The first fossil Hybocephalini (Coleoptera: Staphylinidae: Pselaphinae) from the middle Eocene of Europe and its evolutionary and biogeographic implications

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http://zoobank.org/urn:lsid:zoobank.org:pub:1D57CB0C-56C4-4DA5-91E1-CF7E9BB40E74

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Received 23 February 2022
Accepted 21 June 2022
Published 19 July 2022


Abstract

The extant tropical tribe Hybocephalini is a morphologically highly derived group of the subfamily Pselaphinae (Coleoptera: Staphylinidae), which is characterized most notably by the modified squamous setae that cover various parts of the body. Ten genera and 69 extant species have been found in the Afrotropical and Oriental regions, with one species found in northern Australia. Prior to this study the evolutionary history of the tribe has been remained elusive due to the dearth of known fossils. Here, we describe the first fossil representative of Hybocephalini, Europharinodes schaufussi Yin & Cai gen. et sp. nov., based on an adult male preserved in Baltic amber (ca 45.0–38.0 Ma). Using X-ray microtomography, the anatomy including the endoskeletal structures of the head, the full pattern of foveation, and the aedeagus of the beetle were reconstructed. Europharinodes shares most derived traits that are congruent with extant members of Hybocephalini, but it also possesses plesiomorphic and autapomorphic characters unknown in living relatives. In order to constrain the phylogenetic placement of Europharinodes, we created an updated morphological character matrix to explore relationships among this genus and related groups. A monophyletic Hybocephalini was recovered by maximum likelihood and parsimony analyses, with Europharinodes being well-resolved as sister to all modern relatives in the likelihood tree. The fossil thus sheds new light on the morphological evolution of Hybocephalini and suggests a broader palaeodistribution of the tribe during the middle Eocene. The disjunct distribution of an Eocene Baltic amber species and an extant Afrotropical-Oriental distribution of the tribe is probably relictual, and was shaped by global cooling during the Eocene–Oligocene transition.

Keywords

Beetles, 3-D reconstruction, Baltic amber, biogeography, Cenozoic climate cooling, Europharinodes schaufussi, phylogeny, plesiomorphic characters
1. Introduction

Comprising more than 64,000 extant and 400 extinct species, the Staphylinidae (rove beetles) stands for the most species-rich family in the whole animal kingdom, surpassing Curculionidae (true weevils) (Yin et al. 2020; Shin et al. 2017). Among the 32 currently recognized extant subfamilies of Staphylinidae, the Pselaphinae are the second most diverse lineage (following Aleocharinae) containing over 10,000 extant species classified in 40 tribes and 1,259 described genera worldwide (Newton and Chandler 1989; Yin et al. 2019), albeit this perhaps represents only a small fraction of their true diversity (Löbl and Kurbatov 2001; Yin 2022).

Six supertribes of Pselaphinae have been recognized and are applied to current taxonomic practice (Newton and Thayer 1995; Chandler 2001): the basal-most Faroniatae, and its sister clade including the other five supertribes (Euplectitae, Goniaceritae, Batrisitae, Pselaphitae, Clavigeritae) forming the so-called ‘higher Pselaphinae’ (Parker et al. 2016). The phyletogenetic relationships among these supertribes, except for the position of Faroniatae, remains unstable because most of them and many included large tribes (e.g., Trichonychini) were shown to be paraphyletic in recent taxonomic or phyletogenetic studies (e.g., Chandler 2001; Parker 2016; Jaloszynski et al. 2022). This poor state of knowledge is further exacerbated by a paucity of direct (fossil) evidence pertaining to the evolutionary history of major pselaphine groups. The research of the fossil history of pselaphines experienced two stages. The first stage lasted from the 1890s to the 1920s (for a review of taxa see Spahr 1981; Newton and Chandler 1989), during which Schaufuss (1890) described a diverse pselaphine fauna from the middle Eocene Baltic amber. The Baltic Pselaphinae, like most other insect groups (Weitschat and Wichard 2010), shows affinities to extant lineages, thus providing little information on how and when the higher lineages may have originated. Furthermore, meaningful re-interpretations of this fauna become almost impossible because of Schaufuss’ limited species descriptions usual for his time, and the fact that his type materials were lost during World War II. A second surge of interest in fossil Pselaphinae started only recently, tracking an increasing discovery of the Mesozaic amber inclusions originating from northern Myanmar (Ross 2019–2021). Several stem-group members of Euplectitae and Goniaceritae were described from this deposit (Parker 2016; Yin et al. 2017; 2019a, b, 2021; Yin and Cai 2021), which shed new light on the paleobiogeography and certain trends in morphological evolution within these two supertribes. Not long ago, a critical fossil representative of stem-group Clavigeritae, Protoclaviger trichodens Parker and Grimaldi, was described (Parker and Grimaldi 2014) from the Ypresian Cambay amber (Rust et al. 2010) of western India, which shows a transitional body form foreshadowing the extreme myrmecophily of recent clavigerites before the rise of modern ants.

The tribe Hybocephalini is a morphologically highly derived group of the supertribe Pselaphitae, characterized most remarkably by the presence of squamous setae that cover various parts of the body, combined with its dorsoventrally convex body, and greatly transverse antennomeres (Nomura 1991a; Sugaya 2003), from under stones (Yin and Jiang 2017), by flight intercept traps, or more often, attracted by ultraviolet light traps (e.g., Jeannel 1950; Chandler 2001). Aphelinodites sinensis Yin & Jiang was found to exhibit male wing dimorphism (Yin and Jiang 2017), suggesting complex trade-offs may exist during the life history of this species. Prior to the present study no fossil representatives of Hybocephalini have been known, complicating attempts at disentangling the evolutionary history of this tribe. Here, the first fossil hybocephaline, Europharinodes gen. nov., is described from the middle Eocene Baltic amber. Aided by X-ray microtomography, the fine anatomy of the beetle has been reconstructed, including the endoskeletal structures of the head. An updated morphological character matrix was constructed to further determine the placement of the fossil, and the biogeographic implications of the new findings are discussed. Europharinodes represents the first extinct Pselaphitae described in detail since the century-old Schaufuss species descriptions.

2. Material and methods

2.1. Location, age and processing of the amber

The Baltic amber (Figs 2–5) studied here was collected at the Yantarny settlement, Sambian Peninsula, Kaliningrad Oblast, Russia (54°52′N, 19°58′E). The age of Baltic amber follows that discussed in Bukejs et al. (2019), dated as 45.0–38.0 Ma (Bartonian to Priabonian, mid-late Eocene). The material is deposited in the Insect Collection of the Shanghai Normal University (SNUC), under the accession number ‘SNUC-Paleo-0102’. The amber piece was cut using a handheld rotary tool equipped with a diamond blade, ground with sandpapers of different grain sizes, and then polished with rare earth polishing powder. The base map (Fig. 6A) showing the palaeolocation of the amber forest was retrieved from Poblete et al. (2021), indicating an age of 40 Ma. The distribution map of recent Hybocephalini (Fig. 6B) was created using QGIS 3.10.8, with the base map acquired from the Web Map Service at https://www.simplemappr.net (Shorthouse 2010). The distributions of a majority of modern species were estimated from published literature, usually with only the country/region known. Since many of the distribution spots are identical, extant species density of
the tribe is shown and was estimated by the ‘heatmap renderer’ function (Kernel Density Estimation) of QGIS.

2.2. Fossil imaging and 3-D reconstruction

Photographs under incident light were taken using a Canon 5D Mark III camera equipped with a Canon MP-E 65 mm macro lens (Figs 2B; 3A), with an attached Canon MT-24EX twin flash as the light source; or using a Canon G9 camera mounted on an Olympus CX31 microscope (Figs 2G; 3C, D, I). Zerene Stacker Version 1.04 was used for image stacking. Using the same method as Li et al. (2021), the amber inclusion was imaged using high-resolution X-ray microtomography (micro-CT) to uncover fine morphological detail. Scans were made using a Zeiss Xradia 520 versa at the micro-CT laboratory of the Nanjing Institute of Geology and Palaeontology, CAS. A CCD-based 4× objective was used, providing isotropic voxel sizes of 2.6365 μm with the help of geometric magnification. During the scanning, the acceleration voltage of the X-ray source was 40 kV. To improve the signal-to-noise ratio, 992 projections over 360° were collected, and the exposure time for each projection was 2 s. The tomographic data were analyzed using Avizone ver. 2019.1. An Isosurface threshold value between 15.000 and 17.500 was used. Images were further processed and arranged into plates in Adobe Photoshop CC ver. 20.0.1.

2.3. Phylogenetic analysis

To test the phylogenetic position of the new fossil taxon within Pselaphinae, we incorporated the new material into previously published datasets (Parker 2016; Yin et al. 2017, 2019b). In addition to Apharinodes papageno Nomura, which was included in the original dataset, we added four more taxa belonging to the genera of Hybocephalini to expand focus on the tribe. A newly described fossil of the tribe Brachyagluta (Yin et al. 2019a) was also included, adding up to 58 non-additive and unordered adult morphological characters coded for 63 taxa (Supplementary material 1). Inapplicable character states are indicated by ‘en’ dashes (–), and missing data are indicated by question marks (?). The data matrix (Supplementary material 2) was assembled in WinClada 1.00.08 (Nixon 2002); characters are numbered starting from 1.

Maximum likelihood (ML) analysis was performed using IQ-TREE v. 2.1.3 (Nguyen et al. 2015) with a single partition. The Mk+FQ+ASC+G4 model was selected as the best-fitting model by the built-in program ModellFinder (Kalyaanamoorthy et al. 2017). Branch support values were estimated by 1,000 duplications of ultrafast bootstraps. Ten independent runs were executed and the result with the highest likelihood was selected as the best ML tree. Bayesian analysis was performed using MrBayes 3.2.6 (Ronquist et al. 2012) under the Mk model with Gamma distributed rates (Lewis 2001; Yang 1994). The search consisted of two Markov chain Monte Carlo (MCMC) runs of two chains and was terminated at ten million generations. Convergence was determined by the standard deviation of split frequencies having dropped below 0.0075, and further verified by estimated sample sizes higher than 200 in Tracer v1.7.1 (Rambeau et al. 2018), indicating sufficient estimation of the posterior values. The first 25% of trees were discarded as burn-in. Both maximum likelihood and Bayesian analyses were rooted on Scirtes hemisphericus. Clades with bootstrap values of 95–100% were considered as being strongly supported, 80–94% moderately supported, and 50–79% weakly supported (Hoang et al. 2018). Maximum parsimony (MP) analysis (Supplementary material 3) was conducted in TNT v1.5 (Goloboff and Catalano 2016) under implied weighting (default weighting function K = 3) using the ‘Traditional search’ strategy; the collapsing rule was switched to ‘none’. Standard Bootstrap value was also calculated in TNT. Character mapping on the consensus tree was made in WinClada 1.00.08 (Nixon 2002). The trees shown in the text (Fig. 1) were annotated in FigTree v1.4.3 (http://tree.bio.ed.ac.uk/software/figtree), and graphically edited using Adobe Illustrator CS5.

3. Results

3.1. Phylogenetic analyses

To test the placement of the new fossil taxon with Pselaphinae, both maximum likelihood and parsimony, as well as Bayesian analyses were performed based on the morphological dataset. In maximum likelihood analysis (Fig. 1) Europharinodes was retrieved in a strongly supported (bootstrap value = 94) monophyletic Hybocephalini, as the basal-most group sister to its modern counterparts. In parsimony analysis the monophyly of Hybocephalini was recovered but with low support (bootstrap value < 50), and the position of Europharinodes was not solved. Nevertheless, neither the monophyly of Hybocephalini nor the position of Europharinodes were resolved in Bayesian analysis, in which the fossil was included in a clade (pp value = 0.69) comprising all modern hybocephalines and a lineage (pp value = 0.84) including Caccoplectus Sharp (Arhytodini), Rhytus Westwood (Arhytodini) and Clavigerinae. The unstable placement of Europharinodes in these analyses was likely a result rooted from the limited taxa sampling and character choice of the tribe and related groups, as all species of Hybocephalini are rarely represented in collections and are difficult to access. Morphologically, Europharinodes possesses most derived characters of modern Hybocephalini as currently defined (see Discussion section below), combined with the morphological evidence and the results of our phylogenetic analyses, the fossil is tentatively placed as a stem-group member of Hybocephalini.
Figure 1. Maximum likelihood and Bayesian trees showing the placement of *Europharinodes schaufussi* gen. et sp. nov. Bootstrap values in maximum likelihood analysis and posterior probabilities in Bayesian analysis are annotated below each branch.
3.2. Systematic paleontology

Family Staphylinidae Latreille, 1802
Subfamily Pselaphinae Latreille, 1802
Tribe Hybocephalini Raffray, 1890

Europharinodes Yin & Cai gen. nov.

http://zoobank.org/0B631F8C-D490-4174-89F9-EE6274592F92

Figs 2–5

Type species. Europharinodes schaufussi sp. nov.

Diagnosis. Most of body covered with squamous setae; body generally compact; head, pronotum and femora coarsely punctuate. Head roundly-triangular, with short and narrow frontal rostrum; large vertexal and frontal foveae present; antennal insertions close, antennomeres slightly elongate to sub-moniliform, clubs formed by apical three enlarged antennomeres; lacking ocular-mandibular carina; clypeus sharply sloping, anterior margin carinate and rounded, lateral margins straight to eyes; maxillary palpi small, four-segmented, with short apical palpal cone. Pronotum with median and lateral antebasal foveae obscured by squamous setae; with antero-hypomeral foveae, lacking hypomeral carinae. Elytra each with two large basal foveae and two distinct discal striae. Each tarsus plesiomorphically with two subequal claws. Abdomen with tergite 1 (IV) slightly longer than 2 (V), tergites 1–4 (IV–VII) broadly sulcate at bases; paratergites moderately broad and laterally protruding. Aedeagus symmetrical, basal capsule enlarged, paired parameres elongate.

Description. Habitus (Figs 2B–D; 3A, B) stout, compact; most of body with squamous setae. Head (Fig. 3E) roundly triangular; vertex coarsely punctate, vertexal foveae (= dorsal tentorial pits; Fig. 3E; \( \gamma_f \)) relatively large, obscured by squamous setae; frontal fovea (Fig. 3E; \( ff \)) distinct, rostrum short and narrow, antennal insertions located at ventral surface of rostrum, tubercles barely raised; compound eyes (Fig. 3G; \( ce \)) large, prominent, lacking ocular-mandibular carina; clypeus (Fig. 3G; \( cl \)) sharply sloping, with broadly rounded, ridged anterior margin; labrum (Fig. 3G; \( la \)) transverse, subtrapezoidal; mandible (Fig. 3G; \( ma \)) with single distinct apical and preapical teeth; maxillary palpus small (Fig. 3H, I), four-segmented, with palpomere 1 small, indistinct, 2 (Fig. 3H; \( p2 \)) pedunculate basally and broadened toward apex, 3 (Fig. 3H; \( p3 \)) roundly triangular, 4 (Fig. 3H; \( p4 \)) sub-fusiform, with short palpal cone at apex. Venter with small, widely separated gular foveae (= posterior tentorial pits; Fig. 3F; \( gf \)) in shared transverse impression, gular moderately raised along middle, weakly impressed admesally; neck region broad. Paired tentorial arms (Fig. 3E; \( ta \)) V-shaped, each branched at base and extending anteriorly to reach inner wall of clypeus (right arm broken at apex in holotype), Pharynx (Fig. 3E; \( ph \)) about 2/3 of head length, posteriorly broadened. Antenna 11-segmented, moderately elongate, extending to approximately half of elytral length when extending posteriorly, antennomeres each slightly elongate to sub-moniliform, club (Fig. 3F) formed by enlarged apical three antennomeres.

Pronotum (Fig. 4A) approximately as long as broad, sides rounded, broadest at middle, anteriorly and posteriorly narrowed, surface with dense squamous setae (Fig. 3C); disc coarsely punctate, with squamous setae all over surface, covering median and lateral antebasal foveae (Fig. 4A, B; \( maf, laf \)), lacking sulcus or carina. Hypomeron extended, lacking carina, with anterior hypomeral fovea (Fig. 4B, C; \( ahf \)). Prosternum (Fig. 4C) with widely separated lateral precoxal foveae (Fig. 4C; \( lpcf \)), anterior part shorter than coxal part, margins of coxal cavity moderately carinate.

Elytra broadly truncate at bases, each elytron with two large basal foveae (Fig. 4D; \( bef \)), with two long discal striae (Fig. 4G; \( ds \)) extending from foveae to posterior elytral margin, lacking subhumeral fovea or marginal sulcus. Metathoracic (hind) wings (Fig. 2D; \( hw \)) fully developed.

Mesoventre with median foveae (Fig. 4E; \( mmsf \)) originating from shared transverse impression, moderately separated, with pairs of large lateral and distinct anterolateral mesoventral foveae (not shown in figure); metaventrite with large, setose lateral coxal foveae (Fig. 4F; \( lmcf \)), with single median metaventral fovea (Fig. 4E; \( mmhf \)), posterior margin with small, narrow split at middle (Fig. 4E; \( ms \)); metacoxae broadly separated. Marginal carina of meso- and metaventrite complete (Fig. 4F; \( mc \)). Legs (Fig. 5A–C) moderately elongate; femora roughly punctate; with short tarsomere 1 and long tarsomere 2 and 3, 2 slightly longer than 3, each tarsus with two subequal pretarsal claws (Fig. 2G).

Abdomen constricted at base, with dense squamous setae (Fig. 3D); tergite 1 (IV) slightly longer than 2 (V), 2–4 (V–VII) subequal in length, tergites 1–4 (Fig. 4G, H; \( t1–4 \)) each deeply and broadly sulcate at base, at least with one pair of basolateral foveae (Fig. 4G; \( blf \)), tergite 5 (VIII) (Fig. 4H; \( t5 \)) roundly triangular, transverse, medi ally roundly emarginate at posterior margin; sternite 2–5 (IV–VII) (Fig. 4H, I; \( s2–5 \)) each broadly sulcate at base, with one pair of basolateral foveae (Fig. 3H; \( blf \)), 6 (VIII), sternite 6 (Fig. 4H, I; \( s6 \)) transverse.

Males have modified sternites 4 and 5 (V I and VII), Aedeagus (Fig. 5D–F, I–K) dorso-ventrally symmetrical.

Etymology. The new generic name is a combination of Latin ‘Eurōpa (Europe)’ and genus Apharinodes, referring to the origin of the fossil in Baltic amber and its affinity with Apharinodes. The gender is feminine.
Europharinodes schaufussi Yin & Cai sp. nov.

http://zoobank.org/5BB9EDF8-BE3F-43D5-854B-89585BF7E453

Figs 2–6

Type material. Holotype (#SNUC-Paleo-0102), deposited in SNUC; a complete, well-preserved male in a 11.6 mm × 7.1 mm × 7.0 mm transparent yellow amber piece, without syninclusions; two surfaces regarding beetle’s lateral and dorsal aspect were cut and polished for observation and photography.

Locality and horizon. Amber mined from the open-pit mine in Yantarny (Fig. 6), Kaliningrad region, Russia; layers between the Bartonian-Priabonian “Wilde Erde” plus “Bläue Erde” and the lower Lutetian “Untere Bläue Erde”; mid-Eocene, 45.0–38.0 Ma (Bukejs et al. 2019).

Diagnosis. As for the genus (vide supra), plus the following: body length approximately 2.1 mm; male antennae lacking modifications; sternites 4 and 5 each with a nodule at middle; aedeagus relatively stout, with short basoventral projection, median lobe with large basal capsule and dorsal diaphragm, sclerotized endophallus present, parameres elongate, each with two long setae at the apex.

Description. Male. Body (Figs 2B–D; 3A, B) length approximately 2.1 mm. Most surface of body covered with squamous setae. Head (Fig. 3E–G) roundly triangular, sub-rectangular at base, slightly longer than wide, length 0.47 mm, width across eyes 0.45 mm, length/width 1.04; vertex roughly punctate, almost flat, distinct vertexal foveae (dorsal tentorial pits) located above level of posterior margin of eyes; frons with narrow and short rostrum, anteriorly confluent with sharply declining elyptes, impressed between slightly raised antennal tubercles; clypeus with smooth surface, anterior margin broadly rounded, carinate and moderately raised; ocular-mandibular carina absent; postgenal region moderately projected. Venter with small, broadly separated gular foveae (posterior tentorial pits) in transverse impression, longitudinally ridged along middle, weakly impressed admesally. Compound eyes large and prominent, each composed of approximately 30 ommatidia, vertical length of eye/temple 2.1. Antenna moderately elongate, length 0.90 mm, lacking modification; antennomeres with rough surfaces; distinct club (Fig. 2B–D, F) formed by enlarged apical three antennomeres; antennomere 1 thick, subcylindrical, 2 and 3 each slightly elongate, 2 slightly longer and wider than 3, 4–7 subequal in width, approximately as long as wide, 8 shortest, slightly transverse, 9 enlarged, slightly longer than wide (including basal stalk), 10 as long as and slightly wider than 9, 11 largest, approximately as long as 9 and 10 combined, 1.24 times as broad as 10.

Prothorax with dense squamous setae (Fig. 3C). Pronotum (Fig. 4A) approximately as long as wide, length 0.42 mm, width 0.41 mm, length/width 1.02, widest at middle; sides rounded, convergent apically and basally; disc moderately convex; with distinct median and lateral antebasal foveae. Hypomeron confluent with prosternum, with antero-hypomeral fovea (Fig. 4B, C; abhf), lacking hypomeral ridge. Prosternum with anterior part much shorter than coxal part, with small, broadly separated lateral procoxal foveae (Fig. 4C; lpcf); margin of coxal cavity moderately carinate.

Elytra (Fig. 4D) with squamous setae finer than those of pronotum and abdomen, much wider than long, length 0.71 mm, width 0.90 mm, length/width 0.79 mm; each elytron with two large basal foveae and two distinct discal striae; humerus weakly prominent, lacking subhumeral fovea or marginal stria. Hindwing fully developed, membranous.

Mesoventrite short, well-demarcated from metaventrite; median mesoventral foveae (Fig. 4E; mnsf) moderately separated, with large lateral mesoventral fovea, mesoventral process short. Metaventrite distinctly raised admesally, inclined towards middle, with well-developed lateral mescoxal (Fig. 4F; lmcf) and single medi-an metaventral fovea (Fig. 4F; mmtf), posterior margin broadly emarginate, convex at middle, with small, short median split (Fig. 4F; ms).

Legs moderately elongate, lacking modification; mesotrochanter elongate; all femora coarsely punctate; tarsi with short tarsomeres 1 and long tarsomeres 2 and 3, with 3 slightly longer than 2; each tarsus with two sub-equal pretarsal claws (Fig. 2G).

Abdomen widest at lateral margins of paratergite 1 (IV), length 0.64 mm, width 0.66 mm; whole surface covered with broad squamous setae. Tergite 1 (IV) slightly longer than 2 (V), deeply and broadly sulcate at base, at least with one pair of basolateral foveae, lacking discal carina; tergite 2–4 (IV–VII) subequal in length along midline, each distinctly sulcate at base and with one pair of basolateral foveae (Fig. 4G; blf), tergite 5 (VIII) semicircular, transverse, posterior margin broadly emarginate at middle; accompanying paratergites 1–3 (Fig. 4G; pt1–3) broad, 4 triangular. Sternites successively shorter; sternites 2–5 (IV–VII) medially slightly impressed, each with broad sulcus and one pair of basolateral foveae (Fig. 4G; blf), lacking carina, 4 and 5 each with single nodule at middle (Fig. 4I; mn), sternite 6 (VIII) transverse, posterior margin broadly emarginate.

Aedeagus (Fig. 5D–F, I–K) 0.28 mm long, dorso-ventrally symmetrical, median lobe (Fig. 5E, J; ml) with large basal capsule (Fig. 5E, J; ml) and dorsal diaphragm (Fig. 5D, I; dd), narrowed towards apex and moderately bent ventrally, basoventral projection (Fig. 5E, J; bp) short; endophallus (Fig. 5G–J; en) well-sclerotized; parameres (Fig. 5E, J; pa) paired, elongate, rounded at apices, each with two long apical setae.

Female. Unknown.

Etymology. The new species is named after the German naturalist Ludwig W. Schaufuss (1833–1890), who described most of the known fossil pselaphines from Baltic amber.
Figure 2. Amber piece (A) containing *Europharinodes schaufussi* gen. et sp. nov., holotype, SNUC-Paleo-0102, and its morphological details (B–G) of (A, B, G: under incident light; C–F: X-ray microtomographic reconstruction). A Original amber piece containing the holotype before cutting and polishing. B, C Left lateral habitus. D Right lateral habitus. E Head in lateral view, show tentorial arms and pharynx. F Right antennal club. G Pro- and metatarsus and respective pretarsal claws. Abbreviations: aed, aedegus; hw, hind wing; ph, pharynx; ta, tentorial arm. Scale bars: 0.5 mm in B–D, 0.2 mm in E, F.
4. Discussion

A monophyletic clade comprising the supertribes Pse- 
laphitae and Clavigeritae was recovered in all analyses, 
with strong to moderate support (bootstrap value in ML 
tree = 100; pp value in MB tree = 1; bootstrap value in 
MP tree = 40) (Fig. 1, Supplementary material 3). Such a 
general relationship between these two higher groups was 
similarly recovered by previous studies focusing on dif- 
f erent target groups (Parker 2016; Yin et al. 2017; Hlávě-
ět al. 2021) or based on different datasets (Jałoszyński

Figure 3. Morphology of Europharinodes schaufussi gen. et sp. nov., holotype, SNUC-Paleo-0102 (A, C, D, I: under incident light; 
portion of the abdominal base, showing squamous setae. E Head dorsum. F Head venter. G Head, in antero-lateral view. H, I Left 
maxillary palpus. Abbreviations: ce, compound eye; cl, clypeus; ff, frontal fovea; gf, gular fovea; la, labrum; ma, mandible; p2–4, 
maxillary palpomere 2–4; vf, vertexal fovea. Scale bars: 0.5 mm in A, B, 0.2 mm in E–I.
Figure 4. X-ray microtomographic reconstruction of *Europharinodes schaufussi* gen. et sp. nov., holotype, SNUC-Paleo-0102. 
A–C: prothorax, dorsal (A), lateral (B) and ventral (C). D Right elytron. E, F Meso- and metathorax, ventral (E) and lateral (F). 
G–I Abdomen, dorsal (G), lateral (H) and ventral (I). Abbreviations: ahf, antero-hypomeral fovea; bef, basal elytral fovea; blf, basal lateral fovea; ds, discal stria; laf, lateral antebasal fovea; lmf, lateral metaventral fovea; lpf, lateral procoxal fovea; maf, median antebasal fovea; mmsf, median mesoventral fovea; mc, marginal carina; mmtf, median metaventral fovea; mn, median nodule; ms, median split; pt1–3, paratergite 1–3; s2–6, sternite 2–6 (IV–VIII); t1–5, tergite 1–5 (IV–VIII). Scale bars: 0.2 mm.
et al. 2022). Within the clade, the placement of Europharinodidae varies in each analysis, likely due to limited taxa sampling and insufficient character selection. The strongest support was observed in the maximum likelihood tree (Fig.), in which a monophyletic Hybocephalini (bootstrap value = 94) was recovered as sister to a lineage composed of Arhytodini + Clavigeritae. Europharinodidae was well-resolved as the basal-most group of the tribe, sister to all other modern hybocephalines. A similar topology from parsimonious analysis (Supplementary material 3) recovered a weakly supported monophyletic Hybocephalini (bootstrap value = 20), and Europharinodidae was included in a probably soft polytomy. Neither the position of the fossil nor the monophyly of Hybocephalini were resolved in the Bayesian tree. The fossil was included in a weakly supported clade (pp value = 0.69) together with the other hybocephalines, Caccoproctus, Rhytius, and Clavigeritae.

Aside from the results inferred from phylogenetic analyses, the position of Europharinodidae was indicated also by the fossil’s unique combination of morphological traits. Within Pselaphinae the presence of squamous setae covering various parts of the body is a distinctive character state occurring in several tribes belonging to the supertribe Pselaphitae: Hybocephalini, Arhytodini, Ctenistini, Odontalginini, and Pselaphini. Europharinodidae can be quickly ruled out from the latter three tribes by the small, reduced maxillary palpi that are only partially visible from the dorsal side. The members of Ctenistini often have maxillary palpomeres greatly extended laterally and with a distinct pencil-like apical projection (e.g., Li et al. 2021); Odontalginini is characterized by the long and basally pedunculate palpomeres 2 and 4, and a maximum number of foveae on the pronotum (Yin et al. 2016); and species of Pselaphini usually possess markedly extending palps that are often longer than the head and pronotum combined, and the squamous setae are usually confined to the basal impression of first visible tergite (Yin and Jiang 2016) (note: short maxillary palpi can be found in Curculionella Westwood and a few more genera, but each genus is characteristic in the form of the palpi and other morphological characters). Both Hybocephalini and Arhytodini share the reduced size of maxillary palps, however, Europharinodidae does not possess the derived characters that define Arhytodini: a) presence of ocular/mandibular carinae; b) characteristic antennae modified in various forms, often greatly increased in length c) often enlarged eyes (normal size in Sabarhynys Lobl), d) femora and tibiae often with spines arranged in rows, e) variously modified tarsomeres, (f) single pretarsal claws, and g) squamous setae usually confined to sulci, foveae, or articulations of body parts (Chandler and Wolda 1986; Chandler 1992, 2001; Lobl 2000).

Although the general morphology of Europharinodidae is largely congruent with modern Hybocephalini (for tribal diagnosis see Chandler 2001: 495), the fossil exhibits a combination of characters found in different recent genera: heavy squamous setae that cover most areas of the body (Figs 2B, 3A, C, D) (Apharinodidae Raffray), four-segmented maxillary palpi (Fig. 3H, I) (Mestogastert Schmidt-Göbel), antennal club formed by enlarged and unmodified three apical antennomeres (Fig. 2C, F) (Hybocephalini Motschulsky, Hybocephalodinae Raffray, Filigerinidae Jeannel, Filigerodinae Jeannel, Mestogastert), projecting paratergites (Figs 3A, 4G) (Mecochelidae Motchulsky), and visible tergites subequal in length along the midline (Figs 3A, 4G) (Apharinodidae, Filigerinidae, Filigerodinae, Mecochelidae, Stipesa Sharp) (Raffray 1890; Jeannel 1950, 1951; Nomura 1989; Chandler 2001; Yin and Jiang 2017). Other than a mosaic morphological combination, Europharinodidae also possesses two presumably plesiomorphic characters which are unknown or rarely presented in modern species. The first is the presence of two subequal pretarsal claws on all tarsi (Fig. 2G), in contrast to one major anterior claw plus a reduced, posterior (accessory) claw in all extant species. The second, revealed by X-ray microtomography, is the dorso-ventrally symmetric aedeagus with an enlarged, bulbous basal capsule, a short, non-protruding endophallus, and large, elongate parameres. All extant members of Hybocephalini except for Apharinodidae and a few Stipesa have a tubular aedeagus with a strongly constricted basal capsule (e.g., Jeannel 1950) similar to that of the genus Pseudophanias Raffray belonging to the tribe Tmesiphorini (Yin et al. 2015; Yin 2019; Inoue and Nomura 2020; Inoue et al. 2020); while Apharinodidae has the aedeagus with a moderately bulbous basal capsule, but the endophallus is asymmetric and often protruding, and the parameres are short and reduced in size (Nomura 1989; Yin and Jiang 2017). Notably, Europharinodidae bears a pair of antero-hypomeral foveae (Fig. 4B, C; ahf) on the prothorax, and a pair of anterolateral foveae (not shown in the figure) on the mesoventrite, two presumably autapomorphic characters that are absent among modern Hybocephalini but variously present in other pselaphine groups. Europharinodidae also have more elongate, subquadrature antennomeres, opposed to the moderately to strongly transverse antennal segments in most extant species. The combination of the above morphological characters readily separates Europharinodidae from all extant genera. Combining the morphological evidence and the results of our phylogenetic analyses present above, Europharinodidae is tentatively postulated as a stem-group member of Hybocephalini.

For the first time, the endoskeletal structure of the head of a fossil Pselaphinae was partially reconstructed thanks to the application of X-ray microtomography technology. The tentorium (Fig. 2E; ta) of Europharinodidae is more generalized and corresponds more to the ground plan of free-living groups such as Batrisitae (Nomura 1991b; Luo et al. 2021) than to Clavigeritae, of which the tentorium is distinctly reduced in size (Jaloszyński et al. 2020) as an adaptation to extreme myrmecophily. Surprisingly, the tentorium of Europharinodidae shows a conspicuous difference from that of Pselaphus heisei Herbst (Pselaphitae: Pselaphini) which lacks anterior arms (Beutel et al. 2021). The dorsal tentorial arms of Europharinodidae derived immediately from the inner wall of the large, distinct vertexal foveae (dorsal tentorial pits) (Fig. 3E; vf), and extending ventrally to connect posterior tentorial arms fusing with the inner wall of the widely separated
Figure 5. Morphology of Europharinodes schaufussi gen. et sp. nov., holotype, SNUC-Paleo-0102 (A–H: X-ray microtomographic reconstruction; I–K: schematic). A Right foreleg. B Right middle leg. C Left hindleg. D–F, I–K Aedeagus, dorsal (D, I), lateral (E, J) and ventral (F, K). G, H endophallus, dorsal (G) and lateral (H). Abbreviations: bc, basal capsule; bp, basoventral projection; dd, dorsal diaphragm; en, endophallus; ml, median lobe; pa, paramere. Scale bars: 0.3 mm in A–C; 0.1 mm in D–K.
gular foveae (posterior tentorial pits) (Fig. 3E; gf). The tentorium divergent anteriorly near the base of posterior arms to form curved and thin anterior arms, which extend anteriorly and end at the inner wall of the clypeus; the tentorial bridge is absent. Other inner structures of the head except for the pharynx cannot be clearly examined. The pharynx (Fig. 2E; ph) is the anterior-most part of the foregut (Beutel et al. 2013). In Europharinodes it extends from the anatomical mouth (which cannot be clearly seen) posteriorly to approximately the anterior 1/3 of prothoracic length. The posterior half of the pharynx is roughly the same width as the anterior half, and the pharyngeal lumen in cross-section appears to be suboval to slightly cordiform. The generalized pharynx, combined with the form of the mandibles, may indicate predacious habits of Europharinodes, albeit the biology of its modern relatives remains largely, if not at all, unknown. For the endoskeletal structures of the other main body segments, not much except for the three pairs of furcae can be observed. The profurcal arms are widely separated at the base, and in anterior view, each arm is slightly curved laterally. Only parts of the mesofurca and the basal part of the metfurca remain, but it would not be unreasonable to postulate that their overall morphology was generally concordant with that of modern Pselaphitae (e.g., Yin et al. 2013).

Different theories explaining the seemingly contradictory co-existence of thermophilic and temperate insect lineages in Baltic amber (Wheeler 1914), termed as the ‘Wheeler’s dilemma’ (Archibald and Farrell 2003), have been proposed. Among them, the theory of an equable terrestrial palaeoclimate of the amber forest with temperate summer and mild winter of low-temperature seasonality (Archibald and Farrell 2003; Archibald et al. 2010) appears to be broadly favored by recent researchers (Wedmann et al. 2010; Perkovsky 2016; Alekseev 2017; Bogri et al. 2018; Schmidt et al. 2019), and corroborated by studies of floras (e.g., Sadowski et al. 2017). Here we adopt Archibald and Farrell (2003)’s explanation as the most convincing theory regarding the ‘mixed’ fauna from Baltic amber. On the other hand, discoveries of present-day arthropod groups showing affinities with Afro-tropical or Oriental regions in Baltic amber have been well-documented in published literature (e.g., Larsson 1978; Engel 2001), and a similar biogeographic connection also holds true for Hybocephalini. The present-day Hybocephalini are exclusively found in the Afrotropical and Australo-Oriental regions, with a higher species diversity occurring in sub-Saharan Africa (Fig. 6B). Notably, most species, if not all, are difficult to collect in the field and are rarely represented in museum collections. Insufficient available data, both morphological and molecular, prevented any meaningful studies tracing the origin and historical biogeography of this group. In this regard, the discovery of the first fossil member of the tribe is significant. The new fossil provides evidence that members of the stem-group Hybocephalini had already been well-established in Europe by the middle Eocene, which have since become extinct. During the Eocene–Oligocene transition, the global climate dramatically transformed from a ‘greenhouse’ to an ‘icehouse’ (Zachos et al. 2001; Hren et al. 2013), with an increase of seasonality (Eldrett et al. 2009; Mosbrugger et al. 2005; Utescher et al. 2015). Although dating the origin of Hybocephalini at this time appears to be premature due to the scarcity of paleontological data, this tribe may have been relatively widespread before the Eocene, and the northern Europe perhaps served as an important migration route for African-Asian spreading of the group. Following the Eocene–Oligocene Transition, the European representatives may have experienced significant declines in diversity and eventually become extinct, leaving the tropical survivors arriving in the Recent and forming isolated distributions as we observe today.

5. Data availability

The original micro-CT data are available from the Zenodo repository (https://doi.org/10.5281/zenodo.6058375).
6. Competing interests

The authors have declared that no competing interests exist.

7. Acknowledgements

We are grateful to the two anonymous reviewers who provided critical comments on an earlier version of the manuscript, which improved the paper. We are thankful to Su-Ping Wu for technical help with micro-CT reconstruction. Financial support was provided by the National Natural Science Foundation of China (grant no. 31872965), the Second Tibetan Plateau Scientific Expedition and Research project (grant no. 2019QZKK0706), the Strategic Priority Research Program of the Chinese Academy of Sciences (grant nos. XDB26000000 and XDB18000000) and the Science and Technology Commission of Shanghai Municipality (grant no. 19QA1406600).

8. References


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Supplementary material 1

Characters and character states

Authors: Yin et. al (2022)
Data type: .docx
Explanation note: List of morphological characters and character states used in phylogenetic analyses (adapted from Parker 2016; Yin et al. 2017, 2019b).
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Link: https://doi.org/10.3897/asp.80.e82644.suppl1

Supplementary material 2

Morphological dataset

Authors: Yin et. al (2022)
Data type: .nex
Explanation note: Morphological dataset used for the analyses.
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Link: https://doi.org/10.3897/asp.80.e82644.suppl2

Supplementary material 3

Results of the maximum parsimony analyses

Authors: Yin et. al (2022)
Data type: .tif
Explanation note: Fifty percent majority-rule consensus cladogram of 4400 most parsimoniuous trees obtained by the ‘Traditional search’ analysis of a data matrix of unordered adult morphological characters under implied weighting (K = 3; tree length = 173; consistency index = 0.34; retention index = 0.82), showing placement of Europharinodes schaufussi gen. & sp. n. Standard Bootstrap (≥ 50) are shown below branches. Unambiguously optimized character changes are plotted along internodes. Black circles indicate unique character changes; white circles indicate parallelisms or reversals; character numbers and states are shown above and below circles, respectively.
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