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Ninety million years of chasing mites by ant-like stone beetles

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Abbreviations. IGR, Geological Institute at University Rennes 1.

ABSTRACT

Among insects, the largest group of the Animal Kingdom, rove beetles (Staphylinidae) have undergone an enormous adaptive radiation that resulted in over 62,000 extant species (A.F. Newton, unpublished database) showing diverse body forms, structures and feeding specializations combining predaceous, mycophagous, saprophagous and

phytophagous habits in one family. The morphology of extinct and extant species is well studied, but the evolutionary history of such a broad range of adaptations is scarcely documented in the fossil record, and therefore poorly understood. One of the most puzzling specializations is that of predaceous ant-like stone beetles (Scydmaeninae), a staphylinid subfamily whose members choose not a soft-bodied prey, but the most heavily sclerotized, well-protected armoured mites. Scydmaenines have evolved a unique prey capturing apparatus with adhesive suckers to capture their prey, and the feeding process is remarkably long, often exceeding 30 h. The mouthparts with paired suckers cannot be used to catch any other kind of prey, and therefore finding such a device in extinct taxa implies specialized acarophagy. For the first time, we demonstrate that this very narrow specialization has ancient origins, and the Mesozoic (Turonian) *Hyperstenichnus vendeanus* Jałoszyński & Perrichot, gen. et sp. nov. from Vendean (French) amber was already an advanced, specialized mite killer. Surprisingly, the mouthpart modifications of the new species are more advanced than those in its extant relatives, suggesting that its (possibly too) narrowly specialized lineage has gone extinct. A long stasis of morphological structures is well known among Staphylinidae, and now also antiquity of narrow feeding specializations in rove beetles can be postulated, with unique habits remaining unchanged for over 90 million years.

KEYWORDS

Fossil, Beetle, Evolution, Turonian, Vendean, Staphylinidae, feeding adaptation

1. Introduction

Fossils, especially amber inclusions, contribute markedly to the knowledge of the systematics and evolution of insects, the largest animal group. However, it is necessary to reconstruct the history of novel ecological adaptations, especially those related to specialized behaviour, to understand factors driving differentiation and responsible for the evolutionary success of the largest and most diverse taxa. Fossils infrequently reveal the history of behaviour, yet they sometimes yield data on specialized morphological adaptations. If similar structures are known in extant taxa, and they can be unambiguously associated with unique behaviour, extrapolation can be made to infer function from structure in fossils. This method has been used to demonstrate Mesozoic origins of such complex ethological phenomena as social insect behaviour (summarized by Arillo, 2007), social parasitism in rove beetles (Yamamoto et al., 2016), or parental care in carrion beetles (Cai et al., 2014). Fossil records documenting major shifts in feeding preferences (or simply indicating when certain feeding adaptations might have originated) are even scarcer, as the structure of the mouthparts can not always be unambiguously associated with a particular feeding method or source of food.

The evolutionary history of morphological novelties that allowed for conquering new habitats is especially interesting in megadiverse groups of arthropods, comprising enormously large numbers of morphologically and ecologically diverse species. Among insects, the beetles include such groups, and one of them is the cosmopolitan family Staphylinidae (rove beetles) that currently includes over 62,000 species (A.F. Newton, unpublished database). Rove beetles include forms with strongly shortened elytra and long, slender abdomens, but also stout beetles with secondarily shortened abdomens nearly entirely covered by long elytra; their body lengths range from less than a half millimetre to nearly 4 cm; they live in all types of terrestrial habitats (except the polar zone), and their feeding adaptations include predaceous, mycophagous, saprophagous and phytophagous habits (Thayer, 2016). Staphylinids also include highly specialized beetles, such as spore feeders, larval

ectoparasites, inquilines of ants and termites, or troglobites (Thayer, 2016). Evolutionary pathways of such diverse adaptations within a single monophyletic group are expected to be very complex. Fossils make it possible to understand the origins of such adaptations, by providing data for reliable dating of major advances in exploring novel ecological niches.

Among Staphylinidae, some ant-like stone beetles (Scydmaeninae) show very unusual feeding preferences. Some of these tiny (typically 1–2 mm) beetles, predominantly associated with the forest floor, feed on the most heavily sclerotized mites (Oribatida and Mesostigmata: Uropodina), which are protected by their thick cuticle against most other predators. This is a puzzling adaptation, as in the leaf litter, soil and rotten wood where scydmaenines live, there are thousands of much less protected potential prey organisms. They include soft-bodied mites, springtails, nematodes, oligochaetes, insect larvae and others, extensively used as a source of food by nearly all remaining arthropod predators. Some scydmaenines show only behavioural adaptations to feed on armoured mites, such as the ability to attack vulnerable mouthparts, anal or genital openings of their prey, or to use noxious digestive juice exuded onto the mite to weaken its defences (Jałoszyński and Olszanowski, 2013, 2015).

Interestingly, mouthparts of such species do not differ from those that feed on springtails, hence it is not possible to infer their feeding habits solely by comparative morphological studies (Jałoszyński 2012a; Jałoszyński and Olszanowski, 2015). There are, however, specialists among scydmaenines that have evolved bizarre and unique morphological structures with the sole function of capturing and immobilizing heavily sclerotized oribatids and uropodines, adaptations that make it impossible to feed on any other type of prey (Jałoszyński and Beutel, 2012; Jałoszyński and Olszanowski, 2016). The crucial component of such a narrowly specialized feeding apparatus is a pair of suckers located on the labium (i.e., the lower lip). Within Scydmaeninae, the suckers have evolved independently twice: in all genera of the tribe Cephenniini and in *Stenichnus* Thomson, one genus (out of over sixty)

of Glandulariini (Jałoszyński, 2013a). And although a suggestion that scydmaenines may feed on armoured mites was published over a century ago (Reitter, 1909), the functional mouthpart morphology and details of the surprisingly complex feeding process were elucidated only recently (Jałoszyński and Beutel, 2012; Jałoszyński and Olszanowski, 2016).

Adult suckers of Cephenniini have been studied in detail; they are not simple 'adhesive pads' on the labium, but complex structures consisting of several components connected to the cuticle and to the internal sclerotized scaffold of the labium, and operated by strong labial muscles (Jałoszyński and Beutel, 2012). Cephenniini use the suckers to immobilize their prey, which adheres to the predator's labium throughout the entire feeding process. One short mandible grinds a tiny hole in the mite's cuticle, the connection between the beetle's mouth opening and its prey is tightly sealed by specialized membranous structures, digestive juices are injected, and eventually liquefied tissues are ingested (Jałoszyński and Olszanowski, 2016). *Stenichnus*, in contrast, uses its labial suckers only in the initial phase of attack, to catch and lift a mite; then slender falciform mandibles take over the leading role in breaching the prey's defences and the mite is killed by the beetle inserting one mandible into its mouth opening. This is followed by tearing off the prey's movable mouthparts and performing external digestion through the resultant opening (Jałoszyński, 2016). No such structures or similar feeding preferences are known among any others of nearly 400,000 beetle species.

This unusual specialization is still poorly understood, and already several distinct variants of feeding techniques and narrow prey preferences toward only certain mite taxa or particular mite morphological forms have been discovered (Jałoszyński and Olszanowski, 2013, 2015, 2016). The acarophagy of scydmaenines is a challenging research problem in the study of predator-prey system evolution. The feeding process was demonstrated to take sometimes over 30 hours (Jałoszyński and Olszanowski, 2013), and involves an energy- and time-consuming breaching of the mite's defence. This is an unusual feeding strategy in an

aggressive and highly competitive soil environment, where other predators, e.g., abundant ants, spiders, ground and rove beetles, are likely to disturb or interrupt the process. The most interesting question is how and when this strict specialization evolved, especially knowing that Cephenniini and Glandulariini are not sister groups (Jałoszyński, 2012b, 2013b), yet they have developed similar labial modifications to feed on a similar prey. The oldest known cepheniine beetle was recently discovered in Mesozoic amber, but its mouthparts were not visible for study (Jałoszyński and Peris, 2016). Recently, the oldest known glandulariine genera were described from Cenomanian Burmese amber, but representing taxa clearly unrelated to *Stenichnus* (Jałoszyński et al., 2016, 2017); younger and relatively numerous Glandulariini in Eocene-Oligocene deposits have not revealed any mouthpart modifications either (e.g., Jałoszyński and Perkovsky, 2016). In this study, we describe a newly discovered specimen that not only demonstrates ancient origins of a strict feeding specialization, but also sheds light on the direction of evolutionary processes related to the mouthpart modification in *Stenichnus*-like scydmaenines.

2. Material and methods

The amber inclusion described herein was collected in 2002 from a deposit named Garnache 1, that was exposed briefly during work along the road D32 between the towns of Challans and La Garnache, in the Department of Vendée, northwestern France (Fig. 1A). The amber was contained in a lignitic clay that was dated as Turonian (Late Cretaceous, 89.8–93.9 Ma) based on the associated palynomorphs (Néraudeau et al., 2017). A chemical characterization of the amber and analyses of the associated fossil woods indicated that the resin originated from conifers of the family Cupressaceae, and a salt marsh or coastal swamp palaeohabitat was suggested (Nohra et al., 2015; Néraudeau et al., 2017) (Fig. 1B). The

specimen was cut, polished and observed (as a dry specimen and submerged in cedar oil) under a Nikon SMS1500 (Nikon, Tokyo, Japan), Leica M205C and MZ APO (Leica Microsystems, Wetzlar, Germany) stereomicroscopes. Photographs were taken under both incident and transmitted light using an EOS 5D Mark II digital camera (Canon, Tokyo, Japan) mounted to the APO microscope. Image stacks were processed using Helicon Focus 6.7.1 Pro (Helicon Soft Ltd.) and edited with Corel PhotoPaint 9.397. Morphological structures were figured by freehand drawing, with exact proportions and general shapes sketched from photographs. Measurement convention and the terminology of morphological structures follow those of Jałoszyński (2013a). Examples of extant species presented for comparative purposes were ethanol-dehydrated, air-dried and observed as uncoated specimens using a Helios Nanolab 450HP scanning electron microscope (FEI, Hillsboro, USA) at 800 V, 25 pA, using TLD detector. The work is registered in ZooBank under LSID urn:lsid:zoobank.org:pub:BC5ABEAD-9C61-413C-AC9C-269F1F8DC019.

3. Systematic palaeontology

Suborder: Polyphaga Emery, 1886

Superfamily: Staphylinoidea Latreille, 1802

Family: Staphylinidae Latreille, 1802

Subfamily: Scydmaeninae Leach, 1815

Tribe: Glandulariini Schaufuss, 1889

Genus *Hyperstenichnus* Jałoszyński & Perrichot **gen. nov.**

Zoobank LSID urn:lsid:zoobank.org:act:7F3A045E-9B27-4D64-8FE3-3CF69DE216B0

Type species. *Hyperstenichnus vendeanus* Jałoszyński & Perrichot.

Etymology. After the genus name *Stenichnus*; the prefix 'hyper' refers to the labial suckers much larger than those in extant species of *Stenichnus*; gender masculine.

Diagnosis. Anterior surface of labium (i.e., prementum) with one pair of conspicuous labial suckers (Fig. 2B; *lbs*) together broader than frons between antennae and about as wide as 1/3 of maximum width of head, each sucker semicircular and longer than labial palp; basisternal portion of prosternum (Fig. 2B; *bst*) about as long as coxal portion.

Description. Head (Fig. 2A, B) broadest at compound eyes, antennal insertions broadly separated at middle; clypeus not demarcated from frons; labrum strongly transverse; labium with strongly reduced, small and narrow labial palps broadly separated by one pair of premental suckers surrounded by membranous area and separated at middle by narrow longitudinal groove; each sucker semicircular, distinctly concave; maxillary palps long and slender, palpomere 2 pedunculate, palpomere 3 gradually and strongly broadened distally, palpomere 4 minute, subconical with pointed apex. Antenna weakly and gradually thickened, all antennomeres elongate, with especially long antennomere 11, which is more than twice as long as broad, with rounded apex. Pronotum not visible dorsally, only ventral portions of hypomera visible, lacking hypomeral ridges or lateral edges; prosternum lacking intercoxal process or carina, with subtriangular and weakly, evenly convex median precoxal region and with long basisternal portion. Position of procoxae indicative for closed procoxal cavities; notosternal sutures complete. Mesocoxae distinctly separated by moderately broad and weakly convex mesoventral process with distinct median longitudinal ridge. Legs long and slender, femora weakly and gradually clavate; tibiae straight; tarsi slender, with all five tarsomeres elongate. All visible body parts covered with sparse suberect vestiture of setae; head and prothorax lacking thick bristles.

Remarks. *Hyperstenichnus* is unambiguously placed in Glandulariini on the basis of the autapomorphy of this tribe, the maxillary palpomere 4 subconical, elongate and pointed, much smaller than broadened and elongate palpomere 3 (Fig. 2A, B; *mxp*). Although dorsal characters of the prothorax and elytra, and most of ventral structures of the pterothorax are not visible in the specimen, the mouthparts alone are sufficient to distinguish this genus from *Stenichnus*, the only other glandulariine genus with labial suckers. *Stenichnus* (Fig. 2C) has a pair of small labial suckers together about as wide as 1/3 of the frons between antennal insertions and only 1/7–1/10 as wide as maximum width of head, each sucker circular and much shorter than labial palp. Additionally, *Stenichnus* has rudimentary, very short basisternal part of prosternum (typically as long as about 1/4 length of procoxa; Fig. 2C), whereas in *Hyperstenichnus* the basisternum is clearly nearly as long as procoxae (Fig. 2B).

Species *Hyperstenichnus vendeanus* Jałoszyński & Perrichot sp. nov.

Zoobank LSID urn:lsid:zoobank.org:act:A8527200-1FDF-4B2C-93E6-8C2CF94AD402

Material studied. Holotype (IGR.GAR-10), inclusion in Vendean amber, sex unknown, specimen in irregular plate of yellow translucent amber $4 \times 3 \times 0.85$ mm, deposited in the amber collection of the Geological Institute and Museum of the University Rennes 1. Specimen incomplete: head, prothorax and anterior portion of pterothorax preserved with complete labial and maxillary palps, right fore leg and right antenna; left fore and right middle leg partly preserved, missing distal tarsomeres; left antenna missing distal antennomeres.

Etymology. The name *vendeanus* refers to the Vendean amber.

Type locality and horizon. La Robinière, departmental road D32, 2.5 km southwest of La Garnache, Vendée, north-western France (Fig. 1A); Turonian in age (89.8–93.9 Ma).

Diagnosis and description. As in genus, *vide supra*; width of head 0.20 mm, width of pronotum 0.28 mm.

4. Discussion

The Staphylinidae is the largest animal family, with the number of nominal species growing fast and gradually approaching that of all known vertebrates. The remarkable ecological diversity of such a successful animal group attracts much attention, as evolving morphological and behavioural adaptations to certain habitats and sources of food might have been driving factors of megaraadiations. The sequence of major splitting events and ancestral morphology can be reconstructed using phylogenetic methods, whereas the history of highly specialized ecological adaptations can be reliably traced only in the fossil record. For such an enormously large family as staphylinids, with the oldest known fossils possibly dating to the Late Triassic and with over a hundred described extinct Mesozoic taxa (e.g., Chatzimanolis et al., 2012; Grebennikov and Newton, 2012; Peris et al., 2014a), well-documented 'fossilized behaviour' is strikingly scarce. It was demonstrated that Aleocharinae, one of major lineages within the family, showed highly specialized anatomy typical of extant social parasites already during Late Cretaceous, indicating that *Mesosymbion compactus* Yamamoto et al. might have coexisted with stem-group ants or termites ~99 Ma (Yamamoto et al., 2016). Similarly ancient traces of possible specialized feeding adaptation were observed in Late Cretaceous *Megalopinus extinctus* Yamamoto & Solodovnikov, a staphylinid that shows mouthparts modified as those in its extant predaceous congeners, suggesting the same 'rotary mill' or preoral sieving process to strain digestible tissue from indigestible cuticle (Yamamoto and Solodovnikov, 2016). Yue et al. (2011) suggested that the body form and mouthparts of an Early Cretaceous *Oxyporus yixianus* Solodovnikov & Yue demonstrate a history of a

fungus-associated biology of Oxyporinae for over 100 My, and a strong evidence for a specialized mycophagy in Proteininae was found by Cai et al. (2016), who described a spore-feeding *Vetuproteinus cretaceus* Cai, Newton & Thayer from Burmese amber. Cai et al. (2015) hypothesized that *Protolistaerus jurassicus* Cai et al. was a subcortical beetle, just as its similar extant Olisthaerinae relatives. These are the only ecological adaptations inferred from the Mesozoic Staphylinidae fossils, and they all seem to be already well-established, and not representing early or initial stages of acquiring novel features.

In this study, for the first time we provide evidence that glandulariine Scydmaeninae with unique labial suckers had differentiated already by the Late Cretaceous. *Hyperstenichnus* shows a highly modified labium, which in extant species of the presumably most similar genus, *Stenichnus*, is used to capture exclusively heavily sclerotized Oribatida and Uropodina (Fig. 2D–F) (Jałoszyński, 2016). It seems unlikely that such structures have evolved as an adaptation to capture any other kind of prey, as the suckers are suitable to adhere only to rigid surfaces, and would be ineffective in catching soft-bodied invertebrates with flexible cuticle; such prey choice has not been reported for any extant *Stenichnus* or cephenniinae species. The extant species of *Stenichnus* use a mixed technique, relying on their suckers during the initial phase of attack only, and once a prey is captured and lifted, the mandibles play a crucial role in the further process (Jałoszyński, 2016). In Cephenniini, the adhesive surface of the labium is large, with four or six suckers, the labial palps are strongly reduced, and the mandibles are short and modified to 'drill' a hole through the mite's cuticle (Jałoszyński and Beutel, 2012). By comparison to the mouthparts in other Scydmaeninae, it can be concluded that the strict specialization in Cephenniini has been obtained by enlarging the adhesive median area of the labium, reducing the labial palps, and shortening the mandibles. These modifications allow for maintaining the adhesion by a large surface of the suckers throughout the entire attack and feeding process, as the small mandibles can operate without detaching the labium from the

prey. In *Stenichnus* (Fig. 2C, E), the suckers are small, and the labial palps and mandibles large. Long mandibles require the captured prey to be detached from the suckers before it can be killed. *Stenichnus*, therefore, could be hypothesized to represent an intermediary step in the evolution that eventually may lead to the cephenniine-like specialization that relies on the adhesion of suckers for a prolonged period of time.

The newly discovered fossil of *Hyperstenichnus* falsifies this hypothesis. Structures visible in the inclusion are without doubt similar to those of *Stenichnus* (the shape of head and pronotum, antennae, lateral and ventral structures of the prothorax) and these two glandulariine genera may be closely related. However, the labial suckers in *H. vendeanus* are strikingly large, much larger than those in *Stenichnus* (or even those in Cephenniini) in relation to the head, and the labial palps are distinctly smaller. The labium of the ancient *Hyperstenichnus* is surprisingly more modified, its suckers larger, and its palps reduced compared to those in the extant *Stenichnus*. These morphological differences bear important implications for the evolution of *Stenichnus*-like Scydmaeninae. It seems that the more morphologically advanced, ancient *Hyperstenichnus* lineage has gone extinct, whereas the less modified, and apparently more successful *Stenichnus* lineage has survived till today, and radiated into about 200 extant species distributed in the Northern Hemisphere (Jałoszyński, 2013a). Alternatively, *Hyperstenichnus* may represent an ancestral lineage in the evolution of *Stenichnus*, and evolutionary processes led to a partial reversal of what could possibly be too narrow an adaptation, i.e., to reducing large suckers and enlarging the labial palps, which again made the mandibles the main tool and possibly enabled greater flexibility in prey choice. Indeed, the extant *Stenichnus* species can feed not only on smooth Oribatida (which are the only prey for more specialized Cephenniini), but also (and in some instances exclusively) on Uropodina, whose cuticle is finely sculptured (Jałoszyński, 2016). The suckers may lose their adhesion faster on a coarse surface and then a beetle that can use its

mandibles to manipulate the prey and does not need the suckers during the subsequent stages of feeding, gains access to a broader spectrum of prey mites. Under certain circumstances (abundance of sculptured uropodines and a deficit of smooth oribatids, or when oribatids are periodically replaced by uropodines) the less specialized *Stenichnus* might have won competition with more specialized species. Diverse families of mites have been identified in Vendean amber, including a new family of Prostigmata (Sidorchuk et al., 2016; Néraudeau et al., 2017), but there have been no oribatids nor uropodines discovered so far in this deposit that could point to the potential menu of *Hyperstenichnus*, and we do not know whether it could feed on smooth mites only, or also on sculptured ones.

Hyperstenichnus is the only documented case of a peculiar feeding specialization in beetles, attributable to a unique feeding technique and prey choice, being more 'advanced', or morphologically better developed, in a Mesozoic taxon compared to its extant relatives. The specialized feeding on armoured mites in Glandulariini is the first example of such unique morphological modifications in Staphylinidae being that ancient. If the *Hyperstenichnus* lineage gave rise to the extant *Stenichnus*, then consequently the modified mouthparts underwent a partial reduction that ensured a higher level of ecological plasticity, better fitted to periodical fluctuations in available food sources. More similar fossils are required to address these questions.

An interesting implication of the discovery reported here is that we already seem to have sufficient evidence to conclude that not only the general body form and taxonomically important exoskeletal structures of major subfamilies of Staphylinidae have ancient origins, but even some narrow ecological adaptations within this family have differentiated and reached their current form already in, and presumably before the Late Cretaceous. The ancient subfamilies Glypholomatinae, Olisthaerinae, Omaliinae, Oxytelinae, Piestinae, Scaphidiinae and Tachyporinae are present in the fossil record since the Jurassic (Chatzimanolis et al.,

2012; Cai et al., 2012, 2013; Cai and Huang, 2013a); the ground plan of Aleocharinae, Dasycerinae, Euaesthetinae, Osoriinae, Oxyporinae, Phloeocharinae, Pselaphinae, Scydmaeninae, Solieriinae, Staphylininae and Trigonurinae has not changed since the Cretaceous (summarized in Chatzimanolis et al., 2012, with further findings in Chatzimanolis et al., 2013; Peris et al., 2014a, b; Cai and Huang, 2013b, 2015a, b; Yamamoto, 2016; Yamamoto et al., 2016). In the Cenomanian, the Megalopsidiinae, hunters with large eyes and specialized mouthparts, were sieving food particles (Yamamoto and Solodovnikov, 2016), highly specialized Aleocharinae parasites were living as inquilines of social insects (Yamamoto et al., 2016), Oxyporinae species strikingly resembling their extant fungivorous relatives were dwelling in fruiting bodies of mushrooms (Yue et al., 2011), and Proteininae rove beetles were scraping spores off surfaces with their modified maxillae (Cai et al., 2016). Now we also infer that in the Turonian, specialized Scydmaeninae were using labial suckers to catch heavily sclerotized mites, as they do today.

Long morphological stasis, the term so frequently repeated by authors reporting discoveries of Jurassic and Cretaceous representatives of yet another extant Staphylinidae subfamily, can now be expanded to ecological specializations, even very narrow ones, that require unique and profound transformations of body parts, as exemplified by the labial suckers of *Hyperstenichnus vendeanus*.

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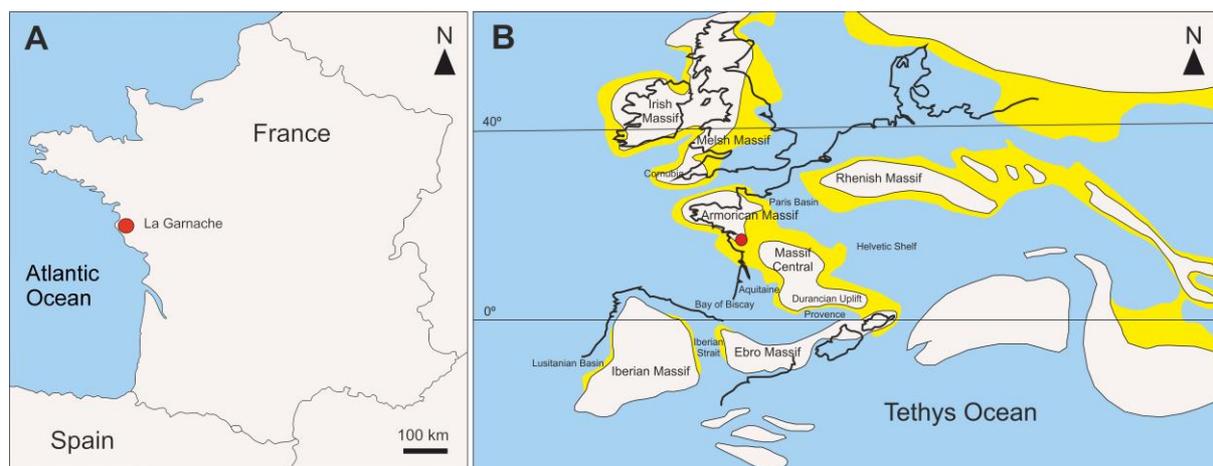
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Figure legends

Fig. 1. The location of the Vendean amber deposit in the present-day France (A), and in a palaeogeographical reconstruction of Turonian (based on Dercourt et al., 2000; grey represents landmasses, yellow - drowned massifs) (B).

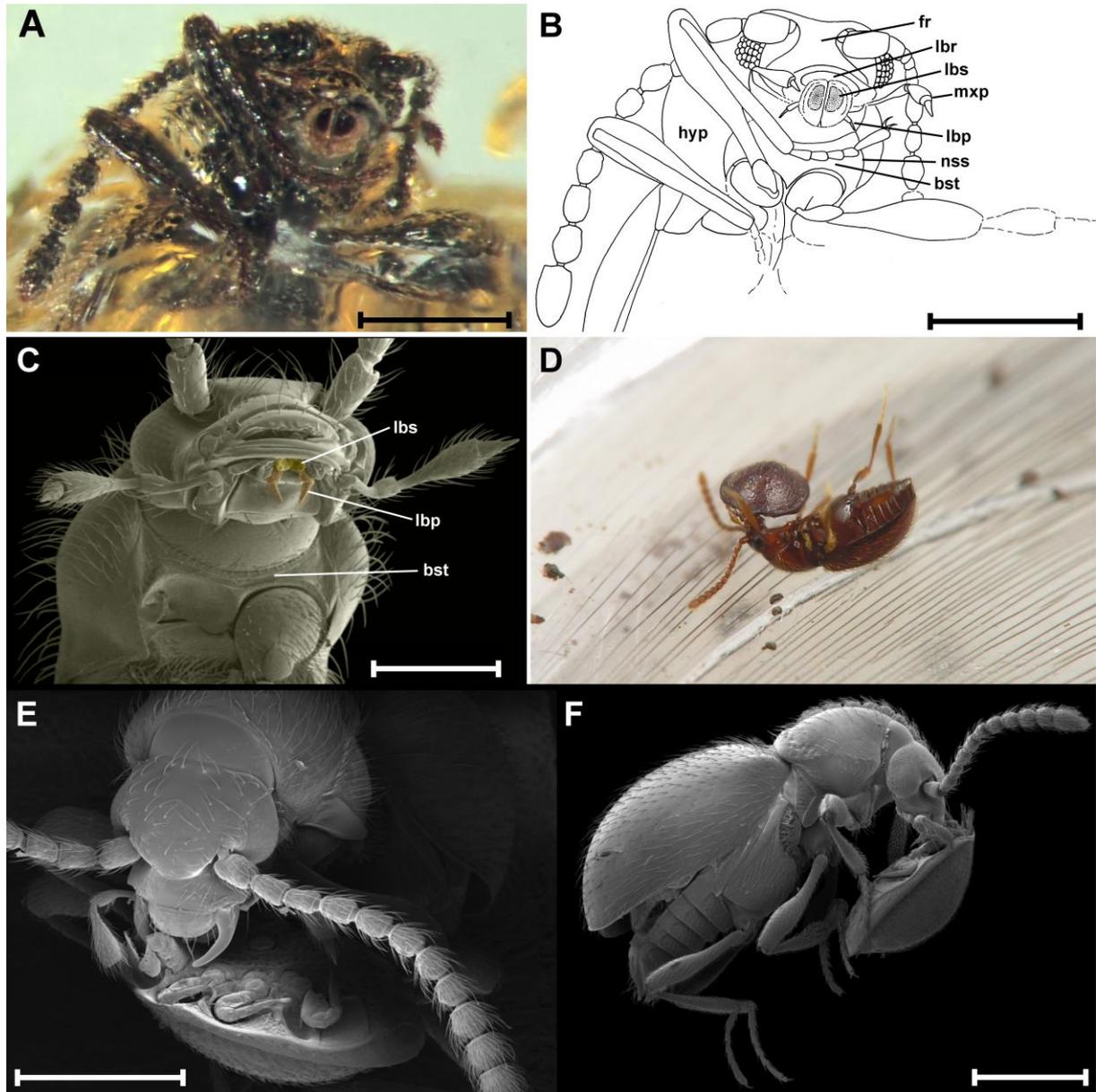
Fig. 2. Holotype (IGR.GAR-10) of *Hyperstenichnus vendeanus* gen. and sp. nov. (A, B) compared to extant *Stenichnus godarti* (Latreille) from Europe (C–F). **A, B.** Anteroventral habitus. **C.** Anteroventral habitus (in artificial colours) with labial suckers and labial palps highlighted. **D.** Beetle feeding on *Trichouropoda* sp. (Mesostigmata: Uropodinae). **E, F.** Beetle preserved in late phase of feeding on *Trichouropoda* sp., with one mandible inserted into the mite's mouth opening. Abbreviations: bst, basisternal portion of prosternum; fr, frons; hyp, prothoracic hypomeron; lbp, labial palp; lbr, labrum; lbs, labial sucker; mxp, maxillary palp; nss, notosternal suture. Scale bars: A–C: 200 μm ; E: 400 μm ; F: 500 μm .

Figure 1



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Figure 2



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Graphical abstract



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Highlights

- Turonian *Hyperstenichnus* gen. n. was a specialized armoured mite killer
- preserved prey catching apparatus is more specialized than that in extant relatives
- strict feeding specialization in scydmaenine staphylinids has ancient origins

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