Systematic
Entomology

Systematic Entomology (2021), **46**, 422–452 DOI: 10.1111/syen.12469

Diversification of myrmecophilous Clavigeritae beetles (Coleoptera: Staphylinidae: Pselaphinae) and their radiation in New Caledonia

PETER HLAVÁČ[1], JOSEPH PARKER[2], MUNETOSHI MARUYAMA[3] and MARTIN FIKÁČEK[1,4,5]

[1]Department of Entomology, National Museum, Natural History Museum, Prague, The Czech Republic, [2]Division of Biology and Biological Engineering, California Institute of Technology, Pasadena, CA, U.S.A., [3]The Kyushu University Museum, Fukuoka, Japan, [4]Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung, Taiwan and [5]Department of Zoology, Faculty of Science, Charles University, The Czech Republic

Abstract. Clavigeritae (Coleoptera: Staphylinidae: Pselaphinae) comprise a supertribe of specialized myrmecophile rove beetles that display numerous behavioural, chemical and anatomical modifications associated with a socially parasitic lifestyle. Due to the extreme morphological diversity of clavigerites, their systematic relationships, patterns of character evolution and host ant use have been challenging to infer. Here, we resolve deep divergences within Clavigeritae by assembling a molecular dataset encompassing the breadth of tribal diversity. We classify Clavigeritae into six tribes: extinct Protoclavigerini, and recent Tiracerini, Mastigerini sensu nov., Clavigerini sensu nov., Lunillini sensu nov. and Disarthricerini stat. nov. The previously recognized subtribes Clavigerodina, Apoderigerina, Dimerometopina, Hoplitoxenina, Miroclavigerina, Theocerina and Thysdarina are demonstrated as polyphyletic or highly derived internal clades of Clavigerini and are hereby synonymized with the latter. *Colilodion* – a highly enigmatic taxon proposed to be the earliest-branching lineage of recent Clavigeritae – is revealed to be unrelated to Clavigeritae and is transferred to Pselaphitae. We provide a systematic treatment of newly-discovered endemic genera from New Caledonia and infer their phylogenetic affinity to the Australian tribe Tiracerini. The zoogeographic distribution of early-branching Clavigeritae lineages in India and the Australian region indicates a possible Gondwanan origin of the supertribe. Extant clades diversified from the Eocene onwards, correlated with the rise of modern ants. We present evidence for island radiations of Clavigeritae in both Madagascar and New Caledonia during the Oligocene-Miocene. Using a newly-created morphological dataset, we analyse patterns of character evolution and demonstrate widespread convergence in morphology that extends to virtually all traits. Counterintuitively, however, characters postulated to be involved in beetle-ant communication are amongst the most invariant, and least convergent. The host ant spectrum of many Clavigeritae genera and species is broad, contradicting co-cladogenesis with hosts and instead implying widespread host switching. We speculate whether morphological variability in Clavigeritae is truly adaptive, as opposed to the product of 'morphological drift' of body parts under weak selection inside ant colonies, in species with potentially very small effective population sizes.

Correspondence: Martin Fikáček, Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung, Taiwan. E-mail: mfikacek@gmail.com

Introduction

Pselaphine rove beetles (Coleoptera: Staphylinidae) comprise a clade of ∼10 000 species of minute (1–5 mm), predatory, litter dwelling beetles (Park, 1942; Chandler, 2001; Parker, 2016a, 2016b). Within this speciose subfamily, a pervasive evolutionary trend exists in which numerous lineages have evolved into ‘myrmecophiles’ – species that engage in symbiotic relationships with ants (Parker, 2016a). Among these symbiont clades, the supertribe Clavigeritae represents the largest radiation, with ca. 370 described species, all of which are believed to be obligately dependent on ant colonies (Kistner, 1982; Parker & Grimaldi, 2014; Parker, 2016a). Clavigerites are tightly integrated into host ant societies where they live as social parasites. The beetles are accepted by their hosts seemingly as nestmates and show numerous behavioural and chemical adaptations for this way of life. Clavigerites interact intimately with worker ants, including receiving food directly via oral trophallaxis, and being licked, groomed and carried around the nest (Kistner, 1982; Parker & Grimaldi, 2014; Parker, 2016a). Most species possess trichomes – clumps of thick setae associated with large glands (the so-called ‘Wasmann’ glands). These structures are positioned near the base of the abdomen and their secretions are highly attractive to host ants, likely promoting the beetle’s acceptance inside the nest (Park, 1932, 1942; Akre & Hill, 1973; Cammaerts, 1992; Parker & Grimaldi, 2014). Anatomically, clavigerite beetles are amongst the most specialized myrmecophiles known: the mouthparts are strongly reduced and internalized to facilitate trophallaxis (Akre & Hill, 1973; Jałoszynski *et al.*, 2020), and the body as a whole is strengthened via extensive fusions of segments. The tergites are combined into a single ‘tergal plate’, and the antennae likewise show a reduction of segments, with all modern species possessing between three and six flagellomeres. In addition to the trichomes, a diversity of smaller glandular structures decorate the integument and appendages (Cammaerts, 1974; Hill *et al.*, 1976). Some of the most anatomically extreme genera are additionally eyeless and wingless (Akre & Hill, 1973; Jałoszynski *et al.*, 2020).

Despite their fascinating biology, the evolutionary history and phylogenetic relationships of Clavigeritae remain poorly resolved. Key insights into the origin of this clade of myrmecophiles came with the recent discovery of a stem-group clavigerite, *Protoclaviger trichodens* Parker & Grimaldi, in Indian Cambay amber (ca. 52 million years old) (Parker & Grimaldi, 2014). *Protoclaviger* shares many synapomorphies with recent Clavigeritae, including trichomes and modified mouthparts that demonstrate unambiguously that it was a myrmecophile. However, *Protoclaviger* is notable in its possession of only a subset of the myrmecophilous adaptations seen in modern species: its abdominal tergites remain unfused and its antennal segments are only partially fused, bearing eight antennomeres. Its mouthparts also protrude more prominently beyond the oral cavity. *Protoclaviger* reveals that the Clavigeritae-ant symbiosis dates to at least the Early Eocene, and fossil-dated molecular trees produced in the same study indicate an even older emergence of the beetle-ant association, in the Late Cretaceous (Parker & Grimaldi, 2014). Such a scenario implies that the radiation of crown-group clavigerites correlates with – and was potentially catalysed by – the Cenozoic diversification of modern ants and their rise to ecological dominance (Barden, 2017).

Modern Clavigeritae are distributed in all zoogeographical regions except Antarctica (Newton Jr & Chandler, 1989), and their cladogenesis has been coupled to dramatic morphological divergence. In addition to being heavily modified relative to ancestral free-living pselaphines, the body plan of clavigerites is also extremely variable between species. Virtually every aspect of external anatomy is prone to radical variation, with exaggerated modifications of head, antennal, leg and dorsal abdominal morphology being common (Parker & Grimaldi, 2014). As a result, Clavigeritae are amongst the most morphologically diverse clades within Pselaphinae, and indeed Staphylinidae as a whole. Historically, this variability has obscured the systematics of these beetles and resulted in a highly fragmented tribal and generic classification: 114 genera have been described, of which 68 are monospecific (Hlaváč, personal database). These genera are classified into four tribes and 11 subtribes, but the monophyly of most of these higher taxa has never been rigorously assessed (Parker & Grimaldi, 2014). Many of these groups were created based on a limited number of characters, including features that are systematically indefensible such as the number of antennomeres – a character prone to extensive variation and convergence across the supertribe.

The monophyly and phylogenetic placement of the Clavigeritae were evaluated by Parker & Grimaldi (2014) and Parker (2016b), as well as by a reanalysis of these same data by Lü *et al.* (2020). All three studies recovered a monophyletic Clavigeritae that was most closely related to Arhytodini and Pselaphini – two pselaphine tribes currently placed in the supertribe Pselaphitae. However, outgroup sampling was limited in these analyses, precluding resolution of Clavigeritae’s definitive sister group. Through morphological cladistic analysis, Parker & Grimaldi (2014) further resolved *Protoclaviger* as sister group to all extant Clavigeritae including the tribe Colilodionini. This latter tribe was erected for the single genus *Colilodion* Besuchet (Besuchet, 1991) – a taxon that appears to combine certain characters of both Pselaphitae and Clavigeritae. Prior to the discovery of *Protoclaviger*, *Colilodion* had been proposed as the sister group of the remaining Clavigeritae (Besuchet, 1991). Parker & Grimaldi (2014) questioned this proposal, suggesting a position either outside of Clavigeritae, or as a highly modified lineage within this supertribe that bears some secondary character state reversals to a more pselaphite-like morphology. The authors emphasized the need for a molecular resolution to the true phylogenetic affinity of *Colilodion*, pending collection of new specimens of this exceptionally rare genus.

Due to limited taxon sampling by Parker & Grimaldi (2014), the internal topology of Clavigeritae was not fully resolved, but certain findings nevertheless emerged. These included strong evidence for a monophyletic radiation of clavigerites in Madagascar – an island containing an extremely high diversity of members of this supertribe, with 29 endemic genera (Hlaváč, personal database). Second, the genus *Tiracerus* Besuchet – at that time the only genus within the tribe Tiracerini, was found to be sister to all other Recent Clavigeritae. Notably, Besuchet (1991) alluded to the existence of potentially multiple genera from New Caledonia that share characters with the Australia-endemic *Tiracerus*, implying an unchartered component to the diversity of Clavigeritae that is relevant for resolving the supertribe's early cladogenesis.

In the present contribution, we build on the findings of Parker & Grimaldi (2014) to address some key outstanding challenges in the systematics of Clavigeritae. Focusing primarily on early-branching relationships within the supertribe, we evaluate the phylogenetic position of the enigmatic *Colilodion*, and have accumulated extensive New Caledonian material, including multiple new genera that show affinities with the early-diverging tribe Tiracerini. We describe these critical taxa and place them molecularly in the Clavigeritae tree. In addition to providing molecular resolution of early Clavigeritae relationships, we present a newly-created morphological dataset for the Clavigeritae as a whole. These morphological data enable us to demonstrate empirically the challenges of using morphological characters for exploring systematic relationships in this phenotypically extreme group of insects. The new dataset has also permitted us to investigate patterns of character evolution and convergence across the clade with respect to different parts of the body. Finally, we also summarize the known data about host ant specificity of Clavigeritae, leading us to hypothesize how clavigerites may have host-switched so frequently during their evolutionary history.

Historical classification and zoogeography of Clavigeritae

Due to the diverse morphology of Clavigeritae, the higher classification has often changed rapidly upon discovery of new taxa (see File S1, Supporting information). The first representative of the group was found by J. D. Preyssler in an ant colony under a stone in Prague (Czech Republic) in 1788 – the first documented discovery of a myrmecophilous beetle. Two years later, Preyssler (1790) described it as *Claviger testaceus*. Leach (1815) first introduced *Claviger* in the system of Coleoptera: he placed it as the tribe 'Clavigerides' in the family 'Phalacrurida', together with the tribe 'Pselaphides'. Dalman (1826) described the second member of the group, *Articerus armatus* from Quaternary copal from Tanzania; both *Claviger* and *Articerus* were treated as 'Clavigerines' in Pselaphinae by Aubé (1833). Hope (1836) was the first to give Clavigeridae family status, which was followed by Saulcy (1874), Reitter (1882, 1885) and other authors until the end of the 19th century.

Schaufuss (1872, 1890) attempted the first internal classification of clavigerines, establishing five tribes: Adranini, Articerini, Clavigerini, Clavigerodini and Clavigeropsini. His classification was ignored by Raffray (1904a, 1904b, 1905a, 1905b) in his *Catalogue et Genera des Psélaphides* in which he recognized 41 genera of clavigerines and included them in Pselaphidae. Jeannel (1949), also ignoring Schaufuss's classification, established a new tribal system with four tribes: Clavigerini, Disarthricerini, Fustigerini and Miroclavigerini. Later, based on his study of clavigerines from Madagascar, Jeannel (1954) found this subdivision unsatisfactory and proposed a new tribal system with 12 tribes. Subsequently, he subdivided the largest tribe, Fustigerini, into five groups (Jeannel, 1959). Célis (1969, 1970) used Jeannel's system for his studies of material from Africa and Madagascar, based on which he added three additional tribes (Lunillini, Hoplitoxenini and Neoceratopsini) and established two subtribes of Neocerini (Neocerina and Theocerina). Besuchet (1986) created a new tribe, Tiracerini, for the Australian genus *Tiracerus* which included all Australian species previously classified in *Articerus*.

The discovery of the morphologically aberrant genus *Colilodion* caused a sudden revolution in the classification of the group and led Besuchet (1991) to reclassify the whole clade into three tribes: the speciose Clavigerini, monogeneric Australian Tiracerini and the monogeneric Colilodionini. All remaining tribes were downgraded to subtribes of Clavigerini, some of which were later synonymized (Besuchet, 2008; Hlaváč, 2011; Hlaváč *et al.*, 2013; Hlaváč & Nakládal, 2016). Newton Jr. & Thayer (1995) demonstrated that pselaphines are a clade within the rove beetles (Staphylinidae) and reduced them from family to subfamily rank. Correspondingly, the rank of the clavigerines changed to the supertribe Clavigeritae, in order not to alter the internal classification proposed by Besuchet (1991) and subsequent authors. Parker & Grimaldi (2014) added the extinct tribe Protoclavigerini, established for the Early Eocene fossil genus *Protoclaviger*, considered to be the sister taxon to all extant Clavigeritae. Hence, four tribes are currently recognized, and Clavigerini is divided into 11 subtribes, the validity of some of which is questionable (Parker & Grimaldi, 2014). One subtribe in particular, Clavigerodina, is highly problematic, being a dumping ground for taxa that resist easy assignment to other subtribes.

Zoogeographically, Clavigeritae occur globally except for the polar areas but are absent from all Atlantic and many Indian and Pacific islands, including New Zealand (see File S15 for details). They are present in La Réunion (Célis, 1974), Seychelles (Hlaváč & Nakládal, 2018) and Fiji and Vanuatu (Besuchet & Hlaváč, 2011). The highest species diversity is known from sub-Saharan Africa (39 genera, 87 species and subspecies) and Madagascar (37 genera, 74 species). The Palaearctic region hosts nine genera and 61 species, but the real diversity may be lower, because many species of *Claviger* and *Diartiger* Sharp require revision. The Australian fauna consists of 12 genera and 67 species but also requires a thorough revision. The Oriental region hosts 19 genera and 43 species. Central and Southern America hosts only two genera and 32 species, while North America is the most species-poor region with two genera and eight species. The reported local diversity strongly corresponds to the sampling effort and taxonomic activity in each region, and the supertribe's true diversity is likely much higher, especially in tropical areas. Additionally, a large number of undescribed species have amassed in museum collections, in particular from the Neotropical, Oriental and Australian regions.

Material and methods

Data used for the analyses

Molecular data. We adopted the data from Parker & Grimaldi (2014), which includes 34 representatives of the Clavigeritae, and added five newly sequenced taxa: the genus *Colilodion* as a contentious early-branching member of the Clavigeritae (Besuchet, 1991), and four of five new genera that are endemic to New Caledonia; these are formally described in the Systematic Part below. The molecular dataset includes representatives of all currently recognized extant tribes and subtribes of Clavigeritae except Disarthricerina and Lunillina. Laboratory protocols for these new sequences follow those of Parker & Grimaldi (2014). Of the outgroup taxa, we kept the members of Pselaphitae used by Parker & Grimaldi (2014) (i.e. *Caccoplectus* Sharp and *Rhytus* Westwood for Arhytodini, *Curculionellus* Westwood and *Pselaphogenius* Reitter for Pselaphini), but reduced the number of the nonmacrosceline groups as their sequences were nontrivial to align with the Clavigeritae data. Ultimately, we kept only *Lasinus* Sharp, *Bryaxis* Kugelann and *Faronus* Aubé as more distant outrgroups from the original dataset and added *Dasycerus* Brongniart (Staphylinidae: Dasycerinae) as the taxon rooting the tree. Data were edited and aligned in Geneious (Biomatters Limited, New Zealand) using a combination of MUSCLE (Edgar, 2004) and Geneious algorithms and translational alignment in the case of protein-coding genes. In most cases, Clavigeritae + Arhytodini + Pselaphini were aligned first, and the more distant outgroups were added in a subsequent step. In all ribosomal genes, many hard-to-align and hypervariable regions were present; these were removed from the final dataset and only the fragments with reliable alignments were kept for the analysis. The final dataset for 47 taxa consists of 3719 bp of two mitochondrial (cytochrome oxidase I, *cox1*, 827 bp; 16S rDNA, 485 bp) and three nuclear fragments (18S rDNA, 1349 bp; 28S rDNA, 536 bp; wingless, *wg*, 522 bp). The list of GenBank accession numbers for all sequences used is listed in File S2. The final DNA dataset in FASTA format is available in File S3.

Morphological data. We prepared a dataset of 82 morphological characters coded for 40 taxa of Clavigeritae including *Colilodion* and the Eocene fossil *Protoclaviger trichodens*, as well as 14 non-clavigerine taxa; *Dasycerus* was included to root the tree. The dataset was newly built to examine morphological diversity within Clavigeritae, and thus does not overlap with that of Parker & Grimaldi (2014) which was designed solely for evaluating the placement of *Protoclaviger*. Taxon selection aimed to include representatives of all clavigerinae tribes and subtribes, and to be compatible with the molecular dataset that was acquired independently. We coded 23 characters from the head + antennae, 30 thoracic characters, 20 abdominal characters including male genitalia, and 9 leg characters. In some taxa, certain characters could not be examined due to absence of males or the inaccessibility of characters in the fossil; all these cases are coded as ‘?’. The final morphology matrix in TNT format is available in File S4. Morphological terminology follows Chandler (2001), except in the use of ‘ventrite’ instead of ‘sternite’ when discussing thoracic structures. Specimens were examined with a Leica S8APO stereomicroscope with diffuse lighting at magnifications up to 128×. Habitus images were taken with a Canon EOS 5D in combination with a Canon MP-E65 1–5× macro lens. Resulting images are focus stacks, aligned and stacked with Zerene Stacker and then postprocessed in Adobe Photoshop. Electron micrographs were taken from gold-coated samples using a JEOL 6380 LV scanning electron microscope. Specimens examined for the morphology matrix are from the collection of the first and second authors.

Combined datasets. Combined DNA + morphology datasets were used for analyses combining both data sources, those testing the position of the taxa without DNA data, and for measuring the fit of morphological data on the molecular tree. In some genera, the species included in the molecular and morphological datasets were not identical but were combined since the characters used are assumed to be invariable within the genus. See File S5 for information regarding which species were used for the combined dataset.

Morphological characters used for phylogenetic analyses

1. Head capsule divided by occipital carina or constriction into larger anterior part and smaller posterior neck region which is more less retracted into prothorax: (0) yes; (1) no.
2. Head capsule divided by: (0) occipital carina; (1) by occipital constriction.
3. Anterior part of head: (0) short, less than 1.5 times as long as wide; (1) long, at least 1.5 times as long as wide.
4. Head, frontal fovea: (0) present; (1) absent.
5. Head, vertexal foveae: (0) present; (1) absent.
6. Head, size of clypeus: (0) relatively small, not or hardly visible dorsally; (1) well-developed, projecting ahead, well visible dorsally.
7. Head, frontal rostrum: (0) pointed anteriorly; (1) anterior margin straight or rounded, sometimes slightly bilobed.
8. Head, length of temples: (0) clearly shorter than frontal rostrum; (1) as long as frontal rostrum, that is eyes situated at midpoint along sides of head; (2) clearly longer than frontal rostrum.
9. Head, eyes: (0) present; (1) absent.
10. Head, form of eyes: (0) simple, approximately round, ovoid or of a shallow-crescent shape, never bisected by a genal protrusion; (1) bisected by genal protrusion and divided into dorsal and ventral parts.
11. Head, neck region: (0) partly visible dorsally; (1) completely retracted into pronotum.
12. Head, buccal cavity: (0) large and transverse, on each side with oval, well-defined lateral cavities for the accommodation of maxillary palpi; (1) smaller and oval, lateral cavities for the accommodation of maxillary palpi absent. A large, transverse buccal cavity with lateral cells to accommodate maxillary palpi is characteristic of most Clavigerini, whereas a smaller, oval buccal cavity lacking lateral cells is

characteristic of Tiracerini, including the newly described genera from New Caledonia.

13. Head venter, surface: (0) smooth, lacking any sculpture; (1) at least partly with fine well-defined sculpture; (2) at least partly with coarse sculpture.
14. Head venter, posterior tentorial pits: (0) completely absent; (1) present but very shallow; (2) well-defined, very often joined into one depression of various shapes. The ventral head almost always exhibits two tentorial pits (Besuchet, 1991: 510) but these are sometimes shallow, and in *Semiclaviger* they are absent.
15. Head venter, posterior tentorial pits: (0) separated; (1) fused, confluent to one large fovea.
16. Head venter, maxillary palpus: (0) small to large, exposed outside of buccal cavity; (1) scarcely visible, largely recessed inside buccal cavity.
17. Head venter, mandibles: (0) not recessed in buccal cavity, at least half of the mandibular length exposed; (1) recessed in buccal cavity.
18. Antennae: (0) with more than six antennomeres; (1) with four to six antennomeres; (2) with three antennomeres. In contrast to the hypotheses by Jeannel (1954), the antennae of Clavigeritae always have with three to six antennomeres, with scape and pedicel always present although hidden under the dorsal shelf of the antennal cavity and hence not visible in dorsal view.
19. Antenna, scape: (0) about as long as or longer than pedicel; (1) minuscule, much shorter than pedicel.
20. Antenna, apex of terminal antennomere: (0) rounded or acute; (1) truncate, with concentric short setae.
21. Antenna, terminal antennomere: (0) clearly shorter than penultimate antennomere; (1) about as long as penultimate antennomere; (2) longest, but maximum twice as long as penultimate antennomere; (3) clearly longest, at least three times as long as penultimate antennomere.
22. Antenna, terminal antennomere: (0) parallel sided, quadratic, rectangular or cylindrical; (1) extended apically, sometimes longly curved; (2) clearly tapering (attenuated) apically.
23. Pronotum: (0) lacking squamous setae; (1) with squamous setae.
24. Pronotum, longitudinal carinae: (0) present; (1) absent.
25. Pronotum, median antebasal fovea: (0) present [sometimes very shallow]; (1) absent.
26. Pronotum, lateral foveae: (0) present; (1) absent.
27. Pronotum, transversal antebasal sulcus connecting median and lateral foveae: (0) present; (1) absent.
28. Pronotum, median longitudinal sulcus: (0) present; (1) absent.
29. Pronotum, lateral margins in posterior half of pronotal length: (0) parallel or convergent; (1) clearly divergent.
30. Pronotum, lateral margins: (0) rounded; (1) ridged at least at part of pronotum length, pronotum separated from prothorax.
31. Prosternum, hypomerae: (0) fused with median part of prosternum; (1) separated from median part of prosternum by hypomeral carinae or stria.
32. Mesoventrite, median carina(e): (0) absent; (1) with one median carina; (2) with more carinae.
33. Mesotrochanter: (0) short, dorsal face of proximal femur nearly touching mesocoxa; (1) much longer, mesofemur and mesocoxa widely separated.
34. Mesocoxae: (0) largely separated, isthmus at least as wide as half the diameter of mesocoxal cavity; (1) narrowly separated, isthmus clearly narrower than half of diameter of mesocoxal cavity; (2) contiguous.
35. Metaventral posterior proces: (0) narrow, sometimes projecting backwards; (1) wide, truncate, convex or concave
36. Metaventrite, surface of metaventrite: (0) flat or convex; (1) with median depression or large fovea.
37. Metaventrite, disc of metaventrite: (0) glabrous or with normal setae; (1) with patch of trichome-like macrosetae.
38. Metaventrite, metaventral horn-like projection: (0) absent; (1) present.
39. Elytron, surface: (0) smooth, lacking any puncturation or sculpture; (1) with fine microsculpture or sparse puncturation; (2) with coarse sculpture at least in anterior half. *Cerylambus* has elytra with all those structures and is coded as 2.
40. Elytron, surface: (0) lacking parallel carinae or striae; (1) with some parallel carinae or striae.
41. Elytron, basal fovea(e): (0) present; (1) absent.
42. Elytron, sutural stria: (0) present; (1) absent.
43. Elytron, discal stria(e) or carina(e): (0) present; (1) absent.
44. Elytron, lateral portion of elytra: (0) round, lacking longitudinal marginal carina; (1) with well-defined marginal carina going from humerus to some length of elytron
45. Elytron, posterolateral corner of elytron: (0) round, rectangular or sharp but lacking any projection; (1) with sharp projection.
46. Elytron, posterior margin: (0) lacking channel-like grooves; (1) with set of small channel-like grooves. Channel-like grooves may conduct substances from the trichomes onto elytra, and are present in *Theocerus* and *Antalaha*.
47. Elytron, setae: (0) not arranged in parallel lines or absent; (1) arranged in parallel lines.
48. Elytron, humeri: (0) rounded or evanescent, always lacking spine; (1) with angled humeral callosity, with or without humeral spine.
49. Elytron, humeral prominent projection: (0) present; (1) absent.
50. Ratio of maximum elytral width/maximum pronotal width: (0) less than 1.4; (1) more than 1.5.
51. Abdomen venter, first visible sternite (III): (0) shorter than IV; (1) as long as IV; (2) longer than IV.
52. Abdomen venter, second visible sternite (IV): (0) shorter than V; (1) as long or at most 1.5 times as long as V; (2) at least twice as long as V.
53. Abdomen venter, basal margin of second visible sternite (IV): (0) simple, lacking depressions or foveae; (1) with basal lateral depressions or foveae.
54. Abdomen venter, basal median carina(e) on second visible sternite (IV): (0) present; (1) absent.

55. Abdomen venter, basolateral fovea(e) or pit (in *Thysdarius* located more far from basal margin) on second visible sternite (IV): (0) absent; (1) with one fovea or pit on each side; (2) with two foveae or pits on each side.
56. Abdominal tergites IV–VI: (0) separated; (1) fused together to form composite tergite.
57. Abdomen, composite tergite (tergites IV–VI fused): (0) simple, at base flat, slightly convex or depressed; (1) with quadratic, rectangular or triangular well-defined basal depression; (2) with pair of keels bearing trichomes dividing it into three sectors; (3) with short keels and channels.
58. Abdomen, paratergites: (0) present; (1) absent.
59. Abdomen, posterior part of composite tergite: (0) lacking long macrosetae; (1) with long, stout macrosetae.
60. Trichomes on head: (0) absent; (1) present.
61. Trichomes on pronotum: (0) absent; (1) present.
62. Trichomes on sutural half of posterior elytral margin: (0) absent; (1) present.
63. Trichomes on posterolateral corner of elytra: (0) absent; (1) present.
64. Trichomes on at least first visible paratergite: (0) absent; (1) present.
65. Trichomes on composite tergite: (0) absent; (1) present.
66. Legs, tarsi: (0) with two tarsal claws; (1) with single claw.
67. Legs, tarsomere II: (0) clearly shorter than tarsomere I; (1) clearly longer than tarsomere I; (2) about as long as tarsomere I.
68. Legs, tarsomere III: (0) simple, lacking any projection or lamella; (1) with well-developed lamella on bottom side of tarsomere III.
69. Male sexual characters on fore legs: (0) absent; (1) present.
70. Male sexual character on mid leg: (0) absent; (1) present.
71. Male sexual characters on hind leg: (0) absent; (1) present.
72. Legs, spine(s) or spur(s) on trochanters in males: (0) absent; (1) present.
73. Legs, spine(s) or spur(s) on femora in males: (0) absent; (1) present.
74. Legs, spine(s) or spur(s) on tibiae in males: (0) absent; (1) present.
75. Aedeagus, median lobe: (0) symmetric or nearly so (in *Pseudacerus* and *Clavister* the apical lobe is slightly asymmetric); (1) clearly asymmetric. Virtually all Clavigeritae have a symmetric aedeagus; very exceptionally some species exhibit a slight asymmetry of the apical lobe (*Pseudacerus*, *Clavister*). A strongly asymmetric aedeagus is only present in two of the five New Caledonian Tiracerini genera described herein.
76. Aedeagus, basal part: (0) bulbous; (1) not bulbous.
77. Aedeagus, separation of apical and basal part: (0) well-separated; (1) not separated, fused together.
78. Aedeagus, length of basal part: (0) as long as apical lobe; (1) longer than apical lobe; (2) shorter than apical lobe.
79. Aedeagus, apex of apical lobe: (0) simple; (1) bifurcate; (2) asymmetric with few apophyses.
80. Aedeagus, apex of apical lobe: (0) slender; (1) wide. This character is inapplicable for all known taxa from New Caledonia.
81. Aedeagus, dorsal diaphragm: (0) present; (1) absent.
82. Aedeagus, parameres: (0) present, partly fused but well-defined; (1) entirely absent, completely fused to aedeagus.

Phylogenetic analyses

Maximum parsimony analyses and character mapping. All unconstrained analyses were performed with TNT (Goloboff *et al.*, 2008) using Traditional Search with 1000 replications and a maximum of 100 trees saved per replicate. All characters were unordered and of equal weight. Standard bootstrap was calculated using 100 replicates. See below for constrained analyses to test the position of selected taxa. Morphological characters were mapped onto trees in Winclada (Nixon, 2002).

Maximum likelihood analysis. Maximum likelihood (ML) analysis was performed in IQ-Tree 1.6.10 (Nguyen *et al.*, 2015) under default settings and with 1000 ultrafast bootstrap replicates, using the best-fitting substitution models selected by PartitionFinder2 (Lanfear *et al.*, 2017). The dataset used and nexus file defining the partitions and their substitution models are available in File S6.

Bayesian analyses. All Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012). Molecular data were subdivided by gene fragments and by codon position (for protein-coding genes); we used a mixed substitution model (Ronquist *et al.*, 2012), and search consisted of two independent runs each with 4 chains and 25 million generations, sampled every 1000 generations. Convergence and sufficient effective sample size of all parameters were checked in Tracer 1.7 (Rambaut *et al.*, 2018); the first 25% of trees were removed as burn-in. For the mixed DNA + morphology analysis, morphology was defined as a single partition and analyses under the *Mk* model for morphology (Lewis, 2001) with the correction for only variable characters scored; we assumed equal state frequencies and gamma-distributed rate variation across characters. Nexus files used for DNA and DNA + morphology analyses are available in Files S7 and S8.

Evaluating position of non-DNA taxa. To test the phylogenetic position of selected taxa for which no DNA data were available, including a reanalysis of the position of *Protoclaviger trichodens*, we employed a topology-constrained analyses of morphology-only data using maximum parsimony and Bayesian inference, as introduced by Fikáček *et al.* (2020). Topology constraints followed the results of the ML analysis of molecular data. The maximum parsimony analysis was run in TNT using exhaustive search after imposing the topology constraints. Bayesian analyses were performed in MrBayes, constraining the topology by a set of partial constraints prepared in R using *createMrBayesConstraints* command in the *paleotree* library (Bapst, 2012); the analysis was run for 1 000 000 generations, and the first 25% of trees were removed as burn-in. The position of the analysed taxon in the final majority rule tree was inspected, along with posterior probabilities of the alternative placements visualized using the R script by Fikáček *et al.* (2020). Nexus files with MrBayes commands and constraints for the *Protoclaviger* analysis are available in File S9.

Molecular dating. To understand the timing of the diversification of the Clavigeritae in New Caledonia, we dated the tree in MrBayes, using three fossil calibrations adopted from Parker & Grimaldi (2014) and implemented as offset-lognormal priors (data in brackets = minimum, mean and standard deviation of the prior in nonlogarithmic scale): (i) *Protoclaviger trichodens* from Cambay amber (52 Ma) which was used to calibrate the stem or crown age of the Clavigeritae [prior = 52, 60.4, 1.8], (ii) an undescribed arhytodine fossil from Cambay amber (52 Ma) used to calibrate the stem age of *Caccoplectus* + *Rhytus* [prior = 52, 60.4, 1.8] and (iii) *Caccoplectus* from Dominican amber (20 Ma) to calibrate the divergence of *Caccoplectus* and *Rhytus* [prior = 20, 40.8, 2]. In addition, we constrained the root age (i.e. the divergence of Pselaphinae and Dasycerinae) by uniform prior with minimum of 135 Ma and maximum of 190 Ma, based on the stem age of Pselaphinae and Staphylinidae revealed by Lü *et al.* (2020). Each analysis consisted of two independent runs each with 4 chains and 25 million generations, sampled every 1000 generations; the first 25% of trees were removed as burn-in. Two alternative positions of *Protoclaviger* were revealed in the analyses: (i) as sister to all modern Clavigeritae, and hence constraining their stem age or (ii) as member of the crown Clavigeritae and hence constraining their crown age. Time tree analyses reflecting both alternative placements of *Protoclaviger* were run and the results compared. Detailed parameter settings for the analysis are available in File S10.

Morphological evolution in Clavigeritae

The extreme morphological diversity of Clavigeritae encompasses a variety of traits that have evolved convergently in two or more lineages. To evaluate the amount of convergence, we first mapped the morphological characters onto the molecular tree and inspected the reconstructed evolution of each character and its retention index (RI) using Mesquite (Maddison & Maddison, 2019). To test whether the evolution of morphological characters follows phylogeny, we performed permutation tests using the dataset containing Clavigeritae taxa only (i.e. without outgroups and *Colilodion*). We generated 1000 random trees using the birth-death model in Mesquite, mapped morphological characters onto each of these trees, and plotted their lengths (i.e. the number of character state changes required) using the core functions of R (R Core Team, 2020). The length distribution of random trees simulates phylogeny-independent evolution. This distribution was compared to the length produced by mapping character state changes of onto the morphology-based and molecular trees (the ML molecular topology was, in all cases, taken as a proxy of the real phylogeny of the group). If these actual tree lengths fall within the distribution of lengths produced by mapping character states to random trees, character evolution cannot be distinguished from a random (i.e. phylogeny-independent) pattern. Conversely, if the length of the molecular tree is shorter than the 95% left-tail percentile of the random tree distribution, then character evolution is non-random, and follows the phylogeny (at least partially). Various character sets were used for the tests: (i) all characters; (ii) all characters without the 'best-performing' ones (these were selected by their RI values, $\mathrm{RI} > 0.3$ was arbitrarily selected as a threshold; 19 characters were excluded from this dataset); (iii) characters corresponding to a particular body part (head, thorax, abdomen without genitalia, male genitalia, appendages) and (iv) characters of superficial trichomes and setation which are potentially at the interface of physical interactions between the beetle and ants. The list of the characters in each of these groups is provided in File S11.

Systematics

The aedeagus was studied using a Zeiss transmitted-light microscope at magnifications of up to 500×. The aedeagus was dissected and preserved in Euparal on a plastic card pinned together with the specimen. All drawings were made using a drawing tube. Body dimensions were measured as follows: length of head capsule = distance from the occipital constriction to the anterior margin of the frontal rostrum (an anterior part of the head extending beyond the antennal insertions and raised above the plane of the clypeus and labrum); elytral length = length of elytron along the suture; body length = combined length of the head, pronotum, elytra and abdomen. Width always refers to the maximum width of a given structure. Label data are cited verbatim. Red holotype or paratype labels were attached to the examined type specimens. The holotypes are deposited in Muséum National d'Histoire Naturelle, Paris, France (MNHN). For a list of depositories of paratypes, see File S17.

Online data deposition and registration required by International Committee on Zoological Nomenclature (ICZN)

All data used for the analyses and complete results are available in Files S1-S17. The same files were also uploaded to the Zenodo research depository (https://zenodo.org/) under http://doi.org/10.5281/zenodo.4422103. Newly generated DNA sequences were submitted to GenBank under accession numbers MW417247–MW417248, MW423303–MW423313 and MW440696–MW440698. To make the new taxa available from the date of the online publication of this paper, the paper was registered in ZooBank under the following ID: http://zoobank.org/urn:lsid:zoobank.org:pub:0EAF81B6-D9EA-48E0-BE4C-366FEDFA0110.

Results

Trees resulting from all analyses performed are available in File S12. Below, we summarize our principal new findings.

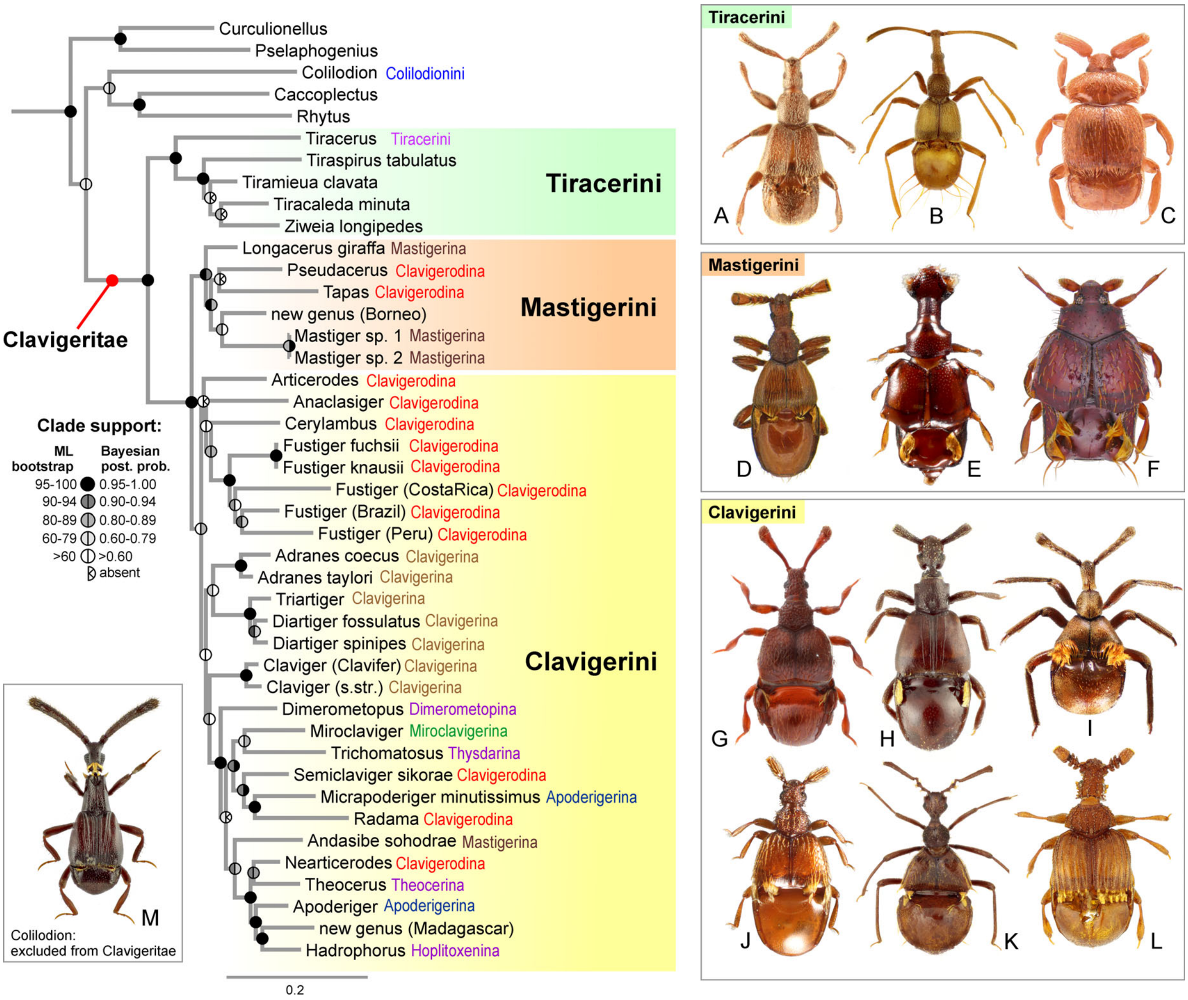

Fig. 1. Results of the maximum likelihood (ML) analysis with clade support indicated for both ML analysis and corresponding clades revealed in Bayesian analysis. Original tribal/subtribal classification is indicated in colour behind taxon names, newly proposed classification by colour shading. Habitus images illustrating the morphological diversity of each group: A, *Tiracerus fortnumi* (Hope); B, *Dzumaca monteithi* gen. & sp.n.; C, *Tiracaleda minuta* gen. & sp.n.; D, *Tapas* sp. (photo by N. Porch); E, *Longacerus giraffa* Hlaváč; F, *Pseudacerus sabahensis* Hlaváč; G, *Cerylambus thailandicus* Nomura, Sakchoowong & Idris; H, *Dimerometopus* sp.; I, *Claviger longicornis* Müller; J, *Radama* sp.; K, *Miroclaviger cervocornis* Wasmann; L, *Antalaha imerinae* Jeannel; M, *Colilodion colongi* Hlaváč. [Colour figure can be viewed at wileyonlinelibrary.com].

Monophyly of Clavigeritae

Both ML and Bayesian analyses based on DNA data revealed that all modern Clavigeritae except *Colilodion* form a strongly supported monophylum (posterior probability pp = 1.0, bootstrap b = 1) (Fig. 1). *Colilodion* is in all analyses revealed as the moderately supported sister group of arhytodine taxa (*Caccoplectus* + *Rhytus*; pp = 0.86, b = 78). The included arhytodine taxa plus *Colilodion* are revealed as sister to Clavigeritae (pp = 0.69, b = 73) and together form a strongly supported monophylum with Pselaphini (pp = 1.0, b = 100). As we argue in the Discussion section, this finding, as well as the discovery of *Protoclaviger* (Parker & Grimaldi, 2014), lead us to remove *Colilodion* from the Clavigeritae and refute the scenario proposed by Besuchet (1991) that this genus bears 'transitional' morphology between Clavigeritae and outgroup Pselaphinae.

Maximum parsimony analysis based on morphology data revealed *Colilodion* as a member of the Clavigeritae (see File S12). Bayesian analyses combining DNA and morphology data revealed *Colilodion* as sister to Clavigeritae (see File S12). Both topologies agree with the original morphology-based ideas by Besuchet (1991); however, we believe these outcomes stem from the challenge of employing morphology to resolve relationships within Clavigeritae. We refute these outcomes on the basis of the molecularly-inferred placement of *Colilodion*, as well as on the grounds of morphological evolution of certain key characters (see Discussion).

Internal topology of Clavigeritae

Three principal clades are revealed in the Clavigeritae by both ML and Bayesian DNA analyses (Fig. 1), all established as

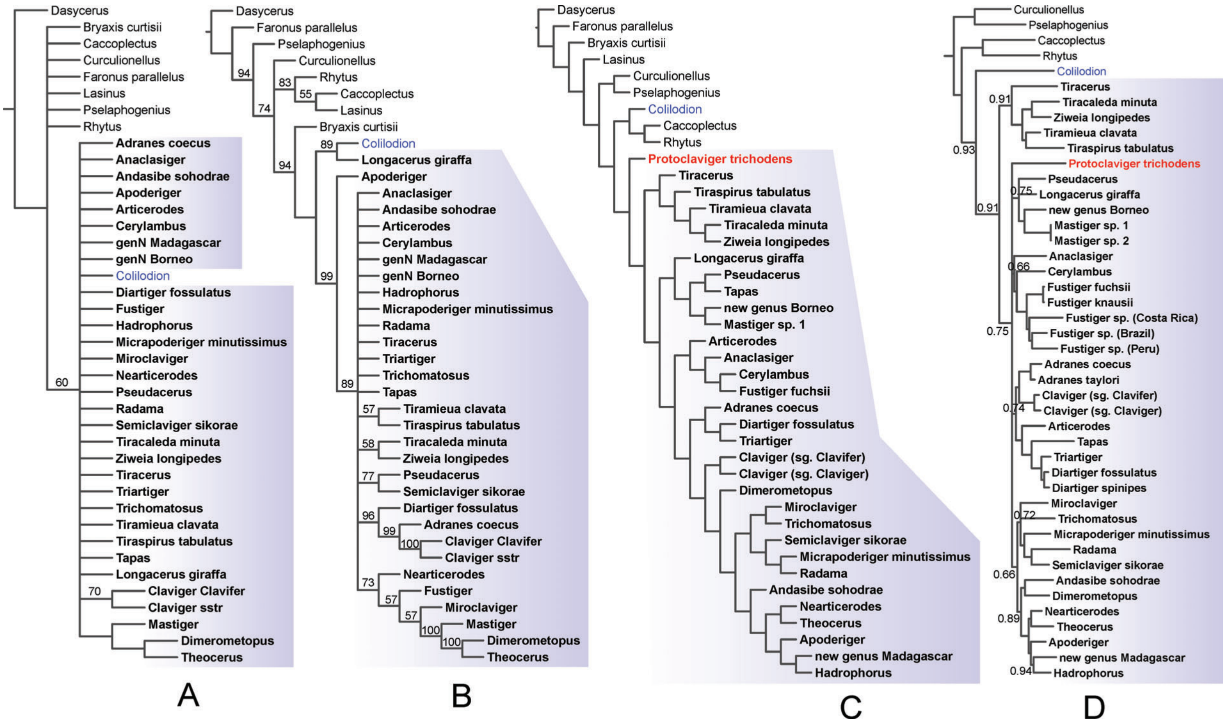

Fig. 2. Results of morphology-based maximum parsimony analyses (A–B) and of the tests of the phylogenetic position of *Protoclaviger* (C–D). A, strict consensus with bootstrap support (only values >50 indicated); B, majority rule consensus with frequency of the clades in the set of most parsimonious trees (only values >50 shown); C, morphology-only maximum parsimony analysis with constrained topology for taxa with DNA data (only *Protoclaviger* was free to move); D, unconstrained total-evidence analysis of morphology+DNA data, Bayesian inference. Blue shading = the revised concept of Clavigeritae. [Colour figure can be viewed at wileyonlinelibrary.com].

tribes in the systematic part below: (i) *Tiracerus* and the New Caledonian species which form an early branching clade with maximum support (pp = 1, b = 100); (ii) the strongly supported (pp = 0.94, b = 98) clade grouping *Longacerus* Hlaváč, *Pseudacerus* Raffray, *Tapas* Besuchet, *Mastiger* Motschulsky and an undescribed genus from Borneo and (iii) moderately to weakly supported clade (pp = 0.81, b = 49) grouping all remaining Clavigeritae. The internal topology of these clades varies among analyses but always groups all New Caledonian taxa (pp = 0.98, b = 96) and all Madagascan taxa (pp = 0.99, b = 97) and subdivides the Madagascan taxa into two large clades, one grouping *Miroclaviger* Wasmann, *Trichomatosus* Célis, *Semiclaviger* Wasmann, *Micrapoderiger* Jeannel and *Radama* Raffray (pp = 0.99, b = 93) and the other *Andasibe* Hlaváč & Baňař, *Nearticerodes* Jeannel, *Theocerus* Raffray, *Apoderiger* Wasmann and *Hadrophorus* Fairmaire (pp = 0.81, b = 75). All Neotropical species form a strongly supported clade (genus *Fustiger* LeConte, pp = 1, b = 100) sister to the Asian *Cerylambus* Newton & Chandler (pp = 0.98, b = 81). The Asian genera *Diartiger* and *Triartiger* Kubota form a strongly supported monophylum (pp = 1, b = 100) that is weakly supported as a sister group to the North American *Adranes* LeConte in the ML analysis (b = 64). The topology of the dated Bayesian analyses (Fig. 3) differ slightly from the nondated one, most importantly in placing *Tiraspirus* gen.n. as the earliest-divergent New Caledonian genus (in agreement with the ML analyses) and in grouping the North American *Adranes* with Palaearctic *Claviger*.

The morphology-based maximum parsimony analysis produced a largely unresolved topology that was wholly incongruent with the molecular trees (Fig. 2A, B). Constrained and combined analyses of modern taxa for which no DNA data are available revealed a reliable position only for *Dzumaca* gen.n. (forming a strongly supported monophylum with *Ziweia* gen.n. and *Tiracaleda* gen.n., pp = 0.95), *Novoclaviger* Wasmann (sister to *Articerodes* Raffray, pp = 0.95) and *Pararticerus* Jeannel (sister to *Articerodes*, pp = 0.96). The position of all other taxa differed between Bayesian and maximum parsimony analyses, and multiple alternative placements, each with a low probability was revealed in Bayesian topology-constrained analyses.

Position of Protoclaviger *and dating analysis*

Protoclaviger was revealed as a sister taxon to all modern Clavigeritae except *Colilodion* in the maximum parsimony analysis (b = 27) (Fig. 2C). In contrast, Bayesian analyses combining DNA + morphology and the topology-constrained ones all revealed *Protoclaviger* as a member of crown-group Clavigeritae, forming a monophylum with non-tiracerine taxa (pp = 0.8) in the combined analysis (Fig. 2D) or with Clavigerini (pp = 0.58) in the topology-constrained analysis. Mapping of alternative placements revealed a moderately high support for a placement of *Protoclaviger* as sister to Mastigerini+Clavigerini (pp = 0.68; see File S12). We consider any crown-group position of *Protoclaviger* as highly unlikely based on its many plesiomorphic character states (Parker & Grimaldi, 2014). These include antennae (eight antennomeres compared to six or fewer in all modern Clavigeritae), abdominal tergites (tergites 4–6 are unfused in *Protoclaviger* but fused in all modern Clavigeritae), maxillary palpi (protruding from oral cavity in *Protoclaviger* but barely so in modern Clavigeritae), abdominal intersegmental membranes (distinct between ventrites in *Protoclaviger*, reduced to absent in modern Clavigeritae) and antennal scape (large and dorsally visible in *Protoclaviger*, reduced and dorsally obscured by shelves of frontal rostrum in modern Clavigeritae). None of these character states is known from any modern member of Clavigeritae, indicating that the position of *Protoclaviger* as a crown clavigerite with numerous reversals is highly unlikely.

We used *Protoclaviger* to calibrate our time tree analyses, using it either as the calibration of the stem age or crown age of the Clavigeritae. The results are summarized in Table 1. The time tree in which *Protoclaviger* was placed as the sister to modern Clavigeritae (i.e. the position we consider most likely), and hence calibrating modern Clavigeritae's stem age, is illustrated in Fig. 3, while both trees are shown together in File S12. As expected, both time trees differ especially in the estimates of the stem and crown ages of the Clavigeritae: 59.1 and 40.5 Ma when *Protoclaviger* is considered as sister to modern taxa, compared to 69.6 and 59.3 Ma when *Protoclaviger* is considered as a member of the crown-group. The differences between analyses are less apparent in divergence times of internal Clavigeritae clades, which are estimated to be 5–10 Ma younger in the analysis where *Protoclaviger* is sister to modern taxa than when *Protoclaviger* is placed in the crown-group. Both analyses indicate that the New Caledonian clade of Tiracerini diverged from the Australian relatives in the Late Eocene or Early Oligocene (39.1/28.1 Ma) and started to diversify in New Caledonia in the Early Miocene (21.5/16.6 Ma). The Madagascan clade diverged from the continental relatives during the Oligocene (29.5/22.3 Ma) and started to diversify shortly after (26.7/20.1 Ma).

Table 1. Comparison of results of the time tree analyses implementing *Protoclaviger* as a calibration of stem or crown age of Clavigeritae. Mean node ages and 95% credibility intervals in million years.

Clade	*Protoclaviger* as sister to modern Clavigeritae	*Protoclaviger* as member of crown group
Clavigeritae (stem age)	59.1 (62.1–56.7)	69.6 (79.6–62.2)
Clavigeritae (crown age)	40.5 (51.8–30.1)	59.3 (62.3–56.7)
NC Tiracetini (stem age)	28.1 (39.7–17.5)	39.1 (54.5–24.7)
NC Tiracerini (crown age)	16.6 (26.7–8.2)	21.5 (34.5–10.0)
Mastigerini (stem age)	30.5 (39.8–22.2)	41.4 (52.3–31.4)
Mastogerini (crown age)	20.4 (29.8–11.9)	26.3 (38.4–15.8)
Clavigerini (stem age)	30.5 (39.8–22.2)	41.4 (52.3–31.4)
Clavigerini (crown age)	26.7 (34.8–19.5)	35.6 (46.3–27.3)
MDG Clavigerini (stem age)	22.3 (29.5–15.8)	29.5 (38.1–20.5)
MDG Clavigerini (crown age)	20.1 (27.6–14.0)	26.7 (36.1–17.9)

Evolution of morphological characters

When mapped onto the ML molecular tree, most characters show low RI values, indicating a high amount of convergent evolution and more character changes than expected under a maximum parsimony criterion. The same trend is seen when characters are grouped by body parts. Nineteen characters show RI > 30, indicating a partial correlation with the ML topology (File S13); these characters are related to head subdivision (char. 2), the form of the buccal cavity (char. 12), the position of tentorial pits (char. 15), the presence/absence of antebasal and lateral pronotal foveae (chars. 25, 26), the position of mesocoxae (char. 34), setation of the metaventrite and elytra (chars. 37, 39, 63), presence/absence of sutural stria, lateral ridges and humeral callosity on elytra (chars. 42, 44, 48), male secondary characters of legs (chars. 72, 73) and male genital characters (chars. 76, 79, 80, 81). When all morphological characters are mapped on the ML tree (Fig. 4A), the tree is significantly shorter than the length distribution of characters mapped onto random trees. However, this result is clearly driven by the 19 characters listed above: the ML tree length falls within the distribution of random trees when these characters are not considered (Fig. 4B, File S14). These findings indicate that the evolution of most morphological characters is not correlated with phylogeny and is highly convergent and hence likely driven by other factors. When body parts are compared, characters of the head, abdomen and appendages produce ML tree lengths indistinguishable from the random tree distribution (Fig. 4C, E, F). In contrast, characters of the thorax, male genitalia and likely also surface trichomes involved in beetle-ant interactions produce a shorter ML tree length than the random tree distribution (Fig. 4D, G, H), indicating a correlation with the phylogeny, although many such characters still exhibit convergent evolution in two or more lineages (compare Fig. 4I, J).

Discussion

Colilodion*: Morphological convergence in a non-clavigerine myrmecophile*

Colilodion is an Oriental genus with nine known species (Fig. 1M). Although it has never been directly collected in association with ants, it exhibits most morphological adaptations for obligate myrmecophily found in the Clavigeritae: (i) antennae with three to four antennomeres, including a hugely enlarged apical segment; (ii) strongly reduced mouthparts; (iii) fused abdominal tergites and (iv) presence of trichomes on the abdomen (as well as other parts of the body). However, Besuchet (1991) and Löbl (1994) noticed that it also bears characters typical of Pselaphitae that are absent from Clavigeritae: (i) tarsomere I short and tarsomere II elongate (both tarsomeres short in all Clavigeritae); (ii) abdominal ventrite VII visible externally (internalized in all Clavigeritae) and

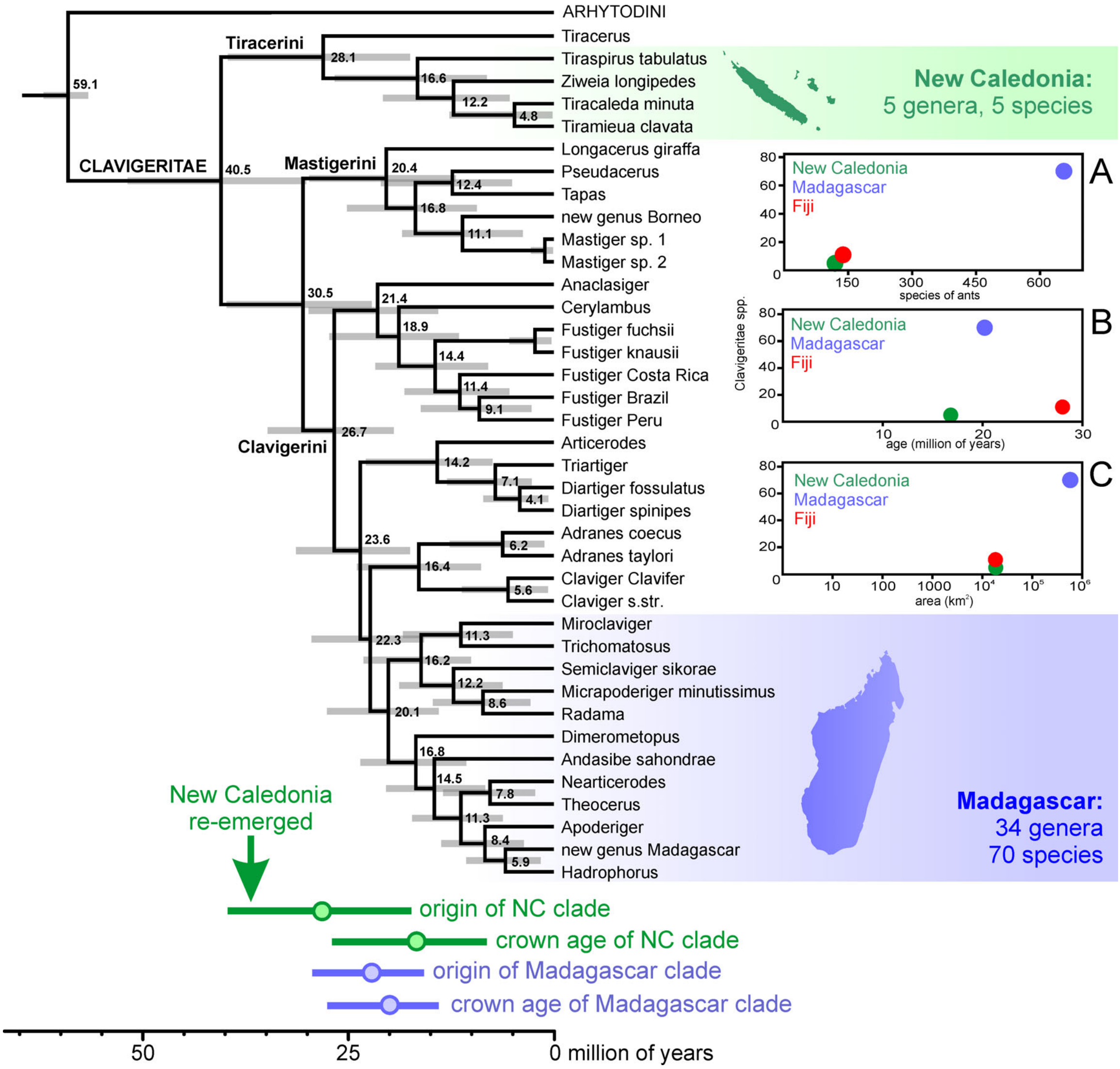

Fig. 3. Fossil-dated tree of the Clavigeritae, showing the timing of the radiation of the group in New Caledonia and Madagascar. Plots: A, relation of number of Clavigeritae species to number of ant species; B, relation of the age of the island radiation and number of Clavigeritae species; C, relation of the island(s) area in logarithmic scale and the number of Clavigeritae species. The ages of radiation for Madagascar and New Caledonia are crown age of the respective clade, for Fiji 28 Ma is used which is age of the oldest emerged part (Beatty *et al.*, 2017). [Colour figure can be viewed at wileyonlinelibrary.com].

(iii) aedeagus with distinct parameres (parameres are completely absent in all Clavigeritae). Based on *Colilodion*'s mixture of character states, Besuchet (1991) proposed that this genus represents a 'missing link' between Clavigeritae and Pselaphitae and is hence the likely sister group of the remainder of the supertribe. However, doubt was cast over this hypothesis with the discovery of *Protoclaviger* by Parker & Grimaldi (2014). This fossil taxon possesses some derived character states typical of clavigerites that are missing in *Colilodion*, including short tarsomeres I and II, and a truncate antennal apex with setose cavity. However, *Protoclaviger* otherwise exhibits a higher number of plesiomorphic states than does *Colilodion*. This led Parker & Grimaldi (2014) to consider whether *Colilodion* may be a highly modified clavigerite with some features that are convergent with Pselaphitae.

Our present molecular analysis (Fig. 1) likewise refutes Besuchet's (1991) hypothesis, but instead reveals that *Colilodion* is not a clavigerite at all: its similarities with Clavigeritae are instead due to convergence. Our molecular analysis reveals that *Colilodion* is more closely related to the genera *Caccoplectus* and *Rhytus* of the tribe Arhytodini (supertribe Pselaphitae). *Colilodion* is hence a prime example of morphological convergence in response to a similar lifestyle (assumedly myrmecophily). We therefore remove Colilodionini from Clavigeritae. However, given our limited outgroup sampling, we refrain from synonymizing Colilodionini with

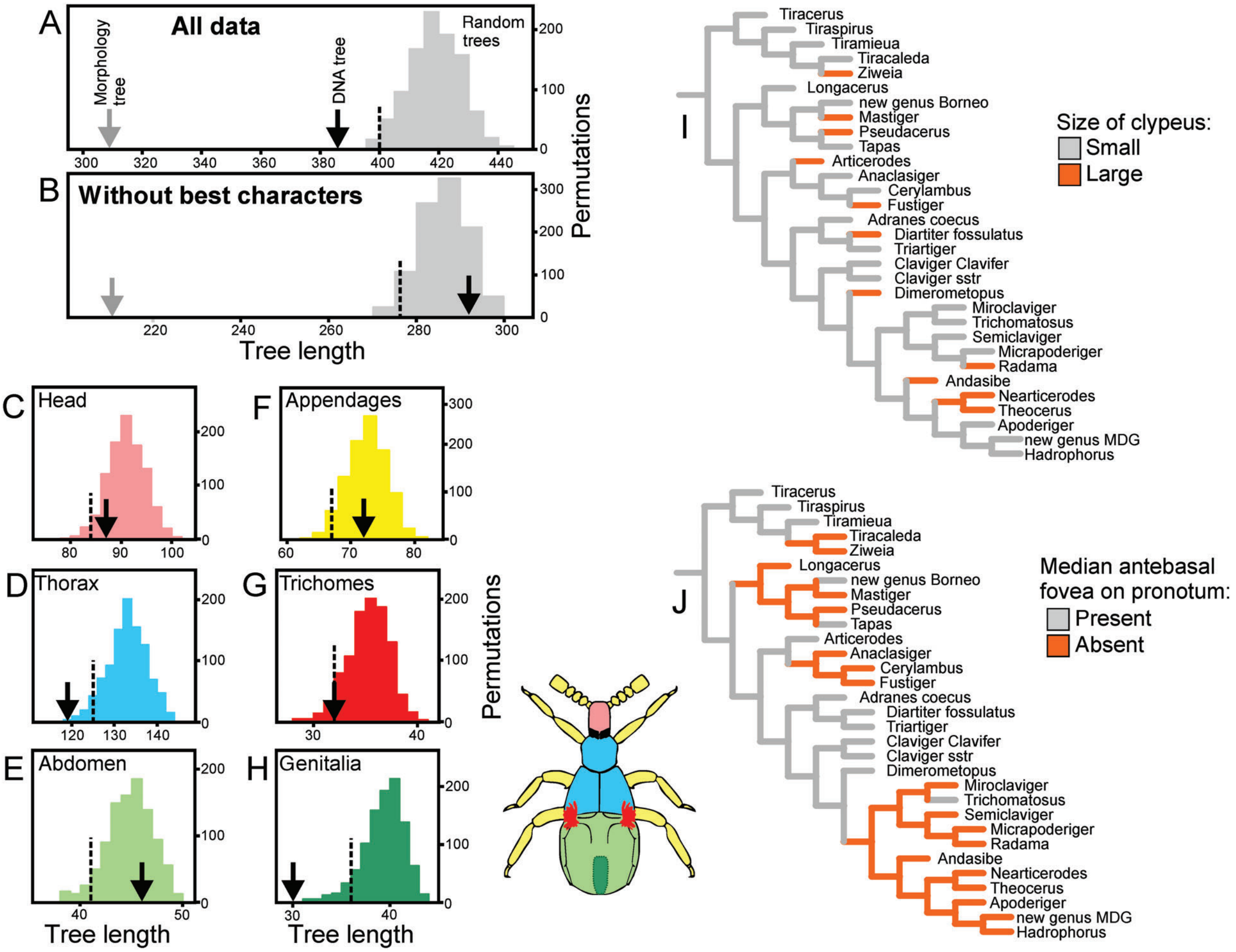

Fig. 4. Morphological evolution in the Clavigeritae: tree length distributions produced by mapping characters onto randomly generated trees (A–H) and examples of convergent evolution of particular characters (I–J). In A–H, grey and black arrows indicate, respectively, the lengths of the morphology-based and DNA-based trees. A, test of all 82 characters; B, test with 19 best-scoring characters excluded (63 characters); C–H, tests of characters by body regions (C, head; D, thorax; E, abdomen except genitalia; F, appendages; G, trichomes; H, male genitalia). I, example of a highly convergent character (character 6) mapped into the molecular phylogeny; J, example of less highly convergent character that partly corresponds to the molecular phylogeny (character 25). [Colour figure can be viewed at wileyonlinelibrary.com].

Arhytodini until a more comprehensive assessment of *Colilodion*'s sister taxon can be carried out. We therefore leave Colilodionini *insertae sedis* within Pselaphitae.

Systematics of Clavigeritae

The traditional classification of Clavigeritae established by Jeannel (1954), Célis (1969, 1970), and Besuchet (1986, 1991) is based on the external morphology, in particular the number of antennomeres, the presence of a constriction or carina on the head, the form of the pronotum and the elytra, the structure of the composite tergite and the position of trichomes. Our analyses reveal that most of these characters are highly convergent and have evolved multiple times independently within Clavigeritae. Consequently, the subtribes represented in our molecular analyses are either polyphyletic (Mastigerina, Clavigerodina, Clavigerina, Apoderigerina) or highly morphologically derived internal branches rather than deeply divergent phylogenetically isolated clades (Miroclavigerina, Thysdarina, Theocerina, Hoplitoxenina). These latter four subtribes are moreover part of the Madagascar adaptive radiation of Clavigeritae characterized by an explosion of morphological diversity (see below). On the basis of these findings (Fig. 1), we hereby update the internal classification of the Clavigeritae as follows (see also Fig. 5A):

1. We recognize three extant tribes corresponding to the three principal Clavigeritae clades revealed in all analyses performed: Tiracerini, Mastigerini **sensu nov.** and Clavigerini **sensu nov.**
2. Two morphologically aberrant subtribes, the representatives of which were not included in the molecular analyses, are temporarily treated as valid tribes pending the study of their

phylogenetic position by DNA data. These are Lunillini **stat. nov.** and Disarthricerini **stat. nov.**,

3 The Early Eocene fossil †*Protoclaviger trichodens*, which is a defensible sister group of all extant Clavigeritae, is kept in a separate tribe, the extinct Protoclavigerini, in agreement with Parker & Grimaldi (2014).

4 All remaining subtribes are synonymized with Clavigerini **sensu nov.**: Clavigerodina **syn. nov.**, Apoderigerina **syn. nov.**, Dimerometopina **syn. nov.**, Hoplitoxenina **syn. nov.**, Miroclavigerina **syn. nov.**, Theocerina **syn. nov.** and Thysdarina **syn. nov.**

Tiracerini is a strongly supported clade containing the Australian genus *Tiracerus* and all New Caledonian genera, as previously supposed by Besuchet (1991). In contrast to remaining clavigerite clades, Tiracerini is characterized by a diverse morphology of the male genitalia (Figs 5B–D, 7), including a strong asymmetry in the early-branching *Tiracerus*, *Tiraspirus* and *Tiramieua* (Fig. 7K–L, N–O). The newly described New Caledonian genera comprise a putative monophyletic group, although greater sampling of both the New Caledonian and Australian fauna will be needed to reliably resolve internal relationships in this tribe.

Mastigerini contains four Asian genera *Longacerus* Hlaváč, *Mastiger*, *Pseudacerus*, *Tasmiger* Besuchet plus the Australian *Tapas*, which is transferred here from Clavigerini. On the other hand, the Madagascan *Andasibe* and *Madastiger* Hlaváč & Baňař originally assigned to Mastigerina are part of the Madagascan clade and are hence transferred to Clavigerini.

Clavigerini is the largest clade of Clavigeritae, distributed worldwide and defined here as containing genera previously classified in Clavigerina and Clavigerodina plus all Madagascar genera irrespective of their previous subtribal placement. Presently, it contains 97 genera and 312 species and subspecies.

Lunillini includes three monotypic genera, *Eurycheiles* Jeannel, *Ischyroceros* Reichensperger and *Lunilla* Jeannel, distributed in the Afrotropical region including South Africa. They are all diagnosed by transverse robust antennomeres I and II, and antennomere III long, composed of three to four fused but still slightly discernable segments.

Disarthricerini includes two oriental genera, *Disarthricerus* Raffray with three species and the monotypic *Kurbatoviella* Hlaváč. The assignment of *Kurbatoviella* to Disarthricerini is tentative (Hlaváč, 2010) and needs confirmation by molecular data. The topology-constrained morphological analyses indicated *Kurbatoviella* as close to the Tiracerini, which can be confirmed or rejected only by the DNA analysis.

The proposed changes in classification (Table 2) are surely not the final word; we consider this a starting point for future, more detailed analyses and studies. Our taxon sampling is limited, especially for the Clavigerini, for which DNA data are only available for 20% of all genera. The inclusion of additional genera and species, as well as other DNA markers, will hopefully result in a more robust phylogeny allowing for a clearer understanding of intratribal phylogenetic relationships. This is a prerequisite for establishing a phylogenetically accurate internal classification, especially of the largest tribe, Clavigerini.

Zoogeography and island radiations of Clavigeritae

Our dating estimates for both stem- and crown-group ages implementing *Protoclaviger* as sister to modern Clavigeritae are considerably younger than those previously proposed (Parker & Grimaldi, 2014), presumably due to fewer total calibrations points on account of the reduced number of nonclavigerite taxa included in our analysis. The analysis is nevertheless consistent with a radiation of clavigerites that began during the Eocene, correlated with the rise of modern ants (Grimaldi & Agosti, 2000; LaPolla *et al.*, 2013; Barden & Grimaldi, 2016; Barden, 2017). Our molecular trees revealed three principal clades of Clavigeritae that originated during the Eocene (52–31 Ma). The earliest-diverging lineage, Tiracerini is a clade confined to the Australian region, with a single Australian genus (*Tiracerus*) and an additional radiation in New Caledonia, described below. The phylogenetic position of Tiracerini indicates a Gondwanan origin of the Clavigeritae, which is further corroborated by the presence of the closest-known sister-group of all extant Clavigeritae (*Protoclaviger*) in Early Eocene Cambay amber from Gujarat, India. The Indian subcontinent started to separate from East Gondwana ca. 120 Ma and in the Early Eocene it was approaching contact with the Asian continent (Royden *et al.*, 2008; Verma *et al.*, 2016; Krause *et al.*, 2019). Following the basal divergence of Australian Tiracerini, the remaining crown-group taxa underwent a further split into the two clades: the moderately speciose Oriental and Australian Mastigerini (five genera and ten species) and the vast Clavigerini with a worldwide distribution. Fully understanding the complex biogeography of Clavigerini will require more extensive taxon sampling as well as a more stable internal topology of the tribe.

Notably, our analyses reveal two island radiations of Clavigeritae (Fig. 3): one in Madagascar (34 genera and 70 species) and another in New Caledonia (five genera and five species known to date, but potentially larger). The Clavigeritae fauna of Madagascar represents nearly 20% of all known species of Clavigeritae and is also diverse morphologically. Due to the considerable morphological differences, the endemic Madagascar genera were previously not considered closely related and were classified in many, often endemic, subtribes. Multiple independent colonizations of Madagascar were therefore expected. Our analyses, in agreement with those of Parker & Grimaldi (2014), revealed that the Madagascan fauna forms a monophyletic group with a most recent common ancestor that colonized Madagascar at the Oligocene-Miocene boundary. The clade subsequently diversified from the Early Miocene (ca. 20 Ma) onwards. Clavigeritae hence parallels the radiation of the obligately myrmecophilous paussine beetles (Carabidae) on Madagascar. The paussine radiation is however of much younger origin, dating back only 2.6 Ma (Moore & Robertson, 2014).

The radiation of the Clavigeritae in New Caledonia is a novel discovery of this study. The presence of three undescribed genera of the tribe Tiracerini was reported for New Caledonia by Besuchet (1991), but these taxa were never described. We now report the presence of at least five monotypic genera, all forming a monophyletic group (Fig. 2). The ancestor of

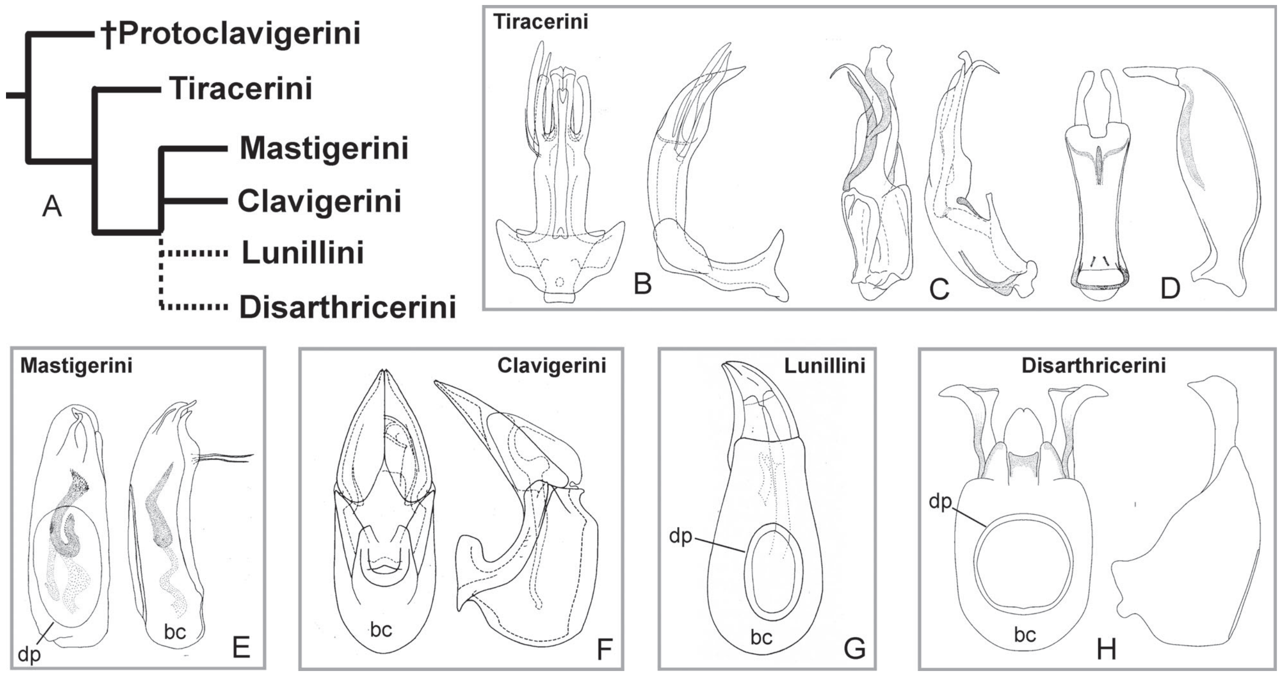

Fig. 5. Updated tribal system of the Clavigeritae (A) and morphological diversity of the aedeagus (B–H). Aedeagus form is more diverse and complex in Tiracerini (B–D) than in the remaining tribes, where it is very simplified and always symmetrical (E–H). Genitalia drawings: B, *Tiracerus foveicollis* (Raffray), unpublished original by C. Besuchet. C, *Tiramieua clavata* gen. & sp.n. D, *Dzumaca monteithi* gen. & sp.n. E, *Pseudacerus furcatus* Raffray, from Hlaváč (2011). F, *Claviger longicornis*, unpublished original by C. Besuchet. G, *Lunilla saprinoides* Jeannel, from Célis (1969). H, *Disarthricerus bruneicus* Nakládal & Hlaváč, from Nakládal & Hlaváč (2018). Abbreviations: bc, basal capsule; dp, dorsal diaphragm.

this group colonized New Caledonia between ca. 28.1–16.6 My ago, that is relatively long after the re-emergence of the island 37 My ago (Grandcolas *et al.*, 2008; Nattier *et al.*, 2017; Giribet & Baker, 2019). The species diversity resulting from this radiation is seemingly much lower than in Madagascar, perhaps the result of the less diverse ant fauna in New Caledonia or the smaller area of the island (more so than to the age of the radiation itself; Table 3, Fig. 3A–C). However, the real species diversity of the New Caledonian clade may be higher than reported here, and discoveries of additional species are expected with greater sampling effort. The five New Caledonian genera and species are treated in detail in the Systematic Part below.

There may be smaller island radiations of Clavigeritae which are not visible in our data due to the absence of DNA-grade material. For example, Fiji hosts 6 genera and 11 species of Clavigeritae. As in New Caledonia and Madagascar, the Fijian endemic genera are morphologically very diverse (Besuchet & Hlaváč, 2011). The monophyly of the Fijian fauna and the age of this possible radiation need to be tested. The oldest parts of the Fiji Archipelago emerged ca. 28 Ma (Beatty *et al.*, 2017), but many ant groups only radiated in Fiji during the Miocene, ca. 14–9 Ma (Economo *et al.*, 2015; Matos-Máravi *et al.*, 2018; Liu *et al.*, 2020). The possible radiation of Fijian Clavigeritae may hence be relatively young. It remains to be explained why islands, when colonized by the myrmecophilous species, tend to host radiations resulting in a boom of morphological diversity. New Caledonia was colonized by Clavigeritae ca. 10–20 My after its emergence when the local fauna was well-established and saturated already, which in theory decreases the probability of successful colonization by a new-comer. However, a well-established fauna of host ants may be a precondition for successful colonization by inquiline clavigerines, causing delayed colonization. This also corresponds well to the relatively late colonization of Madagascar by the Clavigeritae and Paussinae beetles, only possible after ants colonized Madagascar and the ant fauna diversified.

Monophyly and endemicity of island faunas may arise from the low dispersal potential of these symbiotic insects. Clavigerines are believed to be completely dependent on host ants, and unable to pursue a free-living existence outside of host colonies except for a short migration period. Adults of many species are winged and evidently must disperse to some degree, but successful long-distance dispersal to islands – where the beetles must encounter and adapt to novel ant hosts for long term viability – must surely be a relatively rare occurrence. This is reflected in the absence of clavigerites on the majority of small islands as well as some ant-impoverished large islands, such as New Zealand. It also follows that successful dispersal of clavigerites from islands on which they do become established is, in turn, highly unlikely. This may explain why subsequent cladogenesis of clavigerites is strongly constrained within the boundaries of a given island, leading to endemic radiations. This explanation may also apply to other obligate myrmecophiles that have radiated on islands, such as paussine carabids (Moore & Robertson, 2014).

Table 2. An updated classification of the Clavigeritae. Genera in bold were available for the molecular analyses performed in this study. Genera marked by an asterisk are endemic to Madagascar and are (likely) the part of the Madagascan radiation of Clavigerini. For a detailed list of genera with their distribution and number of species, see File S15.

Tribe	Genera
Protoclavigerini	†*Protoclaviger*
Tiracerini	***Tiracerus*, *Tiramieua*** gen.n., ***Tiraspirus*** gen.n., *Dzumaca* gen.n., ***Tiracaleda*** gen.n., ***Ziweia*** gen.n.
Mastigerini	***Longacerus***, ***Mastiger***, ***Pseudacerus*, *Tapas***, *Tasmiger*
Lunillini	*Eurycheiles*, *Ischyroceros*, *Lunilla*
Disarthricerini	*Disarthricerus*, *Kurbatoviella*
Clavigerini	***Adranes***, *Ambohitantella**, *Ambrosiger*, *Amphironchus*, ***Anaclasiger***, ***Andasibe****, *Ankarahitra**, *Antalaha**, ***Apoderiger****, *Archiclaviger*, *Arnoldiella*, ***Articerodes***, *Articerodites*, *Articeronomus**, *Articeropsis**, *Articerus*, *Bironia*, *Braunsiella*, *Burgeonilla*, ***Cerylambus***, ***Claviger***, *Clavigerodes*, *Clavigeropsis*, *Clavister*, *Colletocerus*, *Commatocerodes*, *Corynotopsis*, *Corynotus*, *Dejaegeria*, ***Diartiger***, ***Dimerometopus****, *Elasmatus*, *Fossiger*, ***Fustiger***, *Fustigerillus*, *Fustigerinus*, *Fustigerodes**, *Fustigeropsis*, *Gericlavodes*, *Gomyia**, ***Hadrophorus****, *Hexamerodes*, *Hoplitoxenus*, *Kaisia*, *Leptocorynotus*, *Macrotrachelos*, *Madara**, *Madastiger**, *Madastiger**, *Mataranka*, *Merinia**, *Mesoleptochir*, ***Micrapoderiger****, *Micrelytriger*, *Microconilon*, *Microfustigerinus*, ***Miroclaviger****, *Monodiger*, *Nadarimanu*, ***Nearticerodes****, *Neocerus**, *Neocorynotus**, *Neofustiger*, *Neoradamopsis*, *Novoclaviger*, *Novofustiger**, *Palaeoclaviger*, *Paliger*, *Pararticerus*, *Paussiger**, *Platycerodes**, *Pseudoclavigerodes*, ***Radama****, *Radamellus**, *Radamides*, *Radamira*, *Radamopsis*, *Rhynchoclaviger**, ***Semiclaviger****, *Seychellister*, *Sinoclavigerodes*, *Squamiger**, *Sufifer**, *Syrraphesina*, ***Theocerus****, *Thysdariella**, *Thysdarius**, ***Triartiger***, *Triceratomerus**¸***Trichomatosus****, *Trymalius**, *Vanuatiella*, *Villofustiger*, *Xenalluaudia*, *Xenobesuchetia*, *Xenocelisia*, *Xenomussardia*, ***Zuluclavodes***

Host ant use in Clavigeritae

Although all Clavigeritae species are believed to be obligate myrmecophiles, interactions with ants have only been studied for a handful of taxa (Donisthorpe, 1927; Park, 1932, 1942; Akre & Hill, 1973; Cammaerts, 1996, 1999; Akino, 2002). For the majority of species, adaptive myrmecophilous traits such as trichomes, fusions of segments and modified mouthparts provide indirect evidence of obligate myrmecophily for these species (Parker, 2016a). Additionally, many species have been directly collected from colonies of their putative host ants: ant associations are currently known for 55 genera (i.e. half of known genera) and 197 species and subspecies (i.e. 52.5% of known species/subspecies). In total, 27 extant ant genera and 86 ant species have been recorded as hosts for Clavigeritae (Table 4, File S16), and these hosts span five formicid subfamilies: Dolichoderinae, Ectatomminae, Formicinae, Myrmicinae and Ponerinae. Representatives of Tiracerini have been recorded from all five of these subfamilies, Clavigerini from Dolichoderinae, Formicinae, Myrmicinae and Ponerinae; Mastigerini with Dolichoderinae and Myrmicinae; Disarthricerini only from Formicinae and Lunillini from Myrmicinae. Myrmicinae and Formicinae genera are the most frequent hosts, with the myrmicine genus *Crematogaster* Lund and formicine *Lasius* Fabricius hosting the largest array of Clavigeritae genera and species.

Host switching appears to have happened frequently during clavigerite evolution. Many genera and species are guests of multiple ant species or even genera. For example, the genus *Articerodes* has been recorded from nests of eight genera of ants from the subfamilies Myrmicinae (*Crematogaster*, *Tetramorium* Mayr, *Tapinoma* Foerster), Formicinae (*Lasius*, *Lepisiota* Santschi, *Paratrechina* Motschultsky, *Plagiolepis* Mayr) and Dolichoderinae (*Technomyrmex* Mayr). One of its species, *A. joannae* Jeannel, is known from nests of *Technomyrmex*, *Lepisiota*, *Crematogaster* and *Tapinoma*. Similarly, the Australian *Tiracerus* inhabits nests of six ant genera from four subfamilies: Dolichoderinae (*Iridomyrmex* Mayr, *Ochetellus* Shattuck, *Papyrius* Shattuck), Myrmicinae (*Crematogaster*), Formicinae (*Camponotus* Mayr) and *Rhytidoponera* Mayr (Ectatomminae); several species of *Tiracerus* are known from colonies of more than one of these ant genera. For details see File S16.

The rather loose relationship of many genera and species of Clavigeritae with their host ants indicates that host switches are

Table 3. The number of species and genera of Clavigeritae and ants in New Caledonia, Madagascar, and Fiji, that is, islands in which adaptive radiation of the Clavigeritae is proven or expected. The information about the ant diversity adopted from Fisher & Peeters (2019) for Madagascar, Ward & Wetterer (2006) for Fiji and Jennings *et al.* (2013) for New Caledonia.

	Clavigeritae		Ants			
	Genera	Species	Genera	Species	Radiation age (Ma)	Island age (Ma)
New Caledonia	5	5	49	119	16.8 (8.1–26.4)	37
Madagascar	34	70	62	656	20.2 (14.5–27.3)	88
Fiji	6	11	33	138	?	28

rather frequent, even occurring intraspecifically. Which host ant a given beetle utilizes may depend more on the ant's biology than on the ant's phylogenetic position. Host range may also be influenced by the distribution range of available hosts in a particular locality, with Clavigeritae in temperate regions (e.g. *Claviger* or *Adranes*) potentially more limited in the choice of hosts than beetles from tropical and subtropical areas (e.g. *Fustiger* and *Tiracerus*). It is also unclear whether all ants recorded for particular Clavigeritae species refer to 'true' host ants, in which the beetles survive and complete their life cycle, and to what extent these host records are incidental. What is presumably the case, however, is that the species richness of recent Clavigeritae – one of the most speciose clades of myrmecophiles – has likely been contingent on their capacity to utilize diverse ants as hosts. Host switching opens up potential niche space and provides opportunities for speciation; it can also help to circumvent coextinction with hosts (Zhou *et al.*, 2019). Host switching appears to be characteristic of the most species-rich groups of obligate myrmecophiles, including Paussinae (Moore & Robertson, 2014) and Hetaeriinae (Histeridae) (Zhou *et al.*, 2019). In contrast, highly-host specific clades that show negligible host switching, such as the many convergent lineages of Aleocharinae (Staphylinidae) that utilize specific army ant species as hosts (Maruyama & Parker, 2017), are closely tied to the evolutionary fate of a single host. Their own diversification is strongly contingent on their host's cladogenesis, and consequently, such groups can be very species poor.

Morphological evolution of Clavigeritae

Our analyses reveal a strong conflict between molecular and morphological characters. Although our molecular analyses are affected by limited taxon and gene sampling, several of the recovered clades are well-supported and correspond to zoogeographic distribution. Hence, they seem likely to reflect the true phylogeny of the group. The conflict seems therefore to arise from highly convergent evolution of many morphological characters. This conclusion is corroborated by the maximum parsimony analyses of morphological characters, which resulted in more than 1500 equally parsimonious trees and a largely unresolved consensus tree (Fig. 2A, B). Our randomization tests (Fig. 4A–H) demonstrated clearly that the molecular topology does not, on average, score better than a randomly generated tree when morphological characters are mapped onto it. We found that when different body parts are compared, a somewhat correlated relationship with the molecular phylogeny is revealed for some characters of the head and thorax, those of the male genitalia and likely also trichomes on the body surface. Male genitalia are likely under sexual selection more than under

Table 4. Summary of the host associations of Clavigeritae with ants. For detailed species-level data see File S16. Abbreviations of zoogeographical regions: AFR, Afrotropical; AUS, Australian; MAD, Madagascar; NEA, Nearctic; OR, Oriental; PAL, Palaearctic; RSA, South Africa.

Ants		Clavigeritae			
Genus	Subfamily	Genera	sp. & ssp.	Tribes	Zoogeographical region
Crematogaster	Myrmicinae	33	58	Tiracerini, Clavigerini	AFR, AUS, MAD, NEA, OR, PAL, RSA
Lasius	Formicinae	4	43	Clavigerini	NEA, PAL
Iridomyrmex	Dolichoderinae	2	21	Tiracerini, Mastigerini	AUS
Lepisiota	Formicinae	5	13	Clavigerini	AFR, PAL, RSA
Tetramorium	Myrmicinae	6	12	Clavigerini	AFR, RSA
Pheidole	Myrmicinae	5	11	Clavigerini, Disarthricerini, Lunillini	AFR, AUS, NEO, RSA
Paratrechina	Formicinae	9	11	Clavigerini, Disarthricerini, Tiracerini	AUS, MAD, NEA, OR, PAL
Camponotus	Formicinae	2	6	Tiracerini, Clavigerini	AUS, MAD
Papyrius	Dolichoderinae	1	5	Tiracerini	AUS
Technomyrmex	Dolichoderinae	2	3	Clavigerini	AFR
Aphaenogaster	Myrmicinae	2	3	Clavigerini	NEA, NEO
Ochetellus	Dolichoderinae	2	2	Tiracerini, Clavigerini	AUS
Pachycondyla	Ponerinae	2	2	Clavigerini	AFR, OR
Myrmica	Myrmicinae	1	2	Clavigerini	PAL
Prenolepis	Formicinae	2	2	Clavigerini	AFR, PAL
Philidris	Dolichoderinae	1	1	Clavigerini	AUS
Rhytidoponera	Ectatomminae	1	1	Tiracerini	AUS
Anoplolepis	Formicinae	1	1	Clavigerini	ORT
Nylanderia	Formicinae	1	1	Clavigerini	ORT
Plagiolepis	Formicinae	1	1	Clavigerini	AFR
Brachymyrmex	Myrmicinae	1	1	Clavigerini	NEA
Monomorium	Myrmicinae	1	1	Clavigerini	RSA
Rhoptromyrmex	Myrmicinae	1	1	Mastigerini	OR
Solenopsis	Myrmicinae	1	1	Clavigerini	NEA
Tapinoma	Myrmicinae	1	1	Clavigerini	AFR
Wasmannia	Myrmicinae	1	1	Clavigerini	NEA
Ponera	Ponerinae	1	1	Clavigerini	NEA

selective pressures from the environment or host ants. They are likewise relatively refractory to these selective pressures, being internalized and hence physically isolated from the environment, and not involved in ant interactions. Moreover, genitalia are diverse in the Tiracerini only; in the remaining tribes (i.e. the majority of Clavigeritae) they are very uniform (Fig. 5). For these reasons, limited amounts of homoplasy in these structures is not surprising. On the other hand, the relatively low amount of homoplasy is surprising for trichomes on the dorsal body surface – structures at the interface of beetle-ant communication and physical interaction, and hence conceivably under strong selective pressure.

The tight association and coevolution with ants may be the main driver of morphological evolution in Clavigeritae. The broad host ant spectrum of many genera and species of Clavigeritae, in some cases spanning four different ant subfamilies, contradicts this hypothesis: host switches do not necessarily induce morphological changes as expected under a parallel diversification scenario (Fig. 6A). Rather, rampant host switching across the supertribe implies that clavigerites may have evolved a principal solution to achieving social integration that is potentially effective across a broad spectrum of ant species (Fig. 6B). Consistent with this hypothesis, Donisthorpe (1927) noted that specimens of *Claviger* survived well when experimentally introduced to nests of novel hosts. Such a versatile mechanism of host exploitation may consequently be reflected in the relative morphological stasis of specific body structures that mediate beetle-ant behavioural interactions.

Why some other parts of the body are then seemingly free to evolve so dramatically is unclear; perhaps this marked variation between species is unrelated to myrmecophily but adaptive for other aspects of these beetles' life histories. Alternatively, it might not be the result of adaptation at all, but instead stem from nonadaptive 'morphological drift' of structures in environments where there is only a weak stabilizing selective force to maintain the mean trait value (Fig. 5B). For example, convergent variation in the extent of fusion within the antennal flagella, from one to four flagellomeres, may arise from an absence of strong selection to maintain a precise number of segments. Such a phenomenon may be predicted to occur inside ant colonies, which, despite their many novel ecological pressures, may nevertheless be relatively free of many of the selective constraints on trait performance that are experienced by free-living species in the external environment. Weak stabilizing selection is also expected in

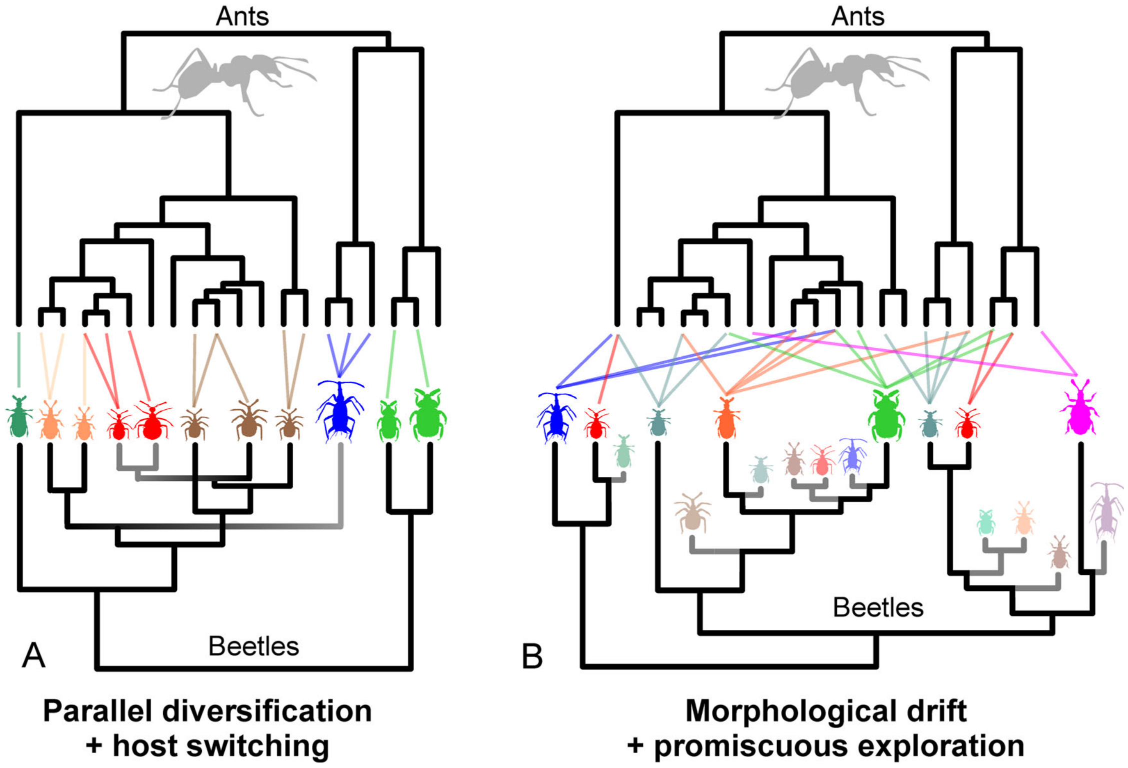

Fig. 6. Alternative models of ant-beetle coevolution. A, parallel diversification + host switching model predicts that each beetle species interacts with one or few closely related host ants; beetle cladogenesis partially mirrors that of the ants, and morphological diversity is generated by rare host switches to distantly related ant lineages (see red and blue beetles). B, morphological drift + promiscuous exploration model, in which a large amount of morphological diversity is generated neutrally under relaxed selection, and the resulting morphotypes are filtered for those broadly compatible with a wide spectrum of unrelated host ants, leading to rampant host switching. In this scenario, drift may also generate morphotypes of low fitness or that exhibit incompatibility with available hosts (depicted as extinct lineages). [Colour figure can be viewed at wileyonlinelibrary.com].

populations of rare species with tiny effective population sizes and hence high genetic drift (Lynch, 2007). Clavigerites may be archetypal examples of such naturally rare species. Examining patterns of gene flow and dispersal efficacy of obligate myrmecophiles such as clavigeritates, and estimating their effective population sizes, will help illuminate how these insects have diversified in the face of the population-level challenges associated with a socially parasitic lifestyle.

Systematic part

Clavigeritae Leach, 1815

Diagnosis. Antennae with three to eight antennomeres (three to six antennomeres in extant taxa), terminal antennomere usually longest (shorter than penultimate antennomere only in *Thysdariella* Hlaváč), apex of terminal antennomere at apex truncate, covered with short, thick setae or simply rounded and setose in Disarthricerina. Mouthparts reduced, barely visible, buccal cavity transverse with or without lateral cavities for the accommodation of maxilla. Abdomen with visible tergites 1–3 (segments IV–VI) either free (*Protoclaviger*) or fused into composite tergite (tergal plate of Chandler, 2001) which usually bears various kind of basal impression (all extant species). Elytra and abdomen with tufts of specialized trichomes (most species), sometimes trichomes completely absent (Disarthricerini). Legs with elongate meso- and metatrochanters; third tarsomere longer than first and second tarsomere combined; tarsus with single tarsal claws. For the diagnosis of the supertribe see also Chandler (2001: 534) and Parker & Grimaldi (2014).

Composition. Six tribes, 3 subtribes, 114 genera with 372 species and subspecies. Many taxa are waiting for description.

Biology. All the members of Clavigeritae are obligate myrmecophiles.

Key to tribes and genus groups of Clavigeritae

1. Antennae with more than six antennomers, visible tergites 1–3 (segments IV–VI) free. .... †**Protoclavigerini**

– Antennae apparently with two to six antennomeres (in reality always with three to six antennomeres, but the scapus is sometimes minuscule and difficult to see), visible tergites 1–3 (segments IV–VI) fused into composite tergite. 2

2 Trichomes entirely absent, antennae apparently with two antennomeres, terminal antennomere unmodified, simply rounded. .... **Disarthricerini**

– Some trichomes always present on elytral posterior apex, composite tergite of abdomen or paratergites. 3

3 Ventral anterior part of head not dilated, sides round; pronotum lacking distinct antebasal foveae, at most with only median impression near base; with three antennomeres, basal two very short, aedeagus lacking basal capsule, lacking dorsal diaphragm opening, (Figs 5B, 7B–C, E–F, H–I, K–L, N–O). **Tiracerini**. 4

– Ventral anterior part of head almost always dilated, sides carinate (except in *Claviger* and *Adranes*); pronotum usually with distinct median and lateral antebasal foveae; antenna with three to six antennomeres; aedeagus with median lobe bulbous, with well-developed basal capsule, with dorsal diaphragm opening circular or elliptical (Fig.5E - H). 6

4 Median lobe of aedeagus in dorsal view asymmetric, spiral-like in shape, parameres absent (Fig. 7K, N) .... ***Tiraspirus* genus group**

– Median lobe of aedeagus in dorsal view symmetric (Fig. 7B, E, H) 5

5 Median lobe of aedeagus not divided into apical and basal part, with prolonged parameres (Fig. 5B) .... ***Tiracerus* genus group**

– Median lobe of aedeagus composed of two parts, apical part bifurcate, considerably smaller than basal part, parameres absent (Fig. 7B,E, H) .... ***Tiracaleda* genus group**

6 Antennomeres I and II usually small, both as long as wide or slightly elongate, lateral margins of pronotum parallel-sided or convergent posteriad .... **Clavigerini + Mastigerini**

– Antennomeres I and II robust, clearly transverse, lateral margin of pronotum divergent posteriad ...... **Lunillini**

Tribe †Protoclavigerini

Diagnosis. Body length about 1.6 mm. Antennae with eight antennomeres, scape large and exposed, terminal antennomere about twice as large as VII, maxillary palpi emerging well outside buccal cavity, abdomen with unfused tergites IV–VI, paratergites IV and V with paired hook-like trichomes, paratergite VI with smaller trichomes (Parker & Grimaldi, 2014).

Composition.†*Protoclaviger trichodens*.

Distribution. India, Gujarat, early Eocene amber.

Biology. Unknown.

Tribe Tiracerini Besuchet, 1986

(Figs 5B–D, 7–10)

Diagnosis. Body length 1.0–3.0 mm. Trichomes always only on abdomen. Antennae with three antennomeres, scape always very small, terminal antennomere long, clearly longer than head, apex of terminal antennomere truncate, covered with short, thick setae. Mouthparts reduced, barely visible, buccal cavity transverse with or without lateral cavities for the accommodation of maxilla. Composite tergite with basal impression of various shape and size. Aedeagus symmetrical or asymmetrical, with (*Tiracerus*) or without parameres (all other genera), dorsal diaphragm opening absent.

Composition. Six genera with 53 species including those described in the present paper are known. More new species will be described from New Caledonia later.

Distribution. Endemic to Australia and New Caledonia.

Biology. Tiracerini have been so far recorded from nests of *Crematogaster* (Myrmecinae), *Camponotus* (Formicinae), from Dolichoderinae ants *Iridomyrmex*, *Ochetellus* and *Papyrius* and from *Rhytidiponera* (Ectatomminae). Tiracerini are usually collected by FIT, sifting of leaf-litter, at light or by applying pyrethrum fogging of trees and logs.

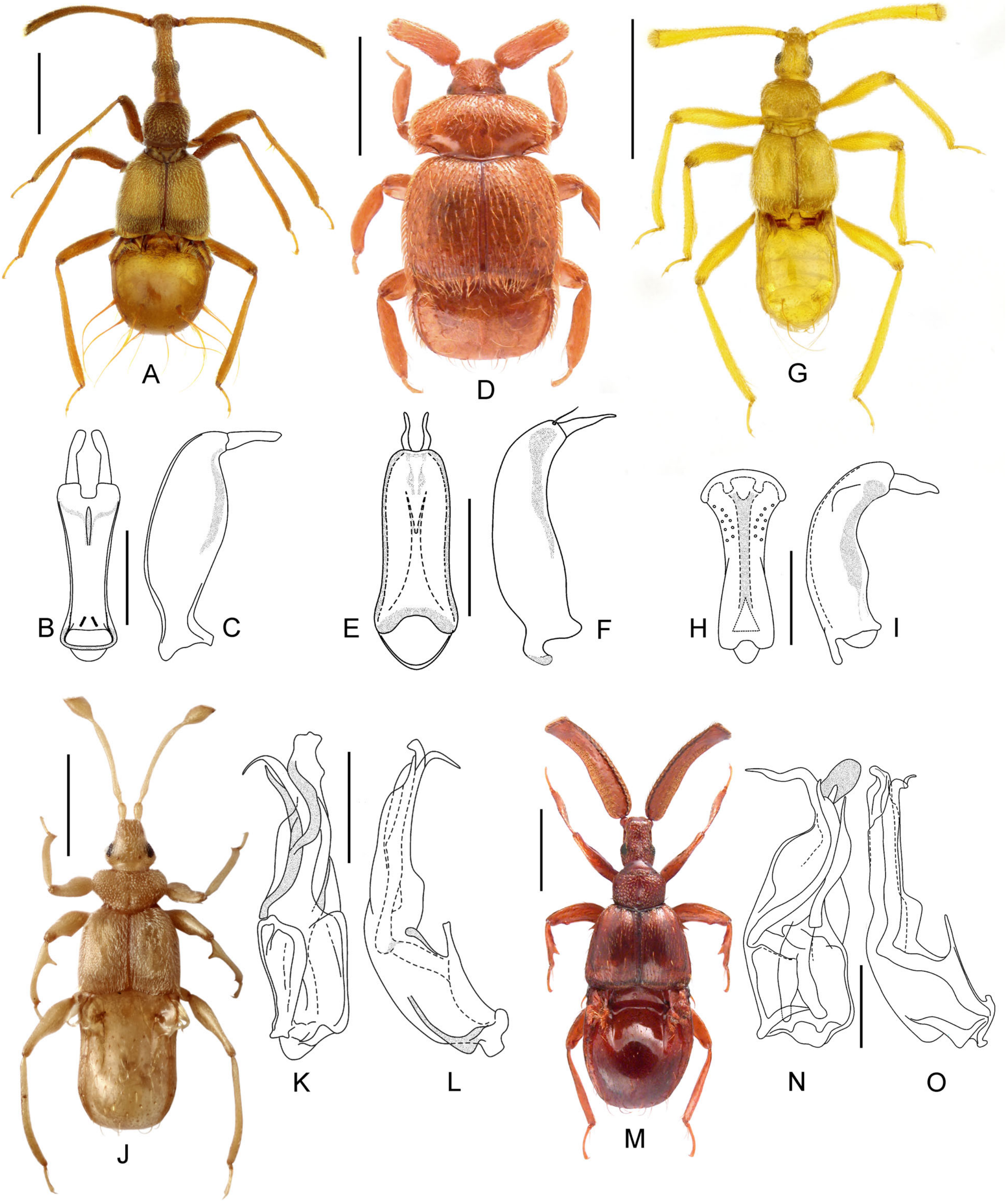

Fig. 7. Habitus and male genitalia (in dorsal and lateral view) of the New Caledonian Clavigeritae beetles. A–C, *Dzumaca montheithi* gen & sp.n.; D–F, *Tiracaleda minuta* gen & sp.n.; G–I, *Ziweia longipedes* gen & sp.n.; J–L, *Tiramieua clavate* gen & sp.n.; M–O, *Tiraspirus tabulatus* gen & sp.n. Scale bars: habitus = 0.5 mm; aedeagus = 0.1 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

Tiracerus **genus group**

(Figs 1A, 5B)

Diagnosis. Body length 1.0–3.0 mm. Trichomes only on abdomen. Buccal cavity transverse without lateral cavities for the accommodation maxilla. Pronotum with well-defined median fovea, lacking lateral foveae. Composite tergite with basal impression. Median lobe of aedeagus symmetric, median lobe reduced, parameres present, prolonged, dorsal diaphragm opening absent. See also Chandler (2001: 537).

Composition. Monogeneric group, the only genus *Tiracerus* has 48 described species.

Distribution. Endemic to Australia.

Tiracaleda **genus group**

(Figs 7A–I, 8–9)

Diagnosis. Body length 1.25–2.0 mm. Buccal cavity with lateral cavities for the accommodation of maxilla. Pronotum lacking sulci and foveae. Composite tergite with basal impression, with one to two small trichomes on each side. Aedeagus elongate, symmetrical in dorsal view, subdivided in two parts, basal part much longer than apical part, apical part formed by bifurcate lobe; ventrolateral foramen absent, dorsal phallobase diaphragm absent.

Composition. Three monospecific genera (*Dzumaca*, *Tiracaleda*, *Ziweia*) described below.

Distribution. Endemic to New Caledonia.

Dzumaca **gen.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:D3144AAF-D939-46FD-A62B-CDC492E17020

(Figs 7A–C, 8)

Type species. *Dzumaca monteithi* sp.n.

Diagnosis. Head distinctly longer than wide, eyes in middle, lacking frontal and vertexal foveae, venter with two largely separated tentorial pits, terminal antenonmeres very long. Pronotum lacking sulci and foveae. Elytra longer and wider than pronotum, lacking basal foveae, striae or carinae. Abdomen with very long macrosetae. Legs long and slender.

Sexual dimorphism. Female unknown. Very likely females lack the bunch of long setae in the basal third of the protibia.

Etymology. Named after the type locality of its only species, Mt. Dzumac. Gender feminine.

Description. ***Body*** (Fig. 7A) yellowish-brown, head and pronotum slightly rugose, elytra and composite tergite smooth, shiny. Length 1.90–2.00 mm. ***Head*** (Fig. 8A, B, F) widest across eyes and at level of occipital constriction, slightly expanded behind eyes to posterior margin of head capsule, head capsule long, separated from short neck region by well-defined occipital constriction (Fig. 8A, F: *occ*), rostrum obtuse, slightly rounded, temples long, clearly longer than diameter of eyes, clearly shorter than rostrum, frontal and vertexal foveae absent. Clypeus (Figs 7B, 8C: *cl*) not visible dorsally, short, not separated from frons. Mouthparts (Fig. 8B, C, E) rudimentary but well-developed, completely hidden in elliptical buccal cavity (Fig. 8E), with bunch of long setae under labrum (Fig. 8B, C), buccal cavity about 1.7 times as wide as high. Labrum (Fig. 8B, C: *lb*) small, strongly wrinkled, semielliptical, lacking setae. Maxilla (Fig. 8E) reduced, cardo (Fig. 8E: *cd*) hemispherical, basistipes (Fig. 8C, E: *bst*) triangular, lacking setae, with one palpomere (Fig. 8C, E: *plp*) of uncertain shape, mentum (Fig. 8E: *mn*) hexagonal, with one pair of long median setae. Venter of head (Fig. 8E, F) with anterior part glabrous, with few setae, posterior part rough, with strong, mesh-like microsculpture, mentum and submentum fused, gular plate large, almost flat, with two largely separated tentorial pits (Fig. 8F: *gp*, *tp*). Antennae very long (Fig. 8D), with three antennomeres, scape and pedicel small, scape slightly larger and longer, both visible dorsally, terminal antennomere very long, slender, curved at apex, about 15 times as long as wide at apex, elliptical in cross section, obliquely truncate at apex with dense, long setae. ***Thorax***. Pronotum about as long as wide, subrectangular with rounded anterior margins, basal margin straight, lacking sulci and foveae. Prosternum (Fig. 8G) slightly longer than half of pronotum, with basisternal part (Fig. 8G: *bs*) short, median prosternal process (Fig. 8G, *pstp*) long and narrow, procoxal foveae absent, procoxal cavities closely separated, prosternal carina absent, replaced by bunch of setae. Hypomera (Fig. 8G: *hy*) large, hypomeral carinae absent. Mesoventrite about three times shorter than metaventrite, fused together, lacking median carinae, mesoventral process (Fig. 8H: *msvp*) triangular, mesocoxae well-separated by short, wide isthmus (Fig. 8H: *ist*), isthmus with median bunch of setae, lacking mesoventral foveae. Metaventrite (Fig. 8H) large, about 1.6 times as wide as long, anterior metaventral process (Fig. 8H: *amtvp*) triangular, wide at base, metacoxae widely separated by wide, short, posterior metaventral process (Fig. 8H: *pmtvp*) which is largely concave and bearing bunch of setae. Elytra wider than long and longer than pronotum, twice as wide as pronotum, lacking basal foveae, striae or carinae, humeri well-defined, posterior corners sharply rounded, lacking trichomes. ***Abdomen*** elongate, slightly wider than long, more than one and half as long as elytra, composite tergite (IV-VI) smooth, basal depression slightly expanded to discal area, with two trichomes on each side, with one laterally strongly expanded paratergite, posterior third on each side with six exceptionally long and stout macrosetae. First visible sternite (III) short (Fig. 8I), in midline about five time shorter than second (IV), in middle with dense bunch of setae and with about ten long setae on each side of sternite, second visible sternite (IV) lacking median basal carina, with two well-defined, transversally elongate basolateral foveae (Fig. 8I: *blf*). ***Aedeagus*** (Fig. 7B, C) elongate, symmetric in dorsal view, basal part clearly longer than apical dorsally bifurcate lobe, ventrolateral foramen absent, dorsal phallobase diaphragm absent. ***Legs*** long and slender, simple, protibiae with bunch of long setae in basal third which is probably male sexual character.

Dzumaca monteithi **sp.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:6D2CCAE1-46F4-4336-AC17-3C5D7A9C8F63

(Figs. 7A–C, 8)

Holotype. ♂: NEW CALEDONIA: Dzumac Rd, junct., 9 November 2002, G. B. Monteith/QM Berlesate 1077,

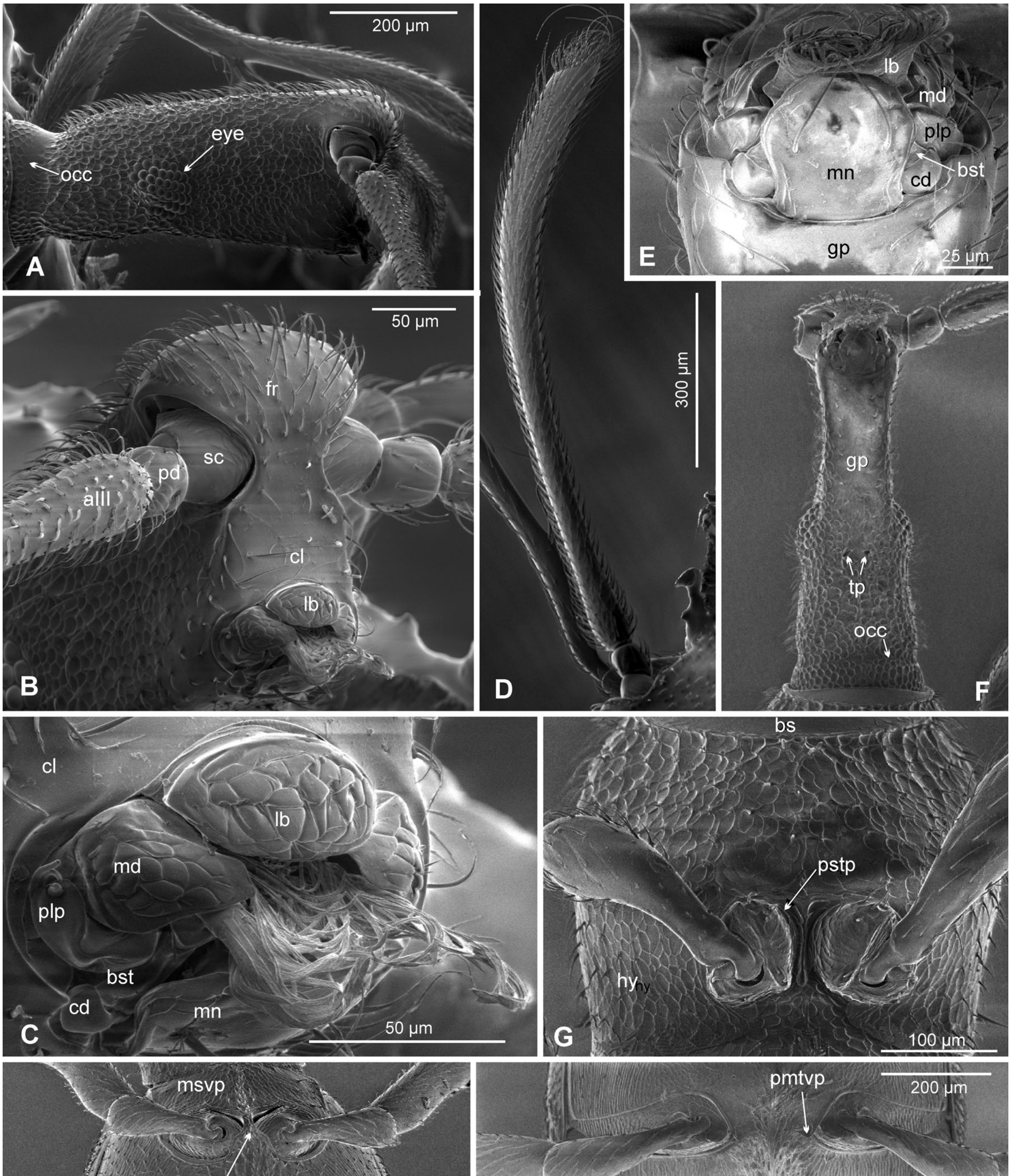

Fig. 8. Morphology of *Dzumaca monteithi* gen. & sp.n., (SEM) micrographs. A, head in lateral view; B, anterior part of the head; C, mouthparts in dorsal view; D, antenna; E, mouthparts in ventral view; F, head in ventral view; G, prothorax, ventral view; H, meso- and metathorax, ventral view; I, basal abdominal ventrites, ventral view. Abbreviations: *aIII*, third antennomere; *amtvp*, anterior metaventral proces; *blf*, basolateral fovea; *bst*, basistipes; *cd*, cardo; *cl*, clypeus; *fr*, frons; *gp*, gular plate; *hy*, hypomeron; *lb*, labrum; *md*, mandible; *mn*, mentum; *msvp*, mesoventral process; *occ*, occipital constriction; *pd*, pedicel; *plp*, palpomere; *pmtvp*, posterior metaventral process *sc*, scape; *tp*, tentorial pits.

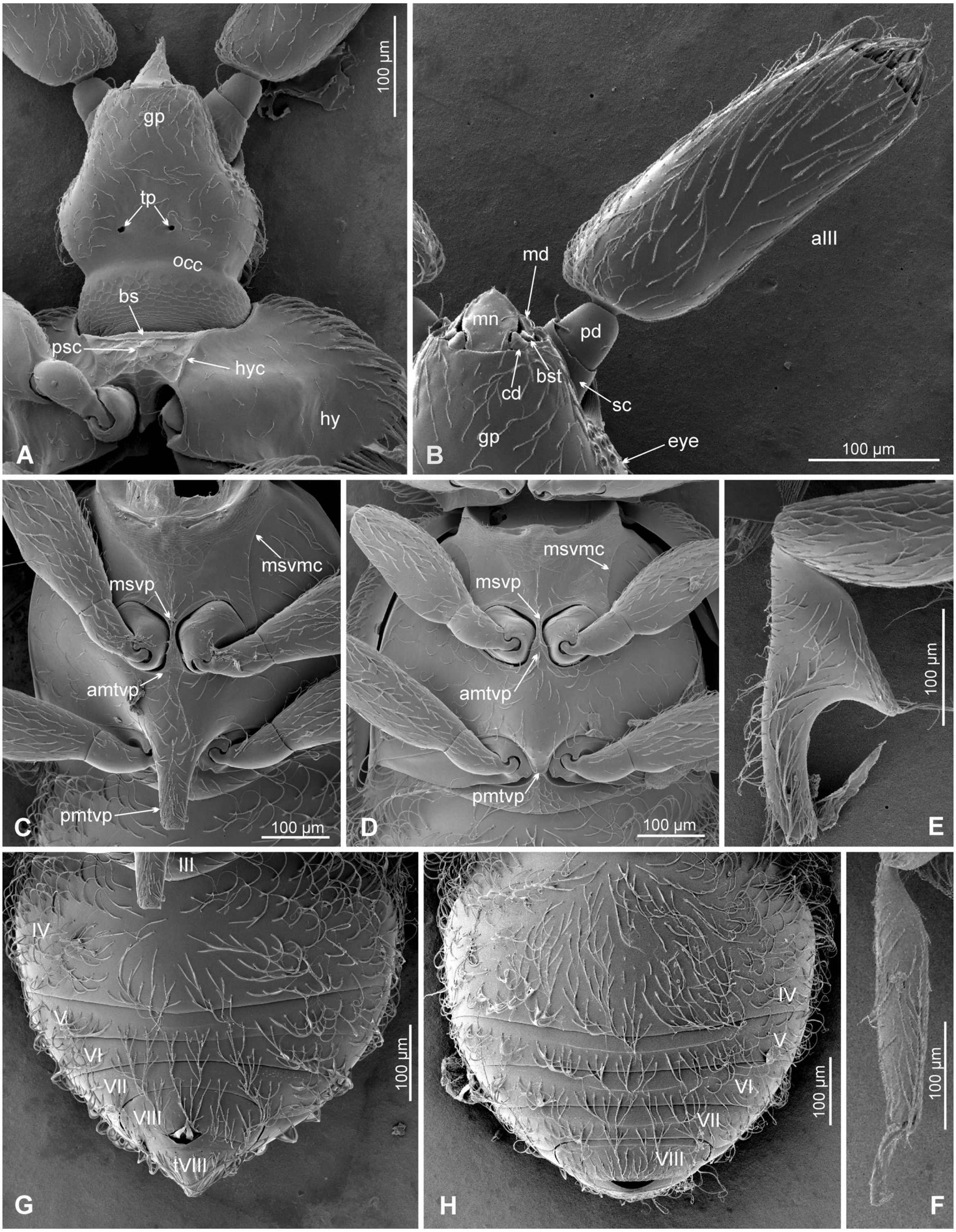

Fig. 9. Morphology of *Tiracaleda minuta* gen. & sp.n., SEM micrographs. A, ventral view of head and prothorax, male; B, antenna and mouthparts in ventral view, female; C–D, meso- and metaventrite (C, male; D, female). E–F, mesotibia in ventral view (E, male; F, female). G–H, abdomen in ventral view (G, male; H, female). Abbreviations: *aIII*, third antennomere; *amtvp*, anterior metaventral proces; *bs,* basisternum; *bst*, basistipes; *gp*, gular plate; *hy*, hypomeron; *hyc*, hypomeral carina; *md*, mandible; *mn*, mentum; *msvmc*, mesoventral median carina; *msvp*, mesoventral process; *occ*, occipital constriction; *pd*, pedicel; *pmtvp*, posterior metaventral process; *psc*, prosternal carina; *sc*, scape; *tp*, tentorial pits; *tVIII*, abdominal tergite VIII; *IV–VIII*, abdominal sternites.

22°02’S × 166°28′E, rainforest, 950 m, sieved material (MNHN). For paratypes, see File S17.

Diagnosis. As for the genus.

Biology. Unknown, three specimens were collected by sifting leaf-litter in rainforest and one by Malaise trap.

Distribution. New Caledonia (Mont Dzumac).

***Tiracaleda* gen.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:2CA4F186-679F-40F2-A94C-5BEEA5427CB5

(Figs. 7D–F, 9)

Type species. *Tiracaleda minuta* sp.n.

Diagnosis. Head short, slightly wider than long, eyes in posterior part, temples invisible, lacking frontal and vertexal foveae, venter with two largely separated tentorial pits, terminal antenonmeres flat, longest, less than three times as long as wide. Pronotum strongly transverse, lacking sulci and foveae. Elytra longer than wide, clearly longer than pronotum and abdomen, lacking basal foveae, with fine sutural striae, lacking discal striae or carinae. Abdomen transverse, lacking macrosetae. Legs short, stout and flat.

Sexual dimorphism. Males differ from females by triangular, sharply projecting mentum, strongly elongate posterior metaventral process and a large baso-median spice on metatibiae.

Etymology. The name combines *Tira-* referring to Tiracerini and *-caleda* referring to New Caledonia. Gender feminine.

Description. ***Body*** (Fig. 7D) lightly reddish-brown, whole body smooth and shiny. Length 1.25–1.30 mm. ***Head*** widest across eyes, convergent behind eyes to posterior margin of head capsule, eyes large, head capsule short, separated from short, smooth neck region by well-defined occipital constriction, longer than wide, rostrum obtuse, slightly rounded, temples slightly shorter than diameter of eyes, clearly shorter than rostrum, frontal and vertexal foveae absent. Clypeus reduced, not visible dorsally, not separated from frons. Mouthparts (Fig. 9B) rudimentary but well-developed, completely hidden in elliptical buccal cavity. Maxilla strongly reduced, cardo subtriangular (Fig. 9B: *cd*), basistipes (Fig. 9B: *bst*) smaller than cardo, mentum in males (Fig. 9A: *mn*) triangular, pointed and strongly projecting, visible dorsally, in females (Fig. 9B, *mn*) leaf linde shaped. Venter of head (Fig. 9A, B) glabrous, with few sparse setae, posterior part rough, with mesh-like microsculpture, mentum and submentum fused, gular plate (Fig. 9A, B: *gp*) large, almost flat, with two largely separated tentorial pits (Fig. 9A: *tp*). Antennae short (Fig. 9B), with three antennomeres, scape and pedicel (Fig. 9B: *sc*, *pd*) minuscule, both visible dorsally, terminal antennomere long, flat and wide, widest at base, slightly narrowing to apex, about 2.6 times as long as wide, elliptical in cross section, slightly obliquely truncate at apex with dense, long setae. ***Thorax*.** Pronotum strongly transverse, about twice as wide as long, with large lateral lobes, strongly narrowed at base, basal margin with weak, wide median lobe, lacking sulci and foveae. Prosternum about twice shorter than pronotum, with basisternal part (Fig. 9A: *bs*) very short, median prosternal process short, sharp and narrow, procoxal foveae absent, procoxal cavities confluent. Hypomera separated from median part of prosternum by well-defined hypomeral carinae, prosternal carina (Fig. 9A: *psc*) weakly defined. Mesoventrite (Fig. 9C, D) slightly shorter than metaventrite, fused together, with two arch-like mesoventral median carinae (Fig. 9D: *msvmc*) which divide mesoventrite in three parts, mesoventral process (Fig. 9D: *msvp*) triangular, mesocoxae well-separated by short, narrow isthmus, lacking mesoventral foveae. Metaventrite (Fig. 9C, D) large, about 2.8 times as wide as long, anterior metaventral process wider than mesoventral process, metacoxae closely separated by narrow, in males very long and prominent, in females shorter posterior metaventral process (Fig. 9C, D: *pmtvp*). Elytra clearly wider than long and much longer than pronotum, about 1.15–1.25 times as wide as pronotum, lacking basal foveae, with fine sutural striae, lacking discal striae or carinae, humeri rounded, well-defined, posterior corners sharp, slightly protuberant, posterior margin with dense long setae, lacking trichomes. ***Abdomen*** strongly transverse and shorter than elytra, composite tergite (IV–VI) smooth, with sparse setae but lacking any macrosetae, transversal basal depression short, with weak trichome on each side located close to well-defined first visible paratergite. First visible sternite (III) short, visible only in median part (Fig. 9G), second visible sternite (IV) lacking median basal carina and basolateral foveae (Fig. 9G, H), longest, in midline about five times longer than third (V) one, sternites V, VI and VII about same in midline length. ***Aedeagus*** (Fig. 7E, F) elongate, symmetric in dorsal view, basal part clearly longer than apical dorsally bifurcate lobe, with one long setae on each side, ventrolateral foramen absent, dorsal phallobase diaphragm absent. ***Legs*** (Fig. 9E, F) short and stout, fore and mid legs simple in both sexes, metatibiae in males with strong, large baso-median thorn.

***Tiracaleda minuta* sp.n**

http://zoobank.org/urn:lsid:zoobank.org:act:34718F4F-153F-4CE4-BB4B-5ADC30D1A3D6 (Figs 7D, E, F, 9).

Holotype. ♂: (p) NEW CALEDONIA (N) – 21.1814/165.2879, Aoupinié 700-900 m, Goipin rd [road] jct [junction] to gate, 20 November 2010, leg. R. Ruta, M. Wanat. (MNHN). For paratypes see File S17.

Diagnosis. As for the genus.

Biology. The host ant collected with the holotype was determined as an unknown species of *Paraparatrechina* Donisthorpe (det. Alan Andersen, 2014), which is actually treated as a synonym of *Paratrechina*.

Distribution. New Caledonia (Aoupinié, Serramea, Mandjelia, Dzumac Mts., Pic d’Amoa, Mt. Rembai),

***Ziweia* gen.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:AF84E5B6-9908-4F7E-8D75-BFE7A1C40304

(Fig 7G–I)

Type species. *Ziweia longipedes* sp.n. Present designation.

Diagnosis. Head short, slightly longer than wide, eyes behind middle, temples well-defined, lacking frontal fovea, with vertexal foveae, venter with two largely separated tentorial pits, terminal antenonmeres very long, slender, expanded to apex. Pronotum slightly transverse, lacking sulci and foveae. Elytra wider than long, longer than pronotum, shorter than abdomen, lacking basal foveae, striae or carinae. Abdomen transverse, lacking macrosetae. Legs long, slender.

Sexual dimorphism. Legs of females simple, lacking preapical spur on mesotibiae and preapical spine on mesotrochanters.

Etymology. Named after Ziwei Yin, a specialist on Pselaphinae from the Shanghai Normal University, China. Gender feminine.

Description. Body (Fig. 7G) light yellowish-brown, head, pronotum and elytra with fine microsculpture, composite tergite smooth, shiny. Length 1.45–1.60 mm. ***Head*** widest across eyes at their posterior margin, convergent behind eyes to posterior margin of head capsule, head capsule short, separated from short, nude, shagreened neck region by well-defined occipital constriction, rostrum obtuse, straight, temples short, about as long as length of eyes, clearly shorter than rostrum, frontal fovea absent, vertexal foveae present. Clypeus well visible dorsally, subrectangular, well-separated from frons by large antennal cavities. Mouth part rudimentary but well-developed, completely hidden in elliptical buccal cavity. Venter of head with gular plate large, almost flat, with two largely separated tentorial pits. Antennae long, with three antennomeres, scape and pedicel small, subequal in length, scape barely visible dorsally, terminal antennomere very long, slender, evenly expanded to apex, at apical third slightly curved, about 12 times as long as pedicel, elliptical in cross section, obliquely truncate at apex with dense, long setae. ***Thorax***. Pronotum clearly wider than long, basal margin with two lateral impressions and weakly defined median lobe, with well-defined antebasal sulcus, lacking median longitudinal sulcus and foveae. Prosternum about half as long as pronotum, procoxal cavities closely separated. Hypomera large, hypomeral carinae absent. Mesoventrite more than twice shorter than metaventrite, fused together, with two arch-like mesoventral carinae which divide mesoventrite in three parts, mesocoxae well-separated by short, wide isthmus, mesoventral and anterior metaventral process with bunch of setae. Metaventrite large, about 1.75 times as wide as long, metacoxae widely separated by wide, short, largely concave posterior metaventral process. Elytra wider than long and longer than pronotum, 1.20–1.40 times as wide as pronotum, lacking basal foveae, striae or carinae, humeri well-defined, posterior corners rounded, posterior margins of each elytron with wide, low median lobe, lacking trichomes. ***Abdomen*** elongate, much longer than elytra and longer than wide, composite tergite (IV–VI) smooth, with deep transverse depression which is expanded in middle to discal area, basal depression bearing two small trichomes, with four well-developed and long paratergites, first visible paratergite with trichome in basal part, posterior third of each side with four long and stout macrosetae. First visible sternite (III) short, covered by dense setae, in midline almost four times shorter than second (IV), second visible sternite about as long as remaining visible sternites, lacking median basal carina and with two well-defined, deep basolateral foveae. ***Aedeagus*** (Fig. 7H, I) elongate, symmetric in dorsal view, basal part clearly longer than apical dorsally bifurcate lobe, ventrolateral foramen absent, dorsal phallobase diaphragm absent. ***Legs*** very long and slender, fore and hind legs simple in both sexes, mesotibiae in males with large preapical spur, mesotrochanters with sharp, long preapical spine.

Ziweia longipedes sp.n.
http://zoobank.org/urn:lsid:zoobank.org:act:06CD3E80-5555-4808-A46D-06D80F413304

Holotype. ♂: (p) NEW CALEDONIA 11760, 22°17′S × 166°53′ E, 250 m, Pic du Grand Kaori, site 1, 22–23 November 2004, rainforest, Burwell, Wright, yellow pan/green label (p) QUEENSLAND MUSEUM LOAN, Date: November 2005, No. LE 05.43. (MNHN). For paratypes see File S17.

Diagnosis. As for the genus.

Biology. Unknown, all known specimens were collected in rainforest by flight intercept trap, yellow pans and by pyrethrum fogging of trees and logs.

Distribution. New Caledonia (Pic du Grand Kaori, Mt. Dzumac, Foret Nord).

Tiraspirus **genus group**
(Figs 7J–O, 10)

Diagnosis. Body length 1.55–1.85 mm. Buccal cavity with lateral cavities for the accommodation maxilla. Pronotum lacking sulci and foveae. Composite tergite with basal transversal depression and with basal rectangular basin in basal half of abdomen bordered by lateral carinae. Aedeagus elongate, strongly asymmetrical, spiral-shape in dorsal view, not divided in basal and apical part, apical lobe with sharp apophysis, ventrolateral foramen absent, dorsal phallobase diaphragm absent.

Composition. Two monospecific genera (*Tiramieua*, *Tiraspirus*), both described below.

Distribution. Endemic to New Caledonia.

Tiramieua **gen.n.**
http://zoobank.org/urn:lsid:zoobank.org:act:1C69B543-ADAB-4733-8E31-9EE927549368
(Fig. 7J–L)

Type species. *Tiramieua clavata* sp.n.

Diagnosis. Head short, slightly wider than long, eyes behind middle, anterior half narrow, rostrum narrow, frontal fovea present, lacking vertexal foveae, venter with two largely separated tentorial pits, terminal antenonmeres very long, slender, strongly clavate at apex. Pronotum clearly transverse, median antebasal fovea well-defined, lacking lateral foveae and sulci. Elytra wider than long, longer than pronotum, clearly shorter than abdomen, lacking basal foveae, striae or carinae. Abdomen very long, lacking macrosetae. Legs long, slender.

Sexual dimorphism. Female unknown.

Etymology. The name is a combination of *Tir-* referring to Tiracerini and *-amieua* referring to Col d'Amieu, the type locality of the only species. Gender feminine.

Description. ***Body*** (Fig. 7J) light yellowish-brown, head smooth, pronotum and elytra with fine microsculpture, composite tergite smooth, shiny. Length 1.55 mm. ***Head*** widest behind eyes, after strongly convergent to posterior margin of head capsule, head capsule short, separated from short, nude, shagreened neck region by well-defined occipital constriction, rostrum obtuse, straight, temples short, about as long as length of diameter of eyes, clearly shorter than rostrum, frontal fovea

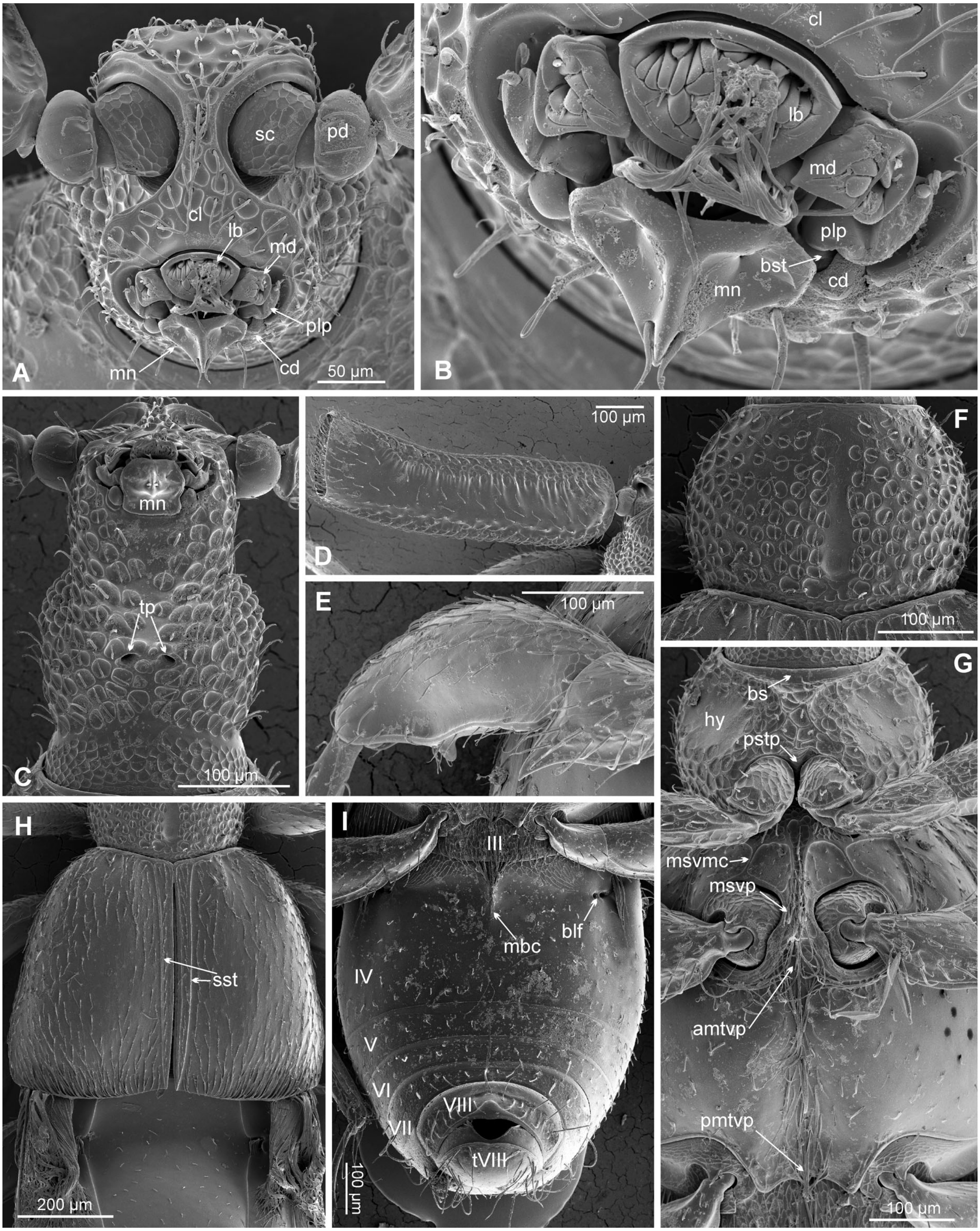

Fig. 10. Morphology of *Tiraspirus tabulatus* gen. & sp.n., SEM micrographs. A, mouthparts in ventral view; B, detail of mouthparts; C, head in ventral view; D, antenna, ventral view; E, male mesofemur in ventral view; F, pronotum; G, ventral morphology of thorax; H, elytra and base of abdomen in dorsal view; I, abdomen, ventral view. Abbreviations: *amtvp*, anterior metaventral proces; *blf*, basolateral fovea; *bs*, basisternum; *cd,* cardo; *cl,* clypeus; *hy*, hypomeron; *md*, mandible; *mn*, mentum; *msvmc*, mesoventral median carina; *msvp*, mesoventral process; *occ*, occipital constriction; *pd*, pedicel; *pmtvp*, posterior metaventral process; *pstp*, posterior prosternal process; *sc*, scape; *sst*, sutural stria; *tp*, tentorial pits; *tVIII*, abdominal tergite VIII; *IV–VIII*, abdominal sternites.

absent, vertexal foveae present. Clypeus not visible dorsally, very short, not separated from frons. Mouth part rudimentary but well-developed, completely hidden in semicircular buccal cavity. Venter of head smooth, with large, almost flat gular plate, with two largely separated tentorial pits. Antennae long, with three antennomeres, scape minuscule, not visible dorsally, pedicel almost twice as long as scape, antennomere III long, slender, strongly clavate at apex, at apical third slightly curved, about six times as long as pedicel, semicircular in cross section, truncate at apex with dense, long setae. ***Thorax***. Pronotum clearly wider than long, cordiform, with well-defined median antebasal fovea, lacking lateral foveae and sulci. Prosternum about two third of length of pronotum, hypomera large, median part of prosternum separated from hypomera by hypomeral carinae, median part rough, procoxal cavities closely separated. Mesoventrite about three times shorter than metaventrite, fused together, mesoventral carinae absent, mesocoxae well-separated by short, wide isthmus, mesoventral process small, narrow, anterior metaventral process clearly wider. Metaventrite large, about twice as wide as long, metacoxae widely separated by wide, short, straight posterior metaventral process. Elytra wider than long and longer than pronotum, about 1.50 times as wide as pronotum, lacking basal foveae, striae or carinae, humeri well-defined, posterior corners sharp, posterior margins largely rounded, lacking trichomes. ***Abdomen*** elongate, much longer than elytra and much longer than wide, composite tergite (IV–VI) smooth, with transverse basal depression and with deep basal rectangular basin in basal half of abdomen, bordered by lateral carinae, with two lateral tubercles, lacking trichomes, with four long paratergites, first visible paratergites with lateral projection and trichome in basal part, composite tergite with sparse, long macrosetae. First visible sternite (III) short, in midline about five times shorter than second (IV) and clearly shorter than third (V), second visible sternite more than twice as long as remaining visible sternites, lacking median basal carina and with two well-defined basolateral foveae. ***Aedeagus*** (Fig. 7K, L) elongate, asymmetric in dorsal view, basal part and apical lobe not separated, ventrolateral foramen absent, dorsal phallobase diaphragm absent. ***Legs*** long and slender, fore and hind legs simple, mesofemora with minuscule median tooth, mesotibiae with long, sharp prebasal spine, mesotrochanters with sharp, very long preapical spine and with bunch of long setae.

***Tiramieua clavata* sp.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:C5AFA347-E18E-4A3D-A5F3-67C89223D4AE

(Figs 7J–L)

Holotype. ♂: (p) NEW CALEDONIA, 11179, 21o37’S × 165 o49’ E. 470 m. Col d’Amieu, west slope. 14 November 2002, Burwell & Monteith. Pyreth [pyrethrin]. trees & logs/green label (p) QUEENSLAND MUSEUM LOAN, Date: November 2005, No. LE 05.43. MNHN. For paratypes see File S17.

Diagnosis. As for the genus.

Biology. Unknown, the holotype was collected by fogging trees and logs by insecticide chemical pyrethrum.

Distribution. New Caledonia (Col d’Amieu).

***Tiraspirus* gen.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:39FF6D5E-B78C-471D-AD9C-E89D0316476C

(Figs 7M–O, 10)

Type species. *Tiraspirus tabulatus* sp.n.

Diagnosis. Head long, clearly longer than wide, eyes behind middle, anterior half wide, rostrum wide, lacking frontal and vertexal foveae, venter with two largely separated tentorial pits, terminal antenonmeres long, wide and flat, longly curved to apex. Pronotum clearly transverse, with median antebasal fovea, lacking lateral foveae and antebasal sulcus, with median shallow sulcus. Elytra longer than wide, almost twice as long as pronotum, clearly shorter than abdomen, lacking basal foveae, sutural striae entire, lacking discal striae. Abdomen very long, lacking macrosetae. Legs moderately long and slender.

Sexual dimorphism. Middle legs of females simple, lacking spines, spurs and teeth.

Etymology. The name is a combination of *Tira-* referring to Tiracerini and *-spirus* referring to the asymmetric, spiral-like apical part of the aedeagus. Gender masculine.

Description. ***Body*** (Fig. 7M) reddish-brown to brown, shiny, antennae and legs lighter, head with large punctures, punctuation on pronotum sparse, elytra with fine, sparse microsculpture, composite tergite smooth. Length 1.75–1.85 mm. ***Head*** widest across eyes, slightly convergent behind eyes to posterior margin of head capsule, head capsule short, separated from short, nude, shagreened neck region by well-defined occipital constriction (Fig. 10C), rostrum obtuse, straight with very shallow median concavity, temples as long as eyes, clearly shorter than rostrum, frontal fovea absent, vertexal foveae absent. Clypeus not visible dorsally, very short, not separated from frons. Mouthparts (Fig. 10A, B) rudimentary but well-developed, completely hidden in elliptical buccal cavity (Fig. 10B), with bunch of long setae under labrum (Fig. 10B), about 2.5 times as wide as high. Labrum (Fig. 10A–B: *lb*) small, strongly wrinkled, semielliptical, lacking setae. Maxilla (Fig. 10B) reduced, cardo (Fig. 10B: *cd*) hemispherical, basistipes (Fig. 10B: *bst*) minuscule, triangular, lacking setae, with one palpomere (Fig. 10B: *plp*) of uncertain shape, mentum (Fig. 10A–B: *mn*) rectangular, wider than long, with constriction in basal third, with strong, sharp projection in middle, projection with two preapical setae (Fig. 10B). Venter of head (Fig. 10C) with rough microstructure, gular plate large, almost flat, with two largely separated tentorial pits. Antennae (Fig. 10D) long and wide, bent, with three antennomeres, scape and pedicel small, subequal in length, scape not visible dorsally, terminal antennomere long and wide, board-like shaped, 15–16 times as long as pedicel, more than four times as long as wide, flat elliptical in cross section, with truncate, transversally thickened apex (Fig. 10A) bearing dense, stout setae. ***Thorax***. Pronotum clearly wider than long, narrowed to anterior margin, basal margin straight, with well-defined median antebasal fovea and shallow median longitudinal sulcus, lacking antebasal sulcus and lateral foveae. Prosternum (Fig. 10G) about two third of length of pronotum, with basisternal part (Fig. 10G: *bs*) very short, hypomera (Fig. 10G: *hy*) large, slightly depressed, depression smooth, lacking hypomeral carinae, median part of prosternum with rough, mesh-like structure, procoxal cavities closely separated. Mesoventrite (Fig. 10G) about three times shorter than metaventrite, fused together, with two mesoventral median carinae (Fig. 10G: *msvmc*) which divide mesoventrite in six parts, mesocoxae well-separated by short, wide isthmus, mesoventral and anterior metaventral process (Fig. 10G: *msvp*, *amtvp*) with bunch of setae. Metaventrite (Fig. 10G) large, about 1.60 times as wide as long, metacoxae widely separated by wide, short, largely concave posterior metaventral process (Fig. 10G: *pmtvp*). Elytra (Fig. 9H) clearly longer than wide and almost twice as long as pronotum and twice as wide as pronotum, lacking basal foveae, sutural striae entire (Fig. 10H: *sst*), discal striae absent, humeri weakly-defined, posterior corners rounded, posterior margins slightly concave in middle, lacking trichomes. ***Abdomen*** elongate, much longer than elytra and longer than wide, composite tergite (IV–VI) smooth, with transverse basal depression and with deep basal rectangular basin in basal half of abdomen, bordered by lateral carinae interrupted by small trichomes, with three well-developed and long paratergites, first visible paratergites with large trichome, posterior part of composite tergite with about eight to ten long and stout macrosetae. First visible sternite (III) short (Fig. 10I), covered by dense setae, in midline more than three times shorter than second (IV) and about as long as third (V), second visible sternite clearly shorter than remaining visible sternites, with short median basal carina and with four well-defined basolateral foveae (Fig. 10I: *mbc*, *blf*). ***Aedeagus*** (Fig. 7N, O) elongate, asymmetric in dorsal view, basal part and apical lobe not separated, ventrolateral foramen absent, dorsal phallobase diaphragm absent. ***Legs*** moderately long and slender, fore and hind legs simple in both sexes, mesotibiae in males with small median spine and large preapical spur, mesofemora with tooth behind middle, mesotrochanters with sharp, long preapical spine (Fig. 10E).

***Tiraspirus tabulatus* sp.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:A1E6CAEB-D086-4C53-8EC9-E8ADC40527A7

(Figs. 7M–O, 10)

Holotype. HOLOTYPE, ♂: (p) NEW CALEDONIA, 11465, 22°02′S × 166 °28′ E. 950 m, Dzumac Road, junction. 5 December 2003–26 January 2004, G. Monteith, flight int. trap/green label (p) QUEENSLAND MUSEUM LOAN, Date: November 2005, No. LE 05.43. MNHN. For paratypes see File S17.

Diagnosis. As for the genus.

Biology. Unknown, all known specimens were collected in rainforests by flight intercept traps, pitfall traps, by sifting litter and by Pyrethrum fogging of trees and logs.

Distribution. New Caledonia (widespread species on the whole main island, collected in Dzumac Mts., Pic d'Amoa, Pic du Grand Kaori, Aoupinie, Mandjelia, Mt. Panié).

Tribe Clavigerini

Diagnosis. Small to large clavigerines, size 1.00–3.00 mm. Trichomes always on elytra and abdomen. Antennae with three to six antennomeres, scape always very small, terminal antennomere from short to very long, apex of terminal antennomere rounded or truncate covered with short, thick setae. Mouthparts reduced, barely visible, buccal cavity transverse with lateral cavities for the accommodation maxilla. Composite tergite with basal impression of various shape and size, aedeagus from symmetric to with slightly asymmetric apex of median lobe, divided in basal and apical part, portion of basal and apical parts varying, dorsal diaphragm opening present.

Composition. Ninety-seven genera (Table 2) with 308 species (i.e. 83% of all described species of Clavigeritrae). Many new genera and species are awaiting description.

Distribution. All zoogeographic regions.

Biology. Highly specialized genera *Claviger*, *Diartiger* and *Adranes* can be almost exclusively collected in nests of host ants. Tropical Clavigerini are living with many different ants (Table 4, File S16), but many species are mainly collected by sifting of leaf-litter and by flight intercept traps in well-preserved primeval forests. Ultraviolet trap is also giving some results, but it is less effective.

Tribe Disarthricerini

Diagnosis. Body length 1.20–1.30 mm. Body lacking trichomes. Antennae with three antennomeres, terminal antennomere considerably longer than antennomere 1 and 2 combined, apex of terminal antennomere rounded. Mouthparts reduced, barely visible, buccal cavity transverse with lateral cavities for the accommodation maxilla. Composite tergite lacking basal transverse impression, with deep basolateral foveae. Aedeagus symmetric, divided in basal and apical part, basal part longer than apical part, dorsal diaphragm opening present.

Composition. Two genera, *Disarthricerus* (three species) and *Kurbatoviella* (one species). Undescribed *Disarthricerus* species from Borneo have been examined (P. Hlaváč, unpublished).

Distribution. Malay Peninsula and Borneo.

Biology. *Disarthricerus moultoni* Bryant was collected on the ground, under dead leaves in the nest of *Paratrechina butteli* (Forel) (Bryant, 1915). Other specimens were collected at light and in rotten wood or under stones with unknown ant (Nakládal & Hlaváč, 2018).

Comments. No DNA-grade specimens were available for our analyses for the tribe.

Tribe Lunillini

Diagnosis. Body stout, length 1.50–1.80. Trichomes present on abdomen. Antennae with three antennomeres, scape and pedicel robust, clearly transverse, terminal antennomere about as long as head, considerably longer than I and II combined, apex of terminal antennomere truncate covered with short, thick setae. Mouthparts reduced, barely visible, buccal cavity transverse with lateral cavities for the accommodation maxilla. Composite tergite with basal transverse impression, with deep basolateral foveae. Aedeagus symmetrical (at most slightly bent, Fig. 6G), divided in basal and apical part, basal part as long as or longer than apical part, dorsal diaphragm opening present.

Composition. Three monospecific genera, *Eurycheiles*, *Ischyroceros* and *Lunilla*. No undescribed species are known to us.

Distribution. Sub-Saharan Africa.

Biology. Most specimens were collected in The Democratic Republic of Congo by sifting of debris of wet leaf-litter and soil around nests of small, thin unidentified ants; ant colonies had about 200–300 ant specimens (Coulon, 1982). *Lunilla* was collected with *Pheidole*. *Ischyroceros* was sifted from the leaf-litter in the forest in Malawi (Hlaváč & Baňař lgt., 2018).

Comments. No DNA-grade specimens were available for our analyses for the tribe.

Tribe Mastigerini

Diagnosis. Body stout, length 1.2–1.7 mm. Trichomes present on abdomen. Antennae with three to six antennomeres, scape and pedicel minuscule, terminal antennomere short, shorter than length of head, apex of terminal antennomere rounded (in *Longacerus*, *Pseudacerus*) or truncate (in *Mastiger*, *Tapas*, *Tasmiger*) covered with short, thick setae. Mouthparts reduced, barely visible, buccal cavity transverse with lateral cavities for the accommodation maxilla. Composite tergite with basal transverse impression, with deep basolateral foveae. Aedeagus from symmetric to slightly asymmetric apex of median lobe, divided in basal and apical part, basal part longer than apical, dorsal diaphragm opening present.

Composition. Five genera, ten described species (Table 2).

Distribution. Tropical Asia (*Longacerus*, *Mastiger*, *Pseudacerus* and *Tasmiger* and one undescribed, monospecific genus from Borneo) and Australia (*Tapas*).

Biology. The majority of known material was collected by sifting of leaf-litter or by flight intercept trap in primeval tropical forests. The host ants are known for one species of *Tapas* (*Iridomyrmex gracilis* (Lowne)) and one species of *Tasmiger* (*Rhoptromyrmex wroughtonii* Forel).

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Historical changes of the higher classification of the Clavigeritae

S2. List of GenBank accession numbers of all sequences used for DNA analyses.

S3. DNA alignment used for molecular analyses (in FASTA format).

S4. Morphology matrix used for morphology-based and mixed analyses (in TNT format).

S5. Description of the composition of the combined DNA + morphology dataset.

S6. Dataset used for IQ-Tree analysis and the description of the partitions.

S7. Nexus file used for the MrBayes analysis of the molecular data.

S8. Nexus files used for the MrBayes analysis of the mixed (DNA + morphology) data.

S9. Nexus files used for the MrBayes topology-constrained analysis of the position of *Protoclaviger*.

S10. Nexus file used for the MrBayes time-tree analysis, showing how calibration points were incorporated.

S11. Groups of morphological characters used for the analyses of phylogenetic signal and their retention indexes.

S12. Results of all phylogenetic analyses performed.

S13. Lengths of 1000 random trees for each group of characters.

S14. Results of the randomization tests of the phylogenetic signal in morphological characters.

S15. List of genera of the Clavigeritae, number of their species and distribution.

S16. Summary of known interactions of Clavigeritae with ants.

S17. Descriptions of new species of New Caledonian Tiracerini.

Acknowledgements

Geoff Monteith collected the majority of New Caledonian Clavigeritae used in this study and kindly provided material to the first author. Donald Chander analysed characters for *Adranes* and provided valuable comments on the new suprageneric system. Al Newton and Margaret Thayer helped to arrange a loan of many Pselaphinae from the Field Museum of Natural History, Chicago, USA, collected by Jarmila and Stewart Peck. Richard Leschen, Marek Wanat and Rafał Ruta made available all pselaphines collected in New Caledonia. The work of PH and MF was supported by the Ministry of Culture of the Czech Republic (DKRVO 2019-2023/5.I.b, National Museum, 00023272). JP is supported by a Rita Allen Foundation Scholars Award, an Alfred P. Sloan Fellowship, a Klingenstein-Simons Fellowship Award and an Army Research Office MURI award W911NF1910269. The authors have declared no conflict of interest.

Data availability statement

All data used for the analyses and complete results are in the Zenodo research depository (https://zenodo.org/) under http://doi.org/10.5281/ zenodo.4422103. Newly generated DNA sequenced were submitted to GenBank under accession numbers MW417247-MW417248, MW423303-MW423313, and MW440696-MW440698.

References

Akino, T. (2002) Chemical camouflage by myrmecophilous beetles *Zyras comes* (Coleoptera: Staphylinidae) and *Diartiger fossulatus* (Coleoptera: Pselaphidae) to be integrated into the nest of *Lasius fuliginosus* (Hymenoptera: Formicidae). *Chemoecology*, **12**, 83–89.

Akre, R.D. & Hill, W.B. (1973) Behavior of *Adranes taylori*, a myrmecophilous beetle associated with *Lasius sitkaensis* in the Pacific Northwest (Coleoptera: Pselaphidae; Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society*, **46**, 526–536.

Aubé, C. (1833) Note sur la famille des Psélaphiens. *Annales de la Société Entomologique de France*, **2**, 502–511.

Bapst, D.W. (2012) Paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution*, **3**, 803–807. https://doi.org/10.1111/j.2041-210X.2012.00223.x, http://onlinelibrary.wiley.com/doi/10.1111/j.2041-210X.2012.00223.x/abstract.

Barden, P. (2017) Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News*, **24**, 1–30.

Barden, P. & Grimaldi, D.A. (2016) Adaptive radiation in socially advanced stem-group ants from the Cretaceous. *Current Biology*, **26**, 515–521. https://doi.org/10.1016/j.cub.2015.12.060.

Beatty, C.D., Sánchez-Herrera, M., Skevington, J.H., Rashed, A., van Gossum, H., Kelso, S. & Sherratt, T.N. (2017) Biogeography and systematice of endemic Island damselflies: the *Nesobasis* and *Melanesobasis* (Odonata: Zygoptera) of Fiji. *Ecology and Evolution*, **7**, 7117–7129. https://doi.org/10.1002/ece3.3175.

Besuchet, C. (1986) Synonymes et homonyme nouveaux de quelques genres de Psélaphides (Coleoptera). *Revue Suisse de Zoologie*, **93**, 257–264.

Besuchet, C. (1991) Révolution chez les Clavigerinae (Coleoptera, Pselaphidae). *Revue Suisse de Zoology*, **98**, 499–515. https://doi.org/10.5962/bhl.part.79801.

Besuchet, C. (2008) Synonymies et combinations nouvelles, revalidations et description de taxa nouveau de Pselaphinae (Coleoptera: Staphylinidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **81**, 61–82.

Besuchet, C. & Hlaváč, P. (2011) Contribution to the knowledge of Clavigeritae (Coleoptera: Staphylinidae: Pselaphinae) from Fiji and Vanuatu, with the catalogue of Clavigeritae of Oceania. *Acta Entomologica Musei Nationalis Pragae*, **51**, 517–528.

Bryant, G.E. (1915) New species of Pselaphidae, sub-fam. Clavigerinae. *Entomologist's Monthly Magazine*, **51**, 211–215 + pl. 19.

Cammaerts, R. (1974) Le systeme glandulaire tegumentaire du coleoptere myrmecophile *Claviger testaceus* Preyssler, 1790 (Pselaphidae). *Zeitschrift für Morfologie der Tiere*, **77**, 187–219.

Cammaerts, R. (1992) Stimuli inducing the regurgitation of the workers of *Lasius flavus* (Formicidae) upon the myrmecophilous beetle *Claviger testaceus* (Pselaphidae). *Behavioral Processes*, **28**, 81–95. https://doi.org/10.1016/0376-6357(92)90051-E.

Cammaerts, R. (1996) Factors affecting the regurgitation behaviour of the ant *Lasius flavus* (Formicidae) to the guest beetle *Claviger testaceus* (Pselaphidae). *Behavioural Processes*, **38**, 297–312.

Cammaerts, R. (1999) Transport location patterns of the guest beetle *Claviger testaceus* (Pselaphidae) and other objects moved by workers of the ant, *Lasius flavus* (Formicidae). *Sociobiology*, **34**, 433–475.

Célis, M.-J. (1969) Contributions à l'étude des Clavigerinae de l'Afrique (Coleoptera Pselaphidae). 3. Démembrement des Fustigerini et création de deux tribus nouvelles ainsi que d'un genre inédit. *Revue de Zoologie et de Botanique Africaines*, **80**, 415–424.

Célis, M.-J. (1970) Contribution à l'étude des Clavigerinae de Madagascar (Coleoptera Pselaphidae). Clavigerinae recueillis par le Professeur Dr H. Franz et par M. J. Vadon. Remaniements apportés à la systématique des Clavigerinae malgaches. *Revue de Zoologie et de Botanique Africaines*, **82**, 237–270.

Célis, M.-J. (1974) Un Clavigérine remarquable de l'Ile de la Réunion (Coleoptera Pselaphidae). *Revue de Zoologie et de Botanique Africaines*, **88**, 771–774.

Chandler, D.S. (2001) Biology, morphology, and systematics of the ant-like litter beetles of Australia (Coleoptera: Staphylinidae: Pselaphinae). *Memoirs on Entomology International*, **15**, 1–560.

Coulon, G. (1982) Résultats de l'Expédition Biologique Belge au Mont Cameroun (1981). 2. Clavigerinae (Coleoptera, Pselaphidae). *Revue de Zoologie Africaine*, **96**, 75–78.

Dalman, J.W. (1826) Om insektar inneslutne i Copal; jemte beskrifning på några deribland förekommande nya slägten och arter. *Kongliga Vetenskaps-Academiens Handlingar*, **46**, 375–410 + pl. 5.

Donisthorpe, H. (1927) *The Guests of British Ants: Their Habits and Life Histories*. George Routledge & Sons, London.

Economo, E.P., Sarnat, E.M., Janda, M. *et al.* (2015) Breaking out of biogeography modules: range expansions and taxon cycles in the hyperdiverse genus *Pheidole*. *Journal of Biogeography*, **42**, 2289–2301. https://doi.org/10.1111/jbi.12592.

Edgar, R.C. (2004) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics*, **5**, 1–19. https://doi.org/10.1186/1471-2105-5-113.

Fikáček, M., Beutel, R.G., Cai, C. *et al.* (2020) Reliable placement of beetle fossils via phylogenetic analyses – Triassic *Leehermania* as a case study (Staphylinidae or Myxophaga?). *Systematic Entomology*, **45**, 175–187. https://doi.org/10.1111/syen.12386.

Fisher, B.L. & Peeters, C. (2019) *Ants of Madagascar: A Guide to the 62 Genera*. Association Vahatra, Antananarivo. 262 pp.

Giribet, G. & Baker, C.M. (2019) Further discussion on the Eocene drowning of New Caledonia: discordances from the point of view of zoology. *Journal of Biogeography*, **46**, 1912–1918. https://doi.org/10.1111/jbi.13635.

Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x.

Grandcolas, P., Murienne, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E. & Deharveng, L. (2008) New Caledonia: a very old Darwinian Island? *Philosophical Transactions of the Royal Society, B: Biological Sciences*, **363**, 3309–3317. https://doi.org/10.1098/rstb.2008.0122.

Grimaldi, D. & Agosti, D. (2000) A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of plants. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 13678–13683. https://doi.org/10.1073/pnas.240452097.

Hill, W., Akre, R. & Huber, J. (1976) Structure of some epidermal glands in the myrmecophilous beetle *Adranes taylori* (Coleoptera: Pselaphidae). *Journal of the Kansas Entomological Society*, **49**, 367–384.

Hlaváč, P. (2010) *Kurbatoviella antennata*, a new peculiar genus and species of the Clavigeritae from Borneo (Coleoptera: Staphylinidae: Pselaphinae). *Acta Entomologica Musei Nationalis Pragae*, **50**, 471–475.

Hlaváč, P. (2011) Contribution to the knowledge of the tribe Mastigerina [sic] (Coleoptera: Staphylinidae: Pselaphinae, Clavigeritae), with a description of new genus from Borneo. *Zootaxa*, **3070**, 51–59. https://doi.org/10.11646/zootaxa.3070.1.6.

Hlaváč, P., Baňař, P. & Parker, J. (2013) The Pselaphinae of Madagascar. II. Redescription of the genus *Semiclaviger* Wasmann, 1893 (Coleoptera: Staphylinidae: Pselaphinae: Clavigeritae) and synonymy of the subtribe Radamina Jeannel, 1954. *Zootaxa*, **3736**, 265–276. https://doi.org/10.11646/zootaxa.3736.3.4.

Hlaváč, P. & Nakládal, O. (2016) The Pselaphinae (Coleoptera: Staphylinidae) of Madagascar. IV. Contribution to the subtribes Hoplitoxenina and Dimerometopina with description of a new species of *Hadrophorus* Fairmaire, 1898. *Zootaxa*, **4105**, 274–284. https://doi.org/10.11646/zootaxa.4105.3.4.

Hlaváč, P. & Nakládal, O. (2018) *Seychelister*, new genus and species of Clavigeritae (Coleoptera, Staphylinidae, Pselaphinae) from Seychelles. *Zootaxa*, **4450**, 293–296. https://doi.org/10.11646/zootaxa.4450.2.9.

Hope, F.W. (1836) Observations on succinic insects. *Transactions of the Entomological Society of London*, **1**, 133–147.

Jałoszynski, P., Luo, X.G. & Beutel, R.G. (2020) Profound head modifications in *Claviger testaceus* (Pselaphinae, Staphylinidae, Coleoptera) facilitate integration into communities of ants. *Journal of Morphology*, **281**, 1072–1085.

Jeannel, R. (1949) Les Psélaphides de l'Afrique orientale. *Mémoires du Muséum National d'Histoire Naturelle*. *Zoology*, **29**, 1–226.

Jeannel, R. (1954) Les Psélaphides de Madagascar. *Mémoires de l'Institut Scientifique de Madagascar*, **4**, 139–344.

Jeannel, R. (1959) Révision des Psélaphides de l'Afrique intertropicale. *Annales du Musée Royal du Congo Belge, 8vo Série*, **75**, 1–742.

Jennings, J.T., Krogmann, L. & Burwell, C. (2013) Review of the hymenopteran fauna of New Caledonia with a checklist of species. *Zootaxa*, **3736**, 1–53. https://doi.org/10.11646/zootaxa.3736.1.1.

Kistner, D.H. (1982) The social insects' bestiary. *Social Insects*, Vol. **3** (ed. by H.R. Hermann), pp. 1–244. Academic Press, New York, New York.

Krause, D.W., Sertich, J.J.W., O'Connor, P.M., Curry Rogers, K. & Rogers, R.R. (2019) The Mesozoic biogeographic history of Gondwanan terrestrial vertebrates: insights from Madagascar's fossil record. *Annual Review of Earth and Planetary Sciences*, **47**, 519–553. https://doi.org/10.1146/annurev-earth-053018-060051.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, **34**, 772–773. https://doi.org/10.1093/molbev/msw260.

LaPolla, J.S., Dlussky, G.M. & Perrichot, V. (2013) Ants and their fossil record. *Annual Review of Entomology*, **58**, 609–630. https://doi.org/10.1146/annurev-ento-120710-100600.

Leach, W.E. (1815) Entomology. *Edinburgh Encyclopaedia*, Vol. **9** (ed. by D. Brewster), pp. 57–172. William Blackwood, Edinburgh.

Lewis, P.O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, **50**, 913–925. https://doi.org/10.1080/106351501753462876.

Liu, C., Sarnat, E.M., Friedman, N.R. *et al.* (2020) Colonize, radiate, decline: unravelling the dynamics of islands community assembly with Fijian trap-jaw ants. *Evolution*, **74**, 1082–1097. https://doi.org/10.1111/evo.13983.

Löbl, I. (1994) The systematic position of Colilodionini with description of a new species (Coleoptera, Pselaphinae). *Revue suissse de Zoology*, **101**, 289–297.

Lü, L., Cai, C.-Y., Xi, Z., Newton, A.F., Thayer, M.K. & Zhou, H.-Z. (2020) Linking evolutionary mode to paleoclimate change reveals rapid radiations of staphylinoid beetles in low-energy conditions. *Current Zoology*, **66**, 435–444. https://doi.org/10.1093/cz/zoz053.

Lynch, M. (2007) The frailty of adaptive hypotheses for the origins of organismal complexity. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 8597–8604. https://doi.org/10.1073/pnas.0702207104.

Maddison, W.P. & Maddison D.R. (2019) *Mesquite: a modular system for evolutionary analysis*. Version 3.61. URL http://www.mesquiteproject.org

Matos-Máravi, P., Clouse, R.M., Sarnat, E.M. *et al.* (2018) An ant genus-group (*Prenolepis*) illuminates the biogeography and drivers of insect diversification in the Indo-Pacific. *Molecular Phylogenetics and Evolution*, **123**, 16–25. https://doi.org/10.1016/j.ympev.2018.02.007.

Maruyama, M. & Parker, J. (2017) Deep-time convergence in rove beetle symbionts of army ants. *Current Biology*, **27**, 920–926. https://doi.org/10.1016/j.cub.2017.02.030.

Moore, W. & Robertson, J.A. (2014) Explosive adaptive radiation and extreme phenotypic diversity within ant-nest beetles. *Current Biology*, **24**, 2435–2439. https://doi.org/10.1016/j.cub.2014.09.022.

Nakládal, O. & Hlaváč, P. (2018) New species and records of Clavigeritae (Coleoptera: Staphylinidae: Pselaphinae) from Africa and Asia. *Zootaxa*, **4402**, 595–600. https://doi.org/10.11646/zootaxa.4402.3.12.

Nattier, R., Pellens, R., Robillard, T. *et al.* (2017) Updating the phylogenetic dating of New Caledonian biodiversity with a meta-analysis of the available evidence. *Scientific Reports*, **7**, 3705. https://doi.org/10.1038/s41598-017-02964-x.

Newton, A.F. Jr & Chandler, D.S. (1989) World catalog of the genera of Pselaphidae (Coleoptera). *Fieldiana: Zoology, (N.S.)*, **53**, 1–93. https://doi.org/10.5962/bhl.title.3209.

Newton, A.F. Jr & Thayer, M.K. (1995) Protopselaphinae new subfamily for *Protopselaphus* new genus from Malaysia, with a phylogenetic analysis and review of the Omaliine Group of Staphylinidae including Pselaphidae (Coleoptera). *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*, Vol. **1** (ed. by J. Pakakuk and S.A. Slipinski), pp. 219–320. Muzeum i Instytut Zoologii PAN, Warszawa.

Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, **32**, 268–274. https://doi.org/10.1093/molbev/msu300.

Nixon, K.C. (2002) *WinClada, version 1.00.08*. Published by the author, Ithaca, New York.

Park, O. (1932) The myrmecocoles of *Lasius umbratus mixtus aphidicola* Walsh. *Annals of the Entomological Society of America*, **25**, 77–88. https://doi.org/10.1093/aesa/25.1.77.

Park, O. (1942) *A study in Neotropical Pselaphidae*. Northwestern University, Evanston and Chicago, Illinois. https://doi.org/10.5962/bhl.title.6838.

Parker, J. (2016a) Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. *Myrmecological News*, **22**, 65–108.

Parker, J. (2016b) Emergence of a superradiation: pselaphine rove beetles in mid-Cretaceous amber from Myanmar and their evolutionary implications. *Systematic Entomology*, **41**, 541–466. https://doi.org/10.1111/syen.12173.

Parker, J. & Grimaldi, D.A. (2014) Specialized myrmecophily at the ecological dawn of modern ants. *Current Biology*, **24**, 2428–2434. https://doi.org/10.1016/j.cub.2014.08.068.

Preyssler, J.D. (1790) *Verzeichniß Böhmischer Insekten*. Schönfeld-Meissnerischen Buchhandlung, Prag, 108 pp. + 2 pls.

R Core Team (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raffray, A. (1904a) Genera et catalogue des Psélaphides. *Annales de la Société Entomologique de France*, **72**, 484–604.

Raffray, A. (1904b) Genera et catalogue des Psélaphides. *Annales de la Société Entomologique de France*, **73**, 1–400.

Raffray, A. (1905a) Genera et catalogue des Psélaphides. *Annales de la Société Entomologique de France*, **73**, 401–476 + pls. 1–3.

Raffray, A. (1905b) Genera et catalogue des Psélaphides. *Addenda. Annales de la Société Entomologique de France*, **73**, 634–658.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, **67**, 901–904. https://doi.org/10.1093/sysbio/syy032.

Reitter, E. (1882) Versuch einer systematischen Eintheilung der Clavigeriden und Pselaphiden. *Verhandlungen der Naturforschenden Vereines in Brünn*, **20**, 177–211.

Reitter, E. (1885) Ueber die bekannten Clavigeriden-Gattungen. *Deutsche Entomologische Zeitschrift*, **38**, 167–168.

Ronquist, F., Teslenko, M., van der Mark, P. *et al.* (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**, 539–542. https://doi.org/10.1093/sysbio/sys029.

Royden, L.H., Burchfiel, C. & van der Hilst, R.D. (2008) The geological evolution of the Tibetan Plateau. *Science*, **321**, 1054–1058. https://doi.org/10.1126/science.1155371.

Saulcy, F. (1874) Species des paussides, clavigérides, psélaphides & scydménides de l'Europe et des pays circonvoisins. *Bulletin de la Société d'Histoire Naturelle de Metz*, **13**, 1–132.

Schaufuss, L.W. (1872) Tabellen-Entwurf zur Bestimmung der Pselaphiden-Gattungen. *Nunquam Otiosus*, **2**, 243–248.

Schaufuss, L.W. (1890) System-Schema der Pselaphiden, ein Blick in die Vorzeit, in die Gegenwart und in die Zukunft. *Tijdschrift voor Entomologie*, **33**, 101–162 + pls 2–6.

Verma, O., Khosla, A., Goin, F.J. & Kaur, J. (2016) Historical biogeography of the Late Cretaceous vertebrates of India: comparison of geophysical and paleontological data. *Cretaceous period: biotic diversity and biogeography*, Vol. **71** (ed. by A. Khosla and S.G. Lucas), pp. 317–330. Albuquerque, New Mexico, USA: *New Mexico Museum of Natural History & Science Bulletin*.

Ward, D.F. & Wetterer, J.K. (2006) Checklist of the ants of Fiji (Hymenoptera: Formicidae). *Fiji Arthropods III*, Vol. **85** (ed. by N.L. Evenhuis and D.J. Bickel), pp. 23–47. Honolulu, Hawaii, USA: *Bishop Museum Occasional Papers*.

Zhou, Y.L., Ślipiński, A., Ren, D. & Parker, J. (2019) A Mesozoic clown beetle myrmecophile (Coleoptera: Histeridae). *eLife*, **8**, e44985. https://doi.org/10.7554/eLife.44985.

Accepted 7 January 2021