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

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

3

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14

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

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

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

15 Dasytinae (treated as family Dasytidae in older works) is a group of mostly uniformly dark or  
16 metallically coloured melyrids with a distinct vestiture. They are regarded as the most diverse and least  
17 taxonomically understood subfamily of Melyridae (Majer 1987). Dasytines can be recognised by their  
18 usually heavily sclerotised body, absence of extrusible glands, apical maxillary palpomere variable but  
19 mostly conical, elytra mostly completely covering the entire abdomen, legs and antennae rarely modified,  
20 basal tarsomere as long or longer than tarsomere 2 on all legs, claws variable but usually with unguis  
21 appendages, basal two ventrites separated by a distinct suture, and median lobe of aedeagus simple (Majer  
22 1994b; Mayor 2002). Larvae are found in leaf litter or rotting plant matter and are usually predaceous,  
23 although some are entirely herbivorous, predatory and herbivorous, or scavenge on small arthropods at  
24 some point during their development (Fiori 1971; Kolibáč *et al.* 2005). The adults visit flowers, often in  
25 large numbers, to feed on pollen and nectar. Due to their seemingly high host specificity, frequently high  
26 abundance, and strongly setose body, melyrids have been regarded as likely important pollinators of some  
27 angiosperms such as daisies (Asteraceae), legumes (Fabaceae), and mustards (Brassicaceae) (Mawdsley  
28 2003). Dasytines are distributed worldwide, although they are the most diverse in arid and semi-arid  
29 regions (Lawrence & Leschen 2010). About 1,500 described species are placed into 50 genera (Mayor  
30 2002; Kolibáč *et al.* 2005).

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

34

## 1 **GEOLOGICAL SETTING**

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

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

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

28

## 29 **MATERIAL AND METHODS**

### 30 *Specimen preparation and photography*

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

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

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

#### 7 *X-ray microtomography*

8 Due to the generally quite opaque nature of Charentese amber, high-resolution X-ray  
9 microtomography (micro-CT) was used to reveal fine morphological detail of the fossil. The specimen  
10 was scanned using Zeiss Xradia 520 versa at the micro-CT laboratory of the Nanjing Institute of Geology  
11 and Palaeontology, CAS in Nanjing, China. A CCD-based 4× objective was used, providing isotropic  
12 voxel sizes of 2.9478 µm with the help of geometric magnification. The acceleration voltage for the X-ray  
13 source was 50 kV. To improve signal-to-noise ratio, 3,001 projections over 360° were collected, and the  
14 exposure time for each projection was 2 s. The tomographic data were analysed using AVIZO (version  
15 2019.01; gold-coloured reconstructions) and VG Studio (version 3.0; Volume Graphics; silver-coloured  
16 reconstructions).

17

### 18 **SYSTEMATIC PALAEONTOLOGY**

19 Order COLEOPTERA Linnaeus, 1758

20 Suborder POLYPHAGA Emery, 1886

21 Superfamily CLEROIDEA Latreille, 1802

22 Family MELYRIDAE Leach, 1815

23 Subfamily DASYTINAE Laporte, 1840

24 Tribe *incertae sedis*

25

26 Genus PROTODASYTES nov.

27

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

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

32 *Type species.* *Protodasytes cretaceus* sp. nov.

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

10

11 *Protodasytes cretaceus* sp. nov.

12 Figures 1–3

13 *LSID.* urn:lsid:zoobank.org:act:C1A31868-5634-4FE8-9B8E-D97BFB1879D114 *Derivation of name.* The specific epithet is derived from the Latin *creta* (=chalk, chalky), in reference to  
15 the Cretaceous age of the fossil.16 *Holotype.* IGR.FRS-7.2, sex undetermined.17 *Diagnosis.* As for genus.18 *Description.* Body elongate and slender, moderately cylindrical, 2.29 mm long from clypeus to elytral  
19 apex, 0.88 mm wide across elytral humeri. All surfaces black, antennae and tarsi with dark brown tints.  
20 Pubescence moderately long, erect, densely scattered on the surface and margins of pronotum and elytra  
21 (Fig. 1).22 Head almost prognathous, not distinctively subrostrate, 0.37 mm long, 1.5 wider than long,  
23 broadest at eyes which are as wide as the base of the pronotum (Fig. 2). Frontoclypeal suture visible.  
24 Clypeus trapezoid, wider than long, with a medial transverse furrow. Labrum transverse, subpentagonal,  
25 with a rounded apex. Mandibles moderately elongate (Fig. 3A, B). Maxillary palpi 4-segmented; basal  
26 palpomere short and narrow; palpomere 2 2.5 times longer than the preceding segment and about twice as  
27 broad apically; palpomere 3 barrel-shaped, approximately as long as wide; palpomere 4 as long as the  
28 preceding two segments together, elongate and subovate, broadest medially. Labial palpi 3-segmented,  
29 apical segment obclavate (Fig. 3E). Eyes large, moderately projecting, finely faceted, without interfacetal  
30 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 indistinct 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. Protrochantins 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

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

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

5  
6 *Note.* Two phoretic mites (Oribatida: Brachypilina) are present on the pro- and mesothoracic legs of the  
7 holotype (Fig. 2B: pm).

8  
9

## 10 DISCUSSION

11 *Systematic position of Protodasytes gen. nov.*

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

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

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

#### 8 *Fossil record of Melyridae*

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

22 Soft-winged flower beetles are more abundant in the Cenozoic fossil record. They are known from  
23 Eocene Baltic and Rovno ambers (Spahr 1981; Hieke & Pietrzeniuk 1984). Majer (1998) reviewed the  
24 melyrid fauna of Baltic amber, and since then several new species have been described (Kubisz 2001;  
25 Tshernyshev 2016, 2019). Two malachiine species are known from Eocene Oise amber (Kirejtshuk & Nel  
26 2008). The recent species *Attalus lusitanicus* Erichson, 1840 reported from Eocene–Oligocene Bembridge  
27 Marls is herein removed from the family and treated as Polyphaga *incertae sedis*, as it is represented by a  
28 single poorly preserved specimen lacking important diagnostic characters supporting its assignment to  
29 this particular species. Fossils described from the late Eocene Florissant Formation in Colorado are all in  
30 need of revision (Wickham 1912, 1914; Mawdsley 1999), as many are very fragmentary. *Troglops*  
31 *punctatissima* Théobald, 1935 was described from the late Oligocene of Puy-de-Dôme, France, based on  
32 only a single elytron without any informative diagnostic characters (Piton & Théobald 1935) and as such  
33 is excluded from the family and treated as Polyphaga *incertae sedis*. *Malachius vertummi* Heer, 1847  
34 from the Miocene of Oeningen, Germany (Heer 1847) is excluded from Melyridae due to the lack of

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

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

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

14 Adult soft-winged flower beetles are believed to be exclusively pollinivorous and nectarivorous. In  
15 summer, they can be collected in large numbers on the inflorescences of diverse angiosperm groups such  
16 as daisies, legumes, and mustards as well as some gymnosperms such as pines. Mawdsley (2003) listed  
17 68 genera of plants belonging to 26 families from North America visited by dasytines. Large quantities of  
18 pollen that adhere to the beetle's setose elytra and abdomen are transported between flowers during the  
19 course of normal feeding (Hawkeswood 1987). At least two Nearctic members of the phlox family  
20 Polemoniaceae depend primarily on pollination by soft-winged flower beetles (Grant & Grant 1965) and  
21 dasytines have also been demonstrated to contribute to the pollination of sunflowers in South Africa (Toit  
22 1990). The body of *Protodasytes* gen. nov. is densely setose and possesses deep grooves, which are  
23 frequently found in pollinating beetles (Cai *et al.* 2018). The occurrence of diverse monocots and eudicots  
24 at Fouras (Peyrot *et al.* 2019) suggests that like its modern relatives, *P. cretaceus* gen. et sp. nov. may  
25 have visited and pollinated early angiosperms in the Cenomanian of western Europe. Further specimens  
26 associated with pollen would be required to directly confirm this association. At the very least, *P.*  
27 *cretaceus* gen. et sp. nov. provides an important calibration point for the Mesozoic diversification of  
28 dasytines.

29

#### 30 **CONCLUSION**

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

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

8  
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## 22 DATA ARCHIVING STATEMENT

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

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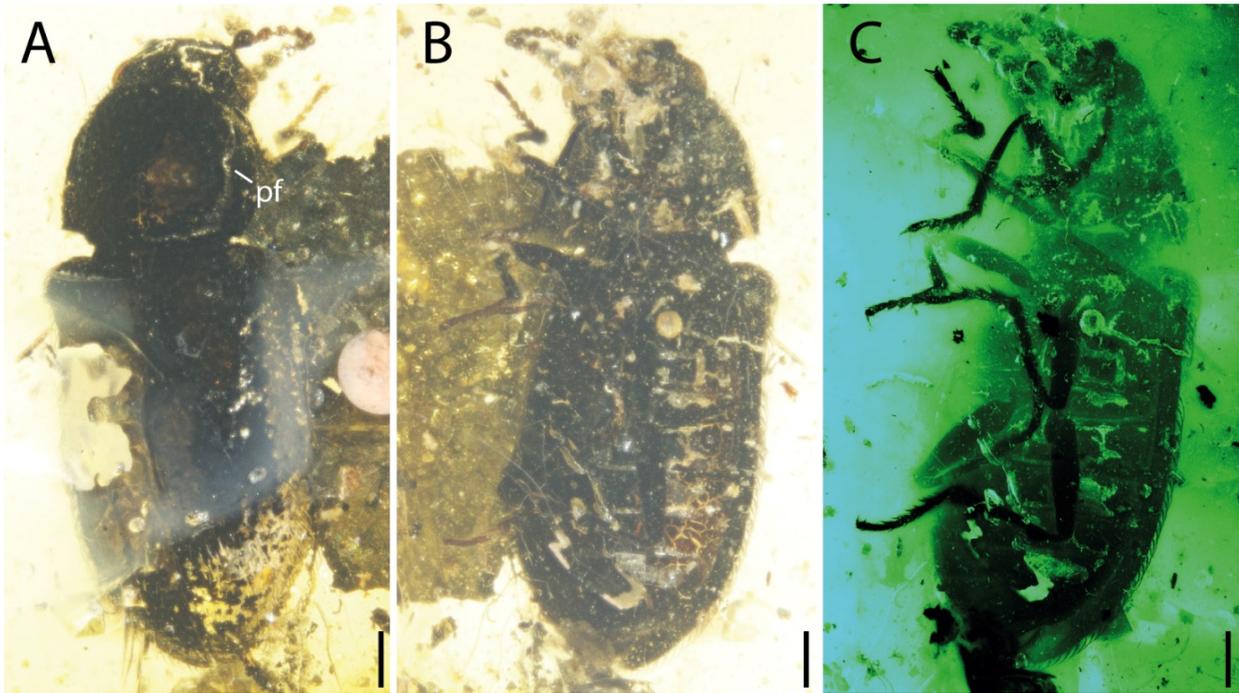
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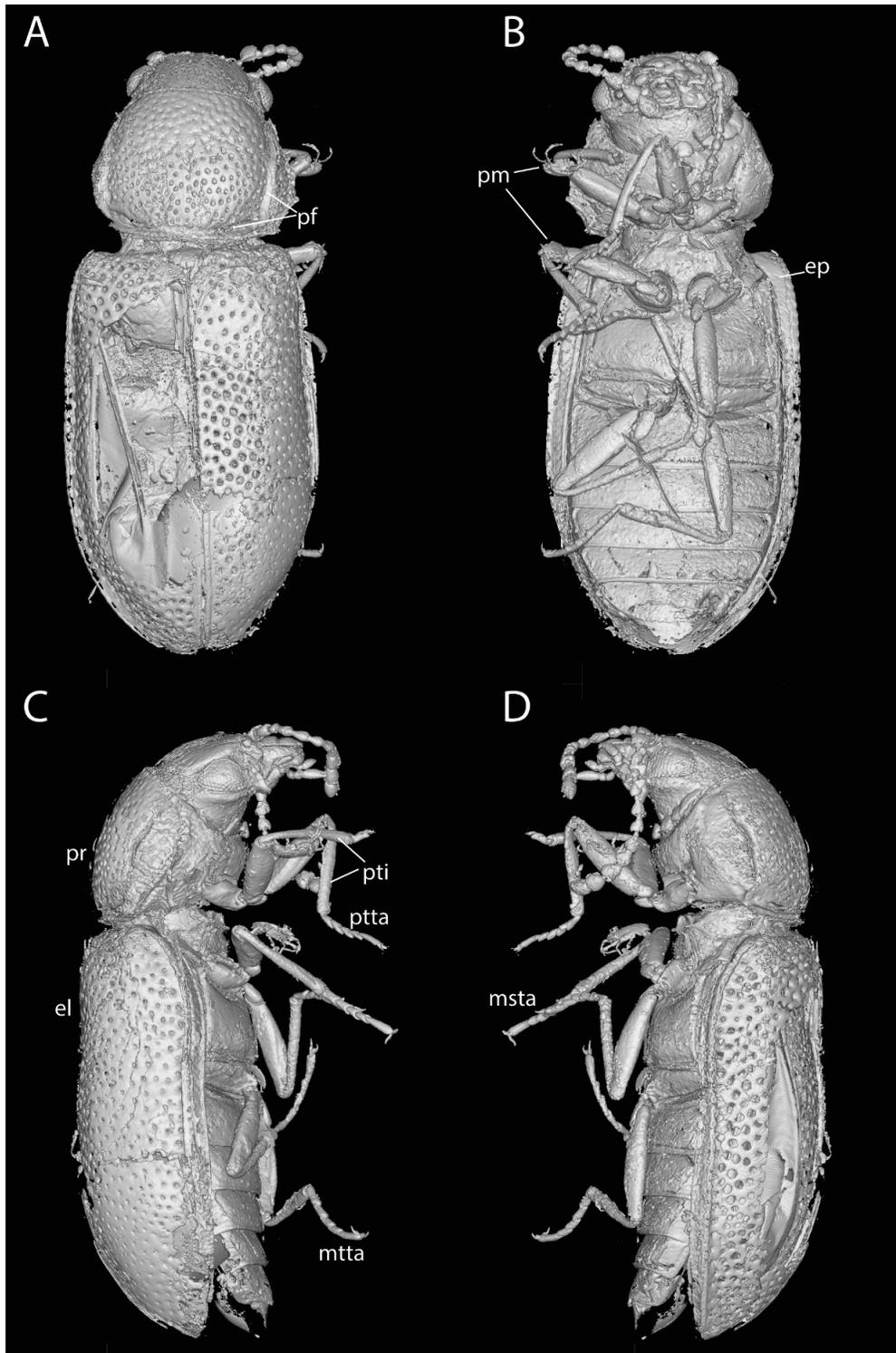


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3 FIG. 1. Habitus view of *Protodasytes cretaceus* gen. et sp. nov. (holotype, IGR.FRS-7.2). A, dorsal view  
4 under normal reflected light. B, ventral view under normal reflected light. C, ventral view under green  
5 epifluorescence. *Abbreviations*: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

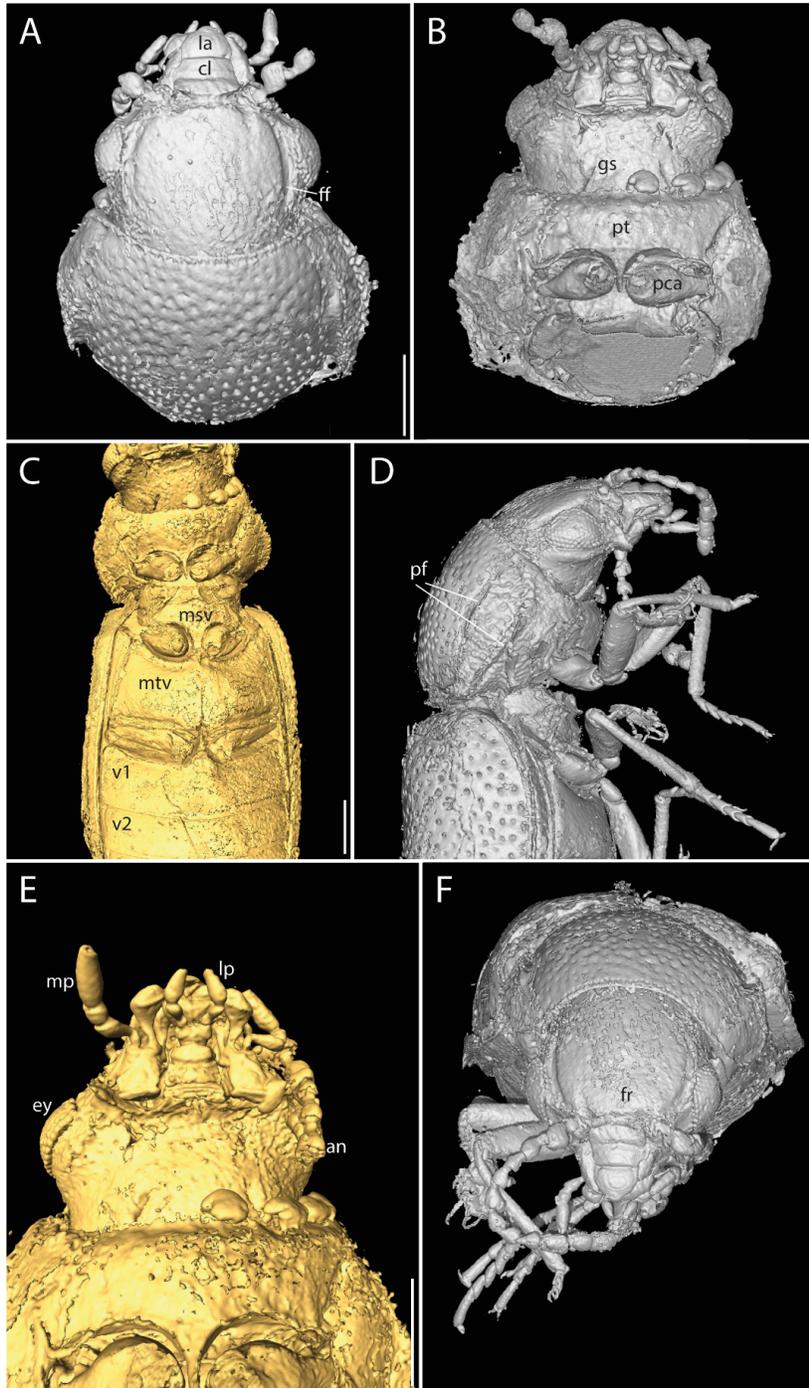
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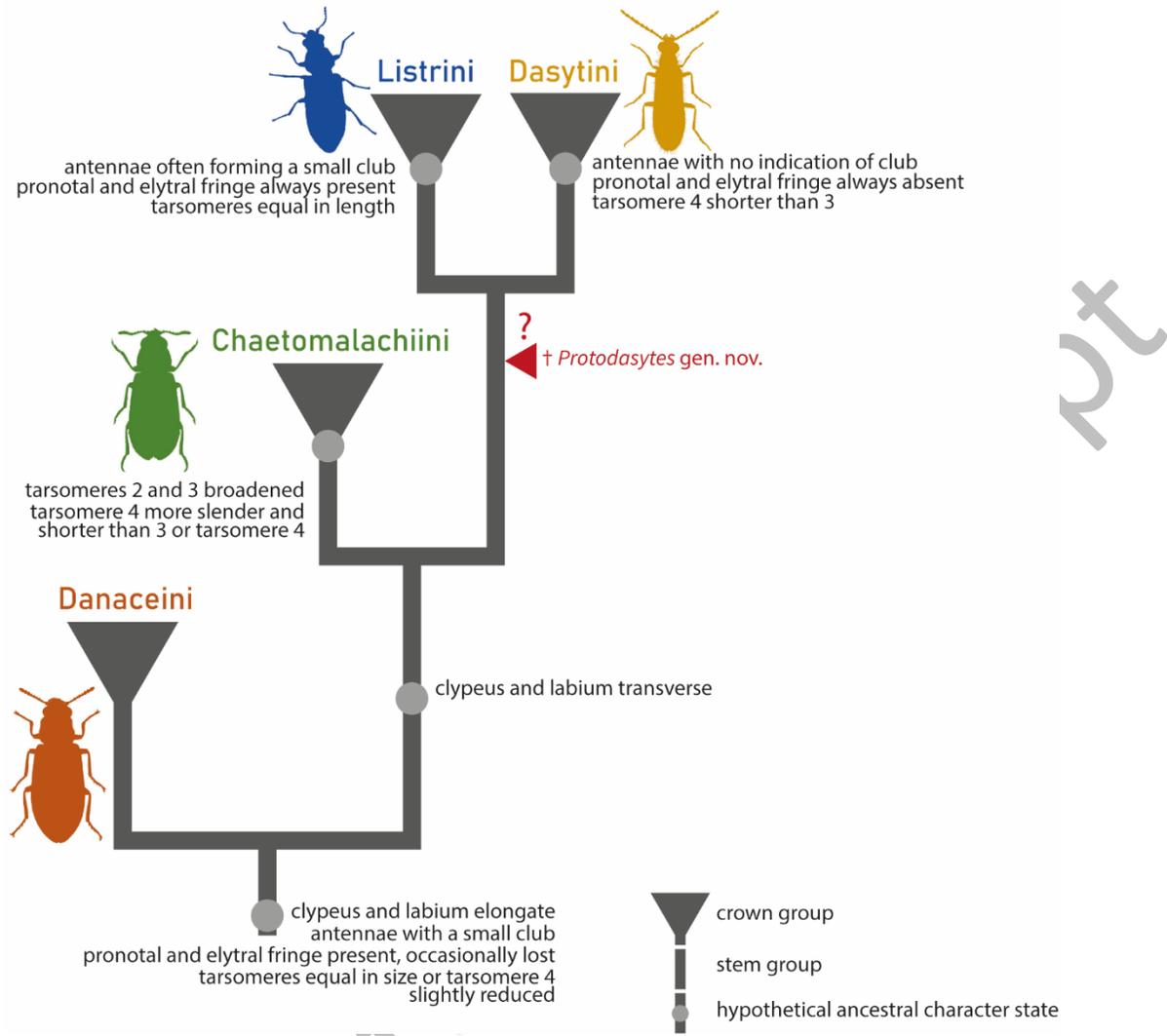
2 FIG. 2. Micro-CT reconstruction of *Protodasytes cretaceus* gen. et sp. nov. (holotype, IGR.FRS-7.2). A,  
 3 dorsal view. B, ventral view. C, D, lateral views. *Abbreviations:* el, elytra; ep, epipleura; msta, mesotarsi;  
 4 mtta, metatarsi; pf, pronotal furrows; pm, phoretic oribatid mites; pr,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



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2 FIG. 3. Enlargements of the micro-CT reconstruction of *Protodasytes cretaceus* gen. et sp. nov. (holotype,  
 3 IGR.FRS-7.2). A, head in dorsal view. B, head in ventral view. C, thorax and base of abdomen in ventral  
 4 view. D, head and thorax in lateral view. E, head and prothorax in ventral view. F, head in frontal view.

5 *Abbreviations:* an, antenna; cl, clypeus; ey, eye; ff, frontal furrow; fr, frons; gs, gular sutures; la, labrum;  
 6 lp, labial palp; mp, maxillary palp; msv, mesoventrite; mtv, metaventrite; pca, procoxa; pf, pronotal  
 7 furrow; pt, prothorax; v1–2, ventrites 1–2. Scale bars represent 200  $\mu$ m.



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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
<i>Sinomelyris praedecessor</i> Kolibáč and Huang, 2019	Melyrinae	<i>incertae sedis</i>	Daohugou Beds, Haifanggou Formation, northeast China	<b>JURASSIC</b> Callovian
<i>Acanthocnemoides sukatshevae</i> Zherikhin, 1977	Dasytinae	Danaceini	Taimyr amber, Taimyr Peninsula, Begichev Formation, Far North Russia	<b>CRETACEOUS</b> Albian
<i>Protodasytes cretaceus</i> Tihelka, Huang, Perrichot and Cai <b>gen. et sp. nov.</b>	Dasytinae	<i>incertae sedis</i>	Charentese amber, Fouras Peninsula, southwestern France	Cenomanian
<i>Colotes constantini</i> Kirejtshuk and Nel, 2008	Malachiinae	Colotini	Oise amber, Le Quesnoy, northern France	<b>EOCENE</b> 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 perkovskyi</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>Eudasytites listriiformis</i> Wickham, 1912	Dasytinae	<i>incertae sedis</i>	Florissant Formation, Colorado, USA	Priabonian
<i>Eutrichopleurus miocenus</i> Wickham, 1912	Dasytinae	Listrini	Florissant Formation, Colorado, USA	Priabonian

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