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A second fossil species of the enigmatic rove beetle genus *Charhyphus* in Eocene Baltic amber, with implications on the morphology of the female genitalia (Coleoptera: Staphylinidae: Phloeocharinae)

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ABSTRACT: Phloeocharinae is a small and likely non-monophyletic subfamily of rove beetles. The enigmatic genus *Charhyphus* Sharp, 1887 has long been placed in Phloeocharinae, whereas recent studies have found it to be phylogenetically very distant from the core members of this subfamily, suggesting the possibility that it actually deserves its own separate subfamily status. So far, the sole definitive fossil record for *Charhyphus* is known based on a single male from Eocene Baltic amber as represented by †*C. balticus* Shavrin, 2020. Here, we describe and illustrate another new *Charhyphus* species, †*C. serratus* Yamamoto & Shavrin, sp. nov., from Baltic amber based on a well-preserved female fossil. Considering the general proportions of the body and the head, this new species is most similar to †*C. balticus*. The new species differs from all known species by the development of strong serration of the lateral edges of the pronotum and features of the shape of the apical margin of the mesoventrite. By using X-ray micro-computed tomography (μCT), we succeeded in visualizing not only the general habitus but also each individual body part, recovering a previously undocumented sclerite on the female internal genital segments in the genus. Morphological features of extinct and extant species of *Charhyphus* are briefly discussed. Figures of all extant *Charhyphus* species and a key for the genus are also provided. Our study is important for considering possible higher palaeodiversity, more common occurrence, and palaeobiogeography of *Charhyphus*.

KEY WORDS: fossil insects, key to species, morphological character, new species, taxonomy, X-ray micro-computed tomography.

Of the 33 recognized extant subfamilies of rove beetles (Yamamoto 2021), Phloeocharinae is comprised of seven genera with about 60 species worldwide, representing only a tiny fraction of the overwhelming mega-diversity of Staphylinidae. Roughly two-thirds of the known species belong to the genus *Phloeocharis* Mannerheim, 1830, and the remaining genera are each monogeneric or containing at most only several species (Newton *et al*. 2000; Chatzimanolis *et al*. 2013; Assing 2015). They are generally small staphylinids that inhabit forest-associated microenvironments such as leaf litter and under bark. Very little is known of their biology, but they are considered to be predatory (Thayer 2016) and frequently flightless (e.g., Assing 2015). Some phloeocharines have reduced eyes, suggesting endogean lifestyles in deep layers of soil (Coiffait 1957; Smetana & Campbell 1980; Hernando 2003). Most phloeocharine species are distributed in the Holarctic region but are also known from North America, Central America, Chile, Australia, and New Zealand (Newton *et al*. 2000; Chatzimanolis et al. 2013).

Phloeocharinae is one of the most problematic subfamilies of Staphylinidae and is not at all likely to be monophyletic based on morphological and molecular evidence (Ashe & Newton 1993; Ashe 2005; Chatzimanolis *et al*. 2013; McKenna *et al*. 2015; Thayer 2016; Gusarov 2018; Lü *et al*. 2020). In fact, it has for a long time been a dumping ground for relatively primitive staphylinids that do not fit well elsewhere (Newton *et al*. 2000). McKenna *et al*. (2015) in their molecular study of Staphyliniformia, showed that *Charhyphus* Sharp, 1887 is a sister group to the non-Osoriini Osoriinae. Consequently, *Phloeocharis*, the type genus of the subfamily, is phylogenetically very distant from *Charhyphus* (McKenna *et al*. 2015). Similarly, the close phylogenetic relationship of *Charhyphus* to Osoriinae has also been confirmed by Lü *et al*. (2020). In general, the placement of the genus within Phloeocharinae is open for discussion. On the other hand, *Phloeocharis* may form a monophyletic group with the two other phloeocharine genera, namely *Phloeognathus* Steel, 1953 and *Pseudophloeocharis* Steel, 1950 occurring in the Australian and Oceanic regions (Newton 1985; Chatzimanolis *et al*. 2013), with the addition of *Dytoscotes* Smetana & Campbell, 1980 from North America and an undescribed genus from Chile (Chatzimanolis *et al*. 2013). In contrast, this generic group is morphologically quite dissimilar from the other three genera of Phloeocharinae (i.e., *Charhyphus*; *Ecbletus* Sharp, 1887; *Vicelva* Moore & Legner, 1973) (Chatzimanolis *et al*. 2013; Yamamoto, pers. obs.). Each systematic placement should be phylogenetically tested in the future to confirm if they are indeed true members in the subfamily or represent new subfamilies.

Charhyphus is a small but distinct genus within the subfamily. In general, members can be distinguished from other taxa of Phloeocharinae by the significantly flattened body, moderately short antennae with antennomeres 6–10 transverse, and serrate lateral margins of the pronotum along with other morphological details (Herman 1972; Newton *et al*. 2000; Brunke *et al*. 2011). Except for *C. picipennis* (LeConte, 1863), other extant species are rare in collections and known mostly only from females. Adults and larvae of *Charhyphus* are known as subcorticolous inhabitants and can be found under tree bark, especially in hardwoods (e.g., Herman 1972). Smetana & Campbell (1980) noted that "…Phloeocharinae has never been adequately characterized and even after Herman (1972) suggested several additional subfamilial characters, the delimitation of the subfamily still remains inadequate" and provided a key to the Nearctic genera of Phloeocharinae including *Charhyphus*. Ashe & Newton (1993) discussed some aspects of the phylogeny of the tachyporine group of Staphylinidae based on the larval morphology and demonstrated the monophyly of *Charhyphus*. Detailed comparative morphological analysis of main internal and external structures of the body of extant species of *Charhyphus* as well as other taxa of Phloeocharinae, Osoriinae, and Piestinae is necessary to determine phylogenetic relationships. Another problem with *Charhyphus* is that they are rarely collected outside of the North-Central Americas resulting in very limited and patchy distributional records for the Palaearctic Region. The recent discovery of the first fossil of *Charhyphus* based on a single male amber inclusion from Eocene Baltic amber has added new insight into the palaeobiogeography on the genus but more information from additional fossils have been needed to consider their morphological evolution, palaeodiversity and palaeodistributions.

The present study provides a description of a new extinct species of *Charhyphus* based on a single female specimen from Baltic amber, representing the first female fossil of the genus. The external and internal morphological characters were explored and visualized using X-ray micro-computed tomography (µCT). The interspecific relations between species of *Charhyphus*, particularly that of the sole extinct species in the genus from the same amber deposit, are briefly discussed. Additionally, a modified key for the entire genus including both extant and extinct species is provided.

1 Taxonomic history of *Charhyphus* and its fossil records

The genus *Charhyphus* was described by Sharp (1887) within "group Phloeocharina" and in the original description, only *C. brevicollis* Sharp, 1887 was included. LeConte (1863) described *Hypotelus picipennis* LeConte, 1863 from "Middle States and Kansas", which was later placed by Fauvel (1878a [=1878b]) to the monotypic genus *Triga* Fauvel, 1878a within "Piestini". Handlirsch (1907) and Bernhauer (1923) moved *Triga* into *Trigites* Handlirsch, 1907 and

Pseudeleusis Bernhauer, 1923 respectively. Bernhauer (1933) described the monotypic "Piestinen" genus *Chapmania* Bernhauer, 1933, with the species *C. paradoxa* Bernhauer, 1933 from the Russian Far East which Blackwelder (1952) later replaced the generic name with *Siberia* Blackwelder, 1952 since the name *Chapmania* was preoccupied. Herman (1972) redescribed *Charhyphus* within Phloeocharinae, synonymized *Trigites* and *Siberia* with it, and described *C. arizoniensis* Herman, 1972. Additionally, one fossil species from Eocene Baltic amber, †*C. balticus* Shavrin, 2020 in Shavrin & Kairišs (2020) was recently described. Another enigmatic fossil species, †*C. coeni* (Scudder, 1900), originally described as a member of *Triga* from the upper Eocene of Florissant, Colorado, USA (Scudder 1900) but later transferred to *Charhyphus* due to the synonymy of *Trigites*, is considered "Staphylinidae incertae sedis" in this study, following such taxonomic treatment by Chatzimanolis *et al*. (2013). The taxonomic position of the fossil was not considered as a member of *Charhyphus* in our study. Thus, four extant and one extinct species of the genus are known at the present time. Newton *et al*. (2000) noted that one species from Mexico and Guatemala still remains undescribed.

2 Materials and methods

The amber piece with the inclusion of †*C. serratus* sp. nov. was polished using emery papers of different grain sizes by the first author (S.Y.) without further treatment. Two fossil specimens examined in this study are deposited in the Institute of Life Sciences and Technologies, Daugavpils University, Daugavpils, Latvia (DUBC [Daugavpils University, beetles collection]; the holotype of †*C. serratus* sp. nov.: Figs 1−6b, 7−9) and the private collection of Vitalii I. Alekseev (Kaliningrad, Russia, but to be deposited in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia [PIN]; the holotype of †*C. balticus*). For comparative purposes, all four extant species of *Charhyphus* were studied for the present study (Figs 8, 9). All of these specimens are deposited in the Gantz Family Collections Center, Field Museum of Natural History (FMNH), Chicago, IL, USA.: 1) *C. arizoniensis* Herman, 1972 (Figs 8a, 9d), 1 female, with the following label data: "Ariz.: Grah. Co., Pinaleno Mtns. Wet Canyon 6000' IV-11-1977", "DSChandler under bark of Arizona Walnut", "*Charhyphus arizonensis* Herman det. L.E. Watrous 1978"; 2) *C. brevicollis* Sharp, 1887 (Figs 8b, 9a): 1 female, with the following label data: "MEXICO: México 19 mi SW Toluca, Mex. 134, 9600 ft ix.12.1973", "under pine bark A. Newton"; 3) *C. paradoxus* (Bernhauer, 1933) (Figs 8c, 9b), 1 female, syntype, with the following label data: "Sibir or. Ussuri Vladivostok Dr. Jureček 1919", "Cotypus", "*Chapmania paradoxa*", "SYNTYPE teste A.Westrich2015 GDI Imaging Project" (Fig. 9c). The photographs of the habitus and type labels of other cotypes (female) are available in the Arthropod Collections Database of FMNH (last access: 08.VI.2021); 4) *C. picipennis* (LeConte, 1863) (Fig. 8d), 1 female, with the following label data: "MASS[ACHUSETTS].: Boxford VI.15.1974", "und[er]. H[ar]dw[oo]d. bark A. Newton".

The accurate age of Baltic amber has been controversial and the subject of great debate, with a broader range of lower–upper Eocene in most modern literature (Bogri *et al*. 2018; Bukejs *et al*. 2019). Here, we tentatively accept the Middle Eocene based on the analysis of the stratigraphy of amber-bearing blue Earth layers in central Europe by Bukejs *et al*. (2019). Rich and abundant staphylinid fossils have been known from Baltic amber, represented by the following 14 subfamilies, each with at least a single formally described species: Aleocharinae, Euaesthetinae, Mycetoporinae, Omaliinae, Oxyporinae, Paederinae, Phloeocharinae, Piestinae, Proteininae, Pselaphinae, Scydmaeninae, Staphylininae, Steninae, and Tachyporinae (e.g., Chatzimanolis & Engel 2011; Alekseev 2013). However, many undescribed rove beetle fossils in Baltic amber await further studies (Shavrin & Yamamoto 2019).

Morphological terminology generally follows Herman (1972) and Shavrin & Kairišs (2020). All measurements are given in millimeters. Observations were made with a stereoscopic microscope equipped with an ocular micrometer, and †*C. serratus* sp. nov. was further checked by Dragonfly PRO (ver. 2020.1) software during preparation of tomographic images; the resulting approximate values are marked with "~". The type labels are cited in inverted commas and separated from each other by a comma, different lines in labels of the types are separated with the vertical line; explanations of the type labels are given in square brackets, necessary notes within the label are given in angle brackets.

The photographs (Figs 1, 6c, 8–9) were taken using a Canon EOS 80D digital camera in conjunction with a Canon MP-E 65 mm f/2.8 1–5× Macro Lens and a Canon MT-24EX Macro Twin Lite Flash used as the light source. Additional figures (Figs 4–6b) were obtained using Dun Inc BK PLUS Lab System equipped with a Camera 6D digital camera and a 10× lens. During the imaging sessions, the amber specimen was completely submerged in clove oil to enhance the visibility of the beetle inclusion and to reduce extra reflection of the amber surface. The obtained images were later processed using the software Helicon Focus 7.5.4 for focus stacking. All figures were edited using Adobe Photoshop Elements 15 software.

Micro-CT observations of the specimen were conducted at the Daugavpils University, Daugavpils (Latvia) using Zeiss Xradia 510 Versa system. Scans were performed with a polychromatic X-ray beam at an energy of 30 kV and power of 2 W. Sample-detector distance was set to 43.2 mm and source to sample distance 27.6 mm. Tomographic slices were generated from 1601 rotation steps through a 360-degree rotation, using a 4× objective, and exposure time during each projection was set to 18 s. Variable exposure was set to 2 times at the thickest part of the amber to achieve similar amounts of photon throughput over the whole sample. Acquired images were binned (2 × 2 × 2) giving a voxel size of 2.6 µm. Since specimen length was longer than the field of view for selected parameters, we carried out image acquisition using an automated vertical stitch function for 2 consecutive scans with identical scanning parameters. Between scans, field of view was set to overlap 42% of data between adjacent fields of view. Images were imported into Dragonfly PRO (ver. 2020.1) software platform for interactive segmentation and 3D visualization. Prior to the full scan a 29-minute warm up scan was conducted with identical stitch parameters but with reduced rotational steps 201 and exposure time was set to 1s. To acquire detailed images of apical part of the abdomen we filtered initial data using Gaussian smoothing with a 3D kernel and standard deviation was set to 1, followed by Laplacian edge detection which was also done with 3D kernel.

The original figures used in this study have been deposited in the Zenodo repository (https://doi.org/10.5281/zenodo.5564635; accessed on 12 October 2021). This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘http://zoobank.org/’. The LSIDs for this publication are: urn:lsid:zoobank.org:pub:065038E1-56FF-4DF4-A367-D2085C071FF6; urn:lsid:zoobank.org:act:45AA361F-62CA-47FB-8D6D-D4C62776CCD7.

3 Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Staphylinidae Latreille, 1802

Subfamily Phloeocharinae Erichson, 1839

Genus *Charhyphus* Sharp, 1887

Type species. *Charhyphus brevicollis* Sharp, 1887 (original designation).

†*Charhyphus serratus* Yamamoto & Shavrin, sp. nov.

LSID: urn:lsid:zoobank.org:act:45AA361F-62CA-47FB-8D6D-D4C62776CCD7.

(Figs 1−6b, 7, Supplementary Videos 1–3)

Type material examined. Holotype: female, complete specimen in a piece of narrow, medium-sized yellow Baltic amber, 24.0 mm × 7.0 mm × 4.0 mm in size (Fig. 1a−1b), deposited in DUBC.

Preservation. The body details of both dorsal and ventral surface are clearly visible except for the dorsoapical part of the right elytron obscured by an oval air bubble and most of the dorsal surface of the abdomen by the hind wings. Syninclusions: an adult of Mycetophagidae (Coleoptera) in the opposite edge of the amber and imago of Ephemeroptera with very long antennae, located very close to the specimen of *Charhyphus*.

Type stratum and age. Mid-Eocene (Bartonian) Baltic amber from amber-bearing Blue Earth layers (Bukejs *et al*. 2019).

Type locality. Baltic Sea coast, Yantarny mine, Sambian (Samland) Peninsula, Kaliningrad Oblast, westernmost Russia.

Description. Measurements: maximum width of head including eyes: 0.55; length of head (from base of labrum to neck constriction along midline of head in dorsal view): 0.36; ocular length: 0.18; length × width of segments III and IV of maxillary palpi: III: 0.07 × 0.05, IV: 0.05 × 0.03; length of antenna: ~0.58; length of pronotum: 0.37; maximum width of pronotum: 0.56; sutural length of elytra from the apex of scutellum to the posterior margin of sutural angle: 0.44; length of elytron from basal to apical margin: 0.57; maximum width of elytra: 0.60; length of metatibia: 0.28; length of metatarsus: 0.18; maximum width of abdomen (at segment IV): 0.56; length of forebody: 1.38; total length (from anterior margin of clypeus to apex of abdomen): ~2.78.

Body long, narrowly elongate (Figs 1c, 2a), flattened (Fig. 3). Body and antennomeres dark brown; legs brown; mouthparts, tarsi, intersegmental membranes and apical part of abdomen yellow-brown. Forebody with regular, semi-erect, short pubescence; lateral margins of pronotum with short and moderately regular setation; setation of elytra slightly denser than that on pronotum; setation of dorsal surface of abdomen invisible in detail but seems to be moderately fine, dense and regular (ventral surface of abdomen with dense, regular, slightly elongate pubescence). Body dorsally as in Figs 1c, 2a; body ventrally as in Figs 1e, 2b; body dorsolaterally as in Fig. 1d; head and pronotum dorsally as in Fig. 4a; forebody ventrally as in Fig. 2c; head and pronotum ventrally as in Fig. 4b; head and pronotum dorsolaterally as in Fig. 4c; forebody lateroventrally as in Fig. 5c.

Head 1.5 times as wide as long, slightly convex in middle; vertex transverse, with moderately straight apical and widely rounded basal margins; latero-apical portion of head weakly convex in middle, gradually narrowing apicad, with lateral margin between apical angles of vertex and antennal insertion slightly concave; postocular portion short, about twice shorter than longitudinal length of eye, from basal margins of eyes gradually narrowing toward neck (Figs 1c, 2a, 4a, 4c). Punctation moderately sparse and fine, irregular in middle, finer on clypeus and around eyes (Figs 1c, 4a, 4c). Microsculpture of dorsal surface dense, isodiametric, finer in apical portion, somewhat oval in middle (Fig. 4a, 4c); microsculpture of ventral surface transverse in middle and moderately large and isodiametric on laterobasal portions (Fig. 4b). Eyes medium-sized, relatively convex (Figs 1c, 4a–4c, *ey*). Labrum wide, distinctly protruding anteriad, with widely concave apical portion and long latero-apical setae. Mandibles strong, wide, each with narrow, elongate and curved apical portions with very acute apices, left mandible with indistinct smooth tooth at about middle (Figs 1c, 1e, 2a–2c, 4a–4b). Mentum and labium wide; two widely and deeply concave medioapical lobes of hypopharynx wide, strongly protruding anteriad, with truncate apices; preapical labial palpomeres moderately wide and transverse, apical segments narrow, about as long as preapical segment (Figs 2b–2c, 4b). Preapical segment of maxillary palpus wide, about 1.4 times as long as wide; apical maxillary palpomere distinctly shorter than preceding segment, narrow, 1.6 times as long as wide, from basal portion gradually narrowed apicad toward rounded apex (Figs 2a–2c, 4a–4c). Gular sutures with widely rounded apical parts, gradually and widely diverging posteriad; shortest, very narrow distance between sutures located at level of posterior third of eyes (Figs 1e, 2b–2c, 4b, 5c). Head with clear neck-like constriction, distinct all around, moderately distant from posterior margins of eyes (Figs 2a, 4a, c, *nc*); neck without visible punctation, covered by dense isodiametric microsculpture, more oval than that in middle portion of head (Figs 1c, 2a, 4a). Antenna moderately short, reaching about anterior third of pronotum, with antennomeres 5–10 progressively widened apicad; antennomeres 4–11 densely covered by short pubescence with additional long latero-apical setae; basal antennomere moderately wide, about twice as long as wide, antennomere 2 distinctly narrower, about 1.6 times as long as antennal scape, antennomere 3 with narrow basal portion, gradually widened apically, about as long as and slightly narrower than antennomere 2, antennomere 4 small, with narrow basal portion, markedly widened apically, longer than wide, shorter and narrower than antennomere 3, antennomere 5 short (indistinctly seen in detail), slightly wider than antennomere 4, antennomere 6 more transverse than antennomere 5, about 1.4 times as wide as long, antennomeres 7–8 transverse, distinctly wider than antennomere 6, antennomere 9 transverse, slightly less than twice as wide as long and markedly wider than antennomere 8, antennomere 10 about as wide as long, slightly longer than antennomere 9, apical antennomere slightly longer than antennomere 10, from apical third sharply narrowed toward subacute apex (Fig. 4d).

Pronotum transverse, 1.5 times as wide as long, about as wide as head, widest in anterior third, from about middle gradually narrowing toward subacute posterior angles (Fig. 4a), with basolateral margins slightly sinuate (Fig. 4b, 4e); laterobasal portions indistinctly impressed (Fig. 4a); anterior angles rounded, slightly protruding anteriad (Figs 1c, 2a, 4a); apical margin somewhat straight, slightly shorter than posterior margin (Figs 2a, 4a); lateral portions narrowly flattened, with almost entire lateral margin irregularly serrate, the teeth indistinct in basolateral and latero-apical portions, more or less progressively and regularly increasing in size lateromedially, with slightly flattened apices directed apically (Fig. 4a). Punctation moderately dense, slightly finer than that on middle portion of head, sparser in middle portion (Figs 1c−1d, 4a, 4c). Medioapical margin of ventral part of prothorax widely rounded, with short, rounded intercoxal process, reaching about middle of procoxae (Figs 1e, 2b−2c, 4b). Mesoventrite narrow, transverse, apical margin, with very wide, rounded pair of portions along medioapical margin (Figs 2c, 6a−6b, *prp*); basal apical ridges (Fig. 6b, *bar*) on anterior margin of mesoventrite (Fig. 6b, *amm*), strongly protruding anteriad laterally, separated by widely and deeply emarginate medial margin (Fig. 6b, *me*), resulting in lack of any modification (e.g., elliptical ridge) on surface; mesoventrite with very long and moderately wide intercoxal process reaching basal portion of mesocoxae (Figs 1e, 2b−2c, 4b). Scutellum large, subtriangular, with rounded apical margin, without punctation, covered with dense, transverse microreticulation (Figs 1c, 4a, 4c). Metaventrite elongate, with wide and deep intercoxal cavities and moderately short, widely rounded intercoxal process apically reaching mesosternal process (Figs 1e, 2b−2c, 4b, 5d, 6a); surface smooth without longitudinal furrow near posteromedial margin (cf. Fig. 9a).

Elytra subparallel, moderately short, somewhat wider than long and slightly longer than pronotum, almost reaching apical margin of abdominal tergite III; hind margins of each elytron slightly truncate toward suture (Figs. 1c, 2a, 5a). Punctation moderately sparse, somewhat finer than on pronotum (Figs 1c, 5a). Hind wings fully developed (Figs 1c−1d, 7a, *hw*).

Legs short, covered by moderately long pubescence, with femora very wide in middle (Figs 1d, 2b, 3a−3b, 5b−5c); procoxal fissure open, with well-exposed protrochantin (Figs 4b, 6a, *ptn*); apical tarsomeres of all legs distinctly longer than previous four segments; tarsomeres 1−4 with very long lateroapical setae; protarsomeres 1–4 transverse, each segment twice as wide as long; meso- and metatarsomeres 1–4 less transverse than those of protarsi (Figs 1e−1f, 5b−5c).

Abdomen slightly narrower than elytra, very long, more or less parallel-sided, indistinctly widened toward tergite VI and insignificantly narrowing apically (Figs 1c, 2a, 3a−3b, 7a).

Abdominal tergites with fine and sparse punctation, presence/absence of small median pair of cuticular combs on tergites IV and V (cf. Fig. 9d, *arrow*) not observable. Ventral part of abdomen as in Fig. 7b.

Male unknown.

Female. Apical margins of abdominal tergite VIII (Fig. 2a) and sternite VIII (Fig. 2b) rounded. Genital segment with very long gonocoxite 2 (Fig. 2d, *gc2*), gradually narrowing apically and bearing a short stylus (Fig. 2d, *sty*), each with a short apical seta; middle portion of genital segment with round structure (Fig. 2d, *arrow*).

Etymology. The specific epithet is the Latin adjective *serratus*, *-a*, *-um* (serrated, toothed like a saw). It alludes to the strongly serrate lateral edges of the pronotum.

Differential diagnosis. †*Charhyphus serratus* sp. nov. differs from the other species of the genus by the darker body, the presence of strong serration on lateral edges of the pronotum (Fig. 4e) and the shape of the basal apical ridges on anterior margin of the mesoventrite (Fig. 6b, *bar*) with very deep medial emargination (Fig. 6b, *me*). Based on the general proportions of the body and shape of the temples which gradually narrow toward neck, it is similar to †*C. balticus* recently described from Baltic amber, from which it can be distinguished by its slightly larger body and eyes, less transverse antennomeres 7−10, narrower distance between gular sutures, finer punctation of the shorter pronotum, structures of the basal apical ridges on the mesoventrite, denser and finer punctation of the elytra, narrower and longer metaventrite, and longer apical segments of tarsi.

Remarks. This new species can unambiguously be assigned to the phloeocharine genus *Charhyphus* based on the distinctly flattened body, structure of the neck-like constriction of the head, crenulate pronotal margins, epipleural keel on elytron, short legs with a 5-5-5 tarsal formula, and other morphological characteristics including those of the maxillary palpi and mesoventrite (Herman 1972; Newton *et al*. 2000; Brunke *et al*. 2011). There are four extant *Charhyphus* species in the fauna of the world, with three species known from North and Central America and one from the Russian Far East (Herman 2001):

Charhyphus arizoniensis Herman, 1972 (Figs 8a, 9d). The species was originally described from "Arizona: Cochise County Chiricahua Mountains: northwest slope of Barfoot Peak, 8250 feet" (Herman 1972). Habitats: specimens were collected under the bark of pine logs.

C. brevicollis Sharp, 1887 (Figs 8b, 9a). The species was originally described form "Guatemala, Totonicapam 8500 to 10,500 feet" (Sharp 1887). It was redescribed by Herman (1972), including a new record from Mexico. The male is unknown (Herman 1972). Habitats: the holotype of *C. brevicollis* was collected under the bark of a pine (Sharp 1887).

C. paradoxus (Bernhauer, 1933) (Figs 8c, 9b). The species was originally described as *Chapmania* from "Ostsibirien: Ussuri, Wladiwostok [=Vladivostok, Khabarovsk Territory, Far Eastern Russia]" (Bernhauer 1933) and redescribed by Herman (1972). Coiffait (1974) recorded the unsexed specimen from Ussuriysk, Maritime Province, Russia. The male of *C. paradoxus* and details of the ecology are unknown.

C. picipennis (LeConte, 1863) (Fig. 8d). The species was originally described as *Hypotelus* from "Middle States and Kansas" and redescribed by Herman (1972). Notably, *C. picipennis* is a widely distributed species in eastern Canada and USA (e.g., Herman 1972, 2001). Habitats: specimens of *C. picipennis* were found from logs and under bark of trees (e.g., *Quercus*, *Ulmus*, *Betula*, or *Abies*) in various types of deciduous or mixed forests (Brunke et al. 2011; Webster et al. 2012).

An extinct species, †*C. balticus* Shavrin, 2020 in Shavrin & Kairišs (2020) was recently described based on a single male adult from Eocene Baltic amber.

All extant species are pale (Fig. 8) and the main interspecific differences are related to punctation of head and pronotum, shape of apical part of the head and relations of length of eyes and temples (see figs 1−4 in Herman 1972), and shape of the anterior margin of the mesoventrite (figs 18−19 in Herman 1972) and apical angles of the pronotum. The male aedeagus is known only for two species (*C. arizonensis* and *C. picipennis*). It has an elongate median lobe and long, thin parameres not or slightly exceeding apex of the median lobe, with a row of relatively short setae along inner edge (figs 23−25 in Herman 1972). Details of the external structure of the aedeagus in males are unknown. Both extinct species have darker colouration of the body (although it could be considered as an artefact of the fossilization processes), finer and sparser punctation of the head which is gradually narrowed toward neck from basal margin of eyes. In general, the shape of the male aedeagus of *C. balticus* (figs 3J−3l in Shavrin & Kairišs 2020) is similar to those of extant species. Based on the shape of the fine and irregular serration of the lateral edges of the pronotum, †*C. balticus* is also more similar to extant species. In contrast, †*C. serratus* sp. nov. has more developed and distinctly larger teeth along lateral edge of the pronotum (Fig. 4e). Additionally, it has a characteristic shape of the medioapical margin of the mesoventrite with paired widely rounded basal apical ridges, strongly protruding anteriad, and a very deep medial emargination between them (Figs 2b−2c, 4b, 6a−6b), which distinguishes it from other known species of the genus. The medioapical portion of the mesoventrite of extant species is located at about the same level with paired rounded portions (see figures 18 and 19 in Herman 1972). The elliptical ridge (see figure 19 in Herman 1972) on the median portion of the base of the mesoventrite in †*C. serratus* sp. nov. is missing. In turn, this portion of the mesoventrite in the specimen of †*C. balticus* is poorly visible within the darker amber but seems to lack both a deep emargination between paired rounded parts on the medioapical margin and elliptical ridges.

4. Key to all extinct and extant species of *Charhyphus*

The key below is significantly modified from that provided for extant *Charhyphus* species by Herman (1972).

1. Punctation of head fine and sparse. Extinct species, Eocene Baltic amber … 2

-. Punctation of head large and dense. Extant species … 3

2. Lateral edges of pronotum with strong serration (Fig. 4e). Anterior margin of mesoventrite with very deep medial emargination (Figs 4b, 6a–6b, *me*) along basal apical ridges on mesoventrite (Figs 4b, 6a–6b, *bar*). Punctation of pronotum and elytra fine. Body length: 2.78 mm. Habitus as in Figs 1c, 2a … †*C. serratus* sp. nov.

-. Lateral edges of pronotum slightly serrate. Apical margin of mesoventrite without emargination along basal apical ridges on mesoventrite. Punctation of pronotum and elytra markedly large and deep. Aedeagus as in fig. 3J (Shavrin & Kairišs 2020). Body length: 2.35 mm. Habitus as in figs 1C, 2A (Shavrin & Kairišs 2020) … †*C. balticus*

3. Medioapical portion of mesoventrite without basal elliptical ridge (fig. 18 in Herman 1972) … 5

-. Medioapical portion of mesoventrite with elliptical ridge on base (Fig. 6c; fig. 19 in Herman 1972) … 6

5. Antennomere 8 narrow, about as wide as long. Male aedeagus as in fig. 25 (Herman 1972). Body length: 2.7–3.9 mm. Habitus as in Fig. 8d. Distribution: Canada, USA … *C. picipennis*

-. Antennomere 8 distinctly transverse, wider than long. Body length: 3.5–3.7 mm. Habitus as in Fig. 8c. Distribution: Far Eastern Russia … *C. paradoxus*

6. Anterior angles of pronotum subacute. Punctation of pronotum large, deep and dense (fig. 4 in Herman 1972). Body length: 3.5–3.9 mm. Habitus as in Fig. 8b. Distribution: Mexico, Guatemala … *C. brevicollis*

-. Anterior angles of pronotum widely rounded. Punctation of pronotum fine and shallow (fig. 3 in Herman, 1972). Male aedeagus as in fig. 24 of Herman (1972). Body length: 2.8–3.3 mm. Habitus as in Fig. 8a. Distribution: USA … *C. arizoniensis*

5. Discussion

Prior to our study, only two definitive fossil taxa of the subfamily Phloeocharinae had been described. The oldest phloeocharine fossil is known from Upper Cretaceous (Turonian) New Jersey amber from the USA suggesting a long-term morphological stasis of the extant genus *Phloeocharis* (Chatzimanolis *et al*. 2013). Another recently described fossil represents the sole extinct species of *Charhyphus* from Eocene Baltic amber based on a single adult male (Shavrin & Kairišs 2020). Our discovery of a new extinct *Charhyphus* species with the first female fossil from the same amber deposit is significant for considering a possible higher palaeodiversity, more common occurrence, and palaeobiogeography of *Charhyphus* in the Eocene. Interestingly, no extant *Charhyphus* species has a distribution which overlaps with another species in the genus (see fig. 1E of Shavrin & Kairišs 2020). For example, the most commonly found species, *C. picipennis*, is restricted to the northeastern part of the USA and its adjacent areas in Canada, whereas the other two species in North America have only been known from Arizona (*C. arizoniensis*) or southwestern Mexico and Guatemala (*C. brevicollis*). No distributional detail is known for an undescribed species mentioned in Newton *et al*. (2000) in the latter region. The sole extant Palearctic species, *C. paradoxus*, has been known only from Vladivostok and Maritime Province (Far Eastern Russia) until now (Bernhauer 1933; Coiffait 1974). Thus, the finding of †*Charhyphus serratus* sp. nov. from Baltic amber demonstrates the co-occurrence of two *Charhyphus* species in the same locality, a case of overlapping distribution found in the genus for the first time. Since there are no extant *Charhyphus* species found from the entire European region, our discovery suggests hidden palaeodiversity of the genus in Europe and even the west Palaearctic region. According to Alekseev (2017), 33 genera of fossil Coleoptera described from Baltic amber are known both from the Palaearctic and Nearctic Regions. Some of these genera have a wide disjunction in the Palaearctic Region between Europe and the Far East (e.g., *Microbregma* Seidlitz, 1889, Ptinidae: see distributional map in fig. 29 in Alekseev 2017). It can be postulated that some extant species survived in high biodiversity refugia in East Asia as determined by climatic factors following glaciations (in our case, possibly *C. paradoxus*). These beetles may be rather easily trapped in tree resin based on a presumably subcortical lifestyle of *Charhyphus* as inferred by its probable adaptative morphological features, particularly the dorsoventrally flattened body (Fig. 3; figs 2C–2D in Shavrin & Kairišs 2020) and the globular procoxae (Figs 2c, 4b, 6a–6b, *pc*; fig. 2B in Shavrin & Kairišs 2020), with potentially a higher flight activity. Thus, it is probable that more

Charhyphus beetles will be found from Eocene European amber. Such discoveries will probably be made mainly from Baltic amber but with some possibility of potential discovery from Bitterfeld and Rovno ambers in the future.

Recently, non-destructive techniques have been used more frequently to examine amber inclusions based on three-dimensional reconstructions (Penney 2016). The recent advancement of X-ray micro-computed tomography (μ-CT) and propagation phase-contrast X-ray synchrotron imaging (PPC-SRμCT) has opened new windows for achiving high quality reconstructions and individual X-ray sliced images for amber beetles (e.g., Chatzimanolis *et al*. 2013; Zanetti *et al*. 2016; Jałoszyński *et al*. 2018, 2020; Bukejs *et al*. 2020a, b; Shavrin & Kairišs 2020, 2021; Perreau *et al*. 2021; Alekseev *et al*. 2021; Schmidt *et al*. 2021). They are useful in exluding extra bubble layers surrounding the surfaces of inclusions (e.g., Yamamoto & Maruyama 2018; Kypke & Solodovnikov 2020; Shavrin & Yamamoto 2020; Kundrata *et al*. 2020) and in removing certain extra bodyparts from reconstructions (e.g., Perreau & Tafforeau 2011; Bukejs *et al*. 2020a, b). Our attempt to visualise the holotype of †*C. serratus* sp. nov. using the X-ray μ-CT recovered remarkably good results. In fact, not only the chitinized external bodyparts but also some internal structures of the female genitalia were successfully reconstructed (Figs 2, 3, Supplementary Videos 1–3). Compared to generally well-chitinized male genitalia, the female genital morphology in Coleoptera has rarely been extracted from amber fossils, likely due to fossil preservation and insufficient sclerotization for scans though notably, Brunke *et al*. (2019) successfully reconstructed the female genital segments of a Staphylininae rove beetle in Baltic amber. Of note, our reconstruction shows an enigmatic rounded structure in the middle of the female abdominal segment (Fig. 2d, *arrow*) which resembles the female accessory sclerite of some phylogenetically unrelated Omaliini McLeay (e.g., Shavrin 2020). The so-called "ring structure", possibly derived from sternum X and apparently homologous to similar female structures in the omaliines, is also known in some genera of Oxytelinae (Makranczy 2006). In contrast, analogous structures have not been described for the extant species of *Charhyphus* (see Herman 1972). It is still unclear if this "ring structure" is important for elucidating the phylogenetic hypothesis of the genus within Staphylinidae pending a thorough investigation for exploring such structures in the related staphylinid subfamilies.

6. Data availability

All fossil material included in the paper is deposited either in the Institute of Life Sciences and Technologies, Daugavpils University (Daugavpils, Latvia [DUBC]; the holotype of †*C. serratus* sp. nov.) or the private collection of Vitalii I. Alekseev (Kaliningrad, Russia); the latter will subsequently be deposited in the collection of the Borissiak Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia [PIN]; the holotype of †*C. balticus*). All the specimens of the extant *Charhyphus* species are housed in the Gantz Family Collections Center, Field Museum of Natural History (Chicago, IL, USA [FMNH]). All data are included in the description and its associated supplementary material. Supplementary videos of X-ray micro-CT volume renderings of †*Charhyphus serratus* sp. nov. are available through the Zenodo repository (https://doi.org/10.5281/zenodo.5564635).

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Figures

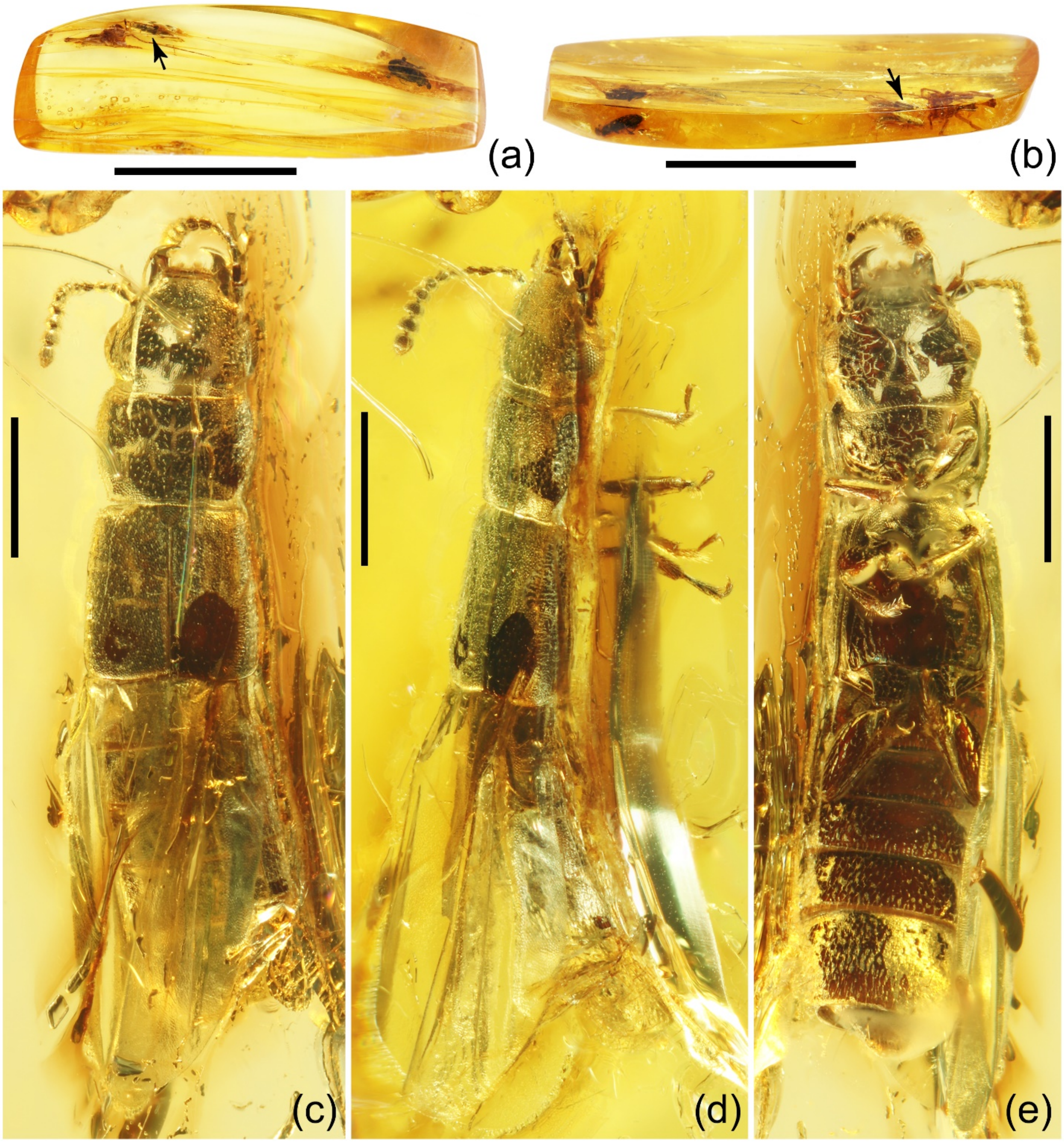

Figure 1 †*Charhyphus serratus* sp. nov., 001 DUBC, holotype: (a) amber specimen with beetle inclusions, holotype (arrow) in dorsal view; (b) amber specimen with beetle inclusions, holotype (arrow) in dorsolateral view; (c) habitus, dorsal view; (d) habitus, dorsolateral view; (e) habitus, ventral view. Scale bars = 1.0 cm (a–b), 0.5 mm (c–e).

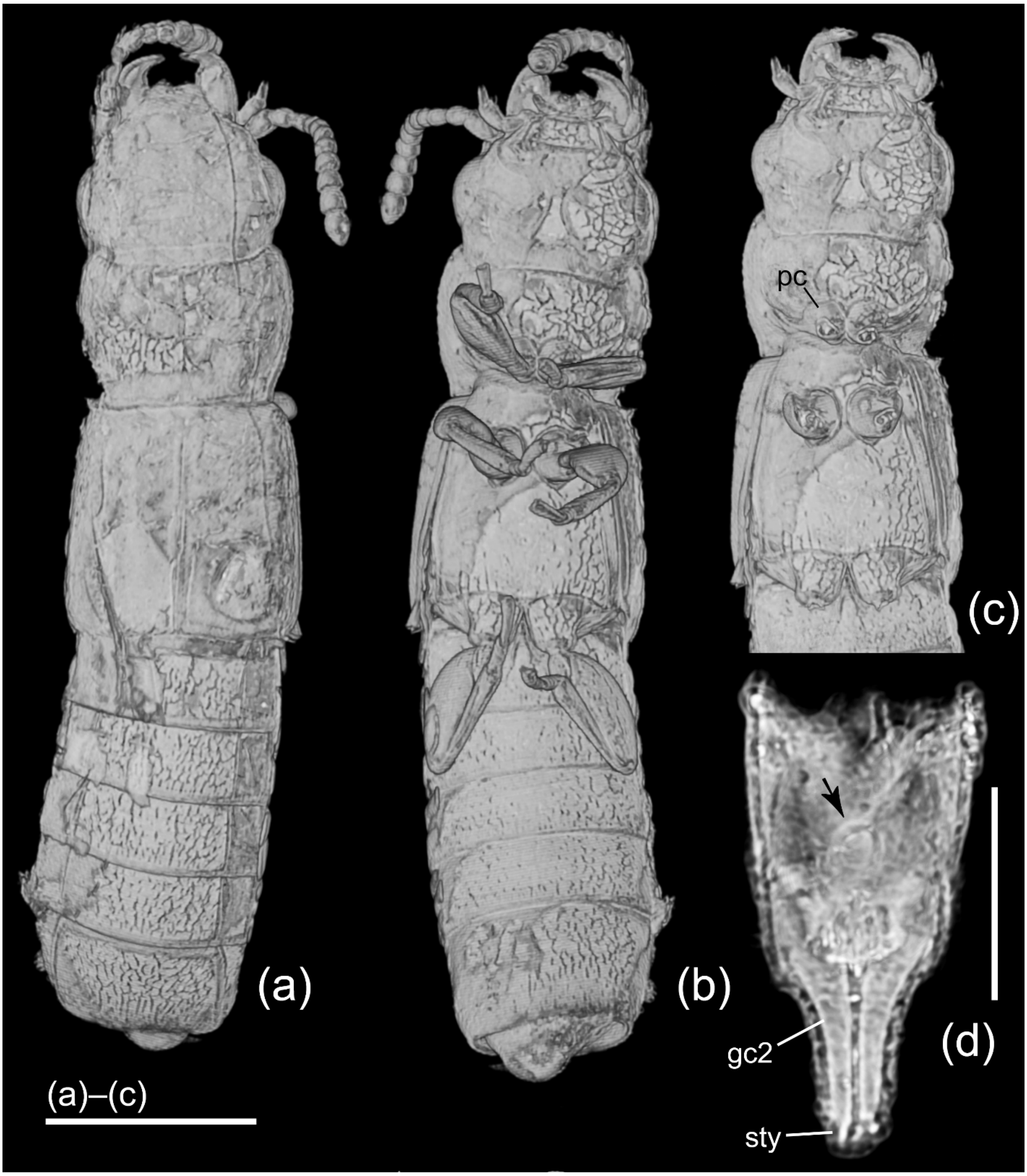

Figure 2 †*Charhyphus serratus* sp. nov., 001 DUBC, holotype, X-ray micro-CT reconstructions: (a) habitus, dorsal view; (b) habitus, ventral view; (c) forebody (without antennae and legs), ventral view; (d) abdominal terminalia with female genital segments, ventral view. Abbreviations: gc2 = gonocoxite 2; pc = procoxa; sty = stylus. Scale bars = 0.6 mm (a–c), 0.1 mm (d).

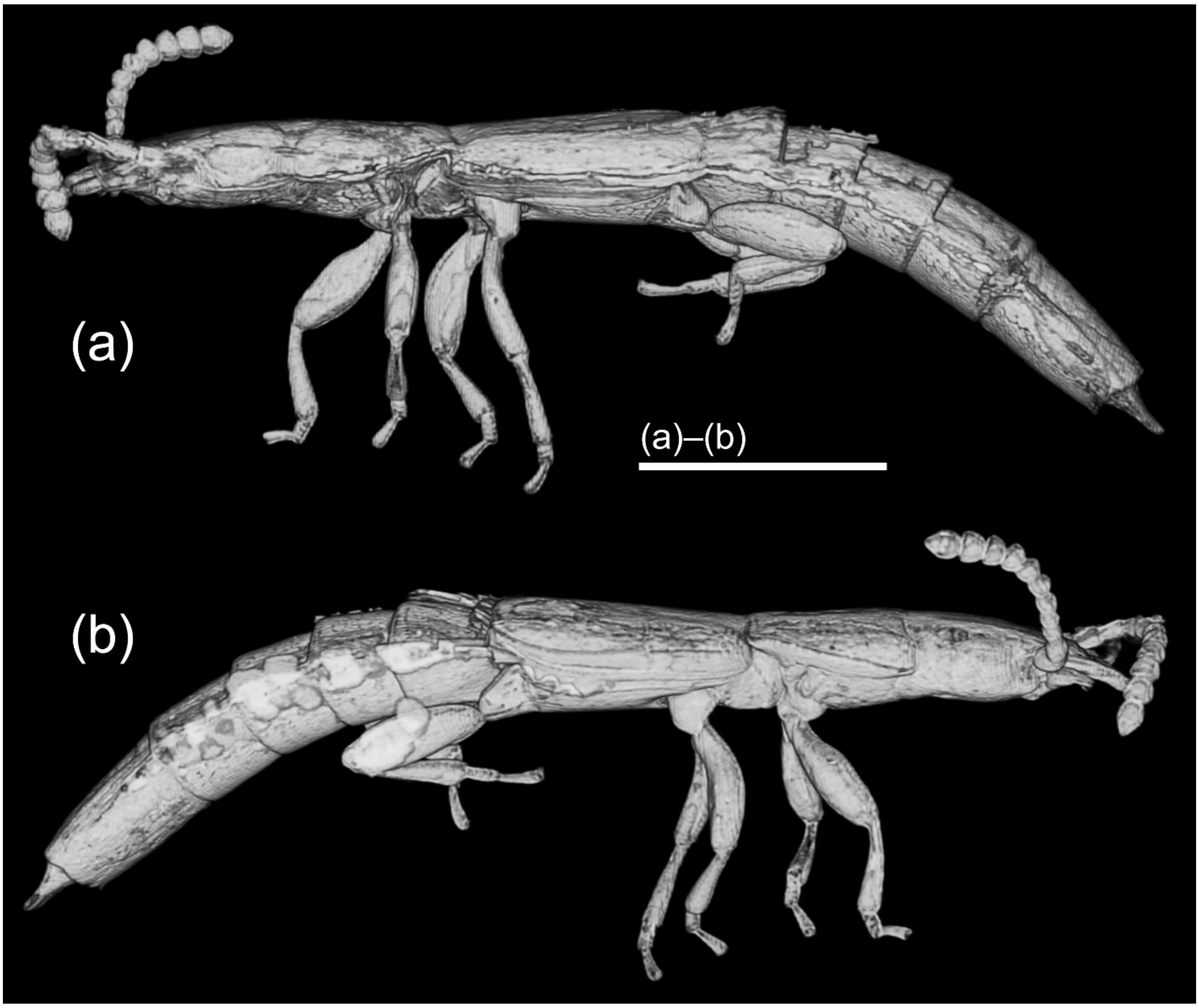

Figure 3 †*Charhyphus serratus* sp. nov., 001 DUBC, holotype, X-ray micro-CT reconstructions: (a) lateral habitus, left; (b) lateral habitus, right. Scale bar = 0.6 mm.

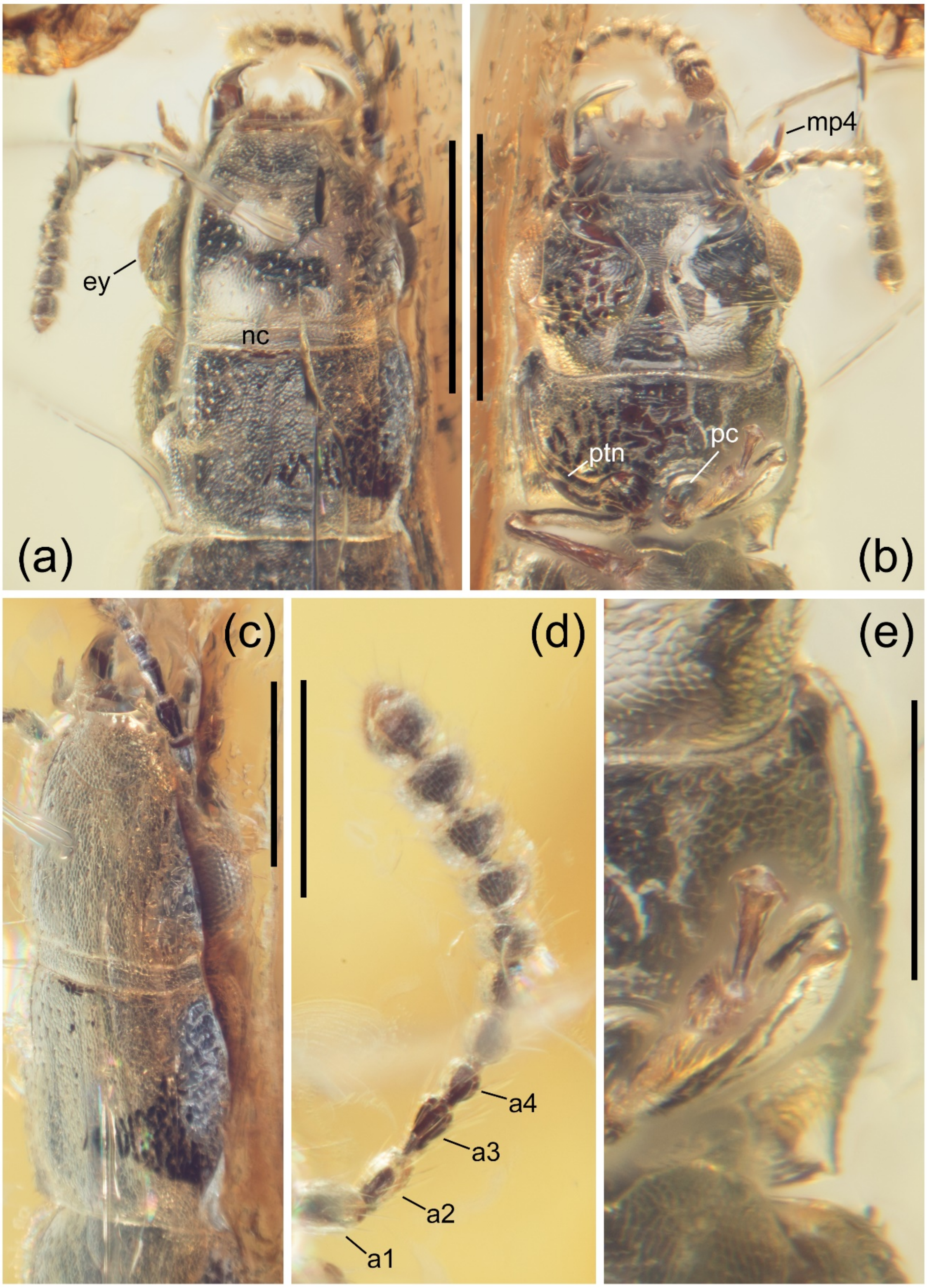

Figure 4 †*Charhyphus serratus* sp. nov., 001 DUBC, holotype, microphotographs: (a) head and pronotum, dorsal view; (b) head and pronotum, ventral view; (c) head and pronotum, dorsolateral view; (d) antenna, left; (E) pronotum and prosternum, ventral view. Abbreviations: a1–a4 = antennomeres 1–4; ey = eyes; mp4 = maxillary palpomere IV; nc = neck-like constriction; pc = procoxa; ptn = protrochantin. Scale bars = 0.5 mm (a–b), 0.3 mm (c), 0.2 mm (d–e).

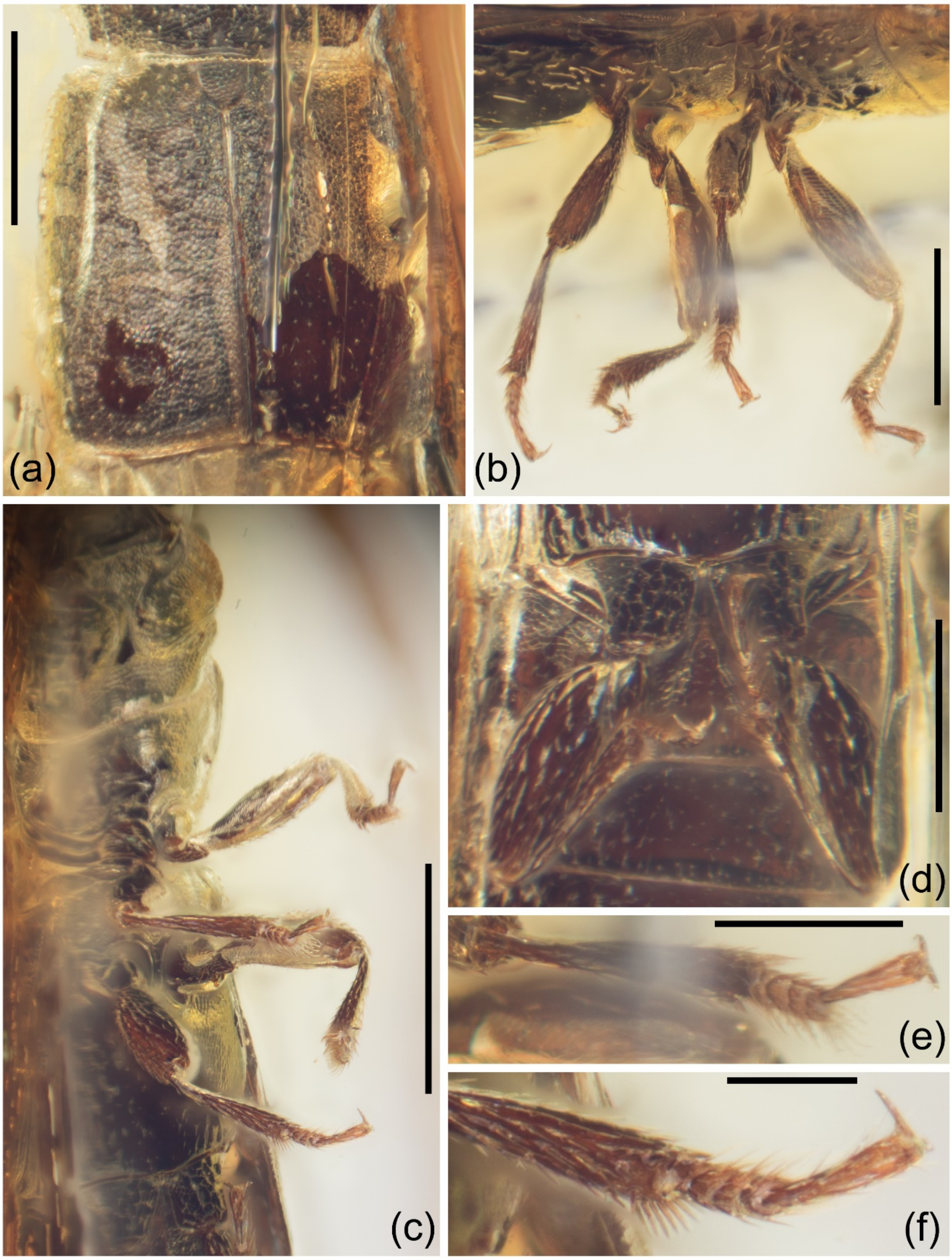

Figure 5 †*Charhyphus serratus* sp. nov., 001 DUBC, holotype, microphotographs: (a) elytra and scutellum, dorsal view; (b) thorax and legs, lateral view, right; (c) head and thorax with legs, ventrolateral view; (d) posterior part of metaventrite and hind legs; (e) protibia and protarsus, right; (f) mesotibia and mesotarsus, right. Scale bars = 0.3 mm (a–b, d), 0.5 mm (c), 0.2 mm (e), 0.1 mm (f).

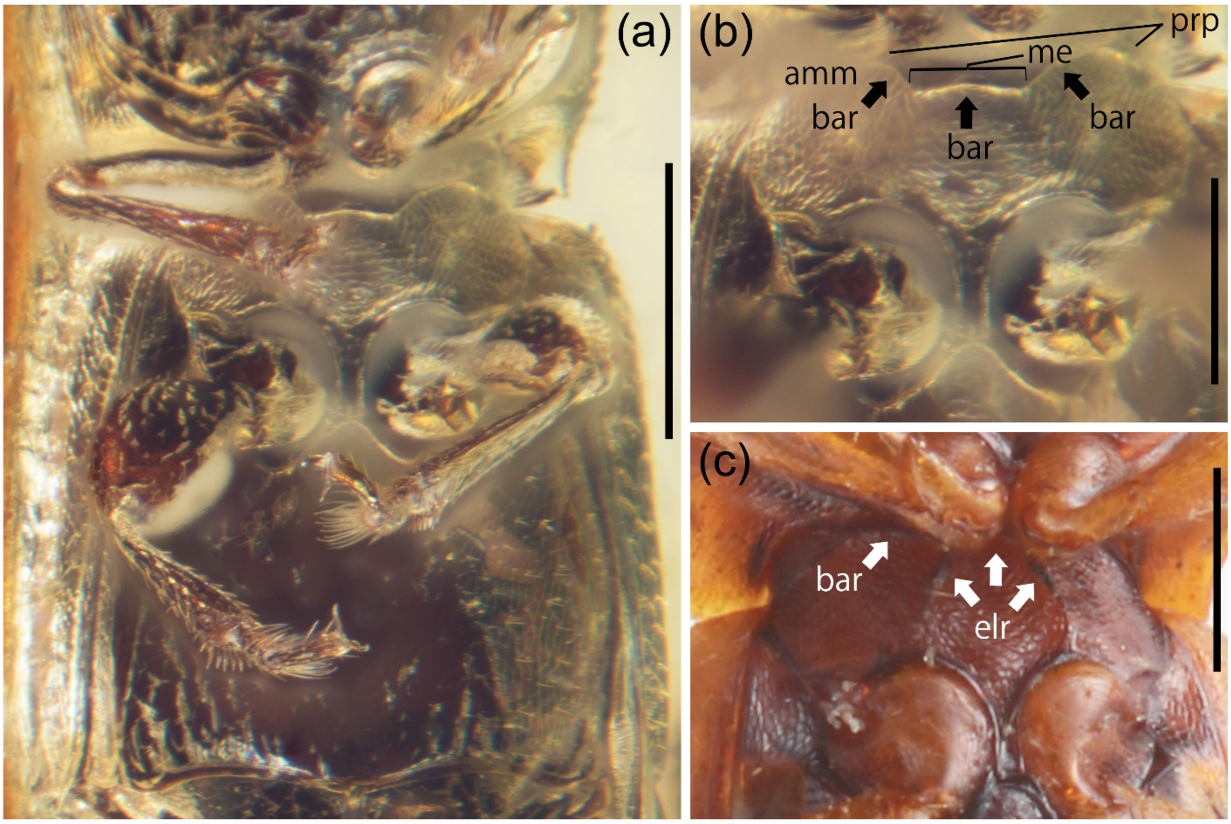

Figure 6 †*Charhyphus serratus* sp. nov., 001 DUBC, holotype, microphotographs: (a) pro-, meso-, and metathorax, ventral view; (b) metaventrite, ventral view. *Charhyphus brevicollis* Sharp, 1887, microphotographs: (c) mesoventrite. Abbreviations: amm, anterior margin of mesoventrite; bar, basal apical ridges on mesoventrite; elr, posteriorly directed elliptical ridge; me, medial emargination of the basal apical ridges on anterior margin of the mesoventrite; prp, paired rounded portions of the medioapical margin of the mesoventrite. Scale bars = 0.25 mm (a), 0.15 mm (b), 0.2 mm (c).

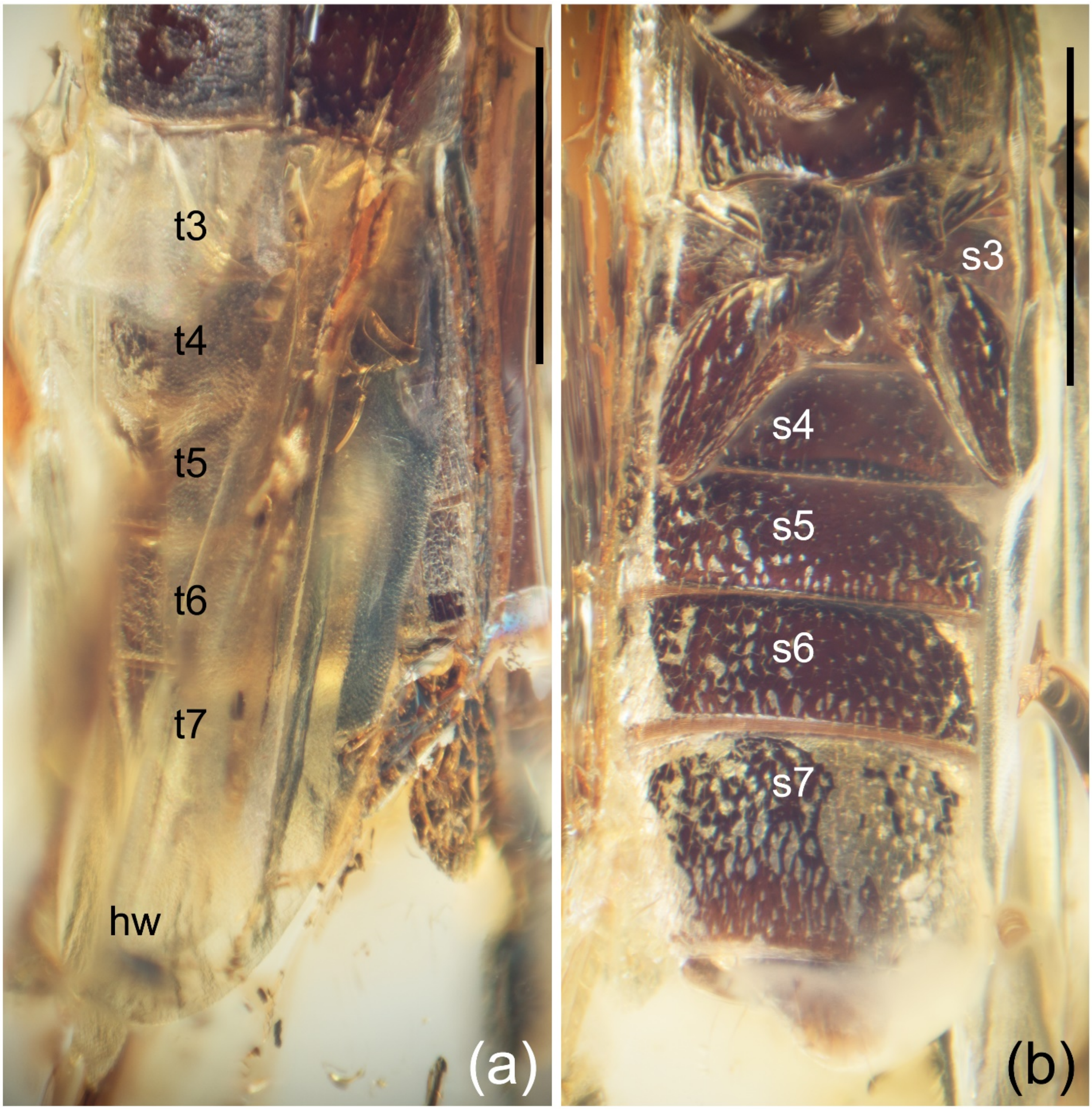

Figure 7 †*Charhyphus serratus* sp. nov., 001 DUBC, holotype, microphotographs: (a) abdomen, dorsal view; (b) abdomen, ventral view. Abbreviations: hw, hind wings; s3–s7, sternites 3–7; t3–t7, tergites 3–7. Scale bars = 0.5 mm (a–b).

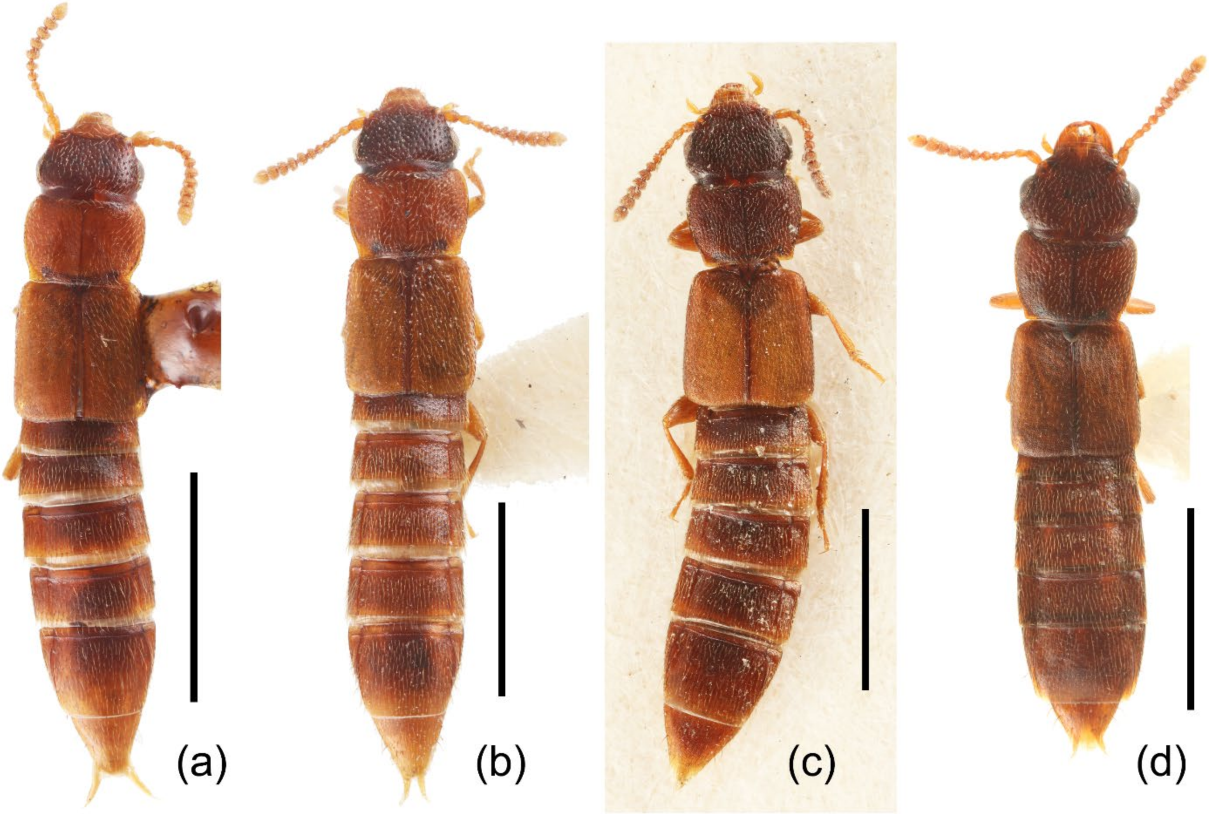

Figure 8 Habitus of all extant species of *Charhyphus*, dorsal view: (a) *C. arizoniensis* Herman, 1972 (USA: Arizona, Pinaleño Mts.); (b) *C. brevicollis* Sharp, 1887 (Mexico: 19 mi SW Toluca); (c) *C. paradoxus* (Bernhauer, 1933), syntype (Russia: Vladivostok); (d) *C. picipennis* (LeConte, 1863) (USA: Massachusetts, Boxford). Scale bars = 1.0 mm.

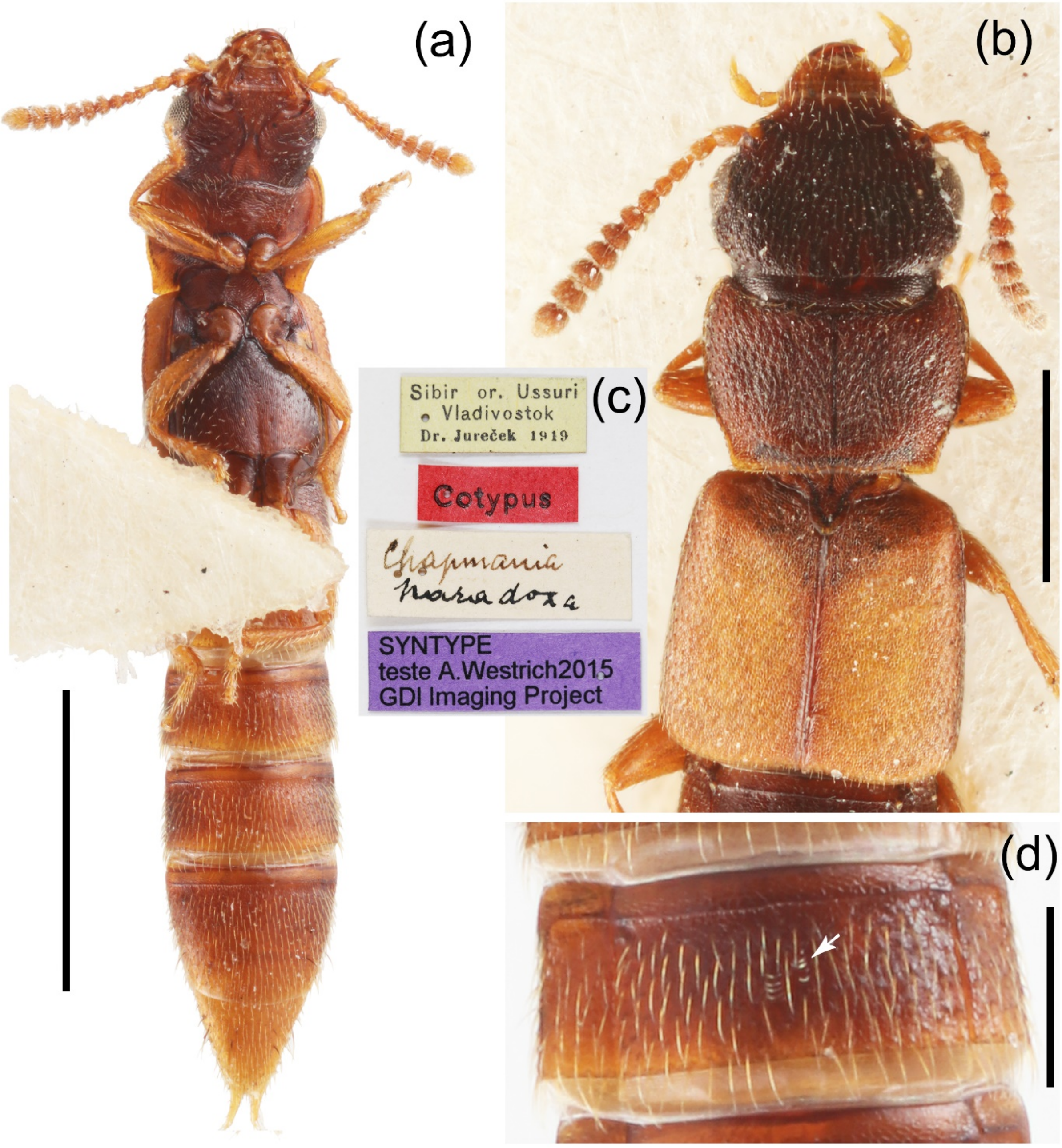

Figure 9 Habitus and body parts of extant species of *Charhyphus*: (a) *C. brevicollis*, habitus, ventral view; (b) *C. paradoxus*, syntype, forebody, dorsal view; (c) syntype labels of *C. paradoxus*, associated with (b); (d) *C. arizoniensis*, abdominal tergite V, arrow showing small median pair of cuticular combs. Scale bars = 1.0 mm (a), 0.5 mm (b), 0.2 mm (d).