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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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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 began 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 vertumnmi 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 angiosperms is discussed.

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

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

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

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

Elytra 1.70 mm long, 1.7 times as long as their combined width, as wide as pronotum at its broadest point, parallel-sided, gradually narrowing in the posterior half, completely covering abdomen. 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 Amauronioidini 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 cretaceous* 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. cretaceous* 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.

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**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.

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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; mtt, metatarsi; pf, pronotal furrows; pm, phoretic oribatid mites; pr, pronotum; pti, protibiae; ptt, protarsi. Scale bar represents 500 μm.

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

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<td>Melyrinae</td>
<td>incertae sedis</td>
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<td>JURASSIC Callovian</td>
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<td><strong>Acanthocnemoides sukatshevae</strong> Zherikhin, 1977</td>
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<td><strong>Protodasytes cretaceus</strong> Tihelka, Huang, Perrichot and Cai <em>gen. et sp. nov.</em></td>
<td>Dasytinae</td>
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<td><strong>Colotes constantini</strong> Kirejtshuk and Nel, 2008</td>
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<td><strong>Colotes impexus</strong> Kirejtshuk and Nel, 2008</td>
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