A previously missing link in the evolution of dasytine soft-winged flower beetles from Cretaceous Charentese amber (Coleoptera, Melyridae)

Erik Tihelka, Diying Huang, Vincent Perrichot, Chenyang Cai

► To cite this version:

Erik Tihelka, Diying Huang, Vincent Perrichot, Chenyang Cai. A previously missing link in the evolution of dasytine soft-winged flower beetles from Cretaceous Charentese amber (Coleoptera, Melyridae). *Papers in Palaeontology*, 2021, 7 (4), pp.1753-1764. 10.1002/spp2.1360 . insu-03196023

HAL Id: insu-03196023

<https://hal-insu.archives-ouvertes.fr/insu-03196023>

Submitted on 15 Sep 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

A previously missing link in the evolution of dasytine soft-winged flower beetles from Cretaceous Charentese amber (Coleoptera, Melyridae)

Journal:	<i>Palaeontology</i>
Manuscript ID	PALA-09-20-4878-OA.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	03-Dec-2020
Complete List of Authors:	Tihelka, Erik; University of Bristol, School of Earth Sciences Huang, Diying; Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences Perrichot, Vincent; Rennes 1 University, Géosciences Rennes Cai, Chenyang; Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences
Key words:	Cleroidea, Charentese amber, Fouras Peninsula, Cenomanian, phoretic mites, Cretaceous

SCHOLARONE™
Manuscripts

A previously missing link in the evolution of dasytine soft-winged flower beetles from Cretaceous Charentese amber (Coleoptera, Melyridae)

by ERIK TIHELKA¹, DIYING HUANG², VINCENT PERRICHOT^{3*} and CHENYANG CAI^{1,2*}

¹ School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8; erik.tihelka@hartpury.ac.uk

² State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, China; dyhuang@nigpas.ac.cn; cycai@nigpas.ac.cn

³ Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, Rennes, 35000, France; vincent.perrichot@univ-rennes1.fr

*Corresponding authors

Abstract: The soft-winged flower beetles are a diverse cosmopolitan family of cleroid beetles with an unresolved higher classification, whose adults feed on nectar and pollen. The fossil record of Melyridae is sparse, with only two described fossils known from the Mesozoic. Here we describe the first representative of the family from the Mesozoic of Europe, from early Cenomanian Charentese (French) amber. Due to the opaque nature of French amber, X-ray microtomography was used to document fine morphological details of the fossil. *Protodasytes cretaceus* gen. et sp. nov. possess a unique combination of characters within the subfamily Dasytinae shared by the tribes Chaetomalachiini, Dasytini, and Listrini, namely the presence of a small antennal club, tarsomere 4 slightly shorter than 3 but not distinctly narrower, symmetrical claws, and a distinct pronotal and elytral fringe. The finding suggests that Dasytinae begun to diversify by the Late Cretaceous, possibly in concert with the radiation of angiosperms. The fossil record of soft-winged flower beetles is critically reviewed, and a checklist of extinct species is provided. The fragmentary Cenozoic fossils *Troglops punctatissima* and *Malachius vertummi* are removed from the family and the record of *Attalus lusitanicus* from Eocene–Oligocene Bembridge Marls is regarded as unlikely. The potential role of *Protodasytes* gen. nov. and Cretaceous melyrids as pollinators of early of angiosperms is discussed.

Keywords: Cleroidea, Charentese amber, Fouras Peninsula, Cretaceous, Cenomanian, phoretic mites

WITH over 6,000 described species placed in 300 genera and four subfamilies, the soft-winged flower beetles (Melyridae) are the most species-rich family of the diverse polyphagan superfamily Cleroidea (Mayor 2002; Ślipiński *et al.* 2011). The group more or less equivalent to modern Melyridae was historically treated as three to five separate families (e.g. Crowson 1955, 1964; Majer 1994a; Bocáková *et al.* 2012), although modern molecular phylogenies indicate that it ought to be treated as a monophylum (e.g. Gimmel *et al.* 2019). Due to their high diversity and convoluted taxonomic history, the higher classification of soft-winged flower beetles is still in its infancies (Mayor 2002). The situation is complicated further by the scarcity of informative Mesozoic fossils that could contribute to elucidating the relationships among modern taxa. Only two Mesozoic melyrids have been described to date: the Middle Jurassic melyrine *Sinomelyris praedecessor* Kolibáč and Huang, 2019 from near the Daohugou village in China, and the enigmatic dasytine *Acanthocnemoides sukatshevae* Zherikhin, 1977 from Albian Taimyr amber, which was formerly regarded as a member of Acanthocnemidae (Arnoldi *et al.* 1977; Kolibáč & Huang 2019; Kolibáč & Perkovsky 2020). Melyrids only become more abundant in the fossil record in the Cenozoic.

Dasytinae (treated as family Dasytidae in older works) is a group of mostly uniformly dark or metallically coloured melyrids with a distinct vestiture. They are regarded as the most diverse and least taxonomically understood subfamily of Melyridae (Majer 1987). Dasytines can be recognised by their usually heavily sclerotised body, absence of extrusible glands, apical maxillary palpomere variable but mostly conical, elytra mostly completely covering the entire abdomen, legs and antennae rarely modified, basal tarsomere as long or longer than tarsomere 2 on all legs, claws variable but usually with ungual appendages, basal two ventrites separated by a distinct suture, and median lobe of aedeagus simple (Majer 1994b; Mayor 2002). Larvae are found in leaf litter or rotting plant matter and are usually predaceous, although some are entirely herbivorous, predatory and herbivorous, or scavenge on small arthropods at some point during their development (Fiori 1971; Kolibáč *et al.* 2005). The adults visit flowers, often in large numbers, to feed on pollen and nectar. Due to their seemingly high host specificity, frequently high abundance, and strongly setose body, melyrids have been regarded as likely important pollinators of some angiosperms such as daisies (Asteraceae), legumes (Fabaceae), and mustards (Brassicaceae) (Mawdsley 2003). Dasytines are distributed worldwide, although they are the most diverse in arid and semi-arid regions (Lawrence & Leschen 2010). About 1,500 described species are placed into 50 genera (Mayor 2002; Kolibáč *et al.* 2005).

Here we describe the first melyrid beetle from Cenomanian Charentese amber from the Charente-Maritime department in southwestern France. The fossil represents the earliest described member of Melyridae from the Mesozoic of Europe and documents the early diversity of the group in the Cretaceous.

GEOLOGICAL SETTING

Charentese amber is a collective name applied to late Albian and early Cenomanian fossil resin collected from several sites in southwestern France, namely in the Charente-Maritime and Charente departments. With over 1,500 arthropod inclusions discovered to date (Perrichot *et al.* 2007, 2010), including insects, arachnids, crustaceans and myriapods, it represents one of the most significant amber deposits from the Cretaceous of Europe. Around 40 well-preserved beetle fossils are known from the deposit, and a further 15 or so specimens are too fragmentary to be determined (Peris *et al.* 2014).

The amber inclusion described herein originates from the ‘Plage de la Vierge’ locality at the Fouras Peninsula, Charente-Maritime, which is a lignitic deposit at times rich in fossil wood and vertebrate remains within a glauconitic sand and clay. The locality is exposed only occasionally during low tides (Néraudeau *et al.* 2003: fig. 1). The location and stratigraphy of the deposit have been discussed in detail in a number of previous publications, which have assigned the amber bed to the ‘lithological subunit B2ms’ (Néraudeau *et al.* 2003; Perrichot 2005; Perrichot *et al.* 2010; Cockx *et al.* 2016), or more recently to the unit ‘B2c/d’ based on palynomorph evidence (Peyrot *et al.* 2019). Based on this latter publication, amber from Fouras is considered early Cenomanian in age (~96 to 100.5 Ma). Palaeontological and sedimentological studies indicate that the Fouras amber locality was an estuarine lagoon-like environment (Néraudeau *et al.* 2003; Perrichot *et al.* 2010). Coastal or riparian forests in the vicinity were dominated by gymnosperms (mostly Cheirolepidiaceae and Cupressaceae), abundant ferns, and rare aquatic angiosperms (Peyrot *et al.* 2019).

To date, Fouras amber has yielded about 110 organismic inclusions, mostly arthropods, including a beetle originally assigned to the family Trogossitidae (Peris *et al.* 2014) and now considered to belong to Thymalidae (Peris 2020), as well as a member of the family Thanerocleridae (Tihelka *et al.* 2020b). The fossil studied herein originates from a highly fossiliferous amber piece that holds 53 arthropods and three conifer fragments including the thaneroclerid beetle mentioned above, three other fragmentary beetle specimens, wasps belonging to the families Bethylidae and Sclerogibbidae (Cockx *et al.* 2016; Perkovsky *et al.* 2020), and conifer remains assigned to the genus *Pagiophyllum* Heer (Cheirolepidiaceae), which may have secreted the resin (Moreau *et al.* 2020).

MATERIAL AND METHODS

Specimen preparation and photography

Since the amber piece #IGR.FRS-7 contained many fossils embedded within different amber flows, it was cut into several smaller fragments using a scalpel blade to enable easier observation of the inclusions. Each fragment containing at least one organic inclusion was embedded into mineralogical-grade epoxy Epotek 301-2 using a vacuum chamber. The resulting blocks were polished for an optimal

view of the fossils. A total of 34 fossiliferous fragments were prepared and numbered IGR.FRS-7.1 to IGR.FRS-7.34. The melyrid specimen described herein is preserved in fragment IGR.FRS-7.2 deposited in the collection of the Geological Department and Museum of the University of Rennes, France.

A Zeiss Discovery V20 stereomicroscope was used for observation and photography. Green epifluorescence microphotographs were taken using the Zeiss Axio Imager 2 light microscope under the eGFP mode.

X-ray microtomography

Due to the generally quite opaque nature of Charentese amber, high-resolution X-ray microtomography (micro-CT) was used to reveal fine morphological detail of the fossil. The specimen was scanned using Zeiss Xradia 520 versa at the micro-CT laboratory of the Nanjing Institute of Geology and Palaeontology, CAS in Nanjing, China. A CCD-based 4× objective was used, providing isotropic voxel sizes of 2.9478 µm with the help of geometric magnification. The acceleration voltage for the X-ray source was 50 kV. To improve signal-to-noise ratio, 3,001 projections over 360° were collected, and the exposure time for each projection was 2 s. The tomographic data were analysed using AVIZO (version 2019.01; gold-coloured reconstructions) and VG Studio (version 3.0; Volume Graphics; silver-coloured reconstructions).

SYSTEMATIC PALAEONTOLOGY

Order COLEOPTERA Linnaeus, 1758

Suborder POLYPHAGA Emery, 1886

Superfamily CLEROIDEA Latreille, 1802

Family MELYRIDAE Leach, 1815

Subfamily DASYTINAE Laporte, 1840

Tribe *incertae sedis*

Genus PROTODASYTES nov.

LSID. urn:lsid:zoobank.org:act: 2C7906D2-3968-440AB3D5-70462AF4E303

Derivation of name. Generic name is a combination of Greek *proto-* (meaning ‘giving rise to’), and *Dasytes* Paykull, in reference to the putatively basal position of the new genus in relation to the tribe Dasytini.

Type species. *Protodasytes cretaceus* sp. nov.

Diagnosis. Body elongate, subcylindrical, setose. Pubescence moderately long, not decumbent, or scale-like. Clypeus and labrum transverse. Maxillary palpomere subovate. Eyes lacking interfacetal setae, moderately projecting. Antennae moniliform, somewhat serrate on inner side, with apical three segments slightly widened. Temples half as long as the length of eyes. Frons with deeply incised and moderately arching longitudinal furrows laterally. Pronotum transverse, no wider than elytra in humeral portion, with oval grooves laterally, connected to a transverse furrow running along pronotal posterior margin. Distinct setose lateral fringe on pronotum and elytra present. Epipleura complete, widest at humeri. Tarsomeres on all legs subequally wide. Tarsomere 4 slightly shorter than 3 on all legs. Claws symmetrical, lacking free membranous appendages.

Protodasytes cretaceus sp. nov.

Figures 1–3

LSID. urn:lsid:zoobank.org:act:C1A31868-5634-4FE8-9B8E-D97BFB1879D1

Derivation of name. The specific epithet is derived from the Latin *creta* (=chalk, chalky), in reference to the Cretaceous age of the fossil.

Holotype. IGR.FRS-7.2, sex undetermined.

Diagnosis. As for genus.

Description. Body elongate and slender, moderately cylindrical, 2.29 mm long from clypeus to elytral apex, 0.88 mm wide across elytral humeri. All surfaces black, antennae and tarsi with dark brown tints. Pubescence moderately long, erect, densely scattered on the surface and margins of pronotum and elytra (Fig. 1).

Head almost prognathous, not distinctively subrostrate, 0.37 mm long, 1.5 wider than long, broadest at eyes which are as wide as the base of the pronotum (Fig. 2). Frontoclypeal suture visible. Clypeus trapezoid, wider than long, with a medial transverse furrow. Labrum transverse, subpentagonal, with a rounded apex. Mandibles moderately elongate (Fig. 3A, B). Maxillary palpi 4-segmented; basal palpomere short and narrow; palpomere 2 2.5 times longer than the preceding segment and about twice as broad apically; palpomere 3 barrel-shaped, approximately as long as wide; palpomere 4 as long as the preceding two segments together, elongate and subovate, broadest medially. Labial palpi 3-segmented, apical segment obclavate (Fig. 3E). Eyes large, moderately projecting, finely faceted, without interfacetal setae. Distance between eyes representing 2.6 times of eye length. Antennal insertions visible from above,

1 separated from eyes by 0.5 times of eye length. Antennae 11-segmented, moniliform, somewhat serrate
2 on inner side, with apical three segments slightly broadened and forming an indistinct club, reaching to
3 pronotal-elytral junction, with short erect setae. Antennomere 1 bulbous, 1.2 times longer than following
4 segment; antennomeres 2–3 elongate and subequal; antennomeres 4–8 somewhat triangular and slightly
5 serrate on inner side, approximately subequal in length; antennomeres 9–11 slightly wider than preceding
6 segments, 1.1 times wide than the preceding segments and not distinctly serrate, gradually lengthening
7 apically; antennomere 11 obclavate, 1.2 times longer than the preceding segment. Temples half as long as
8 the length of eyes. Frons and vertex flat, with deep circular and irregularly arranged punctures. Sides of
9 frons next with deep moderately arching longitudinal furrows, running slightly longer than the length of
10 eyes. Ventral side of head lacking subantennal grooves. Gular sutures well-separated.

11 Pronotum transverse and broadest medially, 0.22 mm long, 2.0 times wider than long. Anterior
12 margin of pronotum shallowly emarginate, with an instinct elevation. Lateral margins not serrated, but
13 with a densely setose fringe. Pronotal disc densely punctate with deep circular pits separated by no less
14 than 3 times their diameter. Each side of disc with a sharply delineated oval groove extending almost the
15 entire length of the pronotum, with the outer part of the furrow lying on the pronotal margin and the inner
16 and deeper part found in the lateral eight of the pronotal disc and connected to a transverse furrow
17 running along pronotal posterior margin (Fig. 1A, 2A, 3D: pf). Posterior margin straight, slightly
18 elevated. Scutellum subtriangular, not abruptly elevated. Precoxal portion of prothorax 0.7 times the
19 maximum width of procoxae. Procoxae strongly transverse, projecting well below prosternum, narrowly
20 separated, externally broadly open, separated by narrow and apically acute prosternal process reaching to
21 the middle of the procoxae. Mesoventrite with mesocoxal cavities strongly transverse and sub-contiguous,
22 separated by less than a quarter of their height. Metathorax with discrimen extending to over half the
23 length of the segment. Postcoxal lines absent. Metacoxae widely separated, extending laterally to meet
24 sides of body.

25 Legs slender and elongate. Protochantins exposed. Femora broadest medially, with a shallow
26 apical groove for the reception of tibiae. Tibiae of prothoracic legs moderately curved (Fig. 2C: pti),
27 straight on meso- and metathoracic legs. Tarsi 5-segmented, slightly shorter than tibia, all tarsomeres
28 subequally wide. Tarsomeres 1 and 2 subequally long, tarsomeres 3 and 4 gradually shortening,
29 tarsomere 5 as long as the preceding two segments together (Fig. 2, 3). Claws symmetrical, lacking free
30 membranous appendages.

31 Elytra 1.70 mm long, 1.7 times as long as their combined width, as wide as pronotum at its
32 broadest point, parallel-sided, gradually narrowing in the posterior half, completely covering abdomen.
33 Disc with deep and irregularly arranged circular pits, separated by more than twice their diameter. Suture

bordered with an elevated ridge. Margin with densely setose fringe (Fig. 1C: ef). Epipleura complete, widest at humeri. Elytral apices meeting at suture.

Abdomen with five ventrites gradually shortening apically, with terminal segment more or less enclosed within the preceding one.

Note. Two phoretic mites (Oribatida: Brachypilina) are present on the pro- and mesothoracic legs of the holotype (Fig. 2B: pm).

DISCUSSION

Systematic position of Protodasytes gen. nov.

The fossil can be unambiguously assigned to the melyrid subfamily Dasytinae on the basis of the presence of a distinct clypeus; procoxae prominent, nearly contiguous, open posteriorly; body lacking obvious eversible vesicles; tarsomere 1 not shorter than tarsomere 2 on all legs; confused elytral punctation that does not form striae; and first two ventrites separated by a by a distinct suture (Mayor 2002; Lawrence *et al.* 2014; Gimmel *et al.* 2019). In its current sense, the subfamily Dasytinae includes the following four tribes: Danaceini, Chaetomalachiini, Listrini, and Dasytini (Gimmel *et al.* 2019). *Protodasytes* gen. nov. possesses an unusual combination of characters that precludes an unambiguous placement into either of the modern tribes. It is excluded from Danaceini by its transverse clypeus and labrum and symmetrical claws. Placement in the tribe Chaetomalachiini is ruled out by tarsomeres 2–3 not distinctly broadened and segment 4 not distinctly slenderer than segment 3. It does not belong to Listrini, as its tarsomeres are not subequal in length and claws lack free membranous appendages.

Protodasytes cretaceus gen. et sp. nov. is the most similar to the tribe Dasytini in its serrate to moniliform antennae; eyes not pubescent; tarsomere 4 slightly shorter than tarsomere 3 on all legs but not distinctly narrower; claws symmetrical, with a basal tooth (Majer 1987, 1994b; Mayor 2002). However, unlike all modern Dasytini, *Protodasytes* gen. nov. has a distinct lateral fringe on the pronotum and elytra. Moreover, the indistinct antennal club of the new genus is unique within crown Dasytini. Both characters, the presence of a pronotal and elytral fringe and a small antennal club, are present in the tribes Danaceini, Chaetomalachiini and Listrini (Majer 1989, 1990). Given that in Majer's (1994) cladogram, Listrini + Dasytini formed a clade, with Chaetomalachiini sister to both and Danaceini as the earliest diverging clade within the subfamily, both characters can be regarded as plesiomorphic. As it shares characters present in both Dasytini and Listrini, we regard *Protodasytes* gen. nov. as a 'fossil link' between the two tribes (Fig. 5). Majer (1994b) provided a list of morphological characters supporting the sister relationship between Dasytini and Listrini, and this relationship has also been recovered by molecular analyses based

on four genes (Gimmel *et al.* 2019). However, the same analysis also recovered a non-monophyletic Danaceini and Chaetomalachiini, and further recovered the tribe Amauronoidini as closely related. Deeper relationships between melyrid tribes vary between molecular studies based on a few genes (Bocáková *et al.* 2012), which may be susceptible to phylogenetic artefacts to insufficient phylogenetic signal and limits of phylogenetic inference software (e.g. Young & Gillung 2020; Tihelka *et al.* 2020a). Given the unresolved higher classification of Dasytinae, we choose to provisionally treat *Protodasytes* gen. nov. as tribe *incertae sedis*.

Fossil record of Melyridae

The earliest fossil melyrid is the Middle Jurassic *Sinomelyris praedecessor* from Daohugou Beds in northeastern China. The fossil has been assigned to the subfamily Melyrinae mostly based on its habitus characters, but a more precise systematic placement was not possible (Kolibáč & Huang 2019). The only other Mesozoic melyrid known to date is the Albian *Acanthocnemoides sukatshevae* from Siberian Taimyr amber. The fossil, known from two fragmentary specimens, has been originally assigned to the family Acanthocnemidae (Arnoldi *et al.* 1977), but a recent re-examination of the type material supported its inclusion in the dasytine tribe Danaceini (Kolibáč & Perkovsky 2020). Two undescribed specimens from Lower Cretaceous Lebanese amber, apparently belonging to Malachiinae and Dasytinae, were mentioned by Kirejtshuk & Azar (2013). Further undescribed specimens from Albian Spanish amber were mentioned by Peris *et al.* (2016). A single Albian–Cenomanian melyrid has been mentioned from Burmese amber in the collections of the Natural History Museum in London (Rasnitsyn & Ross 2000). This makes *P. cretaceus* gen. et sp. nov. the earliest described member of Melyridae from the Mesozoic of Europe.

Soft-winged flower beetles are more abundant in the Cenozoic fossil record. They are known from Eocene Baltic and Rovno ambers (Spahr 1981; Hieke & Pietrzeniuk 1984). Majer (1998) reviewed the melyrid fauna of Baltic amber, and since then several new species have been described (Kubisz 2001; Tshernyshev 2016, 2019). Two malachiine species are known from Eocene Oise amber (Kirejtshuk & Nel 2008). The recent species *Attalus lusitanicus* Erichson, 1840 reported from Eocene–Oligocene Bembridge Marls is herein removed from the family and treated as Polyphaga *incertae sedis*, as it is represented by a single poorly preserved specimen lacking important diagnostic characters supporting its assignment to this particular species. Fossils described from the late Eocene Florissant Formation in Colorado are all in need of revision (Wickham 1912, 1914; Mawdsley 1999), as many are very fragmentary. *Troglops punctatissima* Théobald, 1935 was described from the late Oligocene of Puy-de-Dôme, France, based on only a single elytron without any informative diagnostic characters (Piton & Théobald 1935) and as such is excluded from the family and treated as Polyphaga *incertae sedis*. *Malachius vertummi* Heer, 1847 from the Miocene of Oeningen, Germany (Heer 1847) is excluded from Melyridae due to the lack of

diagnostic characters and treated as *Polyphaga incertae sedis*. Subfossil soft-winged flower beetles are also known from Quaternary sediments (e.g. Elias 1992; Elias *et al.* 2006), these specimens are not included in Tab. 1.

Soft-winged flower beetles: potential pollinators of early angiosperms?

The earliest unequivocal fossil angiosperms date back to the Early Cretaceous (Friis *et al.* 2010). Their diversification during the mid-Cretaceous, when they replaced the previously dominant gymnosperms (Benton 2010) is believed to have drastically altered food chains and lead to the diversification of many terrestrial animal lineages in an event known as the Cretaceous Terrestrial Revolution (Lloyd *et al.* 2008). Together with thrips, lacewings, flies, and scorpionflies (Labandeira *et al.* 2007, 2016), beetles were among the first pollinators of gymnosperms during the Mesozoic (Cai *et al.* 2018; Liu *et al.* 2018). Beetles associated with pollen are known from Cretaceous ambers (Bao *et al.* 2019; Peris *et al.* 2020; Peris & Jelínek 2020) and it has been suggested that the diversification of angiosperms may have contributed to the radiation of phytophagous beetles (Farrell 1998; Ahrens *et al.* 2014).

Adult soft-winged flower beetles are believed to be exclusively pollinivorous and nectarivorous. In summer, they can be collected in large numbers on the inflorescences of diverse angiosperm groups such as daisies, legumes, and mustards as well as some gymnosperms such as pines. Mawdsley (2003) listed 68 genera of plants belonging to 26 families from North America visited by dasytines. Large quantities of pollen that adhere to the beetle's setose elytra and abdomen are transported between flowers during the course of normal feeding (Hawkeswood 1987). At least two Nearctic members of the phlox family Polemoniaceae depend primarily on pollination by soft-winged flower beetles (Grant & Grant 1965) and dasytines have also been demonstrated to contribute to the pollination of sunflowers in South Africa (Toit 1990). The body of *Protodasytes* gen. nov. is densely setose and possesses deep grooves, which are frequently found in pollinating beetles (Cai *et al.* 2018). The occurrence of diverse monocots and eudicots at Fouras (Peyrot *et al.* 2019) suggests that like its modern relatives, *P. cretaceus* gen. et sp. nov. may have visited and pollinated early angiosperms in the Cenomanian of western Europe. Further specimens associated with pollen would be required to directly confirm this association. At the very least, *P. cretaceus* gen. et sp. nov. provides an important calibration point for the Mesozoic diversification of dasytines.

CONCLUSION

The diversification of angiosperms in the Aptian–Albian is believed to have propelled many lineages of phytophagous beetles to their present-day diversity (Farrell 1998; Ahrens *et al.* 2014; Peris *et al.* 2017). Dasytine soft-winged flower beetles are a diverse group of flower-visiting cleroid beetles that feed on nectar as well as angiosperm and gymnosperm pollen (Mawdsley 2003). Here we describe the third

Mesozoic dasytine beetle, from Cenomanian (~96 to 100.5 Ma) Charentese amber from the Plage de la Vierge locality in the Fouras Peninsula, southwestern France, representing the first record of the family in the Cretaceous of Europe. *Protodasytes cretaceus* gen. et sp. nov. possesses an unusual combination of characters that exclude it from the crown group of all four dasytine tribes and most likely belonged to the stem of the lineage Listrini + Dasytini. As such, *P. cretaceus* gen. et sp. nov. provides evidence that pollinivorous dasytines began to diversify by the Late Cretaceous. The fossil provides an important calibration point for testing the co-diversification between beetles and angiosperms in the Cretaceous.

Acknowledgements. We are indebted to Prof. Didier Néraudeau (University of Rennes) who collected and gave access to the amber piece containing the specimen described herein. We also thank David Peris (University of Bonn) for the preliminary identification of beetles in the amber piece studied herein, and our thoughts go to Katya Sidorchuk (1981-2019) who identified the phoretic mites. Financial support for field studies and collection of Charentese amber was provided by the French National Research Agency grant BLAN07-1-184190 (project AMBRACE to D. Néraudeau), and CNRS-INSU grant Intervie (project NOVAMBRE 2 to D. Néraudeau and V. Perrichot). Support for the present study was provided by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000 and XDB18000000), the National Natural Science Foundation of China (41672011 and 41688103), and the Second Tibetan Plateau Scientific Expedition and Research (2019QZKK0706). We are grateful to Dr. Yan Fang and Ms. Su-Ping Wu for technical help with microtomography. We thank anonymous reviewers for their valuable comments.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/3E78BC27-0411-48E7-BE08-D15608EB1073>. Micro-CT scans (full-resolution image stack in .tiff format and model in STL format) are available from Mendeley Data: <https://doi.org/10.17632/zwrcvtjn6n.1>.

REFERENCES

- AHRENS, D., SCHWARZER, J. and VOGLER, A. P. 2014. The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141470.
- ARNOLDI, L. V., ZHERIKHIN, V. V., NIKRITIN, L. M. and PONOMARENKO, A. G. 1977. Mezozoiskie zhestkokrylye. *Trudy Paleontologicheskogo Instituta*, **161**, 1–204.

- BAO, T., WANG, B., LI, J. and DILCHER, D. 2019. Pollination of Cretaceous flowers. *Proceedings of the National Academy of Sciences*, **116**, 24707–24711.
- BENTON, M. J. 2010. The origins of modern biodiversity on land. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3667–3679.
- BOCÁKOVÁ, M., CONSTANTIN, R. and BOCÁK, L. 2012. Molecular phylogenetics of the melyrid lineage (Coleoptera: Cleroidea). *Cladistics*, **28**, 117–129.
- CAI, C., ESCALONA, H. E., LI, L., YIN, Z., HUANG, D. and ENGEL, M. S. 2018. Beetle pollination of cycads in the Mesozoic. *Current Biology*, **28**, 2806–2812.e1.
- COCKX, P. F. D., MCKELLAR, R. C. and PERRICHOT, V. 2016. First records of the subfamilies Bethylinae (Hymenoptera: Bethyridae) and Cleptinae (Hymenoptera: Chrysididae) in Upper Cretaceous amber from France. *Cretaceous Research*, **68**, 1–8.
- CROWSON, R. A. 1955. *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd & Co., Ltd., London.
- . 1964. A review of the classification of Cleroidea (Coleoptera), with descriptions of two new genera of Peltidae and of several new larval types. *Transactions of the Royal Entomological Society of London*, **116**, 275–327.
- ELIAS, S. A. 1992. Late Quaternary zoogeography of the Chihuahuan Desert insect fauna, based on fossil records from packrat middens. *Journal of Biogeography*, **19**, 285–297.
- , KUZMINA, S. and KISELYOV, S. 2006. Late Tertiary origins of the Arctic beetle fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241**, 373–392.
- FARRELL, B. D. 1998. 'Inordinate fondness' explained: why are there so many beetles? *Science*, **281**, 555–559.
- FIORI, G. 1971. Contributi alla conoscenza morfologica ed etologica dei Coleotteri. IX. *Psilothrix viridicaeruleus* (Geoffr.) (Melyridae, Dasytinae). "Studi Sassaressi" Sez. III. *Annali della Facoltà di Agraria dell'Università di Sassari*, **19**, 2–70.
- FRIIS, E. M., PEDERSEN, K. R. and CRANE, P. R. 2010. Diversity in obscurity: fossil flowers and the early history of angiosperms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 369–382.
- GIMMEL, M. L., BOCÁKOVÁ, M., GUNTER, N. L. and LESCHEN, R. A. B. 2019. Comprehensive phylogeny of the Cleroidea (Coleoptera: Cucujiformia). *Systematic Entomology*, **44**, 527–558.
- GRANT, V. and GRANT, K. A. 1965. *Flower Pollination in the Phlox Family*. Columbia University Press, New York, NY.

- 1 HAWKESWOOD, T. J. 1987. Observations on a *Dasytes* species (Melyridae: Coleoptera), a pollen-feeding
2 beetle on daisies (Asteraceae) in northern New South Wales. *Victorian Naturalist*, **104**, 76–80.
- 3 HEER, O. 1847. *Die Insektenfauna der Tertiärgelände von Oeningen und von Radoboj in Croatien. Erster*
4 *Theil: Käfer*. W. Engelmann, Leipzig.
- 5 HIEKE, F. and PIETRZENIUK, E. 1984. Die Bernstein-Käfer des Museums für Naturkunde, Berlin (Insecta,
6 Coleoptera). *Mitteilungen aus dem Zoologischen Museum in Berlin*, **60**, 297–326.
- 7 KIREJTSHUK, A. G. and NEL, A. 2008. New beetles of the suborder Polyphaga from the Lowermost
8 Eocene French amber (Insecta: Coleoptera). *Annales de la Société entomologique de France*
9 (N.S.), **44**, 419–442.
- 10 ——— and AZAR, D. 2013. Current knowledge of Coleoptera (Insecta) from the Lower Cretaceous
11 Lebanese amber and taxonomical notes for some Mesozoic groups. *Terrestrial Arthropod*
12 *Reviews*, **6**, 103–134.
- 13 KOLIBÁČ, J. and HUANG, D. 2019. New cleroid beetles from the Middle–Late Jurassic of China. *Acta*
14 *Palaeontologica Polonica*, **64**, 143–155.
- 15 ——— and PERKOVSKY, E. E. 2020. A reclassification of *Acanthocnemoides sukatshevae* Zherikhin, 1977
16 from the mid-Cretaceous Taimyr amber (Coleoptera). *Cretaceous Research*, **115**, 104548.
- 17 KOLIBÁČ, J., MAJER, K. and ŠVIHLA, V. 2005. *Beetles of the Superfamily Cleroidea in the Czech and Slovak*
18 *Republics and Neighbouring Areas*. Clarion Production, Prague.
- 19 KUBISZ, D. 2001. Beetles in the collection of the Museum of Amber Inclusions, University of Gdansk,
20 with description of *Colotes sambicus* sp. n. (Coleoptera: Melyridae). *Polskie Pismo*
21 *Entomologiczne*, **70**, 259–265.
- 22 LABANDEIRA, C. C., KVAČEK, J. and MOSTOVSKI, M. B. 2007. Pollination drops, pollen, and insect
23 pollination of Mesozoic gymnosperms. *Taxon*, **56**, 663–695.
- 24 ———, YANG, Q., SANTIAGO-BLAY, J. A., HOTTON, C. L., MONTEIRO, A., WANG, Y.-J., GOREVA, Y., SHIH,
25 C., SILJESTRÖM, S., ROSE, T. R., DILCHER, D. L. and REN, D. 2016. The evolutionary convergence
26 of mid-Mesozoic lacewings and Cenozoic butterflies. *Proceedings of the Royal Society B:*
27 *Biological Sciences*, **283**, 20152893.
- 28 LAWRENCE, J. F. and LESCHEN, R. A. B. 2010. Melyridae Leach, 1815. In LESCHEN, R. A. B., BEUTEL, R. G.
29 and LAWRENCE, J. F. (eds.) *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles. Vol.*
30 *2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia Partim)*, De Gruyter,
31 Berlin, 273–280 pp.

- , LESCHEN, R. a. B. and ŚLIPIŃSKI, A. 2014. *Antillipeltis*, a new genus of Antillean Trogossitidae (Coleoptera: Cleroidea) with a key to the Cleroidea. *Zootaxa*, **3794**, 435–454.
- LIU, Z., ŚLIPIŃSKI, A., LAWRENCE, J. F., REN, D. and PANG, H. 2018. *Palaeoboganium* gen. nov. from the Middle Jurassic of China (Coleoptera: Cucujoidea: Boganiidae): the first cycad pollinators? *Journal of Systematic Palaeontology*, **16**, 351–360.
- LLOYD, G. T., DAVIS, K. E., PISANI, D., TARVER, J. E., RUTA, M., SAKAMOTO, M., HONE, D. W. E., JENNINGS, R. and BENTON, M. J. 2008. Dinosaurs and the Cretaceous Terrestrial Revolution. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2483–2490.
- MAJER, K. 1987. Comparative morphology and proposed major taxonomy of the family Melyridae (Insecta, Coleoptera). *Polskie Pismo Entomologiczne*, **56**, 719–859.
- . 1989. Generic classification of the tribe Chaetomalachiini (Coleoptera, Melyridae). *Polskie Pismo Entomologiczne*, **58**, 745–774.
- . 1990. A new tribe Listrini trib. n. including two new genera (Coleoptera, Melyridae). *Acta Entomologica Bohemoslovaca*, **87**, 368–384.
- . 1994a. Gietellidae, full family status for Melyridae: Gietellinae (Coleoptera: Cleroidea). *Entomological Problems*, **25**, 65–72.
- . 1994b. A review of the classification of the Melyridae and related families (Coleoptera, Cleroidea). *Entomologica Basiliensia*, **17**, 319–390.
- . 1998. Rhadalinae from the Baltic Amber (Coleoptera, Dasytidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin: Deutsche Entomologische Zeitschrift*, **45**, 255–264.
- MAWDSLEY, J. R. 1999. Review of the extant and fossil Dasytinae (Coleoptera: Melyridae) of Colorado, U. S. A. *Transactions of the American Entomological Society*, **125**, 251–267.
- . 2003. The importance of species of Dasytinae (Coleoptera: Melyridae) as pollinators in western North America. *Coleopterists Bulletin*, **57**, 154–160.
- MAYOR, A. J. 2002. Melyridae Leach, 1815. In ROSS, A. J., ARNETT, R. H., THOMAS, M. C., SKELLEY, P. E. and FRANK, J. H. (eds.) *American Beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea*, CRC Press, Boca Raton, 281–303 pp.
- MOREAU, J.-D., NÉRAUDEAU, D. and PERRICHOT, V. 2020. Conifers from the Cenomanian amber of Fouras (Charente-Maritime, western France). *BSGF - Earth Sciences Bulletin*, **191**, 16.
- NÉRAUDEAU, D., ALLAIN, R., PERRICHOT, V., VIDET, B., DE BROIN, F. de L., GUILLOCHEAU, F., PHILIPPE, M., RAGE, J.-C. and VULLO, R. 2003. Découverte d'un dépôt paralique à bois fossiles, ambre

- 1 insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans le Cénomanién inférieur
 2 de Fouras (Charente-Maritime, Sud-Ouest de la France). *Comptes Rendus Palevol*, **2**, 221–230.
- 3 PERIS, D. 2020. Coleoptera in amber from Cretaceous resiniferous forests. *Cretaceous Research*, **113**,
 4 104484.
- 5 ——— and JELÍNEK, J. 2020. Syninclusions of two new species of short-winged flower beetle
 6 (Coleoptera: Kateretidae) in mid-Cretaceous Kachin amber (Myanmar). *Cretaceous Research*,
 7 **106**, 104264.
- 8 ———, KOLIBÁČ, J. and DELCLÒS, X. 2014. *Cretamerus vulloi* gen. et sp. nov., the oldest bark-gnawing
 9 beetle (Coleoptera: Trogossitidae) from Cretaceous amber. *Journal of Systematic Palaeontology*,
 10 **12**, 879–891.
- 11 ———, RUZZIER, E., PERRICHOT, V. and DELCLÒS, X. 2016. Evolutionary and paleobiological implications
 12 of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. *Geoscience Frontiers*, **7**,
 13 695–706.
- 14 ———, PÉREZ-DE LA FUENTE, R., PEÑALVER, E., DELCLÒS, X., BARRÓN, E. and LABANDEIRA, C. C. 2017.
 15 False blister beetles and the expansion of gymnosperm-insect pollination modes before
 16 angiosperm dominance. *Current Biology*, **27**, 897–904.
- 17 PERIS, D., LABANDEIRA, C. C., BARRÓN, E., DELCLÒS, X., RUST, J. and WANG, B. 2020. Generalist pollen-
 18 feeding beetles during the mid-Cretaceous. *iScience*, **23**, 100913.
- 19 PERKOVSKY, E. E., MARTYNOVA, K. V., MITA, T., OLMÍ, M., ZHENG, Y., MÜLLER, P., ZHANG, Q., GANTIER,
 20 F. and PERRICHOT, V. 2020. A golden age for ectoparasitoids of Embiodea: Cretaceous
 21 Sclerogibbidae (Hymenoptera, Chrysidoidea) from Kachin (Myanmar), Charentes (France) and
 22 Choshi (Japan) ambers. *Gondwana Research*, **87**, 1–22.
- 23 PERRICHOT, V. 2005. Environnements paraliques à ambre et à végétaux du Crétacé Nord-Aquitain
 24 (Charentes, Sud-Ouest de la France). *Mémoires de Géosciences Rennes*, **118**, 1–310.
- 25 ———, NÉRAUDEAU, D. and TAFFOREAU, P. 2010. Charentese amber. In *Biodiversity of Fossils in Amber*
 26 *from the Major World Deposits*, Siri Scientific Press, Manchester, 192–208 pp.
- 27 ———, ———, NEL, A. and de PLOEG, G. 2007. A reassessment of the Cretaceous amber deposits from
 28 France and their palaeontological significance. *African Invertebrates*, **48**, 213–227.
- 29 PEYROT, D., BARRON, E., POLETTE, F., BATTEN, D. J. and NÉRAUDEAU, D. 2019. Early Cenomanian
 30 palynofloras and inferred resiniferous forests and vegetation types in Charentes (southwestern
 31 France). *Cretaceous Research*, **94**, 168–189.

- PITON, L. and THÉOBALD, N. 1935. La faune entomologique des gisements Mio-Pliocènes du Massif Central. *Revue des Sciences Naturelles d'Auvergne (N. S.)*, **1**, 65–104.
- RASNITSYN, A. and ROSS, A. J. 2000. A preliminary list of arthropod families present in the Burmese amber collection at The Natural History Museum, London. *Bulletin of the British Museum (Natural History), Geology*, **56**, 21–24.
- ŚLIPIŃSKI, A., LESCHEN, R. A. B. and LAWRENCE, J. F. 2011. Order Coleoptera Linnaeus, 1758. in Zhang, Z. (ed.) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. *Zootaxa*, **3148**, 203–208.
- SPAHR, U. 1981. *Systematischer katalog der bersteinund kopal-käfer (Coleoptera)*. Vol. 80. Staatliches Museum für Naturkunde, Karlsruhe.
- TIHELKA, E., THAYER, M. K., NEWTON, A. F. and CAI, C. 2020a. New data, old story: Molecular data illuminate the tribal relationships among rove beetles of the subfamily Staphylininae (Coleoptera: Staphylinidae). *Insects*, **11**, 164.
- , CHENG, G., HUANG, D., PERRICHOT, V. and CAI, C. 2020b. First thaneroclerid beetle from Cretaceous Charentese amber (Coleoptera: Cleroidea: Thanerocleridae). *Palaeoentomology*, **3**, 390–398.
- TOIT, A. P. du. 1990. The importance of certain insects as pollinators of sunflower (*Helianthus annuus* L.). *South African Journal of Plant and Soil*, **7**, 159–162.
- TSHERNYSHEV, S. E. 2016. New taxa of soft-winged flower beetles (Coleoptera, Malachiidae) in Baltic and Rovno amber. *Paleontological Journal*, **50**, 953–962.
- . 2019. New species of malachite beetles (Coleoptera, Dasytidae) in Baltic Amber. *Paleontological Journal*, **53**, 1024–1035.
- WICKHAM, H. F. 1912. A report on some recent collections of fossil Coleoptera from the Miocene shales of Florissant. *Bulletin from the Laboratories of Natural History of the State University of Iowa*, **6**, 3–38.
- . 1914. New Miocene Coleoptera from Florissant. *Bulletin of the Museum of Comparative Zoology, Harvard College*, **53**, 423–494.
- YOUNG, A. D. and GILLUNG, J. P. 2020. Phylogenomics — principles, opportunities and pitfalls of big-data phylogenetics. *Systematic Entomology*, **45**, 225–247.

FIG. 1. Habitus view of *Protodasytes cretaceus* gen. et sp. nov. (holotype, IGR.FRS-7.2). A, dorsal view under normal reflected light. B, ventral view under normal reflected light. C, ventral view under green epifluorescence. Abbreviations: ef, elytral fringe; pf, pronotal furrow. Scale bars represent 200 μm .

FIG. 2. Micro-CT reconstruction of *Protodasytes cretaceus* gen. et sp. nov. (holotype, IGR.FRS-7.2). A, dorsal view. B, ventral view. C, D, lateral views. *Abbreviations:* el, elytra; ep, epipleura; msta, mesotarsi; mtta, metatarsi; pf, pronotal furrows; pm, phoretic oribatid mites; pr, pronotum; pti, protibiae; ptta, protarsi. Scale bar represents 500 μ m.

FIG. 3. Enlargements of the micro-CT reconstruction of *Protodasytes cretaceus* gen. et sp. nov. (holotype, IGR.FRS-7.2). A, head in dorsal view. B, head in ventral view. C, thorax and base of abdomen in ventral view. D, head and thorax in lateral view. E, head and prothorax in ventral view. F, head in frontal view. Abbreviations: an, antenna; cl, clypeus; ey, eye; ff, frontal furrow; fr, frons; gs, gular sutures; la, labrum; lp, labial palp; mp, maxillary palp; msv, mesoventrite; mtv, metaventrite; pca, procoxa; pf, pronotal furrow; pt, prothorax; v1–2, ventrites 1–2. Scale bars represent 200 µm.

FIG. 4. Overview of Dasytinae phylogeny and classification, after Majer (1994b) with mapped hypothetical ancestral character states and the putative position of *Protodasytes* gen. nov.

- 1 TAB. 1. Overview of described fossil Melyridae species. Quaternary subfossils and undescribed material
 2 are omitted from the checklist.

Species	Subfamily	Tribe	Deposit	Age
JURASSIC				
<i>Sinomelyris</i> <i>praedecessor</i> Kolibáč and Huang, 2019	Melyrinae	<i>incertae sedis</i>	Daohugou Beds, Haifanggou Formation, northeast China	Callovian
CRETACEOUS				
<i>Acanthocnemoides</i> <i>sukatshevae</i> Zherikhin, 1977	Dasytinae	Danaceini	Taimyr amber, Taimyr Peninsula, Begichev Formation, Far North Russia	Albian
<i>Protodasytes cretaceus</i> Tihelka, Huang, Perrichot and Cai gen. et sp. nov.	Dasytinae	<i>incertae sedis</i>	Charentese amber, Fouras Peninsula, southwestern France	Cenomanian
EOCENE				
<i>Colotes constantini</i> Kirejtshuk and Nel, 2008	Malachiinae	Colotini	Oise amber, Le Quesnoy, northern France	Ypresian
<i>Colotes impexus</i> Kirejtshuk and Nel, 2008	Malachiinae	Colotini	Oise amber, Le Quesnoy, northern France	Ypresian
<i>Colotes sambicus</i> Kubisz, 2001	Malachiinae	Colotini	Baltic amber, Baltic Sea coast	Priabonian
<i>Dasytes ochraceus</i> Tshernyshev, 2019	Dasytinae	Dasytini	Baltic amber, Baltic Sea coast	Priabonian
<i>Palpattalus baltiensis</i> Tshernyshev, 2016	Malachiinae	Attalini	Baltic amber, Baltic Sea coast	Priabonian
<i>Palpattalus eocenicus</i> Tshernyshev, 2016	Malachiinae	Attalini	Baltic amber, Baltic Sea coast	Priabonian
<i>Protocephaloncus</i> <i>perkovskii</i> Tshernyshev, 2016	Malachiinae	Troglopini	Rovno amber, Ukryantar factory material, Ukraine	Priabonian
<i>Collops desuetus</i> Wickham, 1914	Malachiinae	Malachiini	Florissant Formation, Colorado, USA	Priabonian
<i>Collops extrusus</i> Wickham, 1914	Malachiinae	Malachiini	Florissant Formation, Colorado, USA	Priabonian
<i>Collops priscus</i> Wickham, 1914	Malachiinae	Malachiini	Florissant Formation, Colorado, USA	Priabonian
<i>Eudasytes listriiformis</i> Wickham, 1912	Dasytinae	<i>incertae sedis</i>	Florissant Formation, Colorado, USA	Priabonian
<i>Eutrichopleurus</i> <i>miocenensis</i> Wickham, 1912	Dasytinae	Listrini	Florissant Formation, Colorado, USA	Priabonian