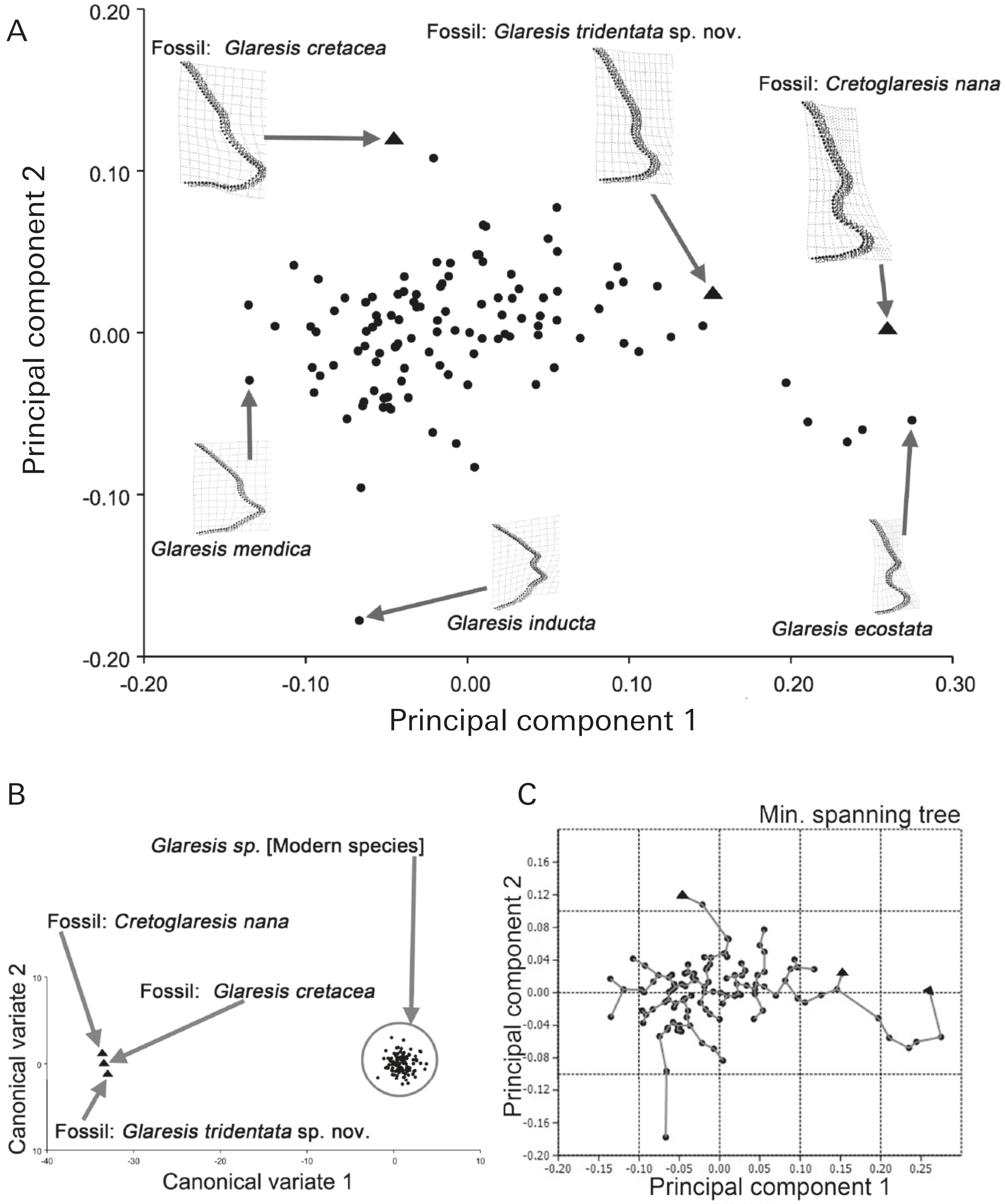

Fig. 7. Metatibia morphological variations of extant and extinct Glaresidae. Relative warps computed from the data set of 60 semi-landmarks, plotted against one another to indicate positions of the relationships among species relative to one another and to the reference configuration (situated at the origin). **B**: Metatibia morphological difference of extant and extinct Glaresidae based on CVA. **C**: Minimum spanning tree mapped onto a PCA plot.

only poorly preserved. If they are recognizable in a beetle fossil, the difference between tergites and sternites is distinct, as the latter have a different shape (evenly tapering twords the abdominal apex) and are more heavily sclerotized. For this fossil, we can definitely say that the preserved abdominal sclerites are sternites. The abdominal feature is clearly present in the fossil described here and tentatively confirms an assignment of the new species to

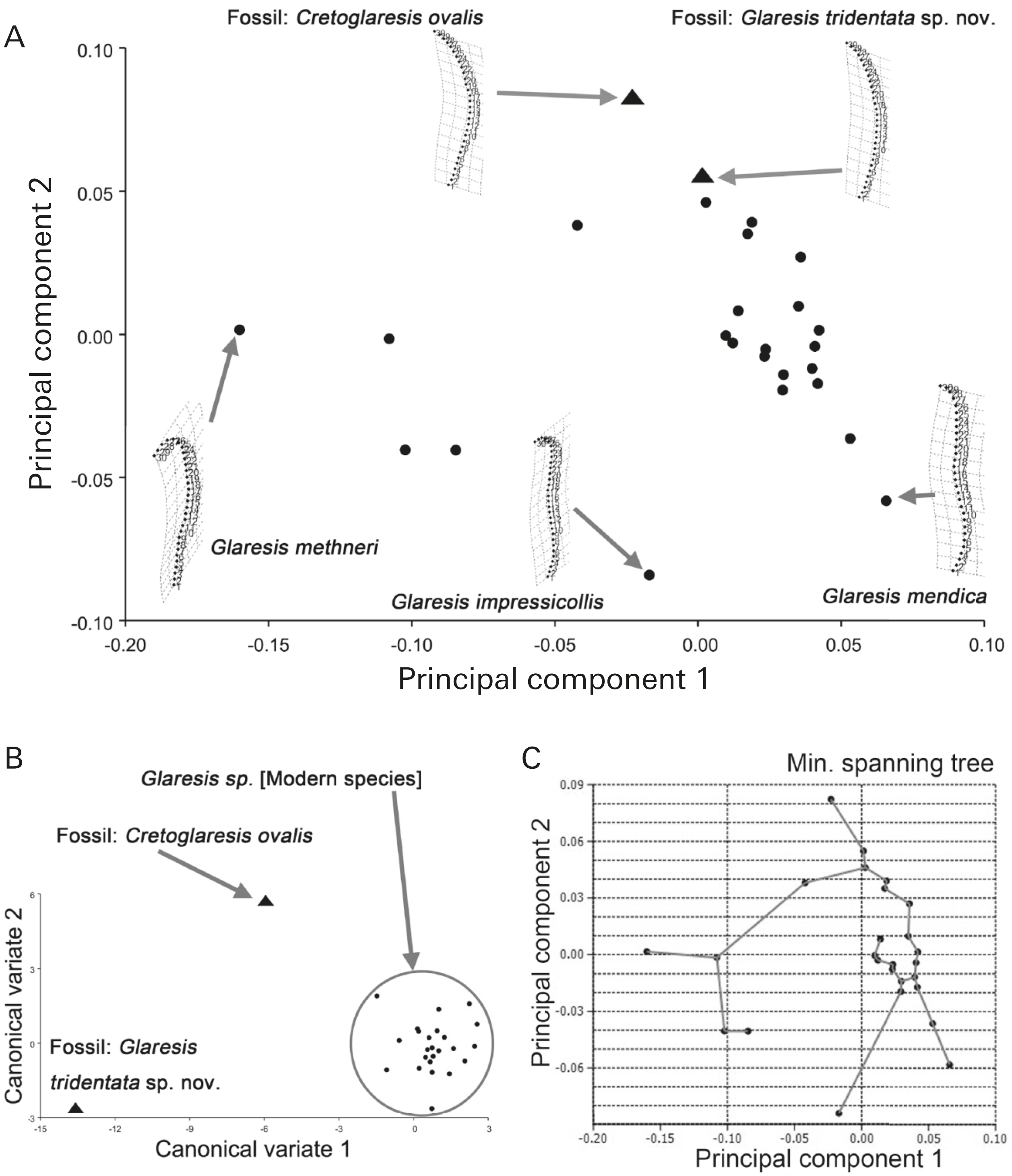

Fig. 8. Aedeagus morphological variations of extant and extinct Glaresidae. Relative warps computed from the data set of 30 semi-landmarks, plotted against one another to indicate positions of the relationships among species relative to one another and to the reference configuration (situated at the origin). **B**: Aedeagus morphological difference of extant and extinct Glaresidae based on CVA. **C**: Minimum spanning tree mapped onto a PCA plot.

Glaresidae. This is at least tentatively supported by the comparison of the head shape between Glaresidae and Aphodiinae, which places the fossil species described here in the glaresid cluster but the aphodiine outgroup taxon clearly outside.

Another typical and derived feature of Glareside is a deep incision between the clypeus and the genal canthus. However, this not only apparently missing in *Glaresis tridentata*, but also in the other described fossils and two extant species, *Glaresis arenata* and *Glaresis handlirschi.* It is conceivable that the absence is a plesiomorphic feature in these species, and the presence an apomorphy linking the glaresids sharing this conspicuous derived feature. However, presently it cannot be fully

Table 2. Shape differences between *Glaresis tridentata* Bai, Beutel & Ren **sp. nov.** and extinct or extant glaresid groups (permutation test=10000).

	Head		Metatibia		Aedeagus	
	Extinct glaresid	**Extant glaresid**	**Extinct glaresid**	**Extant glaresid**	**Extinct glaresid**	**Extant glaresid**
Mahalanobis distances	18.8003	10.7039	150.0336	101.6593	11.3281	14.6102
P-values	0.0136	< 0.0001	0.3337	0.0042	< 0.0001	0.0275
Procrustes distances	0.1240	0.1085	0.1071	0.1800	0.0561	0.0716
P-values	0.0623	0.0471	1.0000	0.0631	1.0000	0.3636

Table 3. Percentage of extinct or extant glaresid groups correctly assigned, compared with *Glaresis tridentata* Bai, Beutel & Ren **sp. nov.** using the Discriminant Function Analysis (DFA) (permutation test=1000).

	Head		Metatibia		Aedeagus	
	Extinct glaresid	**Extant glaresid**	**Extinct glaresid**	**Extant glaresid**	**Extinct glaresid**	**Extant glaresid**
Correctly assigned (discriminant function)	5	113	1	111	–	24
Percentage correctly assigned	100%	100%	50%	100%	–	100%
Correctly assigned (cross-validation)	5	101	2	111	–	23
Percentage correctly assigned	100%	89.4%	100%	100%	–	95.8%
Procrustes distances	0.12402267	0.10845928	0.10709769	0.18002708	–	0.07163842
Mahalanobis distance	2.5389	10.3606	0.2690	103.3319	–	14.6102
T-square	12.0861	313.6973	0.0483	10582.1400	–	204.9210
P-values	0.8649	1.0000	0.8623	0.7127	–	0.8782

excluded that the apparent absence in the fossils is an artifact and that the incision is secondarily missing in the two extant species. Besides this, a reliable interpretation of the character evolution would require a formal phylogenetic analysis with a broad spectrum of characters, which would be beyond the scope of this contribution.

Lithoglaresis Nikolajev was erected as a new genus based on the thin mesotibiae combined with mesofemora broader than in any other glaresid species (Nikolajev 2007, 2009). These features are absent from the new species. The diagnosis of *Cretoglaresis*, another new genus erected by Nikolajev (2009), includes the shape of the meso- and metatibiae, which are much more slender than in *Glaresis*, and the dilated apex of the metatibiae (Nikolajev 2007, 2009). No explicit differential diagnosis separating *Cretoglaresis* from *Glaresis* was provided. Only the distal part of the mesotibia is preserved in the fossil described here, which is close to *Glaresis* but differs distinctly from the condition in *Cretoglaresis* (Fig. 7).

We tentatively place our new species in the genus *Glaresis* as its accessible characters are compatible with the current concept of this genus based on Principal Component Analysis (PCA), Canonical Variate Analysis (CVA), Discriminant function analysis (DFA) and Minimum Spanning Tree (MST) approaches, but do not match with those described for Nikolajev's genera (Nikolajev 2007, 2009).

Presently the classification of Glaresidae with three separate genera – *Glaresis*, *Lithoglaresis* and *Cretoglaresis* – lacks a phylogenetic basis. As it was pointed out in Komarek & Beutel (2006) it is insufficient to erect new genera (or other supraspecific taxa) exclusively based on autapomorphies, without clarifying the monophyly of the remaining groups. It is conceivable that Nikolajev's genera (Nikolajev 2007, 2009) have evolved specialized features, but are in fact deeply nested within *Glaresis.* Autapomorhies of this genus (excl. *Lithoglaresis* and *Cretoglaresis*) are not available. The relationships and taxonomic issues have to be addressed with a phylogenetic analysis including a representative sampling of extant and extinct terminals and a broad spectrum of characters.

The few features of the head analyzed here using geometric morphometrics underline the limitation of morphological data that can be obtained from most fossil beetles. Nevertheless, our results clearly support that the new species differs distinctly in its head shape from other extinct and extant Glaresidae, especially in the shape of the ocular epicanthus and the anterior clypeal margin. Although the fossils are quite distinctly separated from the extant species in the plot (Fig. 6), the head morphology of the extinct species is within the morphological variation of *Glaresis*, which supports the validity of the suggested phylogenetic position of *Glaresis orthochilus* and

Glaresis tridentata **sp. nov**. in this genus. Furthermore, the head shape of the two fossil genera represented by *Cretoglaresis ovalis* and *Lithoglaresis ponomarenkoi* is much closer to extant species, such as *Glaresis oxiana*, *G. rufa* and *G. thiniensis*, which supports the view that the generic status may be phylogenetically unjustified in both cases as pointed out above.

The metatibial shape of *Glaresis tridentata* **sp. nov.** is similar to the condition in an extinct species, *Glaresis orthochilus*, but distinctly separated from that of extant species in the geometric morphometric plot (Fig. 7). Unique features are the outer metatibial margin lacking any projection and the strongly dilated apex. The other three glaresid fossil species, *Cretoglaresis nana*, *Glaresis cretacea*, and *Glaresis orthochilus*, are also distinctly separated from modern species. The metatibial morphology was used as a major diagnostic character for *Cretoglaresis*, which is compatible with our results.

The geometric morphometric analysis suggests that the aedeagi differ greatly between extinct and extant species of Glaresidae (Fig. 8). A sharp apex is apparently always present in the extinct species. The shape varies greatly in the extant species, but the acuminate apical region is always lacking. This is difficult to interpret phylogenetically. However, in this case artifacts in the fossils may play an important role, making a reliable evaluation problematic. An important point underlining this uncertainty is that it was not possible to distinguish the parameres and the phallobase. Additionally, the parameres are a movable part of the aedeagus, which could cause a considerable error in the geometric morphometric result. Consequently, characters of the intromittent organ should presently not be used in a phylogenetic and taxonomic context. Apparently further evidence and improved techniques and methods are needed to solve these problems.

Similar to *Glaresis orthochilus*, *Glaresis tridentata* **sp. nov.** is larger than any extant Glaresidae species, with ca. 8 mm body length versus 2.5 – 6 mm (Scholtz & Grebennikov 2005). This clearly suggests that ancestral species of Glaresidae were larger than today and the small size of extant species is a derived condition in this family. Our results also confirm that the hypothesized sister group of all other extant Scarabaeoidea (Scholtz et al. 1994; Bai et al. 2010, 2013) was already established during the Early Cretaceous.

A formal phylogenetic character evaluation including all described fossil glaresids would be beyond the scope of the present study. Moreover, the scarcity of characters observable in the extinct species would likely have a negative impact on the results, i.e. result in a poorly resolved phylogeny. Even though the results presented here do not reflect a phylogenetic pattern but phenetic affinities, i.e. similarity, they tentatively suggest that all fossil species should be contained in one genus *Glaresis* until there is clear evidence for two or more clearly defined monophyletic subunits of the family.

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