nature COMMUNICATIONS

ARTICLE

Received 25 Sep 2016 | Accepted 8 Feb 2017 | Published 16 Mar 2017

DOI: 10.1038/ncomms14894 OPEN

Mycophagous rove beetles highlight diverse mushrooms in the Cretaceous

Chenyang Cai[1,2], Richard A.B. Leschen[3], David S. Hibbett[4], Fangyuan Xia[5] & Diying Huang[2]

Agaricomycetes, or mushrooms, are familiar, conspicuous and morphologically diverse Fungi. Most Agaricomycete fruiting bodies are ephemeral, and their fossil record is limited. Here we report diverse gilled mushrooms (Agaricales) and mycophagous rove beetles (Staphylinidae) from mid-Cretaceous Burmese amber, the latter belonging to Oxyporinae, modern members of which exhibit an obligate association with soft-textured mushrooms. The discovery of four mushroom forms, most with a complete intact cap containing distinct gills and a stalk, suggests evolutionary stasis of body form for ~99 Myr and highlights the palaeodiversity of Agaricomycetes. The mouthparts of early oxyporines, including enlarged mandibles and greatly enlarged apical labial palpomeres with dense specialized sensory organs, match those of modern taxa and suggest that they had a mushroom feeding biology. Diverse and morphologically specialized oxyporines from the Early Cretaceous suggests the existence of diverse Agaricomycetes and a specialized trophic interaction and ecological community structure by this early date.

[1] Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. [2] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. [3] Landcare Research, New Zealand Arthropod Collection, Private Bag 92170, Auckland, New Zealand. [4] Department of Biology , Clark University, Worcester, Massachusetts 01610, USA. [5] Lingpoge Amber Museum, Shanghai 201108, China. Correspondence and requests for materials should be addressed to D.H. (email: dyhuang@nigpas.ac.cn).

Agaricomycetes is the most conspicuous and morphologically diverse group of Fungi[1]. Most agaricomycete fruiting bodies are ephemeral[2], and so their fossils are extremely sparse[2–6]. Evidence indicating the origin and early diversification of Agaricomycetes is very limited. A Jurassic fossil that had been interpreted as a bracket fungus[7] was shown to be the outer bark of a conifer[8]. To date, five definitive species of agarics (gilled mushrooms) have been known exclusively from amber. Among them, two different forms are from the Mesozoic, including the earliest mushrooms, *Palaeoagaracites antiquus* from mid-Cretaceous Burmese amber[3] (~99 Myr old), and the slightly younger *Archaeomarasmius leggetti* from New Jersey amber[2,4] (~90 Myr old). The remaining three species, *Aureofungus yaniguaensis*[5], *Coprinites dominicana*[6] and *Protomycena electra*[4], are known from early Miocene Dominican amber, some 20 Myr old. All known fossil agarics are very small in size. Here we report four new forms of modern-looking gilled mushrooms (Agaricales) and diverse mycophagous rove beetles (Coleoptera, Staphylinidae) from mid-Cretaceous Burmese amber, the latter belonging to Oxyporinae, modern members that exhibit an obligate association with mature soft-textured mushrooms[9–11]. The specialized mouthpart morphology of these beetles sheds light on the early evolution of insect–fungal associations. More importantly, diverse and morphologically specialized oxyporines from the Early Cretaceous[12,13] suggest a probable occurrence of diverse large-sized Agaricomycetes by that period.

Results

Studied material. The material includes fossil mushrooms and beetles: five mushrooms of four distinctive forms (Taxa A–D) in Burmese amber (~99 Myr old) from Hukawng Valley, northern Myanmar, and five species and four genera of oxyporine beetles. The beetles consist of two new *Oxyporus* species (Taxa 1 and 2) and a new genus (Taxon 3) from Burmese amber, and two monotypic genera (*Protoxyporus* and *Cretoxyporus*) from the Lower Cretaceous Yixian Formation (~125 Myr old) of northeastern China. These fossils are extremely rare among the 111,000 Burmese amber inclusions and in our collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Diverse gilled mushrooms from Burmese amber. The mid-Cretaceous fossil mushrooms (Fig. 1; Supplementary Fig. 1) are clearly Agaricomycetes, a derived group of fungi that plays significant ecological roles as decomposers, pathogens, and symbionts in terrestrial ecosystems and that includes most edible mushrooms. Three of the four mushrooms (Fig. 1a,c,e; Supplementary Figs 2a,c and 3a,b) are nearly complete, with an intact cap (pileus), gills (lamellae) and stalk. All are minute, with caps ranging from 2.6 to 3.9 mm in diameter. The caps (Fig. 1a,c–e; Supplementary Figs 2a,c and 3a–c) range from strongly to slightly plano-convex and are mostly radially sulcate. Lamellae (Fig. 1b; Supplementary Figs 2b,d and 3e) are mostly sub-distant and comparatively close in one form. Macromorphological features of these fossils resemble extant mushrooms. In particular, two of four forms (Taxon A and B; Fig. 1a,c; Supplementary Fig. 2a,c) are similar to the extant genera *Marasmius, Marasmiellus* or *Crinipellis*, and the fossil *Archaeomarasmius* from late-Cretaceous New Jersey amber, suggesting that they belong to the family Marasmiaceae (Agaricales). The other two forms are difficult to place in extant families due to the lack of micromorphological features and inadequate preservation. Taxon C (Fig. 1d; Supplementary Fig. 3c) has a slightly convex pileus (Fig. 1d), close lamellae (Supplementary Fig. 3e) and a sub-marginal stalk (Supplementary Fig. 3d), a combination of features that is not easy to compare with modern agarics. Taxon D (Fig. 1e; Supplementary Fig. 3a,b) has a plicate-pectinate cap margin, which is similar to that of the Miocene *Coprinites* from Dominican amber. However, the former differs from *Coprinites* by the short, stout and sub-marginal stalk (Supplementary Fig. 3b). The discovery of four mushroom forms from Burmese amber, together with the known *Palaeoagaracites antiquus* from the same deposit, highlights the palaeodiversity of Agaricomycetes in the mid-Cretaceous. Like their modern counterparts in Marasmiaceae, these mushrooms (Taxa A and B) were probably decayers of leaf litter and wood in ancient ecosystems. Detailed descriptions of the fossil mushrooms are given in Supplementary Note 1.

Mycophagy and mycophagous oxyporine rove beetles. Mycophagy, or fungus-feeding, is widespread in Coleoptera[14–16] and the occurrence of this feeding habit in older clades of many lineages[17–19] suggests that it preceded phytophagy (feeding on

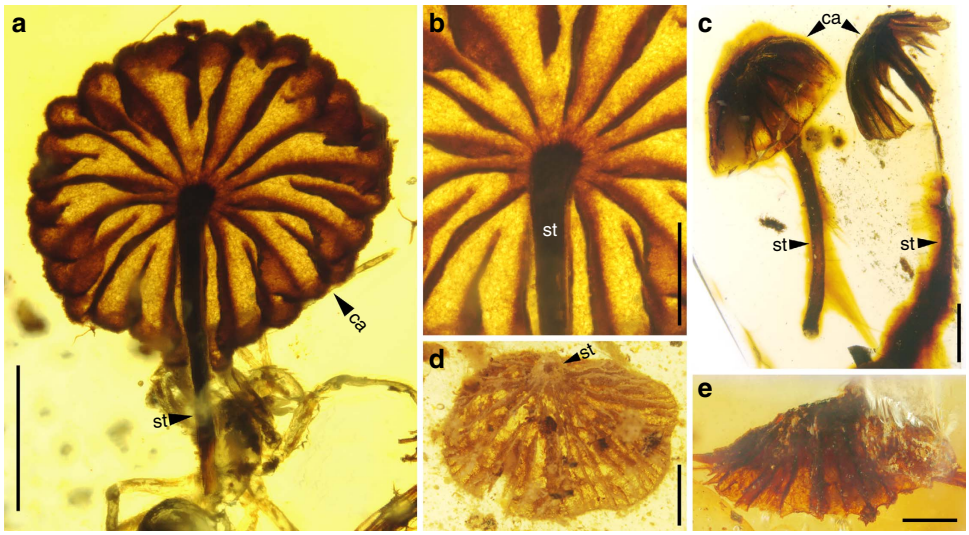


Figure 1 | Diverse mushrooms in mid-Cretaceous amber from northern Myanmar. (**a**) General habitus of Taxon A, FXBA10101, ventral view. (**b**) Enlargement of **a**, showing details of lamellae and top portion of stalk. (**c**) Lateral view of two individuals of Taxon B, NIGP164521 (left) and NIGP164522 (right). (**d**) Ventral view of Taxon C, NIGP164523, showing sub-marginally inserted stalk. (**e**) Lateral view of Taxon D, NIGP164524. Abbreviations: ca, cap; st, stalk. Scale bars, 1 mm (**a**,**c**,**d**); 500 μm (others).

plant tissues). Specialized feeding on mushrooms (including Agaricales, Boletales and Polyporales) occurs in a few beetle lineages and involves species that feed on spores and conidia or those that feed on the hymenium or hyphal tissue, each correlated with specialized mouthparts[17,20]. Recent fossil-based findings shed light on this feeding behaviour, and we report diverse specialized obligately mycophagous rove beetles (Fig. 2a–i; Supplementary Figs 4–9) that set an early date for mushroom specialization and evidence for the existence of diverse Agaricomycete fruiting bodies in the Early Cretaceous.

These brown to black beetles, with a body length ranging from 4.5 to 7.9 mm (Fig. 2a–c; Supplementary Figs 4, 6a,b and 7a), are conspicuous among all staphylinids discovered in Burmese amber. The beetles are definitely oxyporine rove beetles (Staphylinidae: Oxyporinae) as evidenced by the characteristic mouthparts (enlarged mandibles, greatly enlarged apical labial palpomeres; Fig. 3a–e; Supplementary Figs 5a,b,e–i, 6d–f, 7b–f and 8a,b,e), and widely separated mesocoxae present in extant forms (see Supplementary Note 2 for detailed description). These oxyporines include three distinctive species, with two (Taxa 1 and 2) assignable to the extant *Oxyporus* and the third belonging to a new genus (Taxon 3; see Supplementary Note 2).

The most remarkable structure of these beetles is the long, enlarged and anteriorly extended mandibles with the incisor edge well developed. The left mandible (Fig. 3b; Supplementary Fig. 8c) has a notch-like structure on the outer ventral margin to receive the right mandible when at rest just as that found in extant *Oxyporus* species (Supplementary Figs 10a and 11a,b)[10,11,21]. The right mandible (Supplementary Fig. 8c), unlike modern *Oxyporus*, has a jagged incisor edge with dense small, sharp anteriorly directed teeth and a distinct process forming a deep notch-like structure on the ventral margin to receive the left mandible and its ventral notch-like structure. Similar-looking small teeth are found on the mandibles in other soft-tissue

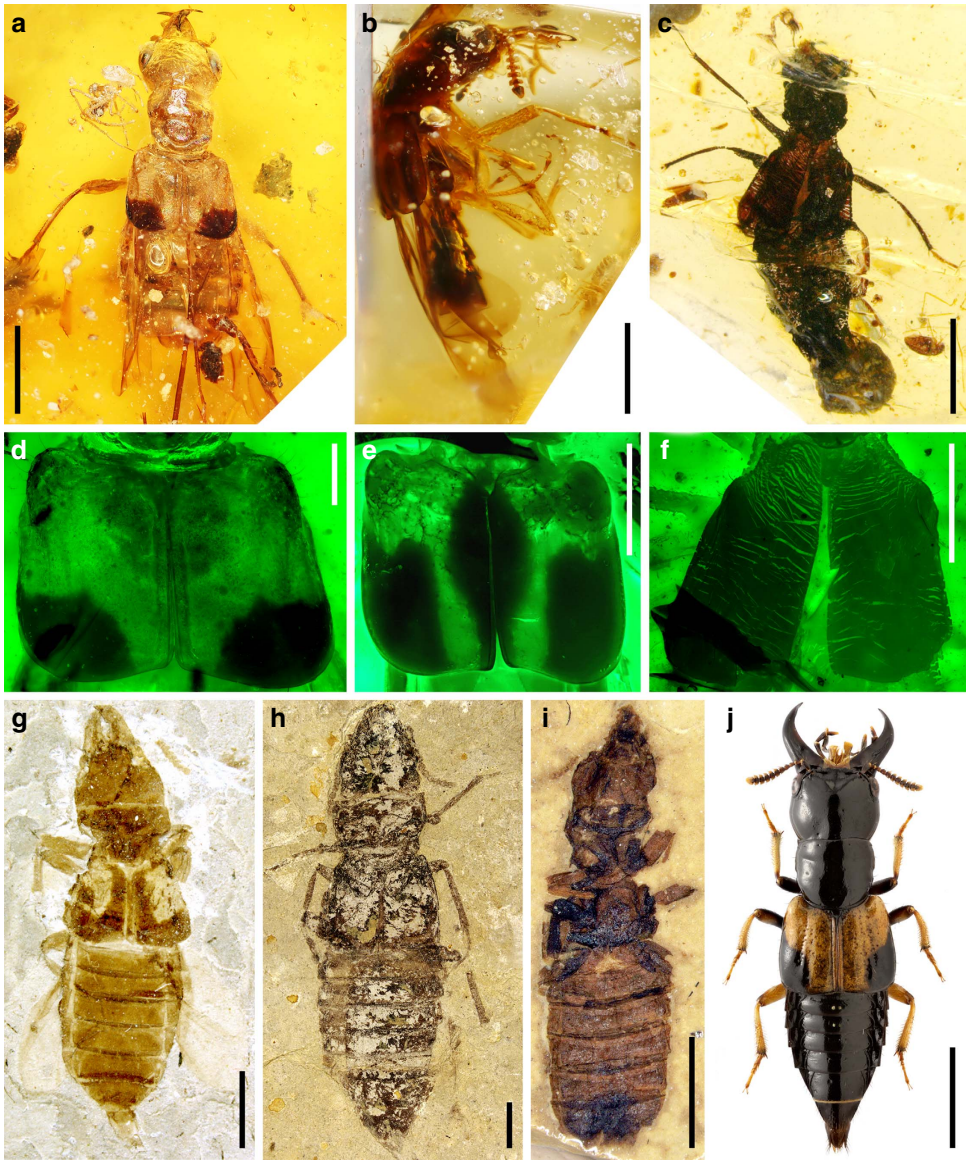


Figure 2 | Diverse mycophagous oxyporine rove beetles. (**a**–**c**) Beetles from mid-Cretaceous Burmese amber, (**d**–**f**) under fluorescence, (**g**–**i**) from the Early Cretaceous Yixian Formation of northeastern China. (**a**) Dorsal view of Taxon 1, NIGP164526. (**b**) Lateral view of Taxon 2, NIGP164528. (**c**) Dorsal view of Taxon 3, NIGP160556. (**d**) Enlargement of elytra from **a**. (**e**) Enlargement of elytra from **b**. (**f**) Enlargement of elytra from **c**. (**g**) *Oxyporus yixianus*; image courtesy of Yanli Yue. (**h**) *Protoxyporus grandis*. (**i**) *Cretoxyporus extraneus*. (**j**) *O. maxillosus*; image courtesy of Maxim Smirnov. Scale bars, 2 mm (**a**,**c** and **g**–**j**); 1 mm (**b**); 500 μm (**d**–**f**).

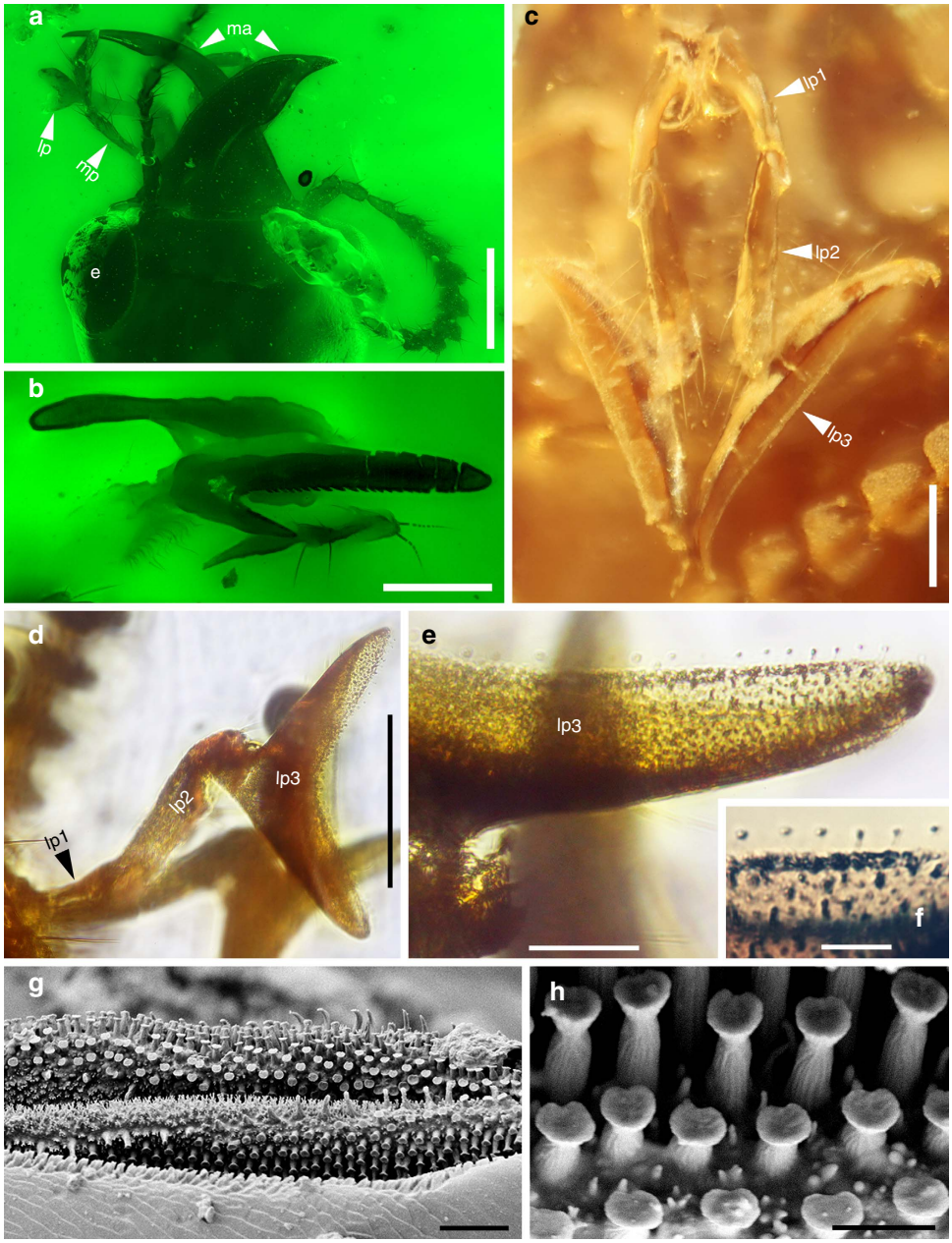


Figure 3 | Details of mouthparts of extinct and extant mycophagous oxyporine rove beetles. (**a**,**b**) Images under fluorescence, (**c**) under reflected light, (**d**–**f**) under transmitted light and (**g**,**h**) under SEM. (**a**) Mouthparts of Taxon 1, NIGP164527. (**b**) Mandibles of Taxon 3, NIGP160556. (**c**) Labial palpi of Taxon 1, NIGP164526. (**d**) Labial palpus of Taxon 2, NIGP164528. (**e**) Enlargement of **d** showing dense peg-like sensory organs. (**f**) Enlargement of **e**, showing details of sensory organs. (**g**) Apex of labial palpus of extant *Oxyporus* sp., showing both peg-like and villiform sensory organs. (**h**) Details of peg-like sensory organs. Abbreviations: e, eye; lp, labial palpomere; ma, mandible; mp, maxillary palpomere. Scale bars, 500 μm (**a**); 200 μm (**b**–**d**); 50 μm (**e**); 20 μm (**f** and **g**); 5 μm (**h**).

specialists, including Scaphidiinae mushroom feeders[20] and the modifications probably represent one of the principal morphological adaptations of Cretaceous oxyporines to mushroom feeding as in extant *Oxyporus* species[10]. Like modern *Oxyporus* (Supplementary Fig. 11a,c,e–h), the mandibles bear a basal pseudomola (Supplementary Fig. 8b), or prostheca, in the form of a brush, a structure assumed as an adaptation to pre-oral digestion in *Oxyporus* adults[22]. The ventral basal area of the mandibles possesses a brush-like structure on the posterior region that serves to increase the surface area for masticating the fungal slices and possibly mixing the material with digestive enzymes produced from the gut. In addition, the closed mandibles probably serve to form a container for the bolus as suggested in its present-day counterparts[23], while the notch-like structures on both mandibles are slightly out-of-line and probably serve as a compression device during mandibular apposition to further macerate fungal tissue.

Another impressive feature of these early beetles is the highly modified labial palpi. The labial palpi (Fig. 3c,d; Supplementary Figs 7f and 8e) are three-segmented, with the apical segment laterally compressed and crescent-shaped (Fig. 3d; Supplementary Fig. 7g), a characteristic feature of modern Oxyporinae (Supplementary Figs 9d, 10a–d, 11d and 12a,b)[10,11] but also found in some staphylinine staphylinids[10]. The first labial palpomere is distinctly shorter than the second, which bears a shallow anterolateral notch at the apex for receiving the base of the

apical palpomere (Fig. 3c,d; Supplementary Fig. 7f). The last labial palpomere is widened and possesses an apical enlarged surface covered with dense, fine peg-like structures (Fig. 3e,f), sometimes appearing as darkened spots from certain angle (Supplementary Fig. 7h) and similar to structures found in extant oxyporines (Fig. 3g,h; Supplementary Fig. 12c–f), although at least three other types of sensory organs (sensillae) are detected from the latter (Supplementary Fig. 12g,h). The sensory areas may aid in the recognition of its host fungi or evaluate quality of the fungal host and are features that also occur on the palpi of obligate mushroom-feeding Erotylidae beetles[10]. Oxyporinae are thought to be members of a predatory group of staphylinines exhibiting different methods of prey handling, including the bizarre stick–capture method for prey–capture by stenines[24,25]. However, the long-held view that the ancestral Oxyporinae had shifted from predation to mushroom feeding is compromised by different placements in recent phylogenetic studies[26,27] (Supplementary Note 3). The exact phylogenetic placement of Oxyporinae remains controversial, complicating the exact nature of the origin of mushroom feeding in the group. Oxyporinae are placed in the predatory Staphylinine group of subfamilies, in a basal position relative to Megalopsidiinae[26], but recently the Staphylinine group is recovered as polyphyletic, and Oxyporinae as a sister to Leptotyphlinae[27]. The peculiar mouthpart structure of fossil oxyporines suggests that the beetles may have been feeding on soft tissues like fleshy mushrooms as do modern oxyporines[10,18], though some of these features are not exclusive to fungus feeding lineages[23] and that host-shifts among widely different food types may occur as long as the texture of the substrates is similar[20].

Discussion

Most extant Agaricomycetes have ephemeral fruiting bodies, although the group also includes taxa with tough, persistent sporocarps, like those of wood-decaying polypores[28]. The fossil record of Agaricomycetes is limited, with only five definitive species of agarics (gilled mushrooms) known previously and four new forms reported here (Supplementary Table 1). All known fossil agarics are small in size, with the pileus ranging from 2.2 to 5.0 mm in diameter (Supplementary Table 1). Their small size and life habits including growing on certain resin-producing plants probably contribute significantly to their amber fossilization. Many extant Marasmiaceae have tough stipes and pilei that can shrivel on drying but then revive on rewetting, which may also promote preservation as fossils. Assuming that the Burmese oxyporines were mushroom specialists with similar habits as the modern species, such as subsocial care on large mushroom fruiting bodies[10], it is unlikely that they fed on the contemporaneous mushrooms from the same deposit described herein, primarily due to the small-sized fruiting body with a pileus <4 mm in diameter. Both larvae and adults of modern *Oxyporus* species construct tunnels in the mushroom cap upon which they feed[9,22,29] and adult females construct brood chambers[30]. The body size of fossil oxyporines were comparatively large (4.5–7.9 mm long), and to construct tunnels and build brood chambers to accommodate up to eight or more eggs[23,30] in fossil mushrooms much smaller than the beetle body length seems unlikely. Therefore, it is likely that during the mid-Cretaceous the Agaricomycetes were more diverse than previously documented and included large mushrooms, related to, but distinct from, the fossil mushrooms reported here.

In addition to multiple oxyporine forms in Burmese amber, oxyporine beetles are known from the older Yixian Formation (*ca.* 125 Myr) of northeastern China (Supplementary Table 2), including *Oxyporus yixianus* (Fig. 2g), *Protoxyporus grandis* (Fig. 2h) and *Cretoxyporus extraneus* (Fig. 2i; Supplementary Fig. 9a–c). All these beetles bear the characteristic oxyporine body shape and prominent mandibles, though the expanded labial

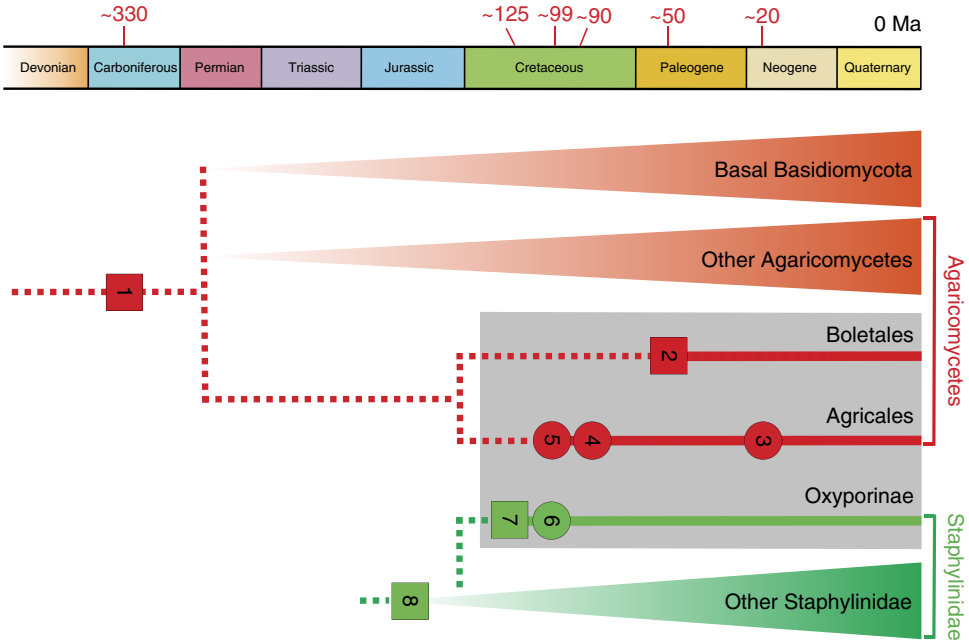


Figure 4 | Associations of higher Agaricomycetes and specialized oxyporine Staphylinidae. Framework for Basidiomycota (red part) based on Taylor and Berbee[31], Floudas *et al.*[36] and Hibbett *et al.*[37] 1: Oldest basidiomycete clamp connections from late Visean (Mississippian, ~330 Myr) of France[38]; 2: oldest Boletales (Ectomycorrhizae) from middle Eocene (~50 Myr) Princeton chert of British Columbia[39]; 3: modern-appearing mushrooms from Miocene (~20 Myr) Dominican amber[3–5]; 4: mushrooms from the Late Cretaceous (~90 Myr) New Jersey amber[1,3]; 5: diverse mushrooms from mid-Cretaceous (~99 Myr) Burmese amber; 6: diverse obligately mycophagous Oxyporinae from mid-Cretaceous Burmese amber; 7: diverse Oxyporinae from the Early Cretaceous Yixian Formation (~125 Myr) of China[1]; 8: oldest known Staphylinidae from the Middle Jurassic (Aalenian – Bathonian) of Kubekovo, Russia[40]. Squares, compression fossils. Circles, amber inclusions.

palpus is present only in *C. extraneus* (Supplementary Fig. 9c). Many mushroom beetles are aposematic, having warning colours that indicate toxicity to potential predators. This is true for many modern *Oxyporus* (Fig. 2j), which are often gaudy and bi- or tricoloured[11]. Although one of the Burmese oxyporines has black elytra (Fig. 2f), the other two species (Fig. 2d,e; Supplementary Figs 5d and 6b,c) and the older fossils (*Protoxyporus* and *O. yixianus*) have distinct bi-coloured elytra, suggesting mushroom-related biology in the Cretaceous. Among Early Cretaceous oxyporines, *P. grandis*, with a body length of 19.7 mm, represents the largest and most conspicuous of the oxyporines, a giant among the entire subfamily when compared with the modern oxyporines that range from 5.5 to 13.0 mm in length[11]. Modern large-sized *Oxyporus* species (>8 mm long), including *O. major* (8.2–12.7 mm long) and *O. rufipennis* (8.5–13.0 mm long), appear to have preferences for large fleshy mushrooms such as *Pleurotus ostreatus* (oyster mushroom, cap 5–25 cm across), *Polyporus squamosus* (8–30 cm across), *Armillaria gallica* (*ca.* 10 cm across), and some *Boletus* species[10,30], though there are a few records for some species that may be associated with large aggregations of moderately sized fungi[22]. Therefore, it is possible that the large-bodied Cretaceous *P. grandis* was associated with large-sized fruiting bodies, such as those produced by extant Agaricales, Boletales or Polyporales, that would accommodate larval growth, especially if these species were subsocial. In addition to having larger body sizes in the Early Cretaceous (8.1–19.7 mm long) the extinct species differ in several significant features, including cephalic and mesocoxal structures, which may indicate that they were adapted to different types of mushrooms present in the Early Cretaceous (Supplementary Fig. 13). Molecular clock dating studies have yielded highly inconsistent age estimates for the Fungi, with the Basidiomycota inferred to have originated from 450 Myr ago to over 1.1 Gyr ago[31–35]. A recent genome-based molecular clock analysis with fossil-based calibrations estimated the mean age of the Agaricomycetes as *ca.* 290 Myr ago[36]. Thus, it is probable that associations between specialized oxyporine rove beetles and Agaricomycetes were well established in the Early Cretaceous (Fig. 4), consistent with the hypothesis that higher fungi, including the main groups of mushrooms, had already diversified by the Early Cretaceous[31,36].

Methods

Specimen preparation and imaging. All specimens (except FXBA10101) are housed at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; FXBA10101 is housed in the Lingpoge Amber Museum in Shanghai. The amber has been polished with sand papers with different grain sizes and diatomite mud. Photomicrographs were taken using the Zeiss Discovery V20 microscope system, and those with green background (Figs 2d–f and 3a,b; Supplementary Figs 2d,e, 5a,c,d, 6a,c and 8) were using fluorescence as light source attached to a Zeiss Axio Imager 2 compound microscope. Finally, a compression fossil (NIGP153699) was examined with a LEO1530VP field emission scanning electron microscope.

Data availability. All data generated during this study are included in this published article (and its Supplementary Information files).

References

1. Hibbett, D. S. & Thorn, R. G. in *The Mycota VII Part B. Systematics and Evolution* (eds McLaughlin, D. I., McLaughlin E. G. & Lemke, P. A.) 121–168 (Springer-Verlage, 2001).
2. Hibbett, D. S., Grimaldi, D. & Donoghue, M. J. Cretaceous mushrooms in amber. *Nature* **377,** 487 (1995).
3. Poinar, G. O. & Buckley, R. Evidence of mycoparasitism and hypermycoparasitism in Early Cretaceous amber. *Mycol. Res.* **111,** 503–506 (2007).
4. Hibbett, D. S., Grimaldi, D. & Donoghue, M. J. Fossil mushrooms from Miocene and Cretaceous ambers and the evolution of homobasidiomycetes. *Am. J. Bot.* **84,** 981–991 (1997).
5. Hibbett, D. S., Binder, M., Wang, Z. & Goldman, Y. Another fossil agaric from Dominican amber. *Mycologia* **95,** 685–687 (2003).
6. Poinar, G. O. & Singer, R. Upper Eocene gilled mushroom from the Dominican Republic. *Science* **248,** 1099–1101 (1990).
7. Singer, R. & Archangelsky, S. A petrified basidiomycete from Patagonia. *Am. J. Bot.* **45,** 194–198 (1958).
8. Hibbett, D., Donoghue, M. & Tomlinson, P. Is *Phellinites digiustoi* the oldest homobasidiomycete? *Am. J. Bot.* **84,** 1005–1011 (1997).
9. Goodrich, M. A. & Hanley, R. S. Biology, development and larval characters of *Oxyporus major* (Coleoptera: Staphylinidae). *Entomol. News* **106,** 161–168 (1995).
10. Hanley, R. S. & Goodrich, M. A. Review of mycophagy, host relationships and behavior in the New World Oxyporinae (Coleoptera, Staphylinidae). *Coleopts. Bull.* **49,** 267–280 (1995).
11. Campbell, J. M. A revision of the New World Oxyporinae (Coleoptera: Staphylinidae). *Can. Entomol.* **101,** 225–268 (1969).
12. Yue, Y.-L., Ren, D. & Solodovnikov, A. The oldest fossil species of the rove beetle subfamily Oxyporinae (Coleoptera: Staphylinidae) from the Early Cretaceous (Yixian Formation, China) and its phylogenetic significance. *J. Syst. Palaeontol.* **9,** 467–471 (2011).
13. Cai, C. & Huang, D. Diverse oxyporine rove beetles from the Early Cretaceous of China (Coleoptera: Staphylinidae). *Syst. Entomol.* **39,** 500–505 (2014).
14. Beutel, R. G. & Leschen, R. A. B. in *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. Volume IV Arthropoda: Insecta; Part 38* (eds Kristensen, N. P. & Beutel, R. G.) XI + 567 (Walter de Gruyter, 2005).
15. Leschen, R. A. B., Beutel, R. G. & Lawrence, J. F. in *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. Volume IV Arthropoda: Insecta; Part 39* (eds Kristensen, N. P. & Beutel, R. G.) XIII + 786 (Walter de Gruyter, 2010).
16. Leschen, R. A. B. & Beutel, R. G. in *Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. Volume IV. Arthropoda: Insecta. Part 38* (eds Kristensen, N. P. & Beutel, R. G.). XII + 675 (Walter de Gruyter, 2014).
17. Lawrence, J. F. in *Insect-Fungus Interactions. 14th Symposium of the Royal Entomological Society of London in Collaboration with the British Mycological Society* (eds Wilding, N., Collins, N. M., Hammond, P. M. & Webber, J. F.) 1–23 (Academic Press, 1989).
18. Newton, Jr A. F. in *Fungus-Insect Relationships: Perspectives in Ecology and Evolution* (eds Wheeler, Q. & Blackwell, M.) 302-353 (Columbia University Press, 1984).
19. Leschen, R. A. B. & Buckley, T. R. Multistate characters and diet shifts: evolution of Erotylidae (Coleoptera). *Syst. Biol.* **56,** 97–112 (2007).
20. Leschen, R. A. B. in *Functional Morphology of Insect Feeding* (eds Schaefer, C. W. & Leschen, R. A. B.) 59–104 (Thomas Say Publications in Entomology, Entomological Society of America, 1993).
21. Hanley, R. S. Mandibular allometry and male dimorphism in a group of obligately mycophagous beetles (Insecta: Coleoptera: Staphylinidae: Oxyporinae). *Biol. J. Linn. Soc.* **72,** 451–459 (2001).
22. Leschen, R. A. B. & Allen, R. T. Immature stages, life histories and feeding mechanisms of three *Oxyporus* spp. (Coleoptera: Staphylinidae: Oxyporinae). *Coleopts. Bull.* **42,** 321–333 (1988).
23. Leschen, R. A. B. & Newton, A. F. Larval description, adult feeding, behavior, and phylogenetic placement of *Megalopinus* (Coleoptera: Staphylinidae). *Coleopts. Bull.* **57,** 469–493 (2003).
24. Weinreich, E. Über den klebfangapparat der Imagines von *Stenus* Latr. (Coleopt., Staphylinidae) mit einem Beitrag zur kenntnis der Jugendstadien dieser Gattung. *Zeitschrift für Morphologie der Tiere* **62,** 162–210 (1968).
25. Betz, O. & Kölsch, G. The role of adhesion in prey capture and predator defense in arthropods. *Arthropod Struct. Dev.* **33,** 3–30 (2004).
26. Grebennikov, V. V. & Newton, A. F. Good-bye Scydmaenidae, or why the ant-like stone beetles should become megadiverse Staphylinidae sensu latissimo (Coleoptera). *Eur. J. Entomol.* **106,** 275–301 (2009).
27. Mckenna, D. D. *et al.* Phylogeny and evolution of the Staphyliniformia and Scarabaeiformia: forest litter as a stepping-stone for diversification of non-phytophagous beetles. *Syst. Entomol.* **40,** 35–60 (2015).
28. Smith, S. Y., Currah, R. S. & Stockey, R. A. Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia. *Mycologia* **96,** 180–186 (2004).
29. Tikhomirova, A. L. *Morfoekologicheskiye osobennosti i filogenez stafilinid (s katalogom fauny SSSR) [Morphological and ecological features and phylogeny of the Staphylinidae (with a catalogue of the fauna of the USSR)]* (Academy of Sciences, USSR, 1973).
30. Setsuda, K. Construction of the egg chamber and protection of the eggs by female *Oxyporus japonicus* Sharp (Coleoptera: Staphylinidae: Oxyporinae). *Jpn J. Entomol.* **62,** 803–809 (1994).
31. Taylor, J. W. & Berbee, M. L. Dating divergences in the fungal tree of life: review and new analyses. *Mycologia* **98,** 838–849 (2006).
32. Douzery, E. J., Snell, E. A., Bapteste, E., Delsuc, F. & Philippe, H. The timing of eukaryotic evolution: does a relaxed molecular clock reconcile proteins and fossils? *Proc. Natl Acad. Sci. USA* **101,** 15386–15391 (2004).

33. Berbee, M. L. & Taylor, J. W. Dating the molecular clock in fungi–how close are we? *Fung. Biol. Rev.* **24,** 1–16 (2010).
34. Gueidan, C., Ruibal, C., De Hoog, G. S. & Schneider, H. Rock-inhabiting fungi originated during periods of dry climate in the late Devonian and middle Triassic. *Fungal Biol.* **115,** 987–996 (2011).
35. Lücking, R., Huhndorf, S., Pfister, D. H., Plata, E. R. & Lumbsch, H. T. Fungi evolved right on track. *Mycologia* **101,** 810–822 (2009).
36. Floudas, D. *et al.* The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* **336,** 1715–1719 (2012).
37. Hibbett, D. S. *et al.* in *Systematics and Evolution, 2nd Edition, The Mycota VII Part A* (eds McLaughlin D. J. & Spatafora J. W.) 373–429 (Springer, 2014).
38. Krings, M., Dotzler, N., Galtier, J. & Taylor, T. N. Oldest fossil basidiomycete clamp connections. *Mycoscience* **52,** 18–23 (2011).
39. LePage, B., Currah, R., Stockey, R. & Rothwell, G. Fossil ectomycorrhizae from the Middle Eocene. *Am. J. Bot.* **84,** 410–412 (1997).
40. Ryvkin, A. B. Beetles of the family Staphylinidae from the Jurassic of Transbaikalia. *Trudy Paleontologicheskogo Instituta, Akademia nauk SSSR* **211**, 88–91 (1985).

Acknowledgements

We are grateful to H.-L. Shi for providing extant oxyporine beetles. Financial support was provided by the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB18000000), the Ministry of Science and Technology (2016YFC0600406), the National Natural Science Foundation of China (41688103, 41602009 and 91514302), and the National Natural Science Foundation of Jiangsu Province (BK20161091). R.A.B. Leschen was supported in part by Core funding for Crown Research Institutes from the Ministry of Business, Innovation and Employment's Science and Innovation Group. Anne Austin reviewed an early draft of the manuscript.

Author contributions

C.C., R.A.B.L., F.X. and D.H. participated in morphological studies; D.H. designed the program; C.C., D.S.H. and R.A.B.L. prepared the manuscript.

Additional information

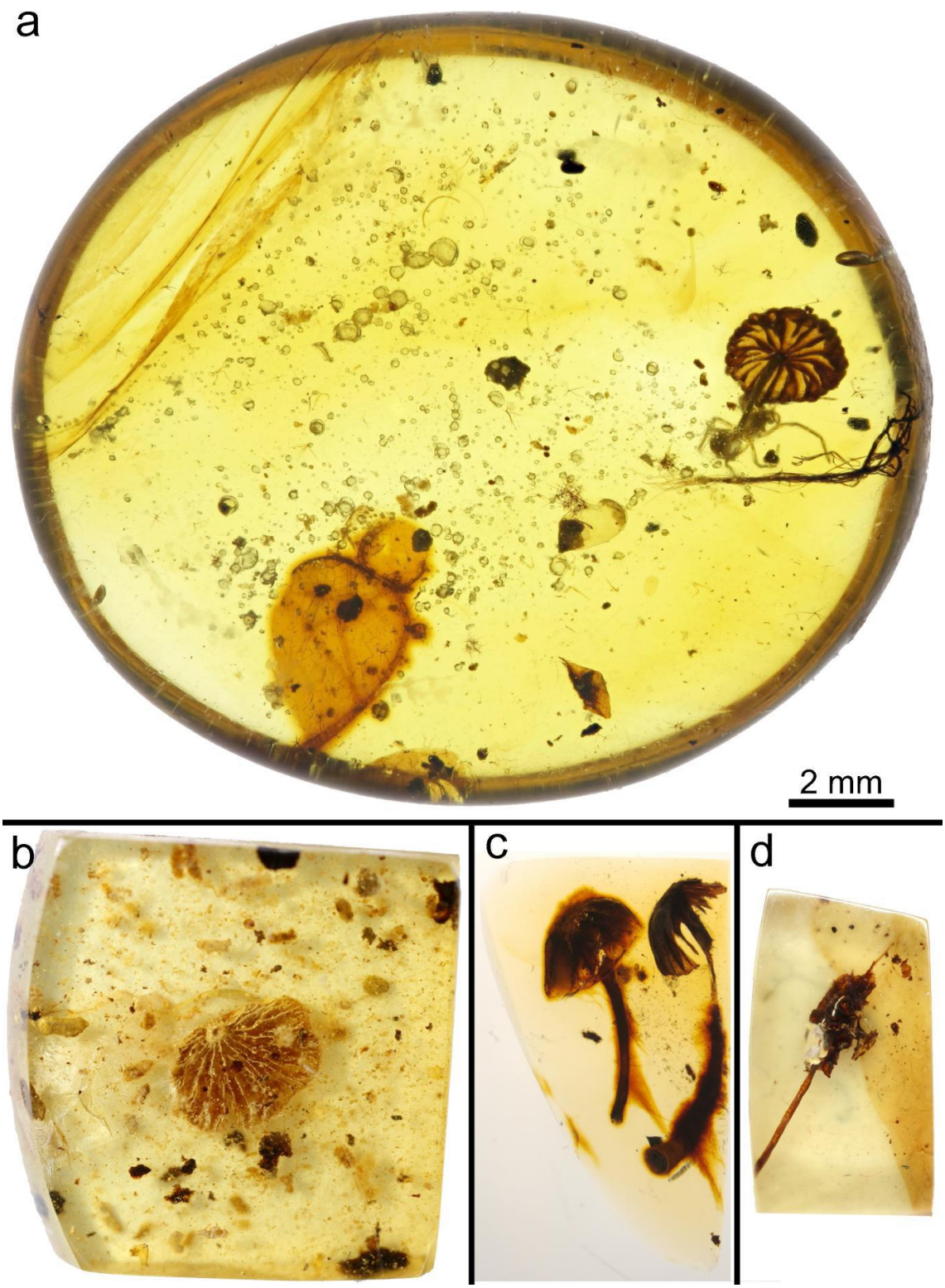
Supplementary Information accompanies this paper at http://www.nature.com/naturecommunications

Competing interests: The authors declare no competing financial interests.

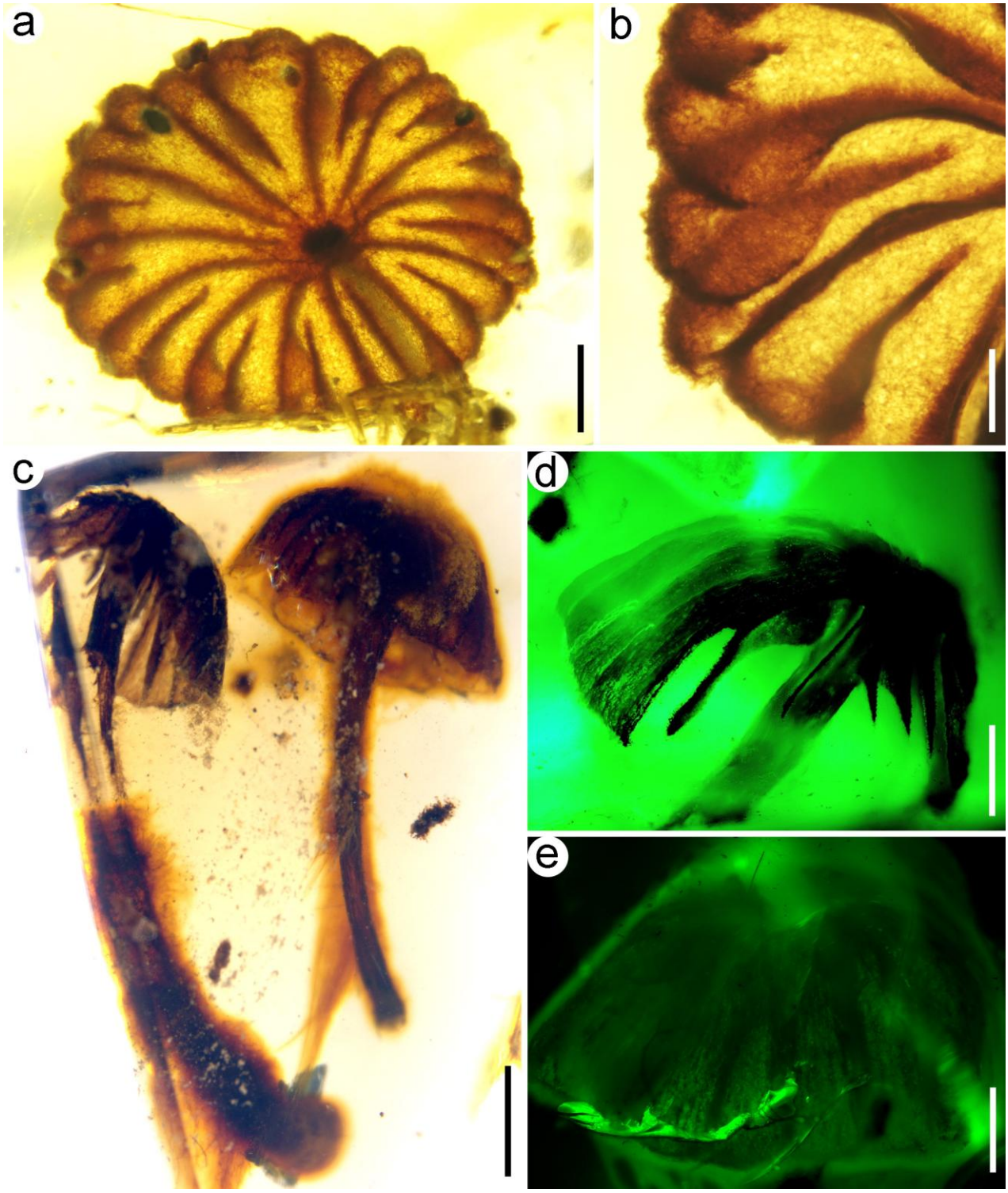
Reprints and permission information is available online at http://npg.nature.com/reprintsandpermissions/

How to cite this article: Cai, C. *et al.* Mycophagous rove beetles highlight diverse mushrooms in the Cretaceous. *Nat. Commun.* **8,** 14894 doi: 10.1038/ncomms14894 (2017).

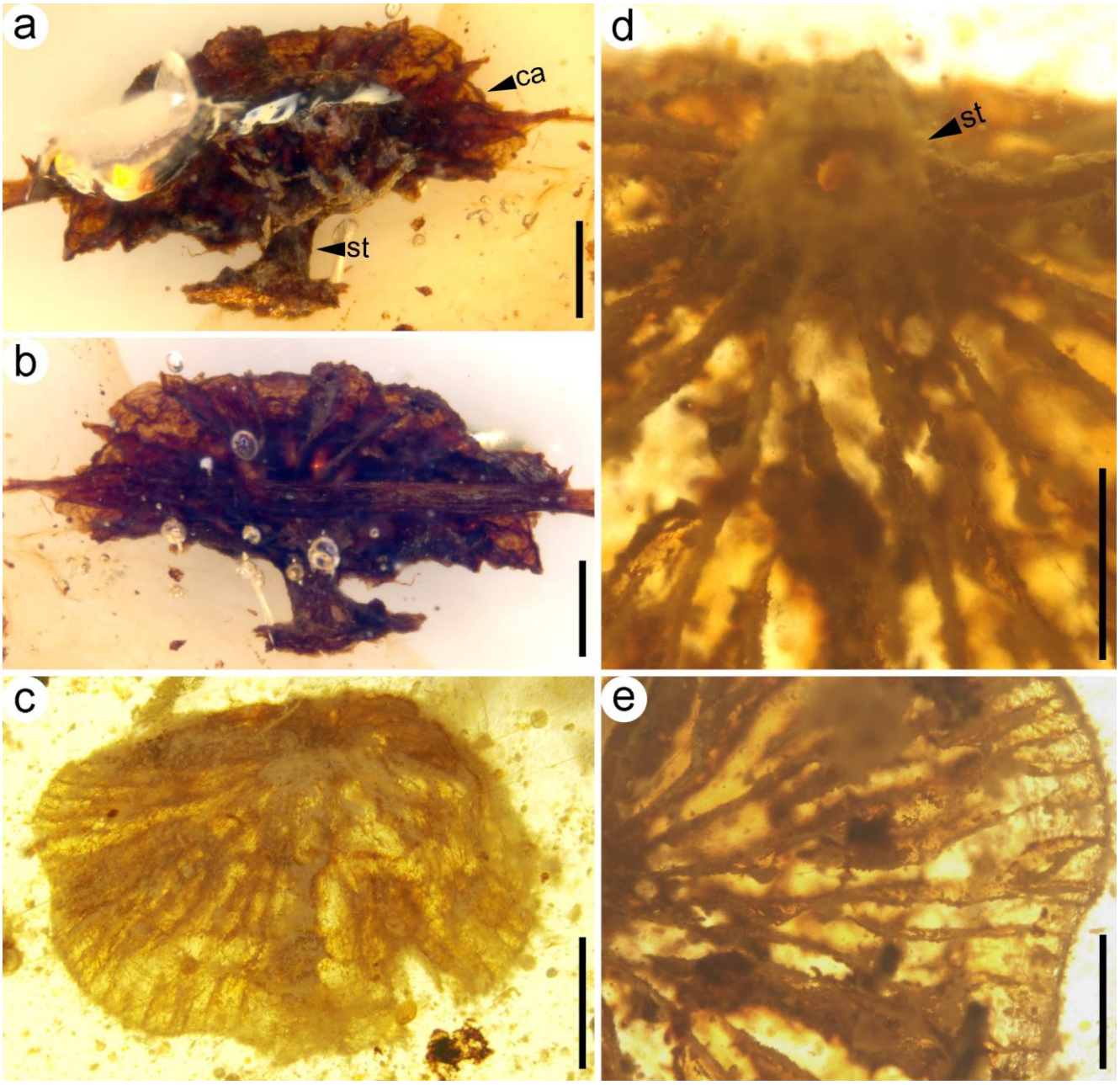
Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



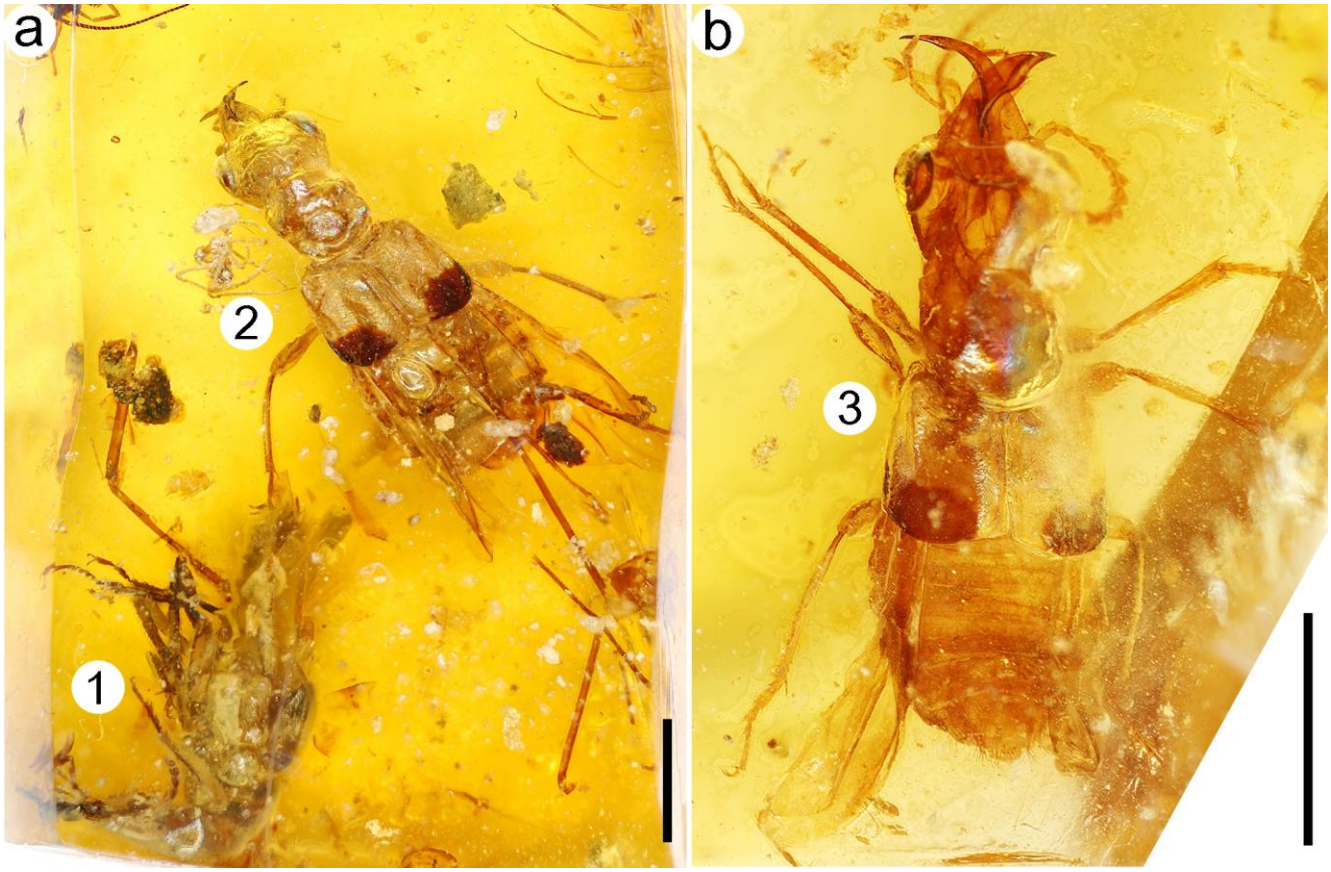
Supplementary Figure 1 | General appearances of mushroom-containing ambers from northern Myanmar. (**a**) Rounded amber piece containing Taxon A, NIGP164520. (**b**) Square-shaped amber piece containing Taxon C, NIGP164523. (**c**) Subtriangular amber piece containing two individuals of Taxon B, NIGP164521 and NIGP164522. (**d**) Rectangle amber piece containing Taxon D, NIGP164524. Scale bar, 2mm.



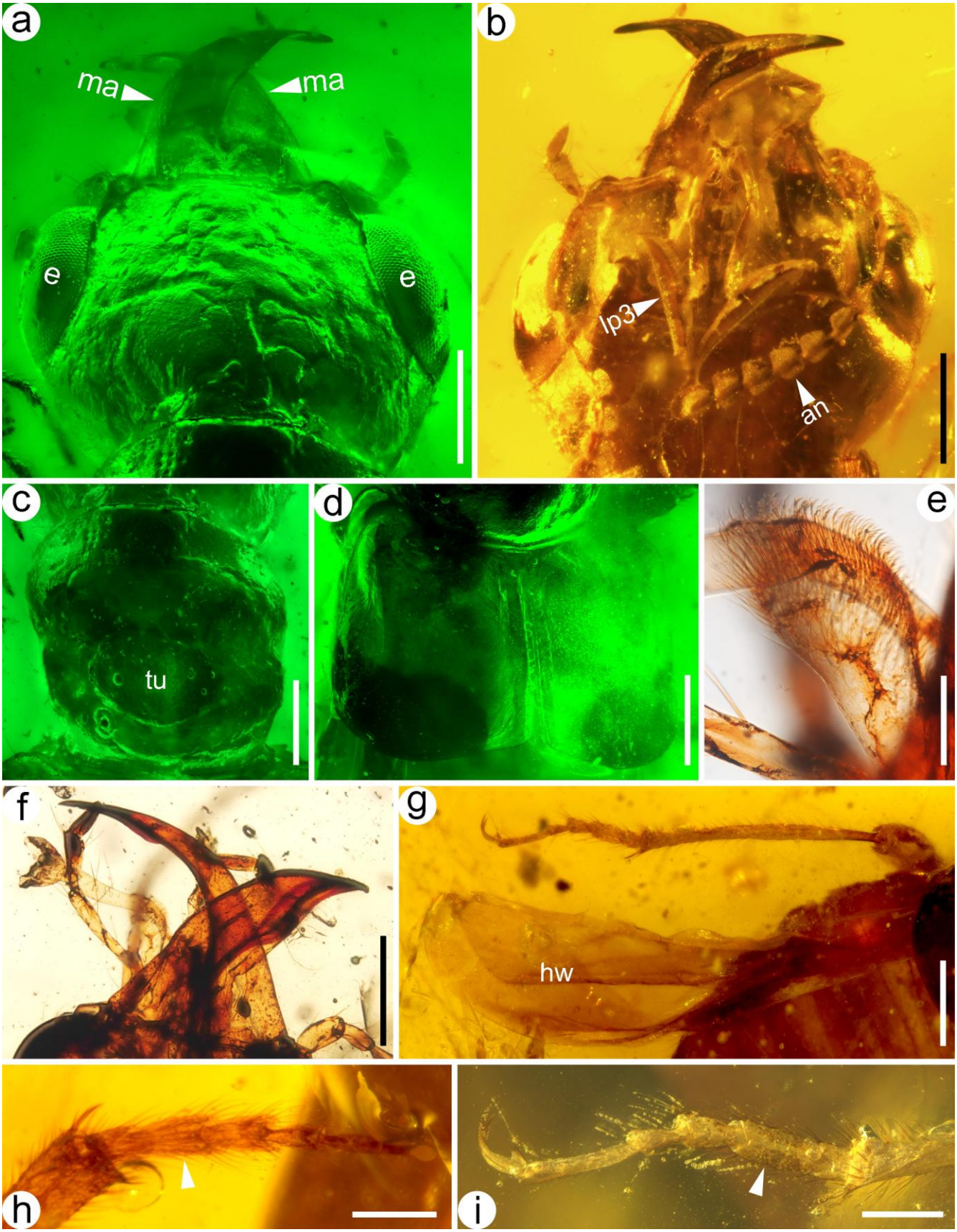
Supplementary Figure 2 | Details of mushrooms in mid-Cretaceous amber from northern Myanmar. **a–c** under normal reflected light; **d** and **e** under fluorescence. (**a**) Top view of Taxon A, NIGP164520. (**b**) Ventral view of Taxon A, showing details of lamellae. (**c**) General appearance of two individuals of Taxon B (NIGP164521 and NIGP164522), showing the strongly plano-convex cap and long stalk. (**d**) Laterally top view of one individual of Taxon B (NIGP164522), showing radially sulcate cap; (**e**) lateral view of the other individual of Taxon B (NIGP164521), showing the median depression on cap. Scale bars, 500 μm in **a**, **d** and **e**; 200 μm in **b**; 1 mm in **c**.



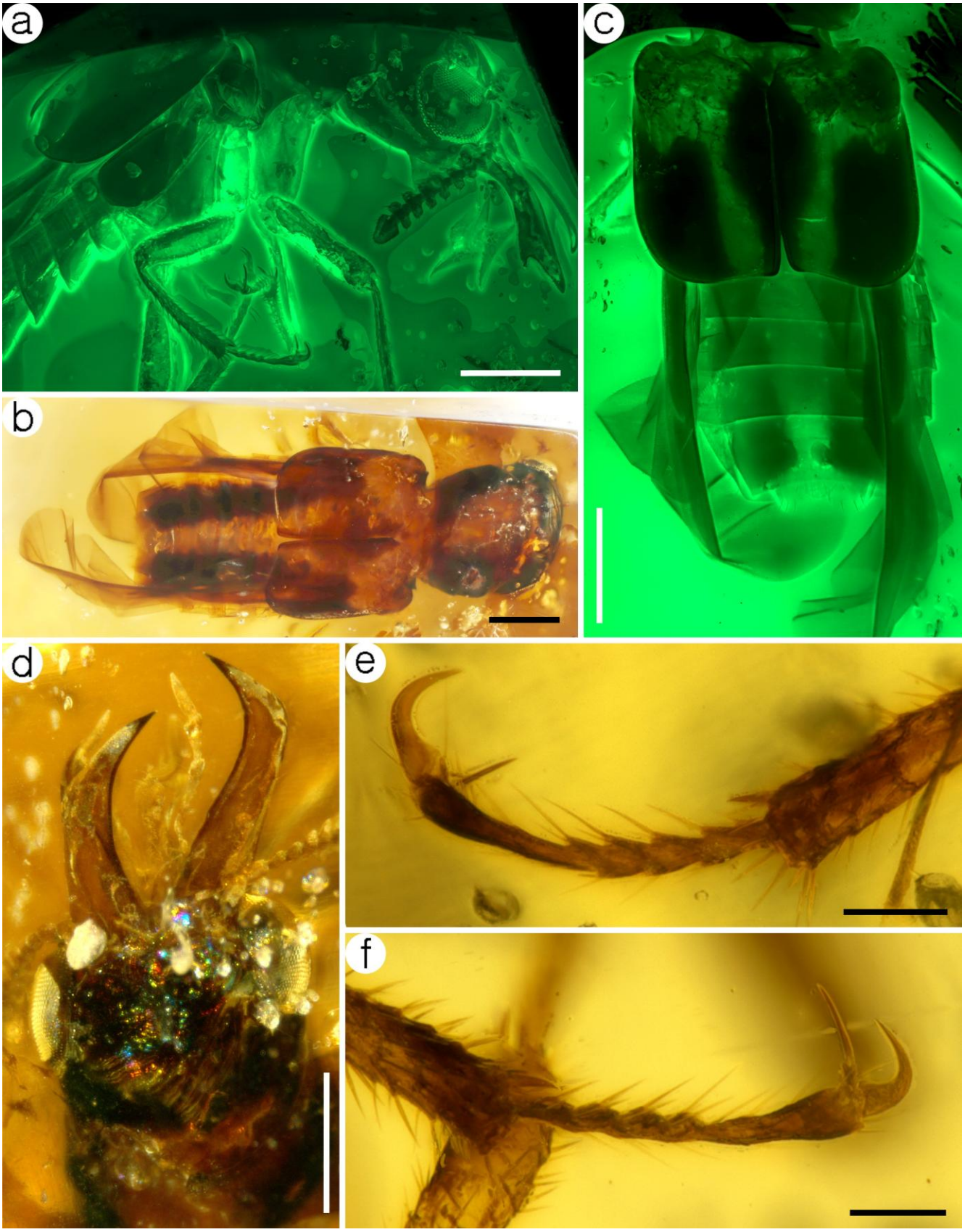
Supplementary Figure 3 | Details of mushrooms in mid-Cretaceous amber from northern Myanmar. (**a**) Top view of Taxon D, NIGP164524. (**b**) Ventral view of Taxon D, NIGP164524. (**c**) Top view of Taxon C, NIGP164523. (**d**) Details of base of stalk and lamellae of Taxon C, ventral view; (**e**) details of lamellae of Taxon C, ventral view. Abbreviations: ca, cap; st, stalk. Scale bars, 500 μm in **a**, **b**, **d** and **e**; 1 mm in **c**.



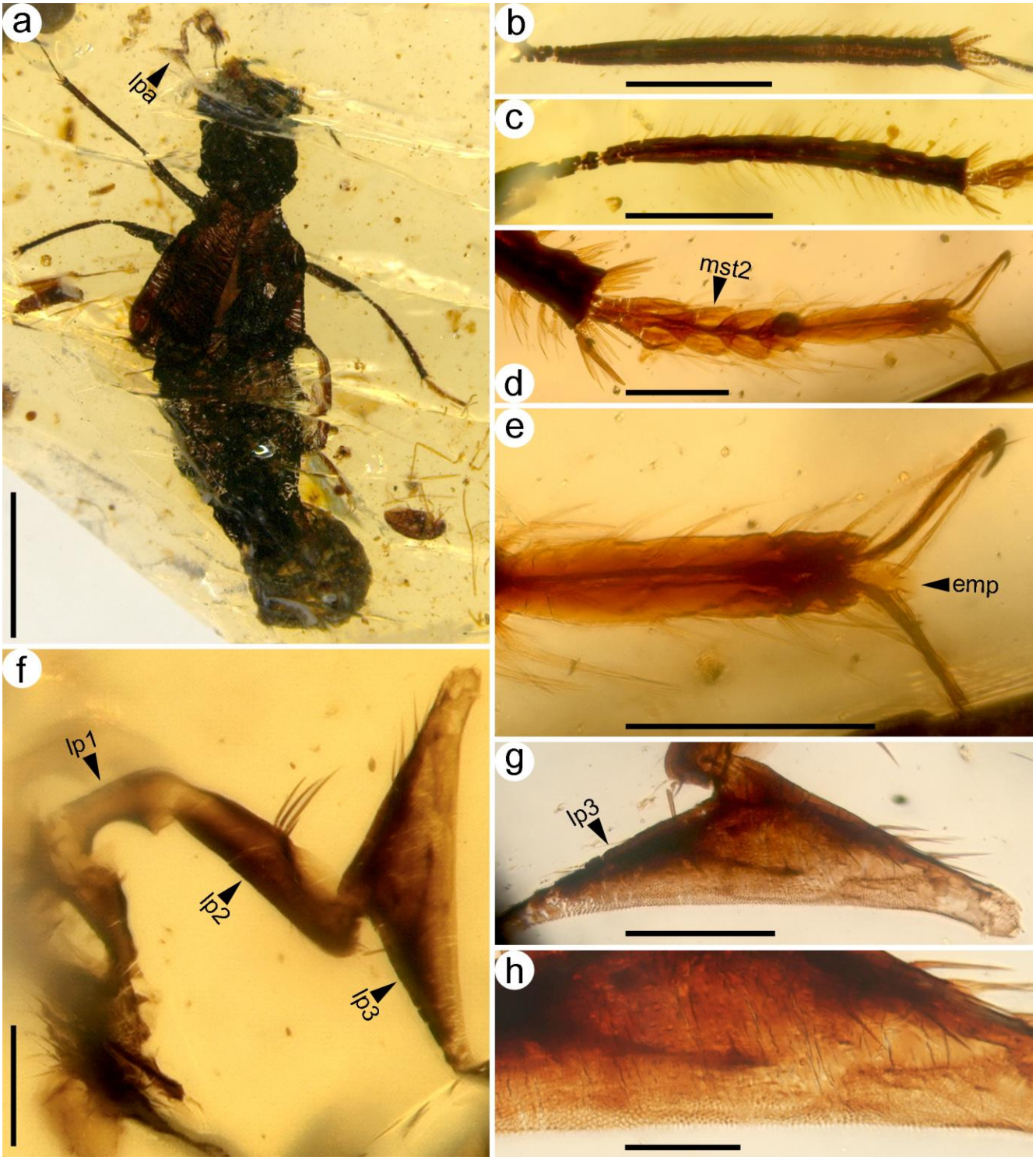
Supplementary Figure 4 | Mycophagous oxyporine rove beetles in mid-Cretaceous amber from northern Myanmar, Taxon 1, preserved in one amber piece prior to preparation. (**a**) Individual 1 (NIGP164525) and individual 2 (NIGP164526) of Taxon 1 preserved together. (**b**) Relatively smaller individual 3 (NIGP164527) of Taxon 1. Scale bars, 2 mm.


a
ma
ma
e
e
b
lp3
an
c
tu
d
e
f
g
hw
h
i

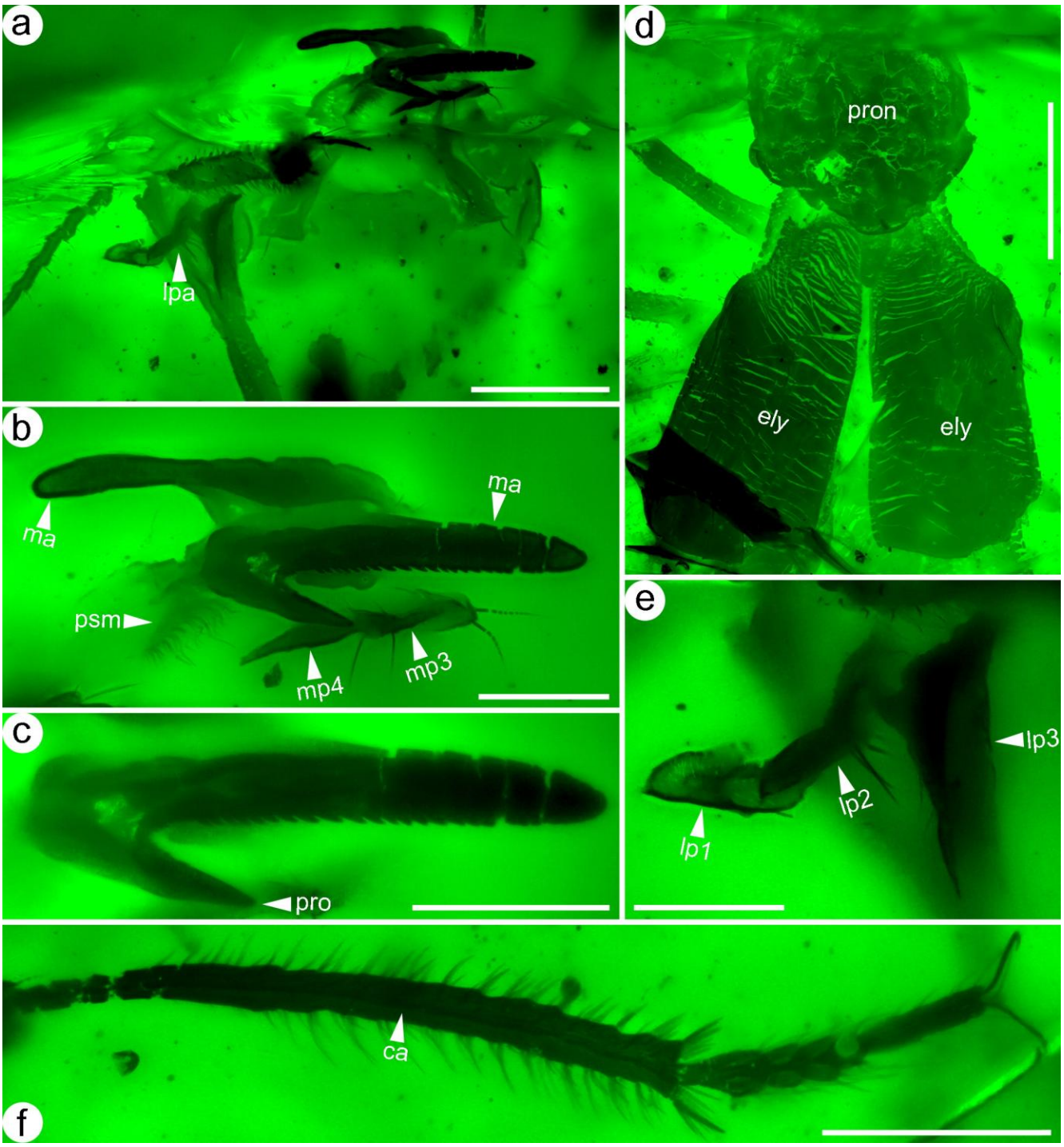
Supplementary Figure 5 | Details of mycophagous oxyporine rove beetles in mid-Cretaceous Burmese amber, Taxon 1. a, c and **d** under fluorescence, others under normal light. (**a**) Dorsal view of head (individual 2, NIGP164526), showing anteriorly protruding mandibles. (**b**) Ventral view of head (individual 2, NIGP164526), showing specialized labial palpi and characteristic antennae. (**c**) Enlargement of pronotum (individual 2, NIGP164526), showing median tubercle. (**d**) Enlargement of elytra (individual 3, NIGP164527). (**e**) Brush-like pseudomola of mouthparts (individual 3, NIGP164527). (**f**) Mouthparts of individual 3, showing mandibles, maxillary and labial palpi. (**g**) Left hind legs and hing wing of individual 3. (**h**) Right protarsus (individual 3, NIGP164527), with elongate tarsomere 2 indicated. (**i**) Left metatarsus (individual 3, NIGP164527), with elongate tarsomere 2 indicated. Abbreviations: an, antenna; e, eye; hw, hind wing; lp, labial palpomere; ma, mandible; tu, tubercle. Scale bars, 500 μm in **a**–**d**, **f** and **g**; 100 μm in **e**; 200 μm in **h** and **i**.


a
b
c
d
e
f

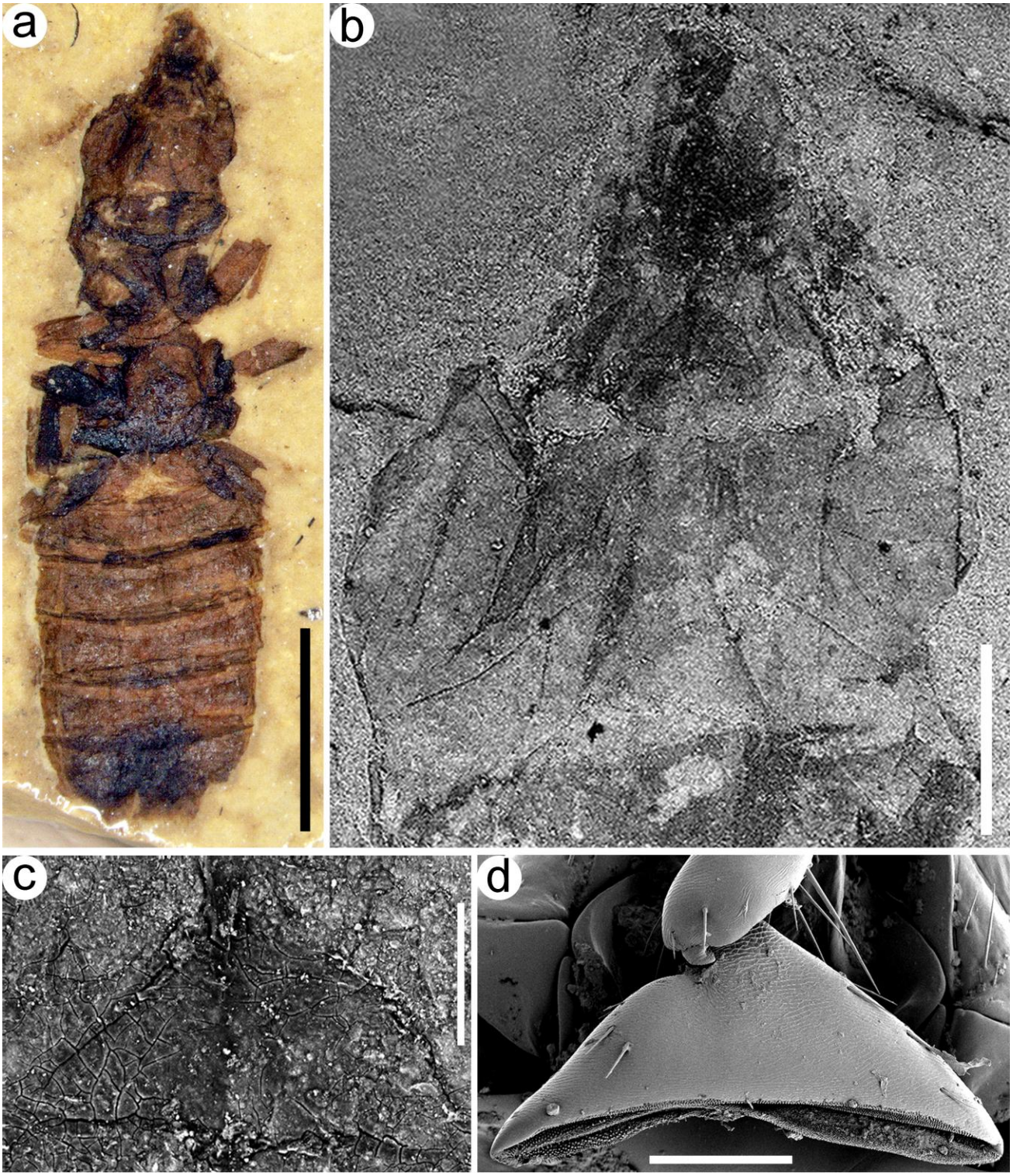
Supplementary Figure 6 | Mycophagous oxyporine rove beetles in mid-Cretaceous amber from northern Myanmar, Taxon 2, NIGP164528. a and **c** under fluorescence, others under normal reflected light. (**a**) Lateral view of head, pronotum, elytra and basal portion of abdomen. (**b**) Dorsal view of pronotum, elytra and abdomen. (**c**) Enlargement of elytra and abdomen, showing colour patterns on them. (**d**) Enlargement of head, showing enlarged and elongate mandibles. (**e**) Left and (**f**) right mesotarsus. Scale bars, 500 μm in **a**–**d**; 100 μm in **e** and **f**.



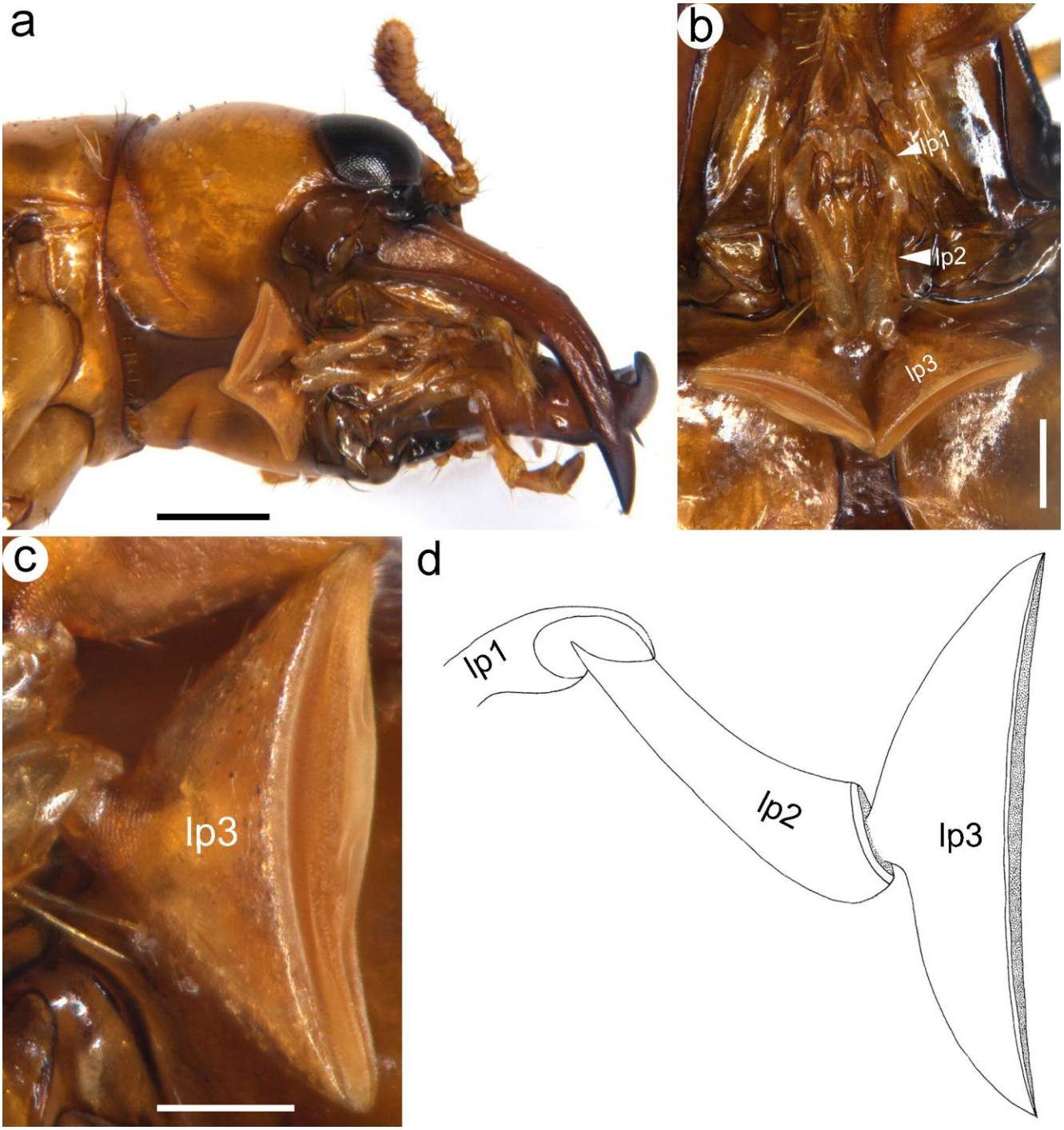
Supplementary Figure 7 | Mycophagous oxyporine rove beetles in mid-Cretaceous amber from northern Myanmar, Taxon 3, NIGP160556, under normal reflected light. (**a**) Dorsal habitus. (**b**) Left protibia. (**c**) Right mesotibia. (**d**) Right mesotarsus. (**e**) Enlargement of **d**, showing apical tarsomere, elongate claw and empodium. (**f**) Left labial palpus. (**g**) Enlargement of **f**, showing apical palpomere. (**h**) Enlargement of **g**, showing dense fine dot-like sensory organs covering its apex. Abbreviations: emp, empodium; lp, labial palpomere; lpa, labial palpus; mst, mesotarsomere. Scale bars, 2 mm in **a**; 500 μm in **b** and **c**; 100 μm in **h**; 200 μm in others.



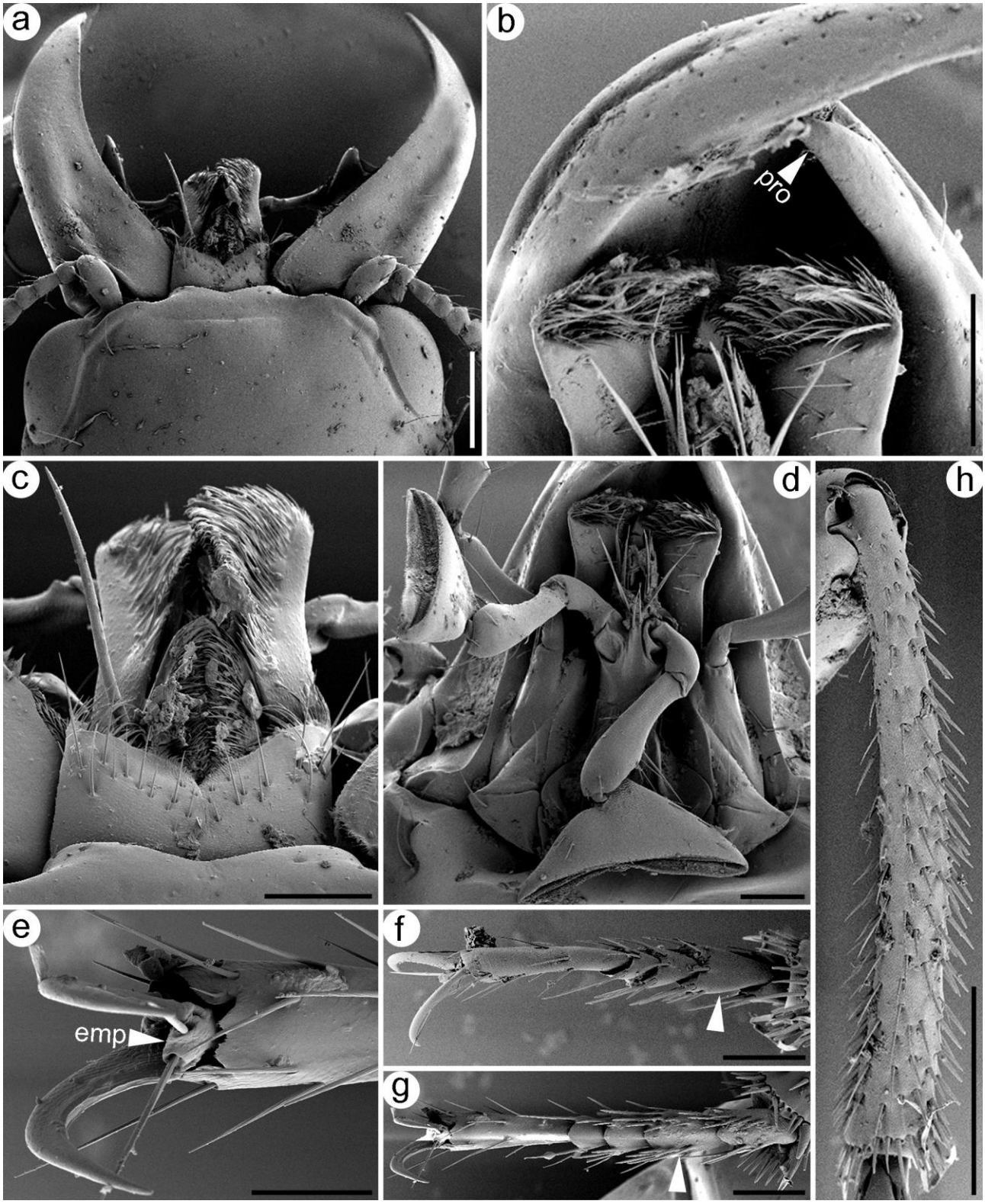
Supplementary Figure 8 | Mycophagous oxyporine rove beetles in mid-Cretaceous amber from northern Myanmar, Taxon 3, NIGP160556, under fluorescence. (**a**) Ventral view of head. (**b**) Enlargement of **a**, showing mandibles, pseudomola and left maxillary palpus. (**c**) Enlargement of **b**, showing right jagged mandible. (**d**) Enlargement of pronotum and elytra. (**e**) Enlargement of **a**, showing right labial palpus. (**f**) Right middle leg, showing keeled tibia. Abbreviations: ca, carina; ely, elytron; ma, mandible; mp, maxillary palpomere; pro, process; pron, pronotum; psm, pseudomola. Scale bars, 500 μm in **a** and **f**; 1 mm in **d**; 200 μm in others.



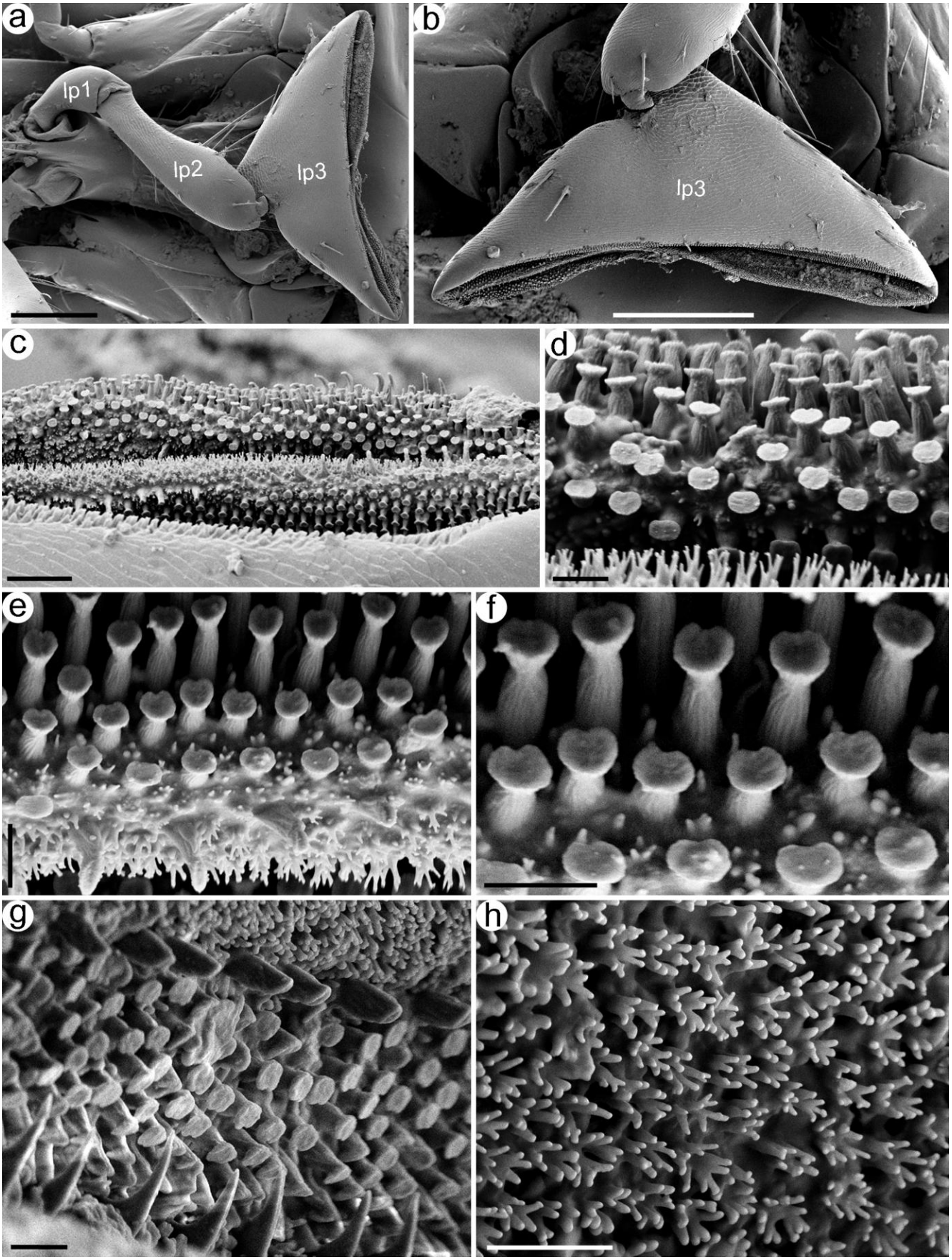
Supplementary Figure 9 | Mycophagous oxyporine rove beetles from Early Cretaceous Yixian Formation of northeastern China and comparison of apical labial palpomere between extinct and extant taxa. a under fluorescence, others under scanning electron microscope. (**a**) *Cretoxyporus extraneus* Cai and Huang, habitus of holotype, NIGP153699. (**b**) SEM of **a**, mainly showing ventral structures of head, including large mandibles. (**c**) Enlargement of **b**, showing the large and strongly securiform apical palpomere. (**d**) Enlargement of apical palpomere of extant *Oxyporus* sp. Scale bars: 2 mm in **a**; 500 μm in **b**; 100 μm in **c**. 200 μm in **d**.



Supplementary Figure 10 | Extant mycophagous oxyporine rove beetles, *Oxyporus* sp. (**a**) Lateroventral view of head, showing details of specialized mouthparts. (**b**) Enlargement of **a**, showing details of labial palpi. (**c**) Enlargement of **b**, showing strongly securiform apical palpomere. (**d**) Line drawing of labial palpus. Abbreviation: lp, labial palpomere. Scale bars: 2 mm in **a**; 1 mm in **b**; 500 µm in **c**.



Supplementary Figure 11 | Details of extant oxyporine rove beetle, *Oxyporus* sp., SEM. (**a**) Anterior part of head, showing large mandibles. (**b**) Ventral view of crossed mandibles, indicating a small process. (**c**) Details of labium and brush-like pseudomola. (**d**) Labial palpi. (**e**) Enlargement of metatarsomere 5, showing elongate claws and empodium. (**f**) Mesotarsus, with elongate tarsomere 2 indicated. (**g**) Metatarsus, with elongate tarsomere 2 indicated. (**h**) Right mesotibia. Abbreviations: emp, empodium; pro, process. Scale bars, 500 μm in **a** and **h**; 100 μm in **e**; 200 μm in others.


a
lp1
lp2
lp3
b
lp3
c
d
e
f
g
h

Supplementary Figure 12 | Details of mouthparts of extant mycophagous oxyporine rove beetle, *Oxyporus* sp., SEM. (**a**) Left labial palpus. (**b**) Enlargement of **a**, showing the apical labial palpomere. (**c**) Enlargement of **b**, showing fine, dense, mainly peg-like sensory organs on the apex of palpomere. (**d**) Enlargement of **c**, showing details of peg-like sensory organs. (**e**) Enlargement of **c**, showing both peg-like and villiform sensory organs. (**f**) Enlargement of **e**, showing peg-like sensory organs. (**g**) Enlargement of **c**, showing four different types of sensilla, including villiform, digitiform, peg-like and acronychius sensilla**.** (**h**) Details of villiform sensory organs. Abbreviations: lp, labial palpomere. Scale bars, 200 μm in **a** and **b**; 20 μm in **c**; 5 μm in others.

Supplementary Figure 13 | Ecological reconstruction of diverse mycophagous oxyporine rove beetles and mushrooms in the Cretaceous; image courtesy of Jie Sun.

Supplementary Table 1 | Checklist of known fossil agarics.

Number	Fossil Agarics	Size & Shape	Systematic Placement	Deposit	Age	Source
1	*Coprinites dominicana* Poinar & Singer, 1990	Pileus 3.5 mm in largest diameter; convex-shaped with a small central depression	Order Agaricales, Family Coprinaceae*	Dominican amber	~20 Ma	ref. 1
2	*Archaeomarasmius leggetti* Hibbett, Grimaldi & Donoghue, 1997	Pileus 3.2–6.0 mm in diameter; circular, plano-convex, radially sulcate; margin incurved	Order Agaricales, Family Tricholomataceae**	New Jersey amber	~90 Ma	ref. 2
3	*Protomycena electra* Hibbett, Grimaldi & Donoghue, 1997	Pileus 5 mm in diameter, 4 mm in height; circular, convex; margin slightly flared; context thin	Order Agaricales, Family Tricholomataceae***	Dominican amber	~20 Ma	ref. 2
4	*Aureofungus yaniguaensis* Hibbett et al., 2003	Pileus 3 mm in diameter; convex, with a broad raised center, glabrous or minutely textured; margin incurved, striated	Order Agaricales, Family incertae sedis	Dominican amber	~20 Ma	ref. 3
5	*Palaeoagaracites antiquus* Poinar & Buckley, 2007	Pileus 2.2 mm in diameter; convex, radially furrowed, hairy; margin slightly incurved	Order Agaricales, Family incertae sedis	Burmese amber	~99 Ma	ref. 4
6	Taxon A	See above	Order Agaricales, Family incertae sedis	Burmese amber	~99 Ma	Present study
7	Taxon B	See above	Order Agaricales, Family incertae sedis	Burmese amber	~99 Ma	Present study
8	Taxon C	See above	Order Agaricales, Family incertae sedis	Burmese amber	~99 Ma	Present study
9	Taxon D	See above	Order Agaricales, Family incertae sedis	Burmese amber	~99 Ma	Present study

[*]*Coprinites* was originally placed in Coprinaceae, but questioned by Hibbet *et al*.[2], who suggested that *Coprinites* could represent either the Agaricaceae or a nondeliquescent member of the Coprinaceae.

[**]*Archaeomarasmius* was suggested to be closely related to the modern genera *Marasmius* and *Marasmiellus*, which were traditionally placed in the polyphyletic family Tricholomataceae. However, both genera have been segregated into Marasmiaceae.

[***]*Protomycena* was compared with extant *Mycena* and placed in the Myceneae, a subfamily was attributed to the family Tricholomataceae. *Mycena* is currently classified in the family Mycenaceae, suggesting that *Protomycena* probably belongs to Mycenaceae, rather than Tricholomataceae.

Supplementary Table 2 | Oldest fossil records of subfamilies of Staphylinidae.

Subfamily	Occurrence of oldest known fossil	Presence in Cretaceous?	Source
Aleocharinae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	ref. 5
Apateticinae	No fossils known	No	–
Dasycerinae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	ref. 6
Empelinae	No fossils known	No	–
Euaesthetinae	Early Cretaceous (~125–135 Ma); Lebanese amber	Yes	ref. 7
Glypholomatinae	Middle Jurassic Haifanggou Formation (~165 Ma); Daohugou beds	No	ref. 8
Habrocerinae	No fossils known	No	–
Leptotyphlinae	No fossils known	No	–
Megalopsidiinae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	ref. 9
Micropeplinae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	ref. 10
Microsilphinae	No fossils known	No	–
Neophoninae	No fossils known	No	–
Olisthaerinae	Middle Jurassic Haifanggou Formation (~165 Ma); Daohugou beds	No	ref. 11
Omaliinae	Middle Jurassic Haifanggou Formation (~165 Ma); Daohugou beds	Yes	ref. 12
Osoriinae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	ref. 13
Oxyporinae	Early Cretceous Yixian Formation (~125 Ma); Jehol biota	Yes	ref. 14
Oxytelinae	Late Jurassic Karabastau Formation, Karatau (~150 Ma)	Yes	ref. 15
Paederinae	Early Cretceous Yixian Formation (~125 Ma); Jehol biota	Yes	ref. 16
Phloeocharinae	Late Cretceous (~90 Ma); New Jersey amber	Yes	ref. 17
Piestinae	Early Cretceous Yixian Formation (~125 Ma); Jehol biota	Yes	ref. 18
Proteininae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	ref. 19
Protopselaphinae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	Cai, personal observation
Pselaphinae	Early Cretaceous (~110 Ma); Spanish amber	Yes	ref. 20
Pseudopsinae	No fossils known	No	–
Scaphidiinae	earliest Late Cretaceous (~99 Ma); Burmese amber	No	Cai, personal observation
Scydmaeninae	Early Cretaceous (~110 Ma); Spanish amber	Yes	ref. 20
Solieriinae	earliest Late Cretaceous (~99 Ma); Burmese amber	Yes	ref. 21
Staphylininae	Early Cretceous Yixian Formation (~125 Ma); Jehol biota	Yes	ref. 16
Steninae	earliest Late Cretaceous (~100 Ma); French amber	Yes	ref. 22
Tachyporinae	Late Jurassic Karabastau Formation, Karatau (~150 Ma)	Yes	ref. 15
Trigonurinae	Late Jurassic Karabastau Formation, Karatau (~150 Ma)	No	ref. 15
Trichophyinae	No fossils known	No	–

Supplementary Note 1

Description of Mushrooms in Burmese Amber

Kingdom: Fungi

Phylum: Basidiomycota

Class: Agaricomycetes

Order: Agaricales

Family: Marasmiaceae

Taxon A

(Fig. 1a, b, and Supplementary Figs 1a and 2a)

Material. NIGP164520; nearly completely-preserved, with an intact cap possessing characterized gills; stalk broken, with basal portion preserved; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and age. Preserved in Burmese amber (Burmite) from Hukawng Valley, northern Myanmar; earliest Cenomaniaas aboven, absolute age 98.79 ± 0.62 million years (myr) ago established by U–Pb dating of zircons from the rind of the unprocessed amber.

Description. Basidiomata dark brown. Pileus 2.86 mm in largest diameter, plano-convex, circular, thin-fleshed, radially sulcate, depressed in middle; margin strongly incurved (Supplementary Fig. 2b). Lamellae sub-distant, with ca. 13 primary lamellae extending from stipe apex to pileus margin and ca. 13 lamellulae (of one length). Stipe slender, base broken, largest diameter 0.22 mm, insertion central, cylindrical.

Taxon B

(Fig. 1c and Supplementary Figs 1c and 2c)

Material. NIGP164521 and NIGP164522. NIGP164521 with complete cap and partial stalk; NIGP164522 with broken cap and stalk; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and age. Preserved in Burmese amber (Burmite) from Hukawng Valley, northern Myanmar; earliest Cenomanian (98.79 ± 0.62 myr).

Description. Basidiomata dark brown. Pileus 2.94 mm in diameter, strongly plano-convex (Supplementary Fig. 2e), circular, thin-fleshed, slightly radially sulcate (Supplementary Fig. 2d); margin slightly incurved; surface minutely textured. Lamellae sub-distant, with about 20 visible lamellae, attached to stipe apex. Stipe slender, slightly curved, base broken, diameter 0.35 mm, insertion central, cylindrical.

Family: incertae sedis

Taxon C

(Fig. 1d and Supplementary Figs 1b and 3c)

Material. NIGP164523; mainly preserved as cap; stalk with only basal part visible; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and age. Preserved in Burmese amber (Burmite) from Hukawng Valley, northern Myanmar; earliest Cenomanian (98.79 ± 0.62 myr).

Description. Basidiomata light brown. Pileus 3.92 mm in largest diameter, slightly convex, sub-oval, thin-fleshed, not sulcate, shallowly depressed in middle; margin not incurved; surface coarsely textured. Lamellae close (Supplementary Fig. 3e), with about 38 visible lamellae and only 10 extend from margin to stipe. Stipe with only apex preserved, insertion sub-marginal, cylindrical (Supplementary Fig. 3d).

Taxon D

(Fig. 1e and Supplementary Figs 1d and 3a, b)

Material. NIGP164524; nearly completely preserved, with a piece of elongate plant remains covering the cap from ventral view; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and age. Preserved in Burmese amber (Burmite) from Hukawng Valley, northern Myanmar; earliest Cenomanian (98.79 ± 0.62 myr).

Description. Basidiomata dark. Pileus 2.65 mm in largest diameter, plano-convex, thin-fleshed, radially sulcate; margin plicate-pectinate, not incurved; surface minutely textured. Lamellae sub-distant, with about 16 visible lamellae. Stipe very short and stout, base preserved, diameter 0.31 mm, insertion sub-marginal, cylindrical.

Supplementary Note 2

Description of Mycophagous Oxyporine Rove Beetles in Burmese Amber

Kingdom: Animalia

Phylum: Arthropoda

Class: Insecta

Order: Coleoptera

Family: Staphylinidae

Subfamily: Oxyporinae

Genus: *Oxyporus* Fabricius, 1775

Taxon 1

(Fig. 2a and Supplementary Figs 4 and 5)

Material. NIGP164525, NIGP164526, NIGP164527; three conspecific individuals preserved in one amber piece prior to preparation (cutting); NIGP164525 and NIGP164526 preserved in one piece after preparation (Supplementary Fig. 4a); all specimens completely preserved, except for the right mesotarsus of NIGP164527; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and age. Preserved in Burmese amber (Burmite) from Hukawng Valley, northern Myanmar; earliest Cenomanian (98.79 ± 0.62 myr).

Diagnostic description. Body moderate, 6.4–7.7 mm long, mostly yellow (except elytral apex); antenna with antennomeres 6–10 strongly transverse, broadly glabrous along axis (of the subgenus *Oxyporus* type; Supplementary Fig. 5b); infraorbital ridge absent; pronotum with a posteromedian tubercle (Supplementary Fig. 5c); elytron impunctate, bicolored, with a small, black and transverse mark on outer apical angle (Supplementary Fig. 5d); mesocoxae widely separated by large metaventral anterior process. Hind wing well developed (Supplementary Fig. 5g).

Remarks: Taxon 1 is undoubtedly placed in the extant Oxyporinae based on the following combination of characters: antenna inserted at sides of head near the eyes; large and strongly protruding mandible (Supplementary Fig. 5a, b); large conical procoxa; transverse metacoxa; tarsal formula 5-5-5 (Supplementary Fig. 5h, i); abdomen with six visible sterna; and two pairs of paratergites each on abdominal segments III–VII. Taxon 1 can be placed in the extant genus *Oxyporus* based on its general habitus, bicolored elytron, absence of infraorbital ridge, and mesocoxae widely separated by large

metaventral anterior process. It can be attributed to the extant subgenus *Oxyporus* by the characteristic antennal morphology (antennomeres 6–10 strongly transverse, broadly glabrous along axis). Taxon 1 is morphologically very similar to some extant *Oxyporus* representatives, but is differs in having a posteromedian tubercule on pronotum, impunctate elytra, and the colour, shape and size of elytral markings.

Taxon 2

(Fig. 2c and Supplementary Fig. 6)

Material. NIGP164528, a nearly complete adult with the head slightly downcurved; median portion of pronotum broken; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and age. Preserved in Burmese amber (Burmite) from Hukawng Valley, northern Myanmar; earliest Cenomanian (98.79 ± 0.62 myr).

Diagnostic description. Body very small, 4.5 mm long, mostly brown and black, head and pronotum black, elytra and abdomen bicolored (Supplementary Fig. 6b, c); mandible elongate (Supplementary Fig. 6d); antenna with antennomeres 6–10 strongly transverse, broadly glabrous along axis (of the subgenus *Oxyporus* type); infraorbital ridge absent; pronotum without median tubercle; elytron impunctate, bicolored, with a large, black and longitudinal mark on outer apical angle, and an elongate distally-tapered mark along sutural margin (Supplementary Fig. 6c); mesocoxae widely separated by large metaventral anterior process. Hind wing well developed (Supplementary Fig. 6c).

Remarks: Similar to Taxon 1, this taxon is undoubtedly a member of the extant genus *Oxyporus* based on its large and strongly protruding mandible, large conical procoxa; tarsal formula 5-5-5 (Supplementary Fig. 6e, f); and two pairs of paratergites on abdominal segments III–VII. Moreover, it can be also attributed to the subgenus *Oxyporus* by the characteristic antennal morphology (antennomeres 6–10 strongly transverse, broadly glabrous along axis). Taxon 2 is similar to some extant *Oxyporus* species, but is differs in having a much smaller body size, bicolored elytron and abdomen, impunctate elytra, and the colour, shape and size of elytral markings.

Taxon 3

(Fig. 2c and Supplementary Figs 7 and 8)

Material. NIGP160556, a complete adult with the body slightly distorted and broken; some structures,

such as the labial palpi, detached from the mouthparts, with one labial palpus below the ventral side of right eye, and the other before the left mandible; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality and age. Preserved in Burmese amber (Burmite) from Hukawng Valley, northern Myanmar; earliest Cenomanian (98.79 ± 0.62 myr).

Diagnostic description. Body moderate, 7.3 mm long, black (including elytra); right mandible jagged-edged with a sharp process near base (Supplementary Fig. 8b, c); antenna with antennomeres 6–10 strongly transverse, broadly glabrous along axis (of the subgenus *Oxyporus* type); infraorbital ridge absent; pronotum without median tubercle; elytron impunctate, unicolored (Supplementary Fig. 8d); mesocoxae widely separated by large metaventral anterior process; tibia keeled (Supplementary Figs 7b, c and 8f); mesotarsus with first tarsomere as long as the second (Supplementary Fig. 7d). Empodium with 2 long setae (Supplementary Fig. 7e).

Remarks: Taxon 3 can be unambiguously placed in Oxyporinae based on its large and strongly protruding mandible, large conical procoxa; transverse metacoxa; 5-segmented mesotarsus, and 6-segmented abdomen with two pairs of paratergites. The taxon resembles *Oxyporus* species in general habitus, but significantly differs by the presence of impunctate elytron, distinctly keeled tibia, and tarsomere 1 as long as the second. In particular, the keeled tibiae are apparently confined to Apateticinae and the related *Mesapatetica* Cai et al., Piestinae, some basal Oxytelinae (*Platydeleaster* Schülke and *Protodeleaster* Cai et al.), and some Scaphidiinae. In *Oxyporus*, the basal tarsomeres (tarsomere 1) are distinctly smaller and shorter than tarsomere 2. However, the basal tarsomere is as long as the second in Taxon 3, making it very distinctive among oxyporines. Therefore, we suggest that taxon 3 represents a new genus belonging to the extant Oxyporinae.

Supplementary Note 3

Evolution of mycophagy in Staphylinidae

Most extant beetle families are thought to have originated in the Cretaceous[23,24] and that diet diversification in Coleoptera was well underway, taking advantage of fully functional ecosystems[25,26]. Of about 60 modern families of beetles known from the Cretaceous[27], those with extant members associated with large-bodied fungi include Ptiliidae, Eucinetidae, Trogossitidae, Nitidulidae, Tetratomidae, Melandryidae, Mordellidae, Tenebrionidae, and Anthribidae. Taxonomic diversity[16] is mirrored in Mesozoic staphylinids, the largest family of the Order Coleoptera[28], which was also diverse in the Cretaceous and consistied of 20 of the 32 extant subfamilies (Supplementary Table 2) belonging to predominantly predatory, mycophagous, and saprophagous lineages[29]. Definitive mushroom feeding by adults and larvae occurs in Oxyporinae and Scaphidiinae (an unconfirmed Upper Jurassic fossil has been identified from the Solenhofen deposits by Weyenbergh[30]; a definitive scaphidiine has recently been discovered from Burmese amber). Saprophagy may be the primitive mechanism for Staphyliniformia as a whole[31,32], which is corroborated by presumed behaviors of Jurassic staphylinids, that also included fungus-feeding Glypholomatinae[8]. Phylogenetic data on staphyliniforms corroborate fossil evidence indicating that staphylinid diversification began in the Jurassic[33]. Character analyses reveal a high number of phylogenetic shifts among various diets and microhabitats, more commonly from leaf litter habitats to subcortical (saproxylic) or to periaquatic microhabitats with fewer shifts from leaf litter to carrion and to fungi[34].

The exact phylogenetic placement of Oxyporinae remains controversial[28,34], complicating the exact nature of the origin of mushroom feeding in the group. Oxyporinae are placed in the predatory Staphylinine Group of subfamilies[35], usually in a basal position relative to Megalopsidiinae, Pseudopsinae, Steninae, Euaesthetinae[36,37]. This staphylinid subgroup is dated to the Cretaceous[38] and contains very diverse prey capture strategies, including the use of a sticky-harpoon method by Steninae that have a protrusible labium[39]. Well-sampled phylogenetic studies place Oxyporinae with low statistical support outside the Staphylinine Group, for example, as sister taxon to Osoriinae[28] or sister to soil-dwelling Leptophylinae[34]. Though the long-held view that Oxyporinae arose from a predatory ancestor remains ambiguous based on recent phylogenetic studies, by the Cretaceous, staphylinid feeding mechanisms had well-diversified.

Supplementary References

1. Poinar, G. O. & Singer, R. Upper Eocene gilled mushroom from the Dominican Republic. *Science* **248**, 1099–1101 (1990).
2. Hibbett, D., Grimaldi, D. & Donoghue, M. Fossil mushrooms from Miocene and Cretaceous ambers and the evolution of Homobasidiomycetes. *Am. J. Bot.* **84**, 981–981 (1997).
3. Hibbett, D. S., Binder, M., Wang, Z. & Goldman, Y. Another fossil agaric from Dominican amber. *Mycologia* **95**, 685–687 (2003).
4. Poinar, G. O. & Buckley, R. Evidence of mycoparasitism and hypermycoparasitism in Early Cretaceous amber. *Mycol. Res.* **111**, 503–506 (2007).
5. Cai, C. & Huang D. The oldest aleocharine rove beetle (Coleoptera, Staphylinidae) in Cretaceous Burmese amber and its implications for the early evolution of the basal group of hyper-diverse Aleocharinae. *Gondwana Res.* **28**, 1579–1584 (2015).
6. Yamamoto, S. The first fossil of dasycerine rove beetle (Coleoptera: Staphylinidae) from Upper Cretaceous Burmese amber: Phylogenetic implications for the omaliine group subfamilies. *Cretaceous Res.* **58**, 63–68 (2016).
7. Lefebvre, F., Vincent, B., Azar, D. & Nel, A. The oldest beetle of the Euaesthetinae (Staphylinidae) from Early Cretaceous Lebanese amber. *Cretaceous Res.* **26**, 207–211 (2005).
8. Cai, C., Huang, D., Thayer, M. K. & Newton, A. F. Jr. Glypholomatine rove beetles (Coleoptera: Staphylinidae): a southern hemisphere Recent group recorded from the Middle Jurassic of China. *J. Kansas Entomol. Soc.* **85**, 239–244 (2012).
9. Yamamoto, S. & Solodovnikov, A. The first fossil Megalopsidiinae (Coleoptera: Staphylinidae) from Upper Cretaceous Burmese amber and its potential for understanding basal relationships of rove beetles. *Cretaceous Res* **59**, 140–146. (2016).
10. Cai, C. & Huang D. The oldest micropepline beetle from Cretaceous Burmese amber and its phylogenetic implications (Coleoptera: Staphylinidae). *Naturwissenschaften* **101**, 813–817 (2014).
11. Cai, C., Beattie, R. & Huang D. Jurassic olisthaerine rove beetles (Coleoptera: Staphylinidae): 165 million years of morphological and probably behavioral stasis. *Gondwana Res.* **28**, 425–431 (2015).
12. Cai, C. & Huang D. *Sinanthobium daohugouense*, a tiny new omaliine rove beetle from the Middle Jurassic of China (Coleoptera, Staphylinidae). *Canadian Entomol.* **145**, 496–500 (2013).
13. Cai, C. & Huang D. The oldest osoriine rove beetle from Cretaceous Burmese amber (Coleoptera: Staphylinidae). *Cretaceous Res.* **52**, 495–500 (2015).
14. Cai, C. & Huang, D. Diverse oxyporine rove beetles from the Early Cretaceous of China (Coleoptera: Staphylinidae). *Syst. Entomol.* **39**, 500–505 (2014).

15. Tikhomirova, A. L. Staphylinid beetles of the Jurassic of the Karatau (Coleoptera, Staphylinidae). in *Jurassic Insects of the Karatau* (ed. Rohdendorf, B. B.) 139–154 (Akademiya Nauk SSSR, 1968) (in Russian).
16. Solodovnikov, A., Yue, Y., Tarasov, S. & Ren, D. Extinct and extant rove beetles meet in the matrix: early Cretaceous fossils shed light on the evolution of a hyperdiverse insect lineage (Coleoptera: Staphylinidae: Staphylininae). *Cladistics* **29**, 360–403 (2013).
17. Chatzimanolis, S., Newton, A. F., Soriano, C. & Engel, M. S. Remarkable stasis in a phloeocharine rove beetle from the Late Cretaceous of New Jersey (Coleoptera, Staphylinidae). *J. Paleontol.* **87**, 177–182 (2013).
18. Yue, Y., Gu, J., Yang, Q., Wang, J. & Ren, D. The first fossil species of subfamily Piestinae (Coleoptera: Staphylinidae) from the Lower Cretaceous of China. *Cretaceous Res.* **63**, 63–67 (2016).
19. Cai, C. *et al*. Specialized proteinine rove beetles shed light on insect–fungal associations in the Cretaceous. *Proc. R. Soc. B* **283**, 20161439 (2016).
20. Peris, D., Chatzimanolis, S. & Delclòs, X. Diversity of rove beetles (Coleoptera: Staphylinidae) in early Cretaceous Spanish amber. *Cretaceous Res.* **48**, 85–95 (2014).
21. Thayer, M. K., Newton, A. F. & Chatzimanolis, S. *Prosolierius*, a new mid-Cretaceous genus of Solieriinae (Coleoptera: Staphylinidae) with three new species from Burmese amber. *Cretaceous Res.* **34**, 124–134 (2012).
22. Schlüter, T. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. A: Geologie und Paläontologie. *Berliner Geowissenschaftliche Abhandlungen* **9**, 1–150 (1978).
23. Grimaldi, D. A. & Engel, M. S. *Evolution of the insects*. (Cambridge University Press, 2005).
24. Hunt, T. *et al*. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **318**, 1913–1916 (2007).
25. Schmidt, A. R., Dörfelt, H., Struwe, S., & Perrichot, V. Evidence for fungivory in Cretaceous amber forests from Gondwana and Laurasia. *Palaeontographica Abteilung B* **283**, 157–173 (2010).
26. Adl, S. *et al*. Reconstructing the soil food web of a 100 million-year-old forest: The case of the mid-Cretaceous fossils in the amber of Charentes (SW France). *Soil Biol. Biochem.*, **43**, 726–735 (2011).
27. EDNA. Fossil Insects Database, hosted by the Palaeontological Association. Available online at http://edna.palass-hosting.org (accessed 10 July 2016) (2016).
28. Grebennikov, V. V. & Newton, A. F. Good-bye Scydmaenidae, or why the ant-like stone beetles

should become megadiverse Staphylinidae sensu latissimo (Coleoptera). *Eur. J. Entomol*. **106**, 275−301 (2009).

29. Thayer, M. K. Staphylinidae Latreille, 1802. in *Coleoptera, Beetles. Vol. 1, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga Partim)*. (eds Beutel, R. G. & Leschen, R. A. B.) in *Handbuch der Zoologie/Handbook of Zoology. Band/Vol. IV: Arthropoda: Insecta; Part 38* (eds Kristensen, N. P. & Beutel, R. G.) 296–344 (Walter de Gruyter, 2005).
30. Weyenbergh, H. Jr. Sur les insectes fossiles du calcaire Iithographique de la Baviere, qui se trouvent au Musee Teyler. *Archives du Musee Teyler* **2**, 247–294, 34–37 pls (1869).
31. Hansen, M. Phylogeny and classification of the staphyliniform beetle families (Coleoptera). *Biol Skr, Det K Dan Vidensk Selsk* **48**, 1–339 (1997).
32. Betz, O., Newton, A. F. & Thayer, M. K. Comparative morphology and evolutionary pathways of the mouthparts of spore-feeding Staphylinoidea (Coleoptera). *Acta Zoologica* **84**, 179–238 (2003).
33. Zhang, X. & Zhou, H.-Z. How old are the rove beetles (Insecta: Coleoptera: Staphylinidae) and their lineages? Seeking an answer with DNA. *Zool. Sci*. **30**, 490–501 (2013).
34. Mckenna, D. D. *et al*. Phylogeny and evolution of the Staphyliniformia and Scarabaeiformia: Forest litter as a stepping-stone for diversification of non-phytophagous beetles. *Syst. Entomol*. **40**, 35−60 (2015).
35. Lawrence, J. F. & Newton, A. F. Jr. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). in *Biology, Phylogeny and Classification of Coleoptera. Papers celebrating 80th Birthday of Roy A. Crowson* (eds Pakaluk, J. & Slipinski, S. A.) 779–1006 (Muzeum i Instytut Zoologii PAN, 1995).
36. Leschen, R. A. B., Newton, A. F. Larval description, adult feeding, behavior, and phylogenetic placement of *Megalopinus* (Coleoptera: Staphylinidae). *Coleopts. Bull*. **57**, 469–493 (2003).
37. Clarke, D. J. & Grebennikov, V. V. Monophyly of Euaesthetinae (Coleoptera: Staphylinidae): phylogenetic evidence from adults and larvae, review of austral genera, and new larval descriptions. *Syst. Entomol*. **34**, 346–397 (2009).
38. Clarke, D. J. & Chatzimanolis, S. Antiquity and long-term morphological stasis in a group of rove beetles (Coleoptera: Staphylinidae): Description of the oldest *Octavius* species from Cretaceous Burmese amber and a review of the "Euaesthetine subgroup" fossil record. *Cretaceous Res*. **30**, 1426–1434 (2009).
39. Koerner, L., Laumann, M., Betz, O., & Heethoff, M. Loss of the sticky harpoon–COI sequences indicate paraphyly of *Stenus* with respect to *Dianous* (Staphylinidae, Steninae). *Zoologischer Anzeiger* **252**, 337–347(2013).