



Fossil *Cymbiodyta* from Baltic amber confirms Euro-American ancient distribution of the genus (Coleoptera: Hydrophilidae)

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Abstract

We describe the first definite fossil of the water scavenger beetle subfamily Enochrinae (Coleoptera: Hydrophilidae): *Cymbiodyta samueli* sp. n. from the Eocene Baltic amber from the Lithuanian coast. The new species is extremely similar and likely closely related to the only European species, *C. marginella* and confirms the European occurrence of the genus since the Eocene. A reanalysis of the historical biogeography of the genus, including the fossil taxon, revealed a wide Euro-American distribution of the ancestor of all modern species of the genus, corresponding to the position of landmasses and existing land connections between North America and Europe in the Late Cretaceous. The biogeographic reconstructions and the fossil both suggest that European *Cymbiodyta* is an ancient relict lineage which used to be more diverse in the past but survived until today in a single species *C. marginella*.

Key words

Water scavenger beetle, amber inclusion, Eocene, Cenozoic, historical biogeography, ancestral distribution

1. Introduction

Beetles (Coleoptera) are among the most diverse and well-known insect groups, inhabiting our planet for c. 300 million years. Recent studies helped us to reconstruct their evolutionary history (Zhang et al. 2018, McKenna et al. 2019, Boudinot et al. 2022), past diversity (e.g., Zhao et al. 2021) and the timing and reasons of radiations of

beetle subgroups (e.g., McKenna et al. 2015, Robertson et al. 2015, Lü et al. 2020, Baca et al. 2021) in unprecedented detail. Dozens of fossils discovered or reexamined every year complement molecular-based evolutionary reconstructions, providing a direct view of the diversity in the past (e.g., Li et al. 2021, 2022, Schädel et al.

2022, Yin et al. 2022) and testing DNA-based estimates. In contrast, surprisingly little is known about the origins and past diversity of most beetle families, subfamilies, or genera: these studies receive much less attention than the questions about early beetle evolution.

Water scavenger beetles (Hydrophilidae) represent a lineage with a comparatively well-studied evolutionary history. The multigene phylogeny by Short & Fikáček (2013) uncovered the relationships among main lineages and most of the genera. Subsequent studies have clarified and refined phylogenetic relationships and evolutionary histories of particular subclades (Toussaint et al. 2016, Toussaint and Short 2018, Arriaga-Varela et al. 2021a, Short et al. 2021) and continue to add details about biology, systematics and diversity of particular clades (e.g., Minoshima et al. 2018, Seidel et al. 2020, Girón and Short 2021). Hypotheses on the timing of the evolution of the Hydrophilidae have also been proposed and explored (Bloom et al. 2014, Toussaint and Short 2018) but the number of fossils documenting the past diversity remains limited. Most Mesozoic and Cenozoic fossils of the family are preserved as compressions (e.g., Fikáček et al. 2010b, 2010a, 2014, 2017, Fikáček and Schmied 2013). Amber inclusions are very rare, representing only five species from Cretaceous Burmese amber (Fikáček et al. 2017), Eocene Baltic amber (Arriaga-Varela et al. 2021b) and Miocene Dominican amber (Fikáček and Engel 2011). Fossils are known for most aquatic subfamilies, with Enochrinae not yet confirmed with certainty since the Early Cretaceous *Alegorius* may represent either Enochrinae or Acidocerinae (Fikáček et al. 2014). No fossils are known for the largely terrestrial Cylominae and Sphaeridiinae.

The subfamily Enochrinae comprises 286 described species in four genera, *Cymbiodyta* (33 spp.), *Notionotus* (25 spp.), *Enochrus* (225 spp.) and *Enochrella* (3 spp.), inhabiting various types of standing waters or seepage habitats (Fikáček 2019). Although frequently collected, the species diversity remains underexplored. Many species remain to be discovered or their status need to be clarified, especially in worldwide *Enochrus* that seems to be a ‘waste basket’ at the moment. The worldwide fauna was only revised in detail for the genus *Cymbiodyta* distributed in three widely disjunct areas of the northern hemisphere: North America (29 species), western Palearctic (one species) and SE Asia (three species) (Smetana 1974, Jia and Short 2010, Jia and Lin 2015, Toussaint and Short 2019). Toussaint and Short (2019) revealed the ancient (Mesozoic) origin of the genus, with the European *C. marginella* having diverged from all remaining species in the Late Cretaceous. SE Asian species were found deeply nested among the American ones, being a result of an Oligocene colonization of Asia from America. They estimated the American origin of *Cymbiodyta*.

In this study, we present the discovery of the first known fossil of the subfamily Enochrinae preserved as an inclusion in Baltic amber from Lithuania. The species seems to be closely related to the only modern European *Cymbiodyta* species, confirming the ancient presence of the genus in Europe, as predicted by the molecular time

tree of Toussaint and Short (2019). To test the impact of the fossil, we rerun the biogeographic analyses and update our idea about ancient distribution and evolutionary history of the genus.

2. Material and Methods

2.1. Morphological study

The fossil was originally found in a larger piece of Baltic amber and uneasy to examine. We polished the amber piece to a smaller one with 600 and 1200 grit wet sandpapers, to make detailed examination possible. After polishing, the specimen was examined using Olympus SZ61 binocular microscope under various light regimes both in dry and wet condition (submerged in glycerine). Photographs were taken using a Canon 850D camera attached to the binocular microscope by an AmScope adapter. Photographs were stacked from a series of original photos with different focus using Helicon Focus software; all photographs, including those not shown here, are available at the Zenodo archive under doi <https://doi.org/10.5281/zenodo.7803930>. Drawings are based on the photographs and were prepared in Clip Studio Paint software using a Wacom One graphical tablet. Morphological terminology follows Fikáček (2019), classification follows Short and Fikáček (2013). Comparison with modern specimens is based on material deposited in the Department of Entomology, National Museum, Prague. SEM micrographs of these specimens were taken using Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum (Prague, Czech Republic), using uncoated specimens in the low vacuum mode.

2.2 Biogeographic analysis

To reveal the impact of the fossil described in this study on the reconstruction of the ancestral distribution of the most recent common ancestor of *Cymbiodyta*, we performed a series of historical biogeography analyses. We used the dated phylogeny of *Cymbiodyta* published by Toussaint and Short (2019) into which we added the fossil species as a sister taxon to the European *C. marginella*, following the close relationship of the fossil and this species revealed by morphology. Since the timing of the divergence between *C. marginella* and the fossil remains unknown, we generated four trees corresponding to four alternative scenarios tested, the age of their MRCA being 38 mya, 50 mya, 70 mya or 90 mya, i.e., arbitrarily selected values ranging from the age slightly predating the youngest estimate for the Baltic amber age (34–48 mya, Seyfullah et al. 2018) to the age only slightly postdating the split of the European lineage of *Cymbiodyta* (96 mya, Toussaint and Short 2019). The distribution of the modern species and the fossil was coded as three areas: Europe

(EU), North America (NA) and southern Asia (AS). The analyses were performed using BioGeoBEARS R package (Matzke 2013), using the tree and the distribution as the only data. Three models (DEC, DIVALIKE and BAYAREALIKE) available in the package and their +j alternatives allowing for jump dispersal were compared; the reconstruction based on the best performing model is presented here. The likelihoods of the three areas and their combinations for all four alternative trees are compared.

3. Systematics

Cymbiodyta samueli sp. nov.

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Figs 1–2

Material examined. Holotype (deposited in the Naturhistorisches Museum Freiburg, Switzerland): 1 specimen in a polished piece of Baltic amber (9×6×4 mm).

Type locality and age. Baltic amber, Lithuanian coast, 34–48 Mya (Seyfullah et al. 2018).

Description. Body: Body size 3.7 mm, maximum width 1.6 mm. Head dark-coloured both dorsally and ventrally, without clear paler preocular patches. Pronotum dark coloured on disc, yellow along margins, pale coloration wide laterally, narrow anteriorly, and very narrow posteriorly. Elytra dark colored, with widely yellow lateral margin. Ventral surface of thorax and abdomen yellowish. Head appendages, antennae and legs yellowish (Figs 1A–C). — **Head** (Figs 1D, G; 2A, C) with large eyes, slightly protruding laterally; interocular distance 3.6× the eye width in dorsal view. Frontoclypeal suture well developed. Clypeus with widely emarginate anterior margin. Dorsal punctation of clypeus and frons identical, moderately coarse. Labrum transverse, slightly bisinuate on anterior margin. Mentum transversely subrectangular, with slightly protruding bisinuate anterior margin. Gular sutures clear, moderately widely separated. Labial palpi with three palpomeres, apical palpomere relatively long. Maxillary palpi not preserved. Antenna with 9 antennomeres: long scapus, moderately long conical pedicel, three minute antennomeres, a cup-like antennomere (cupule) and 3-segmented pubescent antennal club; third antennomere of the club the longest, ca. twice as long as previous two antennomeres each. — **Thorax** (Figs 1D; 2A, D): Pronotum transverse, evenly convex, widening posteriorly, posterolateral corners rounded; dorsal punctation fine, uniform. Prosternum with a transverse groove, without median carina. Mesoventrite with a large triangular projection at midwidth. Mesocoxal cavities transverse, contiguous. Metaventrite ca. 1.7× longer than mesoven-

trite. Metanepisterna relatively wide throughout. Elytra narrowing posteriorly, with at least 8 longitudinal series of fine puctures and a short scutellary series; the series not impressed as striae. Sutural stria present, clearly distinct in apical half of elytron. — **Abdomen** (Figs 1C; 2A, C) with five ventrites, ventrite 5 weakly emarginated at apex, with several stouter setae present (remaining setae of the series have been broken). — **Legs** (Figs 1E, F; 2F, G). Procoxae large, globular, meso- and metacoxae transverse. Profemora relatively shorter than meso- and metafemora, femoral pubescence not visible. Tibiae slender, straight, with several series of spine-like setae, apically with a few longer stout apical spurs. Protarsi with 5 tarsomeres, meso- and metatarsi with 4 tarsomeres; all tarsi without swimming hairs, with fine pubescence ventrally. Claws uniform in size and shape, arcuate.

Genus assignment. Within the family Hydrophilidae, the 5-4-4 tarsal formula is unique for the genus *Cymbiodyta* in the subfamily Enochrinae. The other characters preserved in the fossil correspond with modern species of the genus as well: clypeus widely emarginate anteriorly, antenna with 9 antennomeres, prosternum with a transverse ridge, elytron with a sutural stria, and abdominal apex with an emargination and stouter setae at the apex.

Differential diagnosis. *Cymbiodyta samueli* sp. nov. differs from both Asian *Cymbiodyta* and from most of the American species by the highly elevated triangular projection of the mesoventrite (the other species have a low transverse ridge in that position). Most species with large triangular mesoventral elevation (the American *C. acuminata*, *C. leechi* and *C. vindicata*) are, however larger in body size (3.6–5.3 mm) and with rather deeply emarginate abdominal ventrite 5. The American *C. minima* (Figs 3B,G,H) resembles the fossil species much more, but its mesoventral projection is much lower. The European *C. marginella* (Figs 3A, C–F) is the most similar species to the fossil, but differs from *C. samueli* sp. nov. by dark brown to black ventral body surface (yellowish in *C. samueli*) and absence of elytral series of puctures (with fine elytral series in *C. samueli*).

Etymology. The last author originally purchased the piece of amber with this species as a gift for his son Samuel Rion, but agreed to provide the specimen for the study instead when it was identified as a species important for understanding the evolution of the Hydrophilidae. To compensate Samuel for not getting the piece of amber with this specimen, we dedicate the new species to him.

Historical biogeography. DIVALIKE was the best-performing model for analyses based on all four alternative time trees without the jump dispersal allowed, DIVALIKE+j performed the best among models allowing for jump dispersal. In all analyses (and under all three models), a wide North American and European distribution was estimated for MRCA of *Cymbiodyta*, without any significant effect of the age of MRCA of *C. marginella* and *C. samueli* sp. nov. on the reconstruction and on the

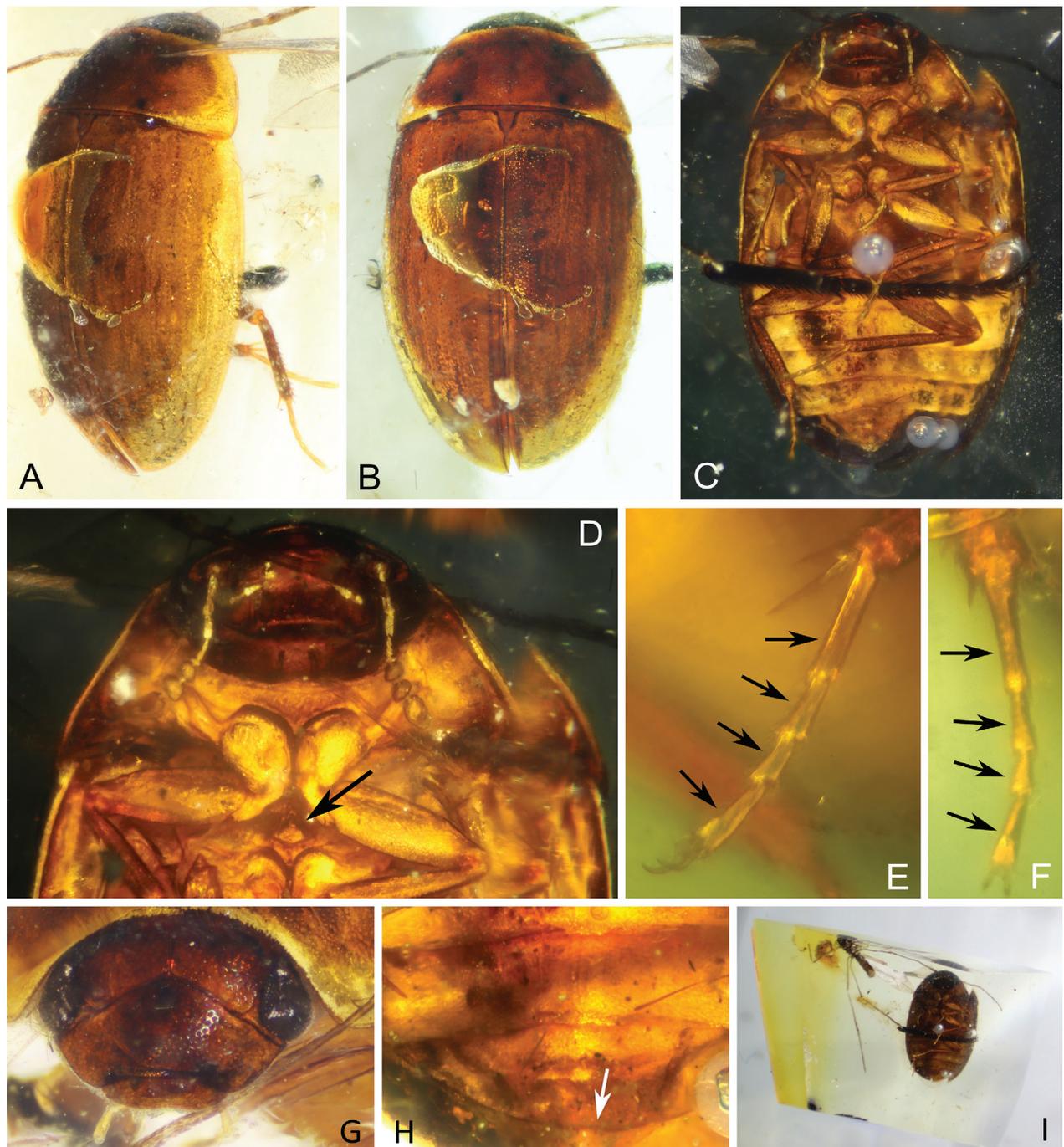


Figure 1. Photographs of *Cymbiodyta samueli* sp. n. in Baltic amber. **A–C** general habitus (**A**, dorsolateral; **B**, dorsal; **C**, ventral). **D** detail morphology of prosternum and mesoventrite, with the large triangular mesoventral projection (see arrow). **E–F** detail of metatarsi with 4 tarsomeres. **G** head in dorsal view, with emarginate clypeus. **H** abdominal ventrite V with shallow emargination (see arrow). **I** complete view of the amber piece after polishing.

likelihood of individual ancestral areas (see Table 1 for results obtained with best-performing models). The models with and without jump dispersal differed in the estimate of the origin of Asian species: DIVALIKE model estimate a widespread (North American+Asian) ancestor, whereas DIVALIKE+j model revealed the long distance dispersal of the North American ancestor. The analyses without the fossil revealed 100% probability of the wide ancestral range under both DIVALIKE and DIVALIKE+j (= best performing models).

4. Discussion

4.1. The phylogenetic position of *C. samueli*

The external morphology of adult *Cymbiodyta* is very uniform, with only a few species being morphologically very distinct (e.g., *C. bifida* which was until recently classified as a separate genus *Helocombus*; Toussaint and Short 2019). Remaining species differ in the shape

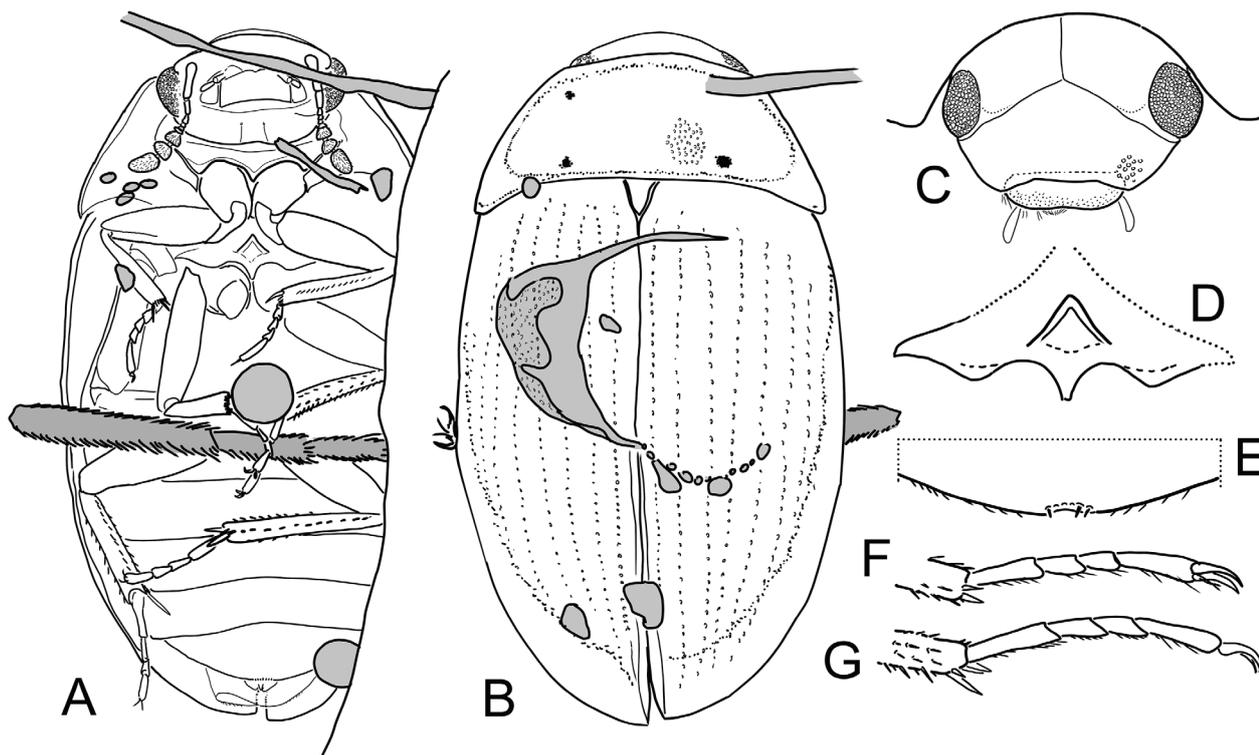


Figure 2. *Cymbiodyta samueli* sp. nov. from Baltic amber, drawings of characters. **A** ventral view; **B** dorsal view; **C** head in dorsal view; **D** mesoventrite (dotted line = reconstruction); **E** abdominal apex; **F–G** metatarsi.

of the mesoventral projection, the presence or absence of elytral striae, the body size and coloration, the size and shape of the emargination on the abdominal apex, and in the morphology of male genitalia (Smetana 1974, Jia and Short 2010, Jia and Lin 2015). Moreover, the molecular phylogeny by Toussaint and Short (2019), albeit including only 13 of 33 known species, indicates that some of these characters originated multiple times independently. For example, the species with the large triangular mesoventral projection (i.e., part of the *C. marginella* group by Smetana 1974) form at least two clades: the European *C. marginella* is sister to all other *Cymbiodyta*, whereas *C. vindicata* (and hence very likely also the other larger-bodied American species with protruding mesoventrite: *C. leechi* and *C. acuminata*) are deeply nested among the American species.

Cymbiodyta samueli sp. nov. described here is undoubtedly very similar to two modern species: the European *C. marginella* and the American *C. minima*. It corresponds with them by a small body size, the high mesoventral projection, the coloration, and the presence of the shallow emargination on abdominal apex. Of these two modern species, it seems to be closer to the European *C. marginella* in the shape of the mesoventral projection: this is highly elevated in *C. marginella* (Fig. 3E) and *C. samueli* (Figs 1D, 2D), but lowly elevated in *C. minima* (Fig. 3G). We hence consider the sister-position *C. samueli* and *C. marginella* as the most probable, further corroborated by the European distribution of both species. Our biogeographic analyses follow this assumption. *Cymbiodyta minima* is widely distributed through northern USA and southern Canada (Smetana 1974), but not included

in the molecular analysis of Toussaint and Short (2019). Based on the morphology, we cannot exclude that it is in fact the member of the the earliest diverging lineage of *Cymbiodyta* (together with *C. marginella* and *C. samueli* sp. n.) but molecular data are needed to resolve this question.

4.2. Historical biogeography of *Cymbiodyta*

Toussaint and Short (2019) reconstructed the historical biogeography of *Cymbiodyta* and revealed the American origin of the genus using the DEC model in Lagrange. In contrast, our re-analysis revealed wide ancestral range (North America + Europe) for MRCA of *Cymbiodyta* for all models compared, with DIVALIKE model fitting our data better than DEC in all cases. We argue that (1) the wider ancestral range corresponds better to data in hand, and (2) is congruent with the position of landmasses in the Late Cretaceous.

The narrower (North American) estimate of ancestral distribution of MRCA of *Cymbiodyta* by Toussaint and Short (2019) was likely caused by the inclusion of out-group taxa (*Notionotus liparus*: South America, *Enochrus testaceus*: Palearctic, *E. ochraceus*: North America). North America alone was not revealed as ancestral range in any of our analyses under any models or settings, with or without *C. samueli* sp. n. It is in fact surprising that the additional information about the lineage presence in Europe 38 mya changed the log-likelihoods only very slightly, without any effect on ancestral reconstructions.

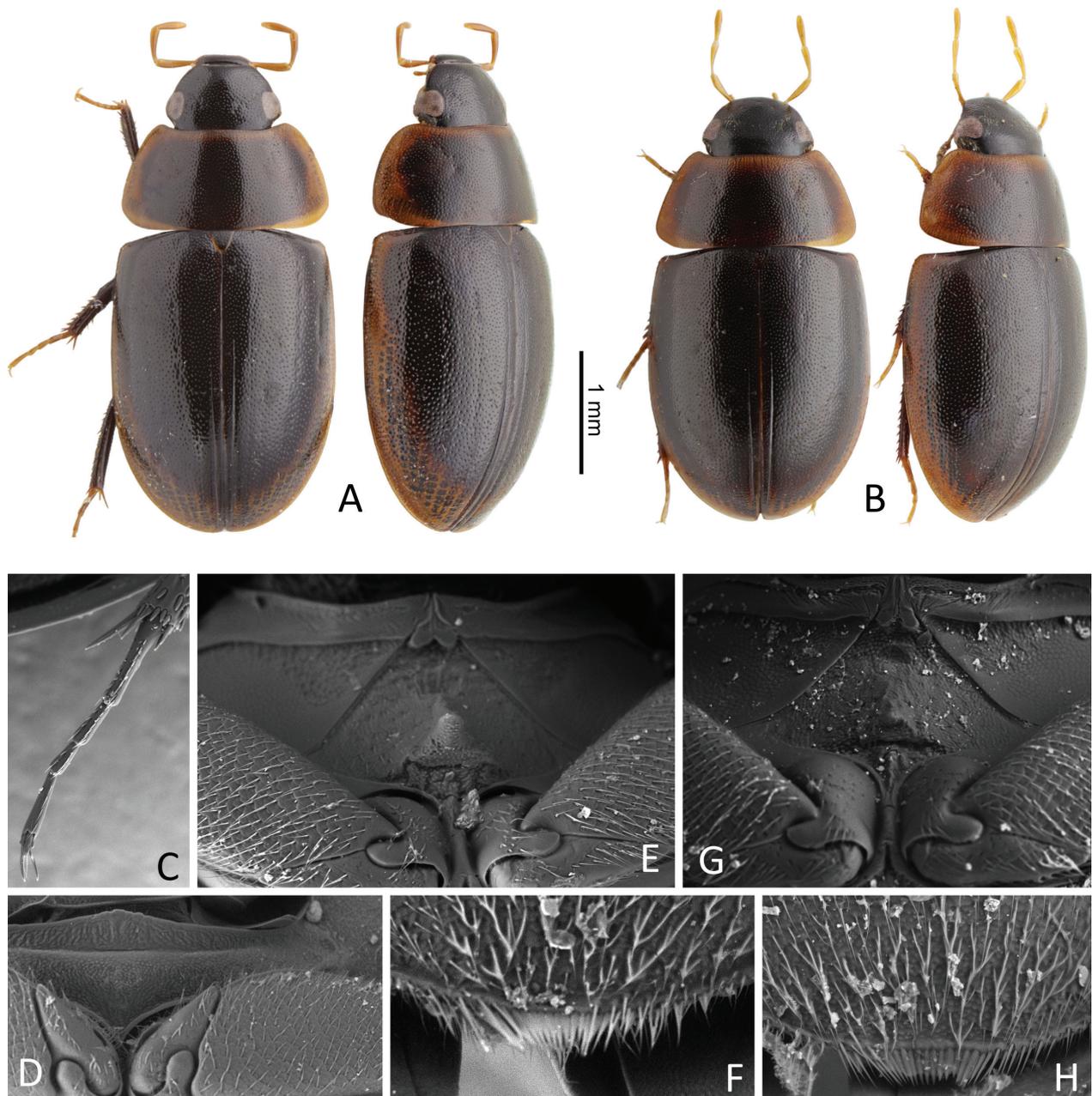


Figure 3. Modern *Cymbiodyta* species most similar to *C. samuelli* sp. n. from Baltic amber. **A, C–F** *Cymbiodyta marginella* (Fabricius, 1792) from Europe; **B, G–H** *C. minima* Notman, 1919 from northern USA and southern Canada. **A–B**, habitus (dorsal and dorsolateral view); **C**, metatarsus; **D**, prosternum; **E, G**, mesoventrite with mesoventral projection; **F, H**, abdominal apex.

This indicates that under the models considered, only the inclusion of fossils contradicting the distribution of modern species affects the analysis significantly, but the information about historical occurrence in the same area is largely ignored. We expect that the effect may be larger in case of time-stratified analyses not performed here.

Our ancestral range of MRCA of *Cymbiodyta* seems to be also congruent with other available data. The stem age of *Cymbiodyta* (Late Cretaceous: Albian) corresponds to the time when eastern North America was situated very close to pieces of future Europe, with occasional land connections between eastern North America, Greenland and Scandinavia (DeGeer Bridge: Brikiatis 2014). The species with wide distribution across the area, with frequent gene flow during the ti-

mes of emergent land bridges, may have really existed, similar to the widespread aquatic beetle species today (e.g., *Helophorus sibiricus* reaching from Scandinavia to Far East, but also inhabiting northern North America: Fikáček et al. 2011). The North American origin of *Cymbiodyta* proposed by Toussaint and Short (2019) cannot be fully excluded, but is not corresponding to the data available at the moment. A detailed molecular phylogeny of Enochrinae, revealing the sister group of *Cymbiodyta* and its modern distribution, will provide further data to reconstruct the origin of *Cymbiodyta* more reliably. The inclusion of *Cymbiodyta minima* into the molecular analyses may be also of interest, especially if it reveals its closer relationship to the European than to the American species; such a discovery would provide further support

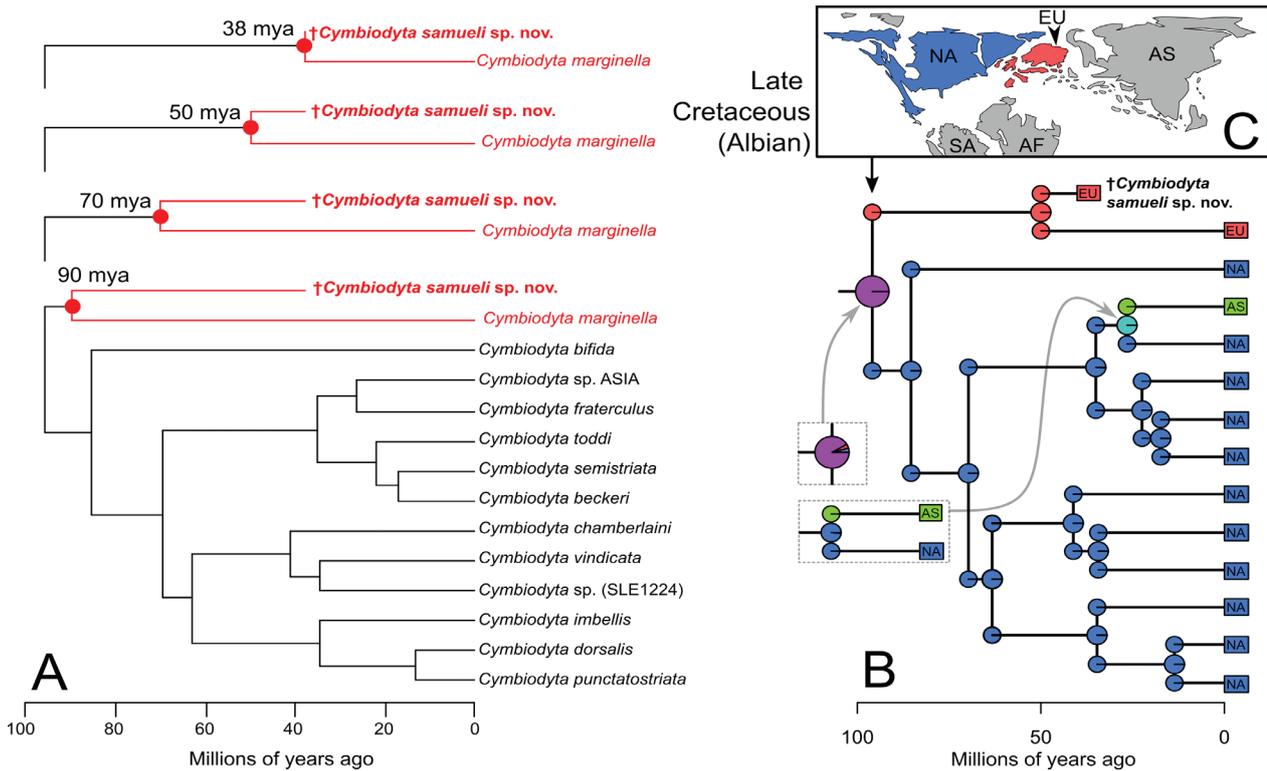


Figure 4. Historical biogeography of *Cymbiodyta*. **A** dated phylogeny of *Cymbiodyta* adopted from Toussaint and Short (2019), with *C. samueli* sp. nov. added as a sister species to modern *C. marginella*, with four alternative ages of their MRCA used for biogeographic analyses. **B** historical biogeography of *Cymbiodyta* following the DIVALIKE model in BioGeoBEARS (dotted rectangles show nodes for which the ancestral reconstruction differed in DIVALIKE+j analysis). **C**, positions of the continents at the end of the Cretaceous (Albian) when European and American *Cymbiodyta* separated (NA, North America; SA, South America; E, Europe; AF, Africa; AS, Asia).

Table 1. Summary of ancestral range reconstruction for MRCA of *Cymbiodyta* (relative probabilities for widespread Euro-American ancestor (NA+EU), European ancestor (EU) and North American ancestor (NA). MRCA = age of MRCA of *C. marginella* and *C. samueli* sp. nov., no fossil indicates the analysis without *C. samueli*. Model = best-performing model. LogLn = log-likelihood of the data under the respective model.

MRCA (mya)	Model	NA+EU (%)	EU (%)	NA (%)	logLn
no fossil	DIVALIKE	100	0	0	-7.38
38	DIVALIKE	100	0	0	-7.38
50	DIVALIKE	100	0	0	-7.40
70	DIVALIKE	100	0	0	-7.43
90	DIVALIKE	100	0	0	-7.46
no fossil	DIVALIKE+j	100	0	0	-5.34
38	DIVALIKE+j	92	4	4	-5.44
50	DIVALIKE+j	92	4	4	-5.44
70	DIVALIKE+j	92	4	4	-5.44
90	DIVALIKE+j	92	4	4	-5.44

to the Euro-American rather than North American origin of the genus.

In any case, European *Cymbiodyta* is clearly an ancient relict lineage. Current data indicate that it survived in Europe since the Late Cretaceous, and our new fossil brings direct evidence of its presence in the Eocene. The fact that *C. samueli* sp. nov. clearly differs from the European species brings also evidence of a higher species diversity and subsequent extinction in Europe in the past.

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