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Research Article

Facing the taxonomic impediment — a reassessment of *Merulanella* Verhoeff, 1926 (Oniscidea, Armadillidae) through historical specimens

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Abstract

The taxonomic impediment has been identified as a problem for conservation biology since 1988. Although several measures have been developed to overcome it, major non-specialized scientific publishers have not fully addressed it. One of the more challenging solutions relies on the identification of taxonomic needs and priorities hampered by the scarcity and inaccessibility of resources. Currently, publishers often consider taxonomy on its own not worth publishing unless supplementary to additional work, such as genetic analyses, pushing publication to a restricted space in specialized journals. A revision of the terrestrial isopod genus *Merulanella*, through the literature and historical specimens, shows that taxonomies outlined before the development of certain key concepts in evolutionary biology need to be urgently revisited before new studies are done on them. Furthermore, some species in this genus are considered endangered due to the pet trade, albeit they are not included on the IUCN Red List. The taxonomy of the genus *Merulanella* was developed before and during the development of zoogeography and before the modern concept of vicariance, explaining the wide distribution of this genus with seven species spanning over three biogeographic realms: *M. carinata*, *M. wahrbergi*, *M. dollfusi* (Australasia), *M. bicolorata*, *M. gibbera*, *M. latissima* (Indomalay), and *M. peltata* (Afrotropics). After revising the literature, the context of the produced taxonomy, and assessing the type material, first-hand and through photographs, the morphological dissimilarity justifies restricting *Merulanella* to the species from New Caledonia (Australasian realm), namely *M. carinata*, *M. wahrbergi*, and *M. dollfusi*. A new genus is proposed for the species from Flores, Indonesia, erecting *Floresiodillo gibberum* **gen. et comb. nov.**, and *F. latissimus* **gen. et. comb. nov.**, a new genus is erected for the species in Myanmar, *Ardentiellabicolorata*, **gen. et comb. nov.** and *A. caerulea* **gen. et comb. nov.** (both in the Indomalayan realm), and a new genus is erected for the species in Seychelles, *Acutodillo peltatus* **gen. et comb. nov.** (Afrotropical realm). Further studies will be needed to determine the phylogenetic relationships between these new genera and the history of their distribution. Still, this new framework better captures the diversity of the family Armadillidae for its conservation.

Key words: Afrotropics, Australasia, Indomalaya, terrestrial isopods, woodlice

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Introduction

Taxonomic impediment

The taxonomic impediment was first identified as a problem of global concern in the Darwin Declaration of 1988 (Environment Australia 1998). It was emphasized as the biggest challenge to conservation during the Earth Summit in Rio de Janeiro in 1992 when the Convention on Biological Diversity was opened for signature (Convention on Biological Diversity 2008; Coleman 2015). The taxonomic impediment was diagnosed as the main challenge to the management of biological diversity since the lack of knowledge on the taxonomic composition of the biota within the boundaries of the signatory parties led to the inability to introduce and enforce policies to protect their biological diversity effectively. At the core of the taxonomic impediment lies the fact that there are far too few taxonomists to identify organisms in collections and databases worldwide. The taxonomic impediment can be understood as a threefold issue: 1) there are large gaps in taxonomic knowledge, 2) there are insufficient human resources, such as the number of trained experts for respective groups being insufficient, 3) the taxonomic infrastructure does not meet the demand, with too few reference collections and lack of resources to develop taxonomy as a career. The Guide to Global Taxonomy Initiative (GTI), published in 2008, proposed several solutions to overcome the taxonomic impediment (Convention on Biological Diversity 2008): 1) identify taxonomic needs and priorities; 2) develop and strengthen human capacity to generate taxonomic information; 3) develop and strengthen infrastructure and mechanisms for generating taxonomic information, and for facilitating sharing of and access to that information; and 4) provide taxonomic information needed for decision-making regarding the conservation of biological diversity, sustainable use of its components, and the fair and equitable sharing of benefits arising out of the utilization of genetic resources. In this paper, we use a case study to propose how scientific publishers can recognize taxonomic needs and priorities.

The GTI was directed towards specific groups that could contribute strategically to solve the taxonomic impediment: governments and government departments, taxonomic institutions, individual taxonomists, conservationists, and funding bodies. In general, it was clear that, at the time of drafting the GTI, taxonomy was considered an afterthought for which resources were not always allocated a priori. Interestingly, scholarly publishers were not mentioned in the GTI of 2008, even though their role was tacitly outlined. For instance, it was acknowledged that one of the key components of the taxonomic impediment is the slowness of the publication of taxonomic guides and national inventories, of national assessments of regional taxonomic needs, of the assessments of national capacity-building, and of catalogues providing the location of type specimens. The interest in the taxonomic impediment started to wane towards the mid-2010s, even if the problem was not really addressed in any international or supranationally concerted way.

In terms of resources, taxonomic literature is the most common problem for the few experts in any group. Many of the resources are behind a paywall and are inaccessible to unaffiliated taxonomists. To describe a new species, taxonomic literature on all the previously identified species is needed. The first problem is that there are many deficiencies in the literature, such as poor or outdated descriptions, lack of illustrations, missing information on or total loss of the type material. This problem is compounded by the fact that there are few or no experts in many groups, thus making taxonomic discussions or revisions even scarcer; moreover there is a lack of interest in the field and a desire for automation (De Carvalho et al. 2007). Scholarly publishers have made the publishing of taxonomic keys, discussions, or revisions a more costly endeavor (Maxted 1992). Outside of specialized taxonomic journals, taxonomy on its own is not always published, and when it is published, it is always a complement to other types of analyses; furthermore, the decentralized nature of taxonomic publications makes it incredibly difficult and costly to index (Page 2016). Therefore, it is hard to diagnose the size of the taxonomic impediment if there is not total access to the literature and a wide view of the current knowledge of the group.

As with anything, interest in certain groups changes over time, and even before the taxonomic impediment was formally recognized in the political sphere, it has always been the center of attention for taxonomists. For instance, Barnard (1958) highlighted the unfavorable conditions that amphipod taxonomists in the United States faced, which included low-paying or non-existing positions in museums and the lack of trained personnel, unlike in the Soviet Union, where amphipod taxonomy was blooming. Barnard (1958) forecasted that by the 1980s, there would be a decline in amphipod taxonomy; luckily, his prediction was not fulfilled, as within the next decades, several publications brought amphipodology to the fore with several monographs (Coleman 2015). Nevertheless, taxonomists have acknowledged the taxonomic impediment as a problem for at least one century.

Taxonomic revisions

A decade ago, the number of described species of terrestrial isopods (woodlice) had plateaued. Between the publication of Schmalfuss (2003) and Sfenthourakis and Taiti (2015), a total of 80 new species were described. Sfenthourakis and Taiti (2015) identified two peaks of species discovery and description for terrestrial isopods: one in the 1920s and another one in the 1960s. These two peaks of discovery are interesting because they are all previous to plate tectonics and historical biogeography (de Queiroz 2005). During that time, we changed our concept of species from a fixist framework to conceiving them as lineages (phylogenetics) and from lineages evolving on static continents to lineages evolving along drifting ones (Barberousse and Samadi 2010; Allmon 2013). Taxonomy is in constant revision as new taxa are defined or recognized in nature — in that way, it is more useful to follow the idea of taxonomy as a map-making activity, where taxonomists are constantly revising the patterns found in nature as our understanding of nature itself changes (Dupré 2001; Thiele et al. 2021).

The first iteration of this publication, for instance, initially submitted elsewhere, was rejected on the grounds that the current revision required genetic analysis. People outside of taxonomy need to acknowledge that for the taxonomic impediment to be addressed, any taxonomic revision that adds to the understanding of biological diversity needs to be published, particularly of species whose naming occurred centuries ago (De Carvalho et al. 2007). The value that has been given to genetic analyses has also exacerbated the taxonomic impediment and can make things more unnecessarily difficult when a genus revision may be possible due to pronounced morphological differences between its constituent species. While certainly not universally applicable —

particularly within groups containing closely related species characterized by subtle morphological variation and close geographic distribution — it is suitable for historically erected groups, most of the time on a highly artificial basis, expressing significant morphological and biogeographical differences.

The taxonomic impediment has manifested itself in genetic archives as well. For instance, online archives of DNA sequence data receive samples without taxonomic identification, creating “dark taxa.” Dark taxa have increased steadily in GenBank since 2010, and, in the case of fungi, DNA samples suggest that only about 10% of the diversity is represented in formal taxonomy (Page 2016).

During the 19th century, taxonomists largely followed the method developed by Carl Linnaeus of using the *differentium*, meaning that the definition of a species should be based on a short diagnosis that separated it from all other taxa (Genus-differentia definition), based on several “principal members” (Witteveen 2016, 2020). Towards the end of the 19th century and the beginning of the 20th century, the need to tie names to a specimen started to grow as the natural collections steadily grew (Farber 1976). Natural collections started to label their specimens and identify collection-type specimens, where each served as a name carrier that contained the characteristics of the species. During the 19th century, taxidermic and preservation techniques advanced, gradually replacing alcohol preservation, and towards the end of that century, several taxidermy and collection-type specimens were established in the literature (Farber 1976). The type-specimen method was quickly adopted as it became the most objective way to define a species: the first specimen described with its narrow variability as a representative of a whole population opposite to a descriptive plaque that was often open to interpretation. The type-specimen concept, however, meant that the collections in Europe and North America became the index of the diversity of all the colonial territories.

With the independence movements of the second half of the 20th century, the type specimens in collections in museums and other institutions became politically disconnected from the population they were extracted from. The GTI recognized the location of type specimens as one of the main dimensions of the taxonomic impediment (Convention on Biological Diversity 2008); studying taxonomy in former colonial territories requires a physical visit to the collections in the former metropoles (Monarrez et al. 2022; Raja et al. 2022; Park et al. 2023). Furthermore, institutions and museums had lists of species without a complete catalogue attached to them, and most institutions holding the type specimens do not have the resources to digitize specimen information and compile the literature where the type specimens were used (Convention on Biological Diversity 2008).

The National Commission for the Knowledge and Use of Biodiversity in Mexico (CONABIO) developed a model that could be used to help countries determine what species had already been recorded in the literature. CONABIO staff were sent to institutions abroad to repatriate or digitize information about the type species (Convention on Biological Diversity 2008). Taxonomists in Mexico benefited from this by understanding the diversity recorded so far within the country, and holder institutions benefitted by acquiring a database about specimens for which they lacked resources in terms of experts, money, justification or time to achieve. However, before this step can be reached, it is important to have publicly available catalogues in one way or another. This taxonomic revision of the genus *Merulanella* is based on historical specimens and we see this as a step in that direction.

The genus *Merulanella* Verhoeff, 1926

Within Isopoda Latreille, 1816, the section Crinocheta Legrand, 1946, within the suborder Oniscidea Latreille, 1802, contains 29 families and about 3069 species distributed in 415 genera as per the World Register of Marine Species (WoRMS) check-list checked in August 2024 — the Catalogue of Life was at the time not yet updated as it missed the new species published that year that were present in WoRMS (Ahyong et al. 2024). The family Armadillidae Brandt in Brandt and Ratzeburg 1831, is the most diverse in the section, totaling 678 species distributed in 81 accepted valid genera, nearly 22% of the species in the section. The maximum number of species within a single genus in Armadillidae is 140 (*Venezillo* Verhoeff, 1928), but a total of 40 genera (roughly 50%) are mono- or bispecific. The more speciose genera are *Venezillo*, *Spherillo* Dana, 1853 (68 species) and *Cubaris* Brandt, 1833 (62), with the next more speciose genera containing at most 28 species. This species richness might be an indication that the genera need revision. For instance, the type genus *Armadillo* Latreille, 1802, currently contains 28 species, from the previously 179 accepted species referred to as *Armadillo*. Nonetheless, the median number of species per genus in the family is seven, with four genera—*Myrmecodillo* Arcangeli, 1934, distributed between Reunion, South Africa and Australia; *Pyrgoniscus* Kinahan, 1859, distributed between Madagascar, New Caledonia, Australia and New Zealand; *Tuberillo* Schutz, 1982, found in Lao and Fiji, and *Merulanella* Verhoeff, 1926, distributed between Myanmar, New Caledonia, Seychelles and the southern Pacific Ocean—having this number. Interestingly, these four genera were proposed at the time when the region was being characterized as a biological transition zone of its own, a geographical overlap between the Australasian and Indomalayan biogeographic realms where there are different degrees of interchange or isolation of taxa. Here, historical specimens of *Merulanella* are reinterpreted, and the morphological differences are explained in biogeographic terms.

While biogeographical patterns and taxonomic revisions provide insights into the distribution and classification of terrestrial isopods, conservation assessments are equally essential for understanding the threats these species face. The International Union for Conservation of Nature (IUCN)'s Red List offers an assessment of the conservation status of some terrestrial isopods, though it highlights significant gaps in knowledge and, more notably, representation. The IUCN Red List currently includes 14 members of the suborder Oniscidea, with 1 species considered as critically endangered, 3 as endangered, 5 vulnerable, 3 near threatened, and 2 data deficient. Population trends are available for only 4 of these species. Notably, species that are well-known to be threatened, such as practically all of the species contained in the family Delatorreiidae (Rodríguez Cabrera and De Armas 2016), are absent from the IUCN Red List. Thus, the listed species likely represent a miniscule fraction of the nearly 4,000 described terrestrial isopod species, with a substantial number of species yet to be formally described. Although other genera in the family Armadillidae span multiple biogeographic realms and are certainly in need of revision, the genus *Merulanella* is herein treated due to its manageable size and conservation concerns arising from exploitation and possible overcollection due to high demand for the genus in the invertebrate pet trade.

Currently, the genus *Merulanella* comprises seven species with a wide range of distribution: *M. bicolorata* (Budde-Lund, 1895), (Myanmar), *M. carinata* Verhoeff, 1926 (New Caledonia), *M. wahrbergi* Verhoeff, 1926 (New Caledonia), *M. peltata* (Budde-Lund, 1904) (Seychelles), *M. dollfusi* (Stebbing, 1900) (southern Pacific Ocean), *M. gibbera* Herold, 1931 (Indonesia), and *M. latissima* Herold, 1931 (Indonesia). *Merulanella*, thus, spans over three biogeographic realms: the Australasian, the Indomalayan and the Afrotropical. The genus was defined and expanded at a time when biogeography was mostly explained through two schools of thought: dispersalism and extensionism. The former considered that rare events of migration or dispersion led to organisms living in disconnected areas of land, whereas the latter considered that the presence of groups separated by land bodies was evidence of submerged land bridges. In the case of *Merulanella*, the dispersalist approach would suppose an origin in the Indochina peninsula towards the islands in the Indan and Pacific Oceans. On the other hand, the taxonomy of several species in this region was underpinned by the possibility of the existence of the now-submerged land of Lemuria, which was hypothesized to have connected the coasts of Africa, India, Southeast Asia, and Australia (Hallam 1967). However, the model of *Merulanella* now implies a very old lineage whose origin can be traced back to 90 million years ago before the Indomalayan and Australasian realms diverged.

Merulanella was erected in 1926 by Karl Verhoeff based on the morphology of what he considered two species from New Caledonia: *Merulanella carinata* Verhoeff, 1926 and *Merulanella wahrbergi* Verhoeff, 1926. Regardless, Verhoeff never provided a concise diagnosis for *Merulanella* and the characters are scattered over the relatively large publication in the form of comparisons and an identification key, albeit with sparse illustrations. Later in the same publication, Verhoeff includes *Cubaris dollfusi* Stebbing, 1900, from the Loyalty Islands, New Caledonia, as part of the genus *Merulanella*. Out of the characters initially mentioned by Verhoeff, Herold (1931) highlighted the frontal shield and the strongly keeled pleotelson as the most diagnostic characters of *Merulanella* and included two additional species from the Island of Flores: *Merulanella gibbera* Herold, 1931, and *Merulanella latissima* Herold, 1931. Both of his species feature a vastly different morphology of the frontal shield, which he acknowledged himself, and neither of his species has a delta-shaped pleotelson. Nevertheless, the distribution of the genus was consistent with the assumption of the original Wallace line (as modified by Huxley) that included the island of Flores, along with all the Lesser Sundas islands and the Philippines, as part of the faunal balance with the Great Australian Bank, now known as Sahul Shelf, along with the archipelago of New Caledonia (Earle 1845; Mayr 1944; Prasetya et al. 2023).

The taxonomic composition of *Merulanella* expanded in subsequent years. In 1946, "*Spherillo peltatus*" Budde-Lund, 1904, from Seychelles, and later on in 1983 "*Spherillo bicoloratus*" Budde-Lund, 1895 were transferred to *Merulanella* (Vandel 1946; Ferrara and Taiti 1979). Verhoeff (1926) acknowledged the morphological similarities between both species of *Spherillo* and *Merulanella* in his "*Isopoda terrestria von Neu-Caledonien und den Loyalty-Inseln*" but notes that both species, representing Budde-Lund's Sectio XI, are remarkably different to the *Merulanella* species he described. This taxonomic confusion is common to many taxa described by Verhoeff (Schmalfuss 2018). Although this model of a Seychelles to Lesser Sunda Islands distribution was still consistent with the notion of the African-Indian Isthmus proposed during the 1930s (Hallam 1967), it failed to acknowledge that New Caledonia would be in a different zoogeographic zone regardless of where the Wallace line was placed. The present revision proposes a new taxonomic system consistent with current biogeographic models for Southeast Asia, Australasia and the Indian Ocean (Fig. 1), and it offers a new framework to produce better population genetic experiments in the future.

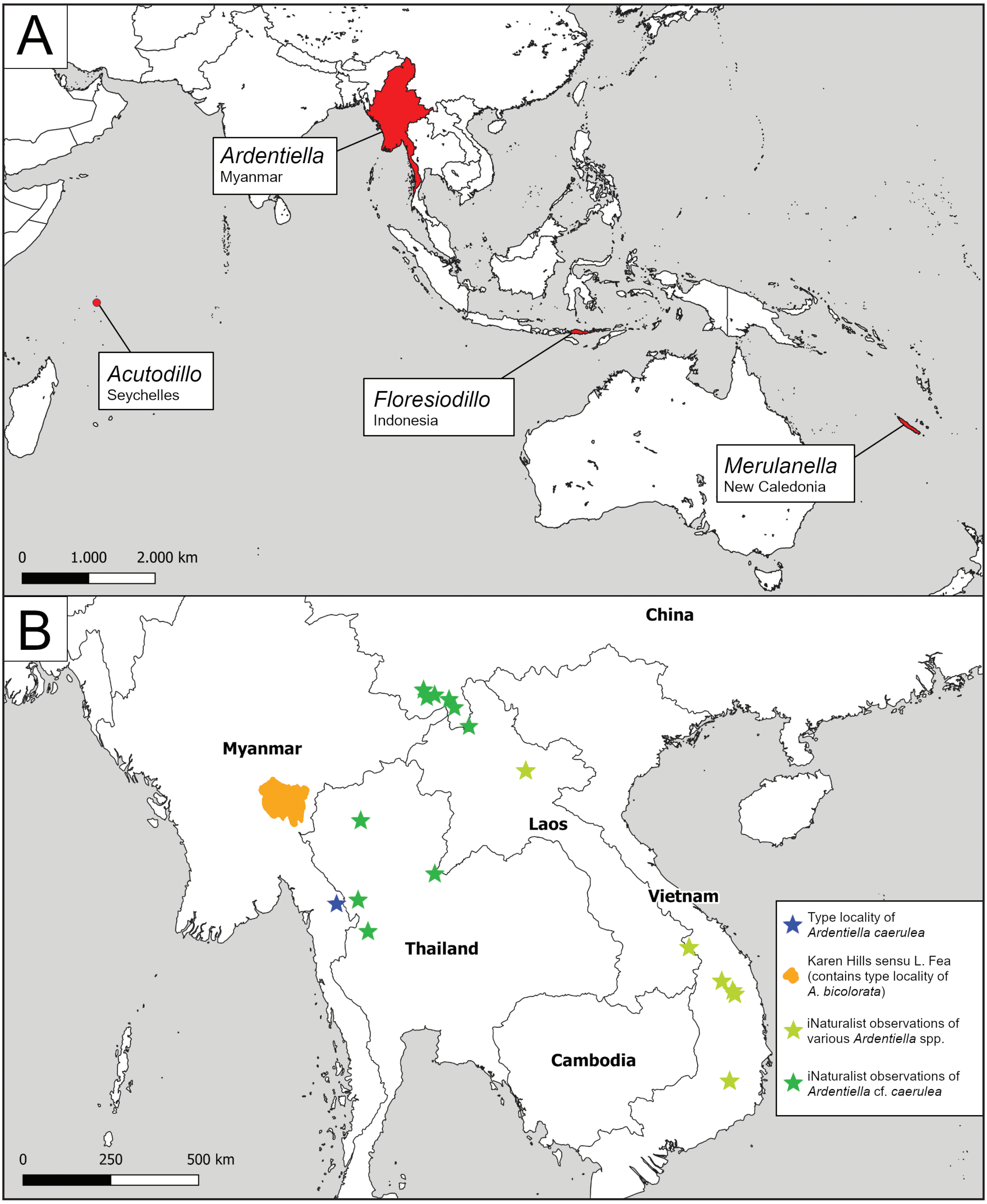

Figure 1. A Distribution of the genera mentioned in this work. Only described species were taken into account **B** distribution of *Ardentiella* gen. nov. species. Boundaries of the Karen Hills sensu L. Fea taken from Bolotov et al. (2019). Observations of *Ardentiella* cf. *caerulea* (Collinge, 1914), comb. nov. and *Ardentiella* spp. taken from iNaturalist (2024a, 2024b). Records very close to each other were combined into a single marker.

Material and methods

We revised the terrestrial isopod genus *Merulanella* Verhoeff, 1926, based on historical specimens deposited in European collections, published literature, and using non-destructive morphological analyses. Some specimens were assessed first-hand (indicated as pers. obs. in the text) and some were assessed through photographs of the specimens provided by the respective collection managers upon request (see text in each taxon for further details).

The taxonomic composition was downloaded from the World Register of Marine Species. Maps were created with QGIS (http://www.qgis.org). Photographs captured by Benedikt Kästle (author) were taken with a Canon EOS 60D and a Canon EF-S 60mm f/2.8 USM Macro Lens.

Institutional abbreviations:

NHMUK	Natural History Museum London (BMNH, old abbreviation)
MSNG	Museo Civico di Storia Naturale Genova
NMB	Naturhistorisches Museum Basel
ZMB	Museum für Naturkunde Berlin
ZMH	Zoologisches Museum Hamburg
ZSIC	Zoological Survey of India

Table 1. Overview of the species treated in this work with the institutions where specimens are deposited. In this table, *Ardentiella* sp. 1 is listed under *Ardentiellabicolorata*, see text for further discussion. When collection data is not known, it is indicated with "n. d.".

Species	Institution	Collection number	Composition (collector, date)
Merulanella carinata	NMB	NMB-131 a–c	a: 3 specimens b: 2 specimens c: 2 specimens (F. Sarasin and J. Roux 1911)
Merulanella wahrbergi	NMB	NMB-132 a	5 specimens (F. Sarasin and J. Roux 1911)
Merulanella dollfusi	?	?	(Willey n. d.)
Floresiodillo gibberum	ZMB	ZMB-CRUST-22987	2 specimens (B. Rensch 1927)
Floresiodillo latissimus	ZMB	ZMB-CRUST-23015	7 specimens (B. Rensch 1927)
Acutodillo peltatus	BMNH	BMNH 1921.10.18.906-907	2 specimens (A. Brauer, n. d.)
*Ardentiella bicolorata**	BMNH	BMNH 1921.10.18.808-813	6 specimens (L. Fea 1885–1889)
	ZMB	ZMB-CRUST-8615	5 specimens (L. Fea 1885–1889)
	ZMH	16851	3 specimens (L. Fea 1885–1889)
	MSNG	Catalogue number not confirmed	Unknown specimen count (L. Fea 1885–1889)
Ardentiella caerulea	ZSIC	Catalogue number not confirmed	Unknown specimen count (F. H. Gravely 1911)

Results

Order Isopoda Latreille, 1816
Suborder Oniscidea Latreille, 1802
Family Armadillidae Brandt, 1831

***Merulanella* Verhoeff, 1926**

Type species. *Merulanella carinata* Verhoeff, 1926, by subsequent designation in Jackson (1941).

Distribution. New Caledonia.

Diagnosis. Dorsum smooth or with rugose muscle spots, epimera of pereon and pleon dorsally with transverse ridges. Cephalothorax with frontal shield protruding above vertex; lamina of frontal shield convexly rounded in dorsal view. Antennae long and slender. Pereonites 1–3 epimera with a small ventral lobe. Pereonites 2–7 epimera rectangular. Pleotelson strongly keeled, medially at least as wide as distally, and with triangular terminal portion. Uropod exopodite reaching posterior margin of protopodite, inserted dorsally, close to medial margin and covered basally by dorsomedial lobe. Endopodite not reaching posterior margin of protopodite. Noduli laterales more or less in straight line, except on pereonite 1 situated further medially.

Remarks. Verhoeff (1926) provided a key to the 2 species discussed here, namely *M. carinata*, and *M. wahrbergi*. *M. dollfusi* is added in a footnote to the genus but not included in the key. The cephalothorax with frontal shield protruding above the vertex is medially only shortly protruding in *M. wahrbergi* and *M. dollfusi*.

***Merulanella carinata* Verhoeff, 1926**

Figs 2A, 3, 4

Merulanella carinata Verhoeff, 1926: 308 (in key), 308–309, figs 71–73.
Merulanella carinata – Jackson, 1941: 18. — Schmalfuss 2003: 157. — Schmidt and Leistikow 2004: 53.
Pyrgoniscus carinatus – Lillemets & Wilson, 2002: 86, 90.

Material examined. ***Lectotype*** (by present designation; table 1) NEW CALEDONIA • 1 ♀; in alcohol; Grande Terre, Poindimié, Négropo Valley; 03. Mar. 1912; F. Sarasin, J. Roux leg.; [assessed through photos] NMB-131 b.

Paralectotypes (table 1) NEW CALEDONIA • 3 ♀♀; 1 in alcohol, 1 dry pinned, 1 slide; New Caledonia, Grande Terre, North Province, Canala; 30. Oct. 1911; F. Sarasin, J. Roux leg.; [assessed through photos]; NMB-131 a • 1 ♀; dry pinned; same data as Lectotype; [assessed through photos]; NMB-131 b • 2 ♀♀; 1 in alcohol, 1 dry pinned; Grande Terre, South Province, La Foa; 16. Jan. 1911; F. Sarasin, J. Roux leg.; [assessed through photos]; NMB-131 c.

Type locality. Négropo Valley, North Province, Grande Terre, New Caledonia.

Diagnosis. Pereon epimera almost horizontally oriented, flattened habitus. Flagellum of antenna with second article about as long as first article. Pleotelson as wide as long. Uropod protopodite elongate.

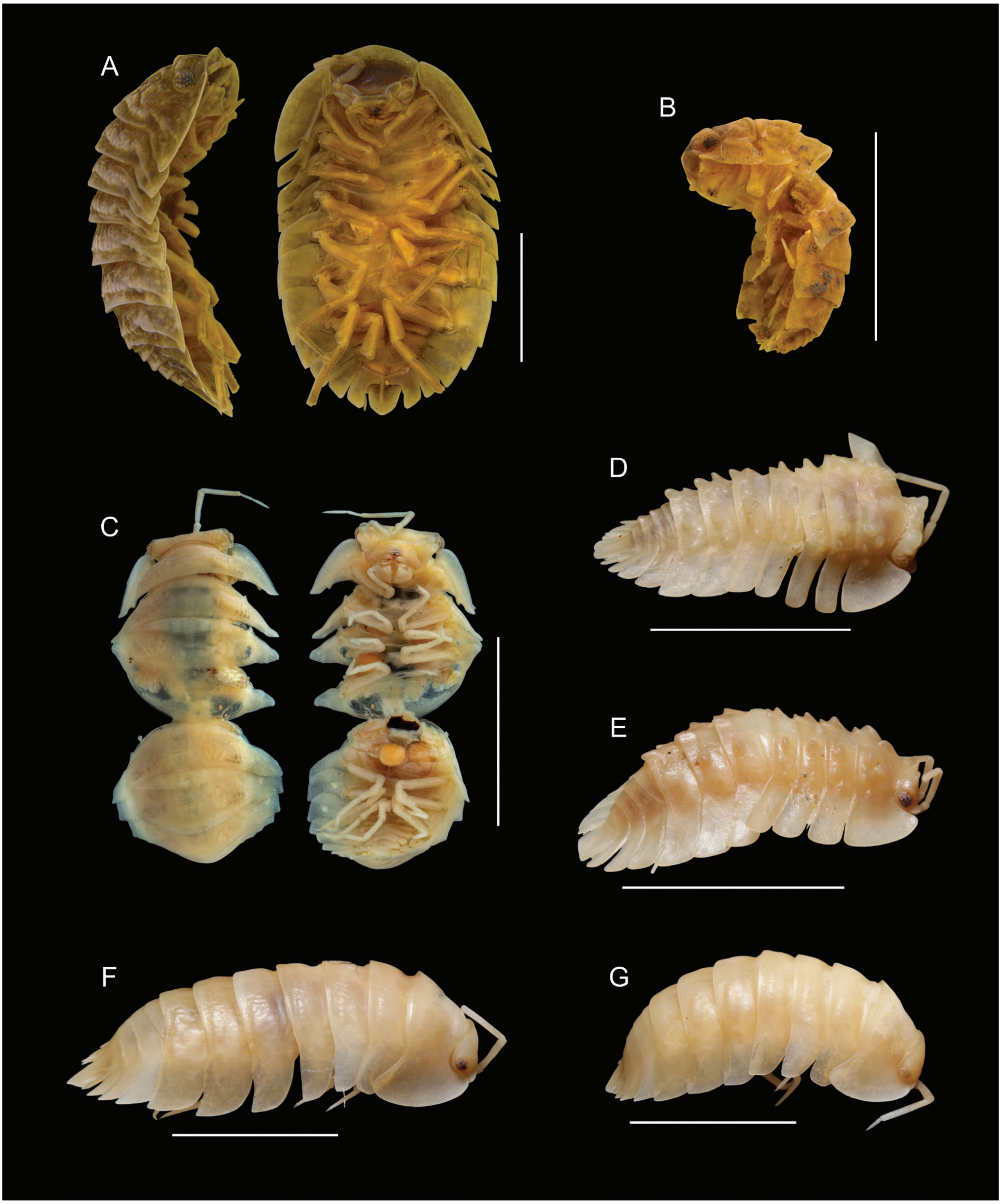

Figure 2. Type material of the different species: **A** *Merulanella carinata* Verhoeff, 1926 Lectotype NMB-131b (Photo: Holger Frick) **B** *Merulanella wahrbergi* Verhoeff, 1926 Lectotype NMB-132a (Photo: H. Frick) **C** *Acutodillo peltatus* (Budde-Lund, 1904), gen. et comb. nov. Paralectotype BMNH 1921.10.18.907 (Photo: Kevin Webb) **D** *Floresiodillo gibberum* (Herold, 1931), gen. et comb. nov. Lectotype ZMB-CRUST-22987 (Photo: Benedikt Kästle) **E** *Floresiodillo latissimus* (Herold, 1931), comb. nov. Lectotype ZMB Crust-23015 (Photo: B. Kästle) **F** *Ardentiella bicolorata* (Budde-Lund, 1895), gen. et comb. nov. Lectotype ZMB-CRUST-8615 (Photo: B. Kästle) **G** *Ardentiella* sp.1 ZMB-CRUST-8615 (Photo: B. Kästle). Scale bars: 5 mm.

Description. Maximum body length 14 mm. Body flattened. Dorsum smooth and covered with small scale setae. Eyes with 20 ommatidia. Cephalothorax with anterior margin strongly convex in dorsal view. Antennae long and slender with first article of flagellum as long as second article. Pereonites 1–4 with the posterior margins strongly concave, pereonites 5–7 with a weakly concave posterior margin. Pereonite 1 epimera with acute posterolateral corner, anterior corner acutely rounded. Pereonites 2–7 epimera rectangular. Pereonites 1–3 ventrally with triangular lobe. Pereonites 4–7 epimera without ventral lobes. Pleotelson about as long as wide, distal portion narrowing weakly. Uropod between pleonite 5 and pleotelson; uropod protopodite elongate, 1.5 times as long as wide, rectangular distal portion; posterolateral distal corner uropod propodite strongly rounded, posteromedial corner acutely rounded; uropod exopodite reaching posteromedial corner of protopodite; uropod endopodite 0.6 times as long as uropod protopodite, not reaching the posterior margin of protopodite. Female exopod of pleopod 1 rectangularly rounded with posterior margin weakly concave and 3.5 times as wide as long. Female pleopod 2 exopod rectangular, 2.6 times as wide as long. Female pleopod 5 exopod subtly triangular, outer margin convex.

Remarks. Unfortunately, some of the type material of *M. carinata* is preserved in a dried state, which leaves the affected specimens highly fragile and brittle. Three specimens of *M. carinata* remained in alcohol. The most intact specimen, NMB-131 b, is chosen as the lectotype. Judging from Verhoeff's

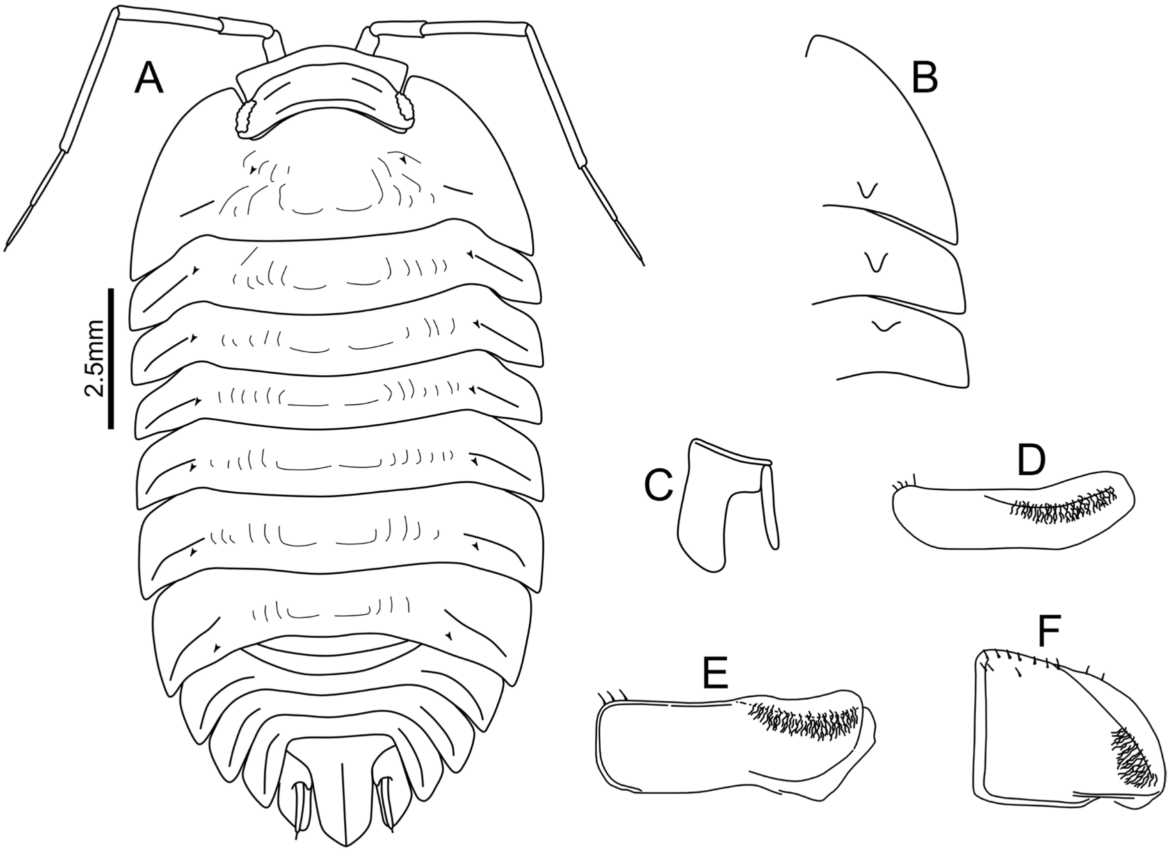

Figure 3. *Merulanella carinata* Verhoeff, 192: **A** habitus **B** ventral lobes **C** right uropod **D** female pleopod exopod 1 traced from Verhoeff (1926) **E** female pleopod exopod 2 traced from Verhoeff (1926) **F** female pleopod exopod 5 traced from Verhoeff (1926).

Figure 4. *Merulanella carinata* Verhoeff, 1926: observed at Les Koghis, New Caledonia **A** photo and observation by Damien Brouste **B** photo and observation by Christian Langner.

illustrations, the species appears to be characterized by polyspiracular-covered lungs. *M. carinata* can be readily distinguished from *M. wahrbergi* and *M. dollfusi* by the frontal shield protruding noticeably along the entire width of the cephalothorax, the more elongate antennae, a 1:1 ratio between the two articles of the relatively long flagellum, the pleotelson being as significantly longer than as wide, as well as a flattened habitus.

***Merulanella wahrbergi* Verhoeff, 1926**
Figs 2B, 5

Merulanella wahrbergi Verhoeff, 1926: 308 (in key), 309–310, figs 74–78.
Merulanella wahrbergi – Jackson, 1941: 19. — Schmalfuss 2003: 158.

Material examined. ***Lectotype*** (by present designation) NEW CALEDONIA • 1 ♀; in alcohol; Grande Terre, North Province, Koné; 04. Aug. 1911; F. Sarasin, J. Roux leg.; [assessed through photos]; NMB-132 a.

Paralectotypes NEW CALEDONIA • 1 ♂, 1 ♀; 1 dry pinned, 3 slides; same data as Lectotype; [assessed through photos]; NMB-132 a.

Type locality. Koné, North Province, Grande Terre, New Caledonia.

Diagnosis. Pereon epimera steep, habitus not flattened. Flagellum of antenna with second article 1.4 times as long as first article. Pleotelson wider than long. Uropod protopodite subtly triangular, not elongate.

Description. Maximum body length 7 mm. Body strongly convex. Dorsum smooth and covered with small scale setae. Eyes with 14 ommatidia. Cephalothorax with anterior margin strongly convex in dorsal view. Antennae long and slender with second article of flagellum 1.4 times as long as first article. Pereonites 1–4 with the posterior margin strongly concave, pereonites 5–7 with a weakly concave posterior margin. Pereonite 1 epimera with acute posterolateral corner. Pereonites 2–7 epimera rectangular. Pereonites 1–3 epimera ventrally with triangular lobe. Pereonites 4–7 epimera without ventral lobes. Pleotelson wider than long, distal portion narrowing weakly, terminating in a flat-angled triangular tip, posterolateral corners weakly rounded. Uropod between pleonite 5 and pleotelson; uropod protopodite as long as wide, distal portion rectangular; posterolateral corner of distal portion of uropod propodite rounded, posteromedial corner acutely rounded; uropod exopodite reaching

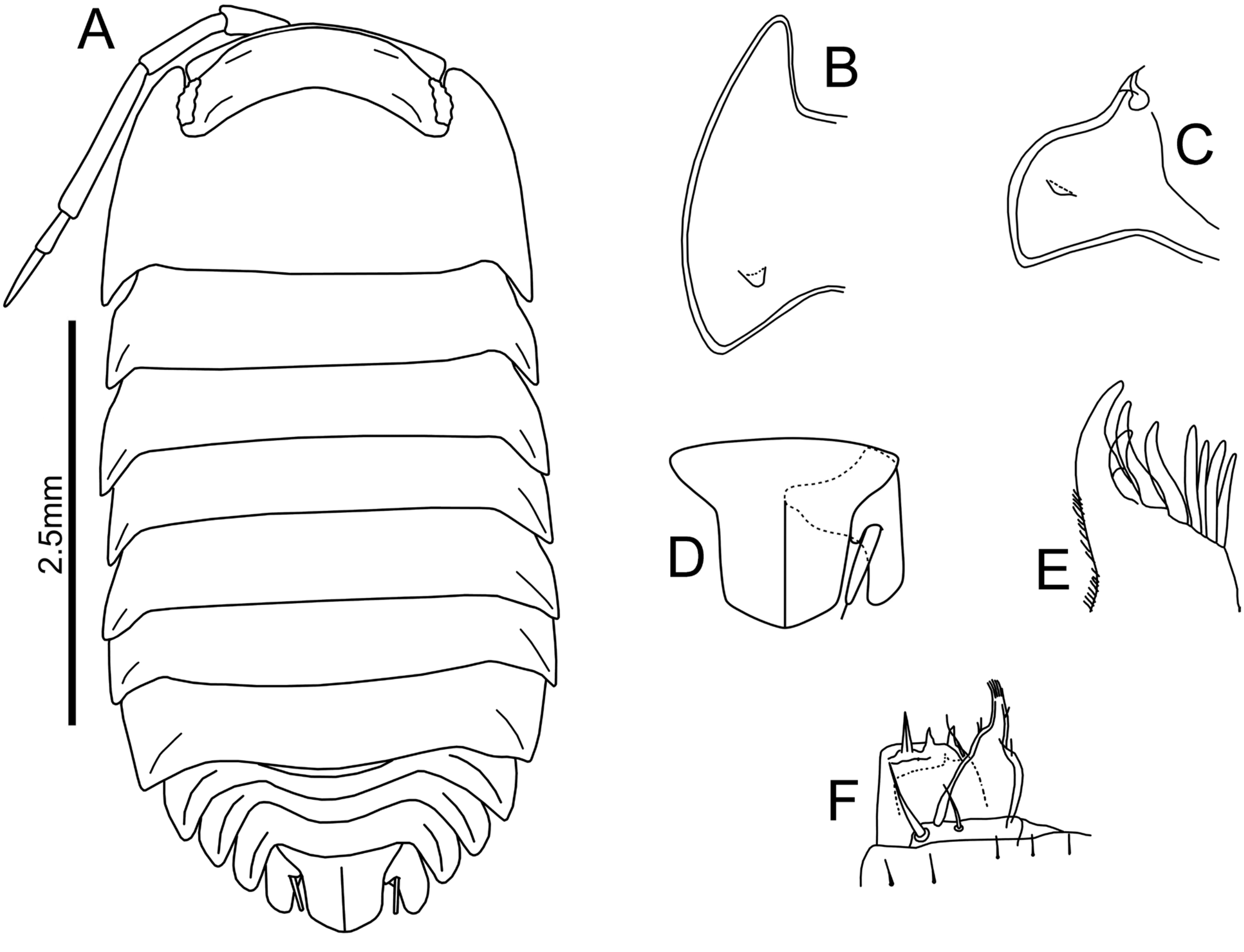

Figure 5. *Merulanella wahrbergi* Verhoeff, 1926: **A** habitus **B** ventral lobe of pereonite 1 **C** ventral lobe of pereonite 2 **D** pleotelson and uropod traced from Verhoeff (1926) **E** maxillula traced from Verhoeff (1926) **F** maxilliped traced from Verhoeff (1926).

posteromedial corner of protopodite and inserted dorsally near medial margin; uropod endopodite about 0.6 times as long as uropod protopodite and not reaching posterior margin of protopodite. Maxillula outer endite with 4+4 simple teeth. Maxilliped endite with straight distal margin and three large terminal setae, the innermost 2 times as long as the two outer setae. Male exopod of pleopod 1 with inner portion separated from outer portion by a small incision, endopod posteriorly bent outwards.

Remarks. As is the case for *M. carinata*, some of the type material is preserved in a dried state. One specimen of *M. wahrbergi* remained in alcohol, which is therefore designated as the lectotype (Fig. 2B).

M. wahrbergi can be distinguished by the shorter lamina of the frontal shield protruding noticeably only in front of the eyes, steep pereon epimera, the pleotelson being as long as it is wide, less elongate uropod protopodites, the smaller ocelli count, as well as a shorter flagellum, with the second article being about 1.4 times longer than the first one. It can be distinguished from *M. dollfusi* by the posterior corners of the pleotelson being more rounded, the lateral corners of the lamina of the frontal shield protruding further in a lobe-like manner, as well as being found on mainland New Caledonia instead of the Loyalty Islands.

Merulanella dollfusi **(Stebbing, 1900)**

Fig. 6

Cubaris dollfusi Stebbing, 1900: 654, pl. LXX, fig. B.
Merulanella dollfusi – Verhoeff, 1926: 357. — Jackson 1941: 19. — Schmalfuss 2003: 157.

Type locality. Lifou, Loyalty Islands Province, New Caledonia.

Diagnosis. Cephalothorax with lateral corners of frontal shield pronounced anteriorly. Pleotelson weakly keeled, wider than long, posterolateral corners strongly rounded. Uropod protopodite subtly triangular, not elongate.

Description. Maximum body length 11 mm. Body convex. Cephalothorax with anterior margin strongly convex in dorsal view with lateral portions protruding in a lobe-like manner. Eyes with 18 ommatidia. Pereonite 1 epimera with an acute posterolateral corner, posterolateral portion weakly raised. Pereonites 1–3 epimera ventrally with triangular lobe. Pereonites 4–7 epimera without ventral lobes. Pleotelson wider than long, weakly keeled, distal portion narrowing weakly and terminating in flat-angled triangular tip, posterolateral corners strongly rounded. Uropod between pleonite 5 and pleotelson; uropod protopodite strongly triangular, as long as wide, distal portion rectangular; posterolateral corner of distal portion of uropod propodite strongly rounded, posteromedial corner acute; uropod exopodite of normal size, reaching posteromedial corner of protopodite and inserted dorsally near medial margin; uropod endopodite almost as long as uropod protopodite.

Remarks. Specimens could not be located. More morphological differences are likely present, but they can only be determined by examining specimens.

Based on the description by Stebbing (1900), *M. dollfusi*, while being of similar appearance to *M. wahrbergi*, differs by having the posterior corners of the pleotelson more rounded, and the lateral corners of the lamina of the frontal

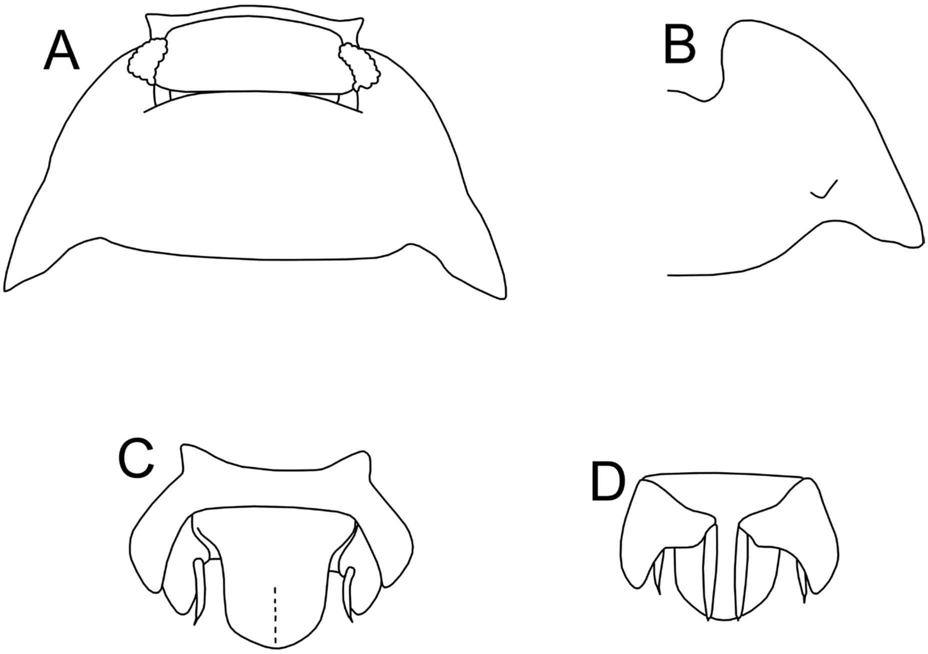

Figure 6. *Merulanella dollfusi* (Stebbing, 1900). Figures traced from Stebbing (1900) **A** cephalon and Pereonite 1 **B** ventral lobe of pereonite 1 **C** telson, uropods and pleonite 5 in dorsal view **D** telson and uropods in ventral view.

shield protruding further anteriorly in a lobe-like manner. It can be distinguished from *M. carinata* by the shorter lamina of the frontal shield protruding noticeably only in front of the eyes, the pleotelson wider than long with more rounded posterolateral corners, as well as less elongate uropod protopodites.

Floresiodillo **gen. nov.**

https://zoobank.org/8A6FE738-BBCC-45E8-A43E-3762D274F4FE

Type species. *Merulanella gibbera* Herold, 1931.

Distribution. Indonesia (Island of Flores).

Diagnosis. Dorsum with small scale setae and with distinct tubercles. Pereon epimera almost horizontally, with wide and flat habitus. Cephalothorax with frontal shield protruding above vertex lobe-like in front of eyes and medially with two small lobes. Flagellum of antennae with second article three times as long as first article. Pereonites 1 and 2 epimera ventrally with small triangular tooth, near inner margin of epimera. Pereonites 2–7 epimera rectangular. Pleotelson longer than wide, lateral margins weakly impressed. Posterior margin of pleotelson straight or weakly concave. Uropod protopodite long and slender, distal portion rounded. Exopodite not reaching posterior margin of protopodite, inserted dorsally close to medial margin, covered basally by dorsomedial tooth. Endopodite not reaching posterior margin of protopodite, longer than half the length of protopodite.

Remarks. Two species are members of *Floresiodillo* gen. nov.: *F. gibberum* (=*Merulanella gibbera*) Herold, 1931, comb. nov. and *F. latissimus* (=*Merulanella latissima*) Herold, 1931, comb. nov. According to Herold (1931) both species can only conglobate imperfectly. Noduli laterales could not be located.

Floresiodillo differs most noticeably from *Merulanella*, *Acutodillo* gen. nov., and *Ardentiella* gen. nov. by the distinct tubercles on the dorsum, the pleotelson shape, and the shape of the lamina of the frontal shield.

Etymology. The genus name *Floresiodillo* gen. nov. (neut.) is derived from the island of Flores, where both members of the genus were discovered.

Floresiodillo gibberum **(Herold, 1931), gen. et comb. nov.**

Figs 2D, 7

Merulanella gibbera Herold, 1931: 317–318, figs 1–5.
Merulanella gibbera – Schmalfuss, 2003: 157.

Material examined. ***Lectotype*** (by present designation) INDONESIA • 1 ♀; in alcohol; Flores, "Geli Mutu" [Kelimutu]; 15.–20. Jul. 1927; B. Rensch leg.; ZMB-CRUST-22987.

Paralectotype INDONESIA • 1 ♀; in alcohol; same data as Lectotype; ZMB-CRUST-22987.

Type locality. Kelimutu, Flores, Indonesia.

Diagnosis. Medial transverse tubercle on cephalothorax wider than lateral pair of transverse tubercles. Largest tubercle of lateral row triangular on pereonites 1–2. Medial tubercles on pleonites inconspicuous. Cephalothorax with the medial lobes of frontal shield small and weakly acute. Ventral lobes on pereonites 1–2 weakly acute. Pleotelson with posterior margin concave and with medial ridge.

Description. Maximum body length 8 mm. Body strongly flattened. Distribution of dorsal tubercles: one medial row of tubercles on pereonites 1–7 and pleonites 2–5, with the tubercle on pleonite 2 inconspicuous. A lateral row of tuberculated muscle spots on pereonites 1–7; lateral row consists of three small and one large triangular tubercles, small tubercles reducing in number on each subsequent segment with one large and one small triangular tubercle remaining on pereonites 3–7, small tubercle inconspicuous on pereonites 4–7; five tubercles between the eyes and close to posterior margin of the head; three medial tubercles transversely expanded and strongly developed, as a high, ridge-like structure at the back of the head with medial tubercle more transversely expanded than the two outer tubercles. Outermost tubercles triangular, significantly smaller and directly above the eyes. Eyes with 16 ommatidia. Maxillula outer endite with 4+6 simple teeth. Pereonite 1 epimera with anterior corner weakly acute, posterolateral corner almost right-angled; posterior margin of pereonite 1 almost straight, posterior margin of successive pereonites increasingly concave. Pereonites 1 and 2 epimera ventrally with small triangular lobe near inner margin of epimera. Ventral lobe of pereonite 1 situated near posterior margin; ventral lobe of pereonite 2 about as far from posterior margin as from anterior margin. Pereonites 2–7 epimera without ventral structures; epimera of pleonites 3–5 rectangular with anterior corner weakly rounded. Pleotelson about as long as wide with medial ridge extending from base of the pleotelson, diminishing posteriorly; posterior margin of the pleotelson weakly concave. Uropod protopodite 1.7 times as long as wide with distal portion tapering weakly posteriorly, terminating in a rounded tip.

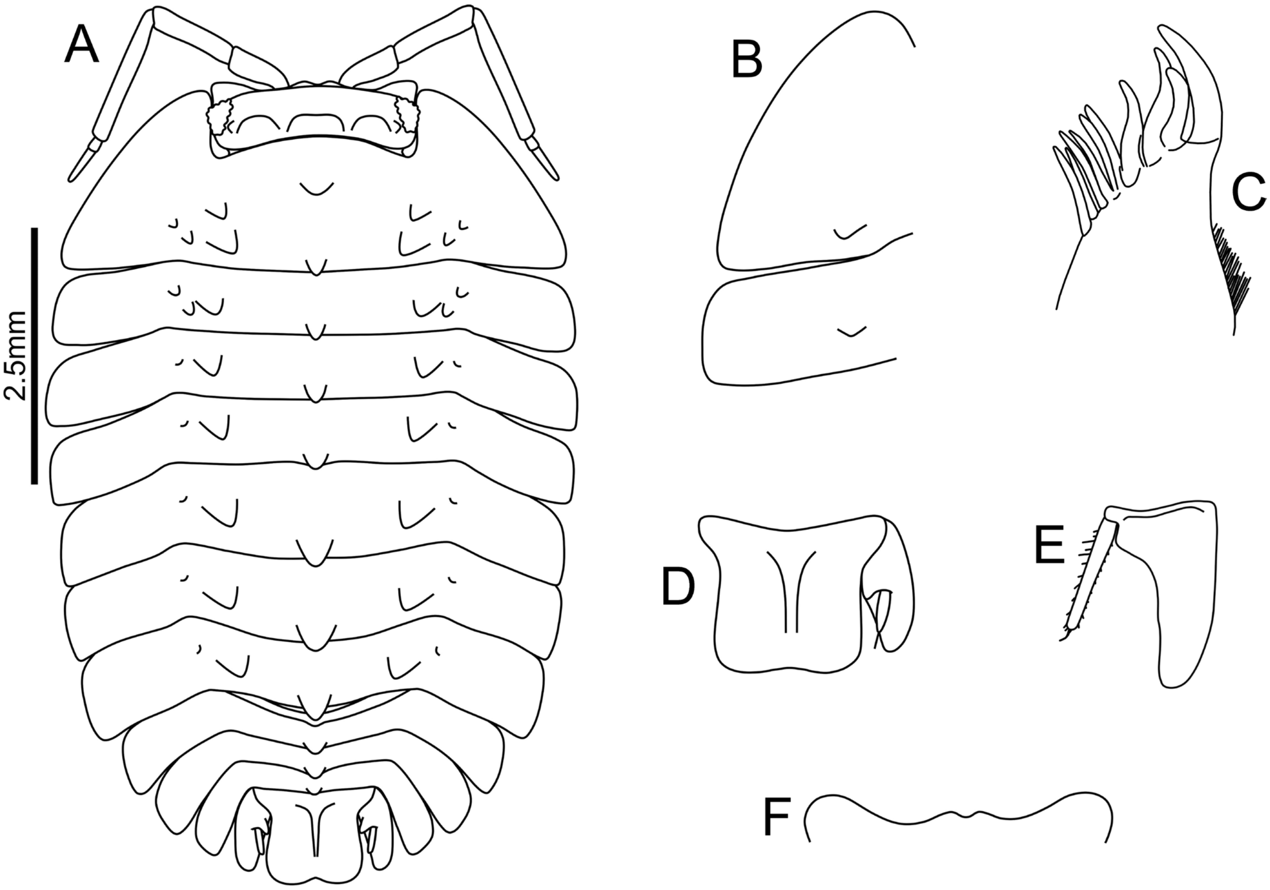

Figure 7. *Floresiodillo gibberum* (Herold, 1931), gen. et comb. nov. **A** habitus **B** ventral lobes of pereonites 1–2 **C** maxillula traced from Herold (1931) **D** pleotelson and right uropod **E** left uropod in ventral view **F** anterior margin of the frontal shield in dorsal view traced from Herold (1931).

Remarks. *Floresiodillo gibberum* gen. et comb. nov. (declination changed as a mandatory change as outlined in ICZN, Chapter 7, Art. 34) can be differentiated from *Floresiodillo latissimus* by the medial tubercle of the cephalon being more transversely expanded than the lateral tubercles. Furthermore, *F. gibberum* can be distinguished by the ventral teeth being less acute, as well as a slightly concave posterior margin of the pleotelson. The pleotelson of *F. gibberum* features a dorsal ridge, but is not truly keeled, as both sides of the pleotelson are forming a flat plane. This ridge is absent in *F. latissimus*.

Floresiodillo latissimus (Herold, 1931), gen. et comb. nov.

Figs 2E, 8

Merulanella latissima Herold, 1931: 318–319, figs 6–8.
Merulanella latissima – Schmalfuss, 2003: 157.

Material examined. ***Lectotype*** (by present designation) INDONESIA • 1 ♂; in alcohol; Flores, Rana Mesé, Mountain Rainforests; 20.–21. Jun. 1927; B. Rensch leg.; ZMB-CRUST-23015.

Paralectotype INDONESIA • 6 ♀♀; in alcohol; same data as Lectotype; ZMB-CRUST-23015.

Type locality. Mountain rainforest of Rana Mesé, Flores, Indonesia.

Diagnosis. Medial transverse tubercle on cephalothorax less wide than lateral pair of transverse tubercles. Largest tubercle of lateral row transversely expanded on pereonites 1–2, triangular on succeeding pereonites. Medial tubercles on pleonites inconspicuous. Cephalothorax with the medial lobes of frontal shield acute. Ventral lobes on pereonites 1–2 acute. Pleotelson with posterior margin straight and without medial ridge.

Description. Maximum body length 12 mm. Body strongly flattened. Distribution of dorsal tubercles: one medial row of small tubercles on pereonite 1–7 and pleonites 3–5, with the tubercles on pleonites inconspicuous. Lateral row of tuberculated muscle spots on pereonite 1–7. Lateral row with one large tubercle and 3 small triangular tubercles; small tubercles reducing in number on each subsequent segment; one large tubercle remaining on pereonites 4–7. Large tubercle transversely expanded on pereonites 1–2 and triangular on pereonites 3–7. Five tubercles between the eyes and close to posterior margin of the head. Three medial tubercles transversely expanded and strongly developed, as a high, ridge-like structure at the back of the head with the two outer tubercles

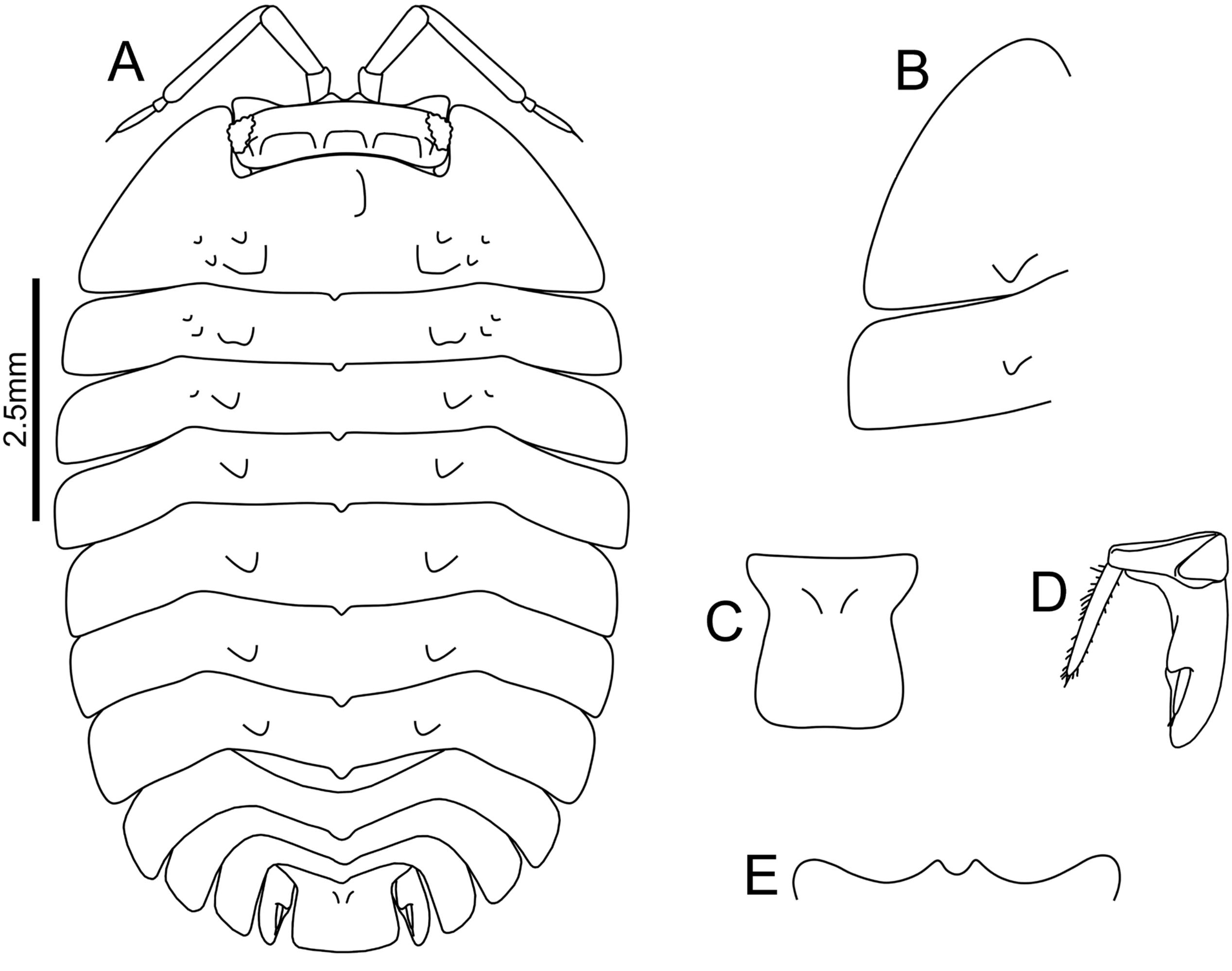

Figure 8. *Floresiodillo latissimus* (Herold, 1931), gen. et comb. nov. **A** habitus **B** ventral lobes of pereonites 1–2 **C** telson in dorsal view **D** right uropod in dorsal view traced from Herold (1931) **E** anterior margin of the frontal shield in dorsal view; traced from Herold (1931).

more transversely expanded than the medial tubercle. Outermost tubercles triangular, significantly smaller and directly above the eyes. Eyes with 16 ommatidia. Pereonite 1 epimera with anterior corner weakly acute and posterolateral corner almost right-angled; posterior margin of pereonite 1 almost straight, posterior margin of successive pereonites increasingly concave; pereonites 1 and 2 ventrally with small, acute triangular lobe, near inner margin of epimera. Ventral lobe of pereonite 1 situated near posterior margin; ventral lobe of pereonite 2 about as far from posterior margin as from anterior margin. Pereonites 2–7 epimera without ventral structures; epimera of pleonites 3–5 rectangular, anterior corner weakly rounded. Pleotelson 1.1 times as long as wide; posterior margin of pleotelson straight. Uropod protopodite 1.9 times as long as wide with distal portion weakly tapering posteriorly and terminating in acutely rounded tip.

Remarks. The distribution of the dorsal tubercles of *Floresiodillo latissimus* gen. et comb. nov. (declination changed as a mandatory change as outlined in ICZN, Chapter 7, Art. 34) is almost identical to *Floresiodillo gibberum* comb. nov., with the medial tubercles on the pleonites being inconspicuous and the big tubercle of the lateral row of the pereonites being slightly transversely expanded on pereonites 1–2 but is triangular on the following segments.

***Acutodillo* gen. nov.**

https://zoobank.org/B12513FB-3F09-4A47-A944-9C0C94A378D3

Type species. *Spherillo peltatus* Budde-Lund, 1904.

Distribution. Seychelles.

Diagnosis. Dorsum smooth, covered with small scale setae. Cephalothorax with frontal shield shortly protruding above vertex. Antennae slender, flagellum long with second article twice as long as first. Pereonites 1 and 2 epimera with small, triangular ventral lobe. Ventral lobe on pereonite 1 epimera continuing laterally as small ridge, not reaching lateral margin. Pereonites 2–4 epimera triangular. Pereonites 5–7 epimera rectangular. Pleotelson keeled, about as long as wide and with distinct posterior tip; lateral margins weakly impressed. Exopodite small, not reaching posterior margin of protopodite, inserted dorsally, close to medial margin, and covered basally by dorsomedial tooth. Endopodite not reaching posterior margin of protopodite. Noduli laterales on pereonites 2–7 in straight line except pereonite 4, with noduli laterales more medially, about as far from median line as from lateral margin.

Remarks. *Acutodillo peltatus* Budde-Lund, 1904, gen. et comb. nov. is the only known member of the genus. While *Acutodillo* shows a habitus reminiscent of *Ardentiella* gen. nov., it can be readily distinguished by the different position of the noduli laterales, the proportion of the antennal segments, as well as the ventral lobes. Considering the geographic distribution and the previously mentioned morphological differences, the similarities in habitus appear to be convergent. It was not possible to assess whether the noduli laterales on pereonite 1 are truly absent or are not preserved.

Etymology. The genus name *Acutodillo* gen. nov. (neut.) refers to the triangular appearance of the epimera of pereonites 2–4 and the acutely pointed tip of the pleotelson.

Acutodillo peltatus **(Budde-Lund, 1904), gen. et comb. nov.**

Figs 2C, 9

Spherillo peltatus Budde-Lund, 1904: 78–79.
Spherillo peltatus – Budde-Lund, 1908: 271. — Budde-Lund 1913: 372.
Merulanella peltata – Vandel, 1946: 254. — Ferrara and Taiti 1979: 178. — Ferrara and Taiti 1983: 61–62, figs 114–118. — Jeppesen 2000: 254. — Schmalfuss 2003: 157.

Material examined. ***Lectotype*** (by present designation) SEYCHELLES • 1 ♀; in alcohol; A. Brauer leg.; [assessed through photographs; specimen in better preservation state] BMNH 1921.10.18.906-907.

Paralectotype (by present designation) SEYCHELLES • 1 ♂; in alcohol; A. Brauer leg.; [not examined; photographs not produced as the specimen is in poor conservation state] BMNH 1921.10.18.906-907.

Type locality. Seychelles.

Diagnosis. As for genus.

Description. Maximum body length 9 mm. Eyes with 20 ommatidia. Cephalothorax with frontal shield protruding over vertex, medially raised, with anterior margin almost straight in dorsal view. Pereonite 1 epimera with broadly rounded posterolateral corner, anterior corner acute. Pereonites 2–4 epimera triangular, pereonite 5 epimera subtly rectangular, and pereonites 6–7 epimera rectangular with convexly rounded anterior margin. Pereonites 4–7 epimera without ventral lobes. Epimera of pleonites 3–5 rectangular with anterolateral corner weakly rounded. Uropod protopodite elongate, with rectangular distal portion, posterolateral corner rounded posteromedial corner strongly acute, almost reaching posterior tip of pleotelson; uropod exopodite relatively short, reaching only halfway from insertion to posteromedial tip of protopodite.

Remarks. Unfortunately, the two specimens of *Ardentiella peltatus* gen. et comb. nov. (declination changed as a mandatory change as outlined in ICZN, Chapter 7, Art. 34) are not preserved in good condition (Miranda Lowe, pers. comm.) and no specific type locality is known. The female specimen is designated the lectotype as it is more suitable as a primary reference due to preservation.

Ardentiella **gen. nov.**

https://zoobank.org/30376EA3-4D71-454F-9C50-0C0BF9B26CC9

Type species. *Armadillo bicoloratus* Budde-Lund, 1895.

Distribution. Myanmar, Thailand [Undescribed species: Vietnam, Laos, and China (Yunnan)].

Diagnosis. Dorsum smooth, covered with small scale setae. Cephalothorax with frontal shield slightly protruding above vertex, medially with small indentation. Antennae long and slender. Pereonite 1 epimera ventrally with broadly rounded lobe, not reaching lateral margin. Pereonite 2 epimera ventrally with small lobe. Pereonites 2–7 epimera rectangular, anterolateral corner often widely rounded, sometimes narrowing apically, resulting in triangular appearance. Pleotelson keeled or convex, lateral margins impressed; posterior margin of pleotelson convex or terminating in posterior tip. Uropod protopodite subtly triangular;

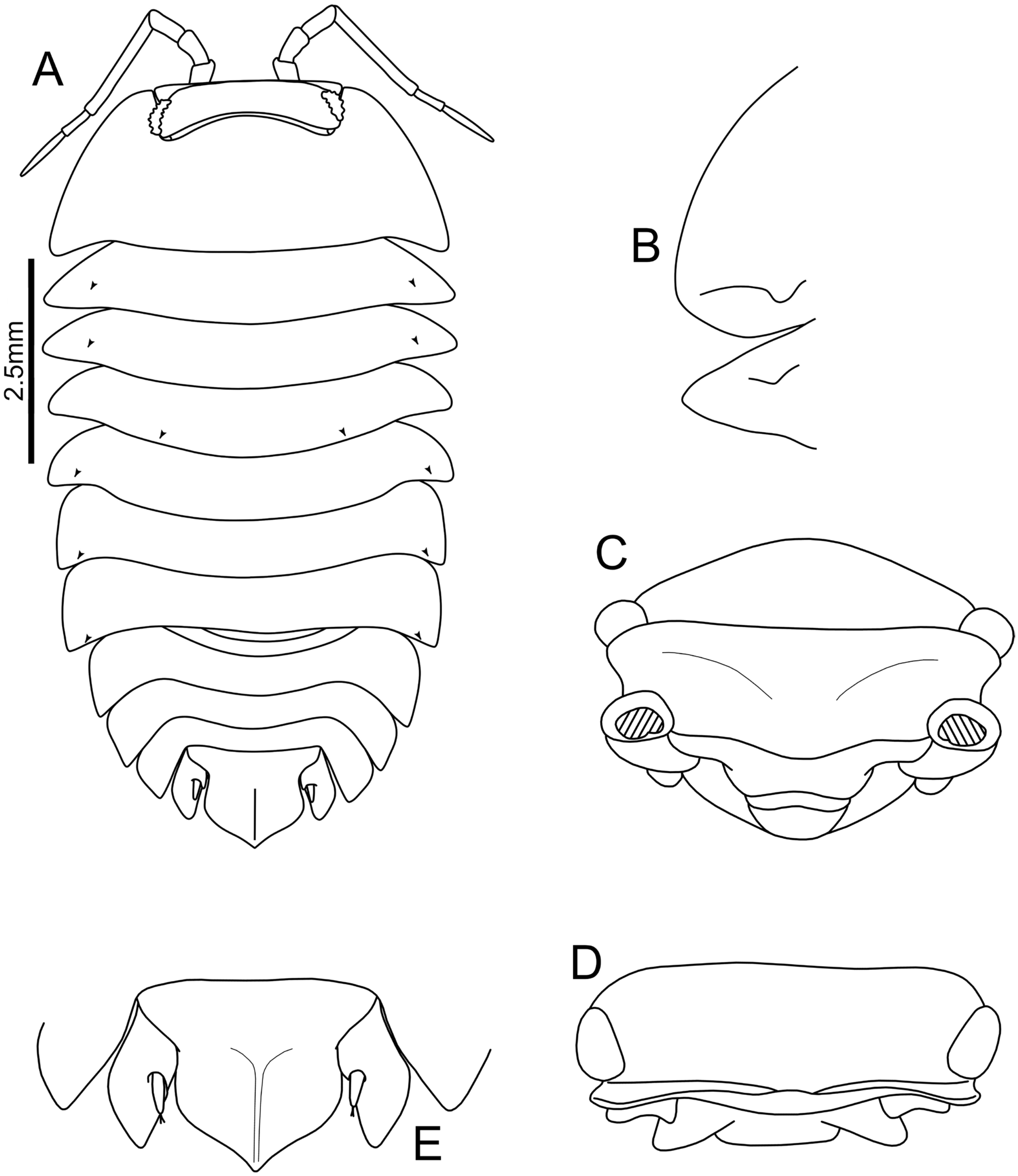

Figure 9. *Acutodillo peltatus* (Budde-Lund, 1904), gen. et comb. nov. **A** habitus **B** ventral lobes of pereonite 1–2 **C** cephalon in frontal view traced from Ferrara and Taiti (1983) **D** cephalon in dorsal view traced from Ferrara and Taiti (1983) **E** telson and uropods in dorsal view traced from Ferrara and Taiti (1983).

uropod exopodite not reaching posterior margin of pleotelson, basally covered by small dorsomedial tooth and inserted near medial margin. Noduli laterales on pereonite 1 and 2 more or less equidistant between anterior and posterior margins with successive pairs progressively closer to posterior and lateral margin; noduli laterales on pereonite 7 not aligned with noduli laterales on pereonites 1–6 and placed significantly more medially, very close to posterior margin.

Remarks. Two previously described species can currently be placed in *Ardentiella* gen. nov.: *Ardentiella bicolorata* (=*Armadillo bicoloratus*) Budde-Lund, 1895, comb. nov. and *Ardentiella caerulea* (=*Cubaris caerulea*) Collinge, 1914, comb. nov. Examination of described as well as undescribed members of the genus revealed that the general pattern of the noduli laterales is consistent, but the exact position appears to be variable between species and may prove to help delimit different species. The striking colors displayed by many members of the genus have been suggested to be an antipredatory strategy (Tuf and Ďurajková 2022). This aligns with observations made by isopod hobbyists and keepers and F. H. Gravely (Collinge 1914), indicating the occurrence of *Ardentiella* on vegetation and other exposed surfaces. Furthermore, members of *Ardentiella* lack alternative defense mechanisms such as tuberculation, and only rarely use the ability to conglobate but instead show behavior that aligns with a runner eco-morphotype, as observed in captivity. Coloration in some undescribed members might seem quite distinct but is often highly variable to the point where different species can only be separated by minor morphological features, as can be seen in *Ardentiella* sp. 2, *Ardentiella* sp. 3, and *Ardentiella* sp. 4 (Fig. 10). The genus has a wide distribution (Fig. 1B) ranging from Eastern Myanmar and Western Thailand to Southern China, Laos and Vietnam (iNaturalist 2023a; Budde-Lund 1904; Collinge 1914; Yao et al. 2023).

Etymology. The genus name *Ardentiella* gen. nov. (fem.) is derived from the word *ardens* (Latin: "burning, fiery, ardent") due to the striking black, yellow, and red colors displayed by many members of the genus (Figs 10, 13).

Ardentiella bicolorata (Budde-Lund, 1895), gen. et comb. nov.

Figs 2F, 11, 13

Armadillo bicoloratus Budde-Lund, 1895: 602–603.
Spherillo bicoloratus – Budde-Lund, 1904: 77–78, pl. VIII, figs 23–35.
Merulanella bicolorata – Ferrara & Taiti, 1983: 62. — Jeppesen 2000: 232–233. — Schmalfuss 2003: 157.
nec Merulanella bicolorata – Uebeler et al., 2022: 14–15, figs 17–19. — Yao et al. 2023: 1312–1314, figs 1–2.

Material examined. ***Lectotype*** (by present designation) MYANMAR • 1 ♀; in alcohol; "Mte. Carin, Viaggio in Birmania; 1000m"; 1885–1889; L. Fea leg.; ZMB-CRUST-8615.

Type locality. Karen Hills.

Diagnosis. Posterolateral corner of pereonite 7 epimera acutely pronounced. Pleotelson strongly keeled and with acute posterior tip. Uropod protopodite with strongly acute posterior corner. Uropod exopodite not reaching posteromedial corner of protopodite. Noduli laterales on pereonite 6 very close to the posterior margin.

Description. Maximum body length 13 mm. Dorsum smooth covered with small scale setae. Eyes with 20 ommatidia. Anterior margin of frontal shield almost straight in dorsal view. Antennae with second article of flagellum twice as long as first article. Pereonite 1 epimera with anterior corner acutely rounded, posterolateral corner acute. Pereonites 2–7 epimera with anterolateral corner

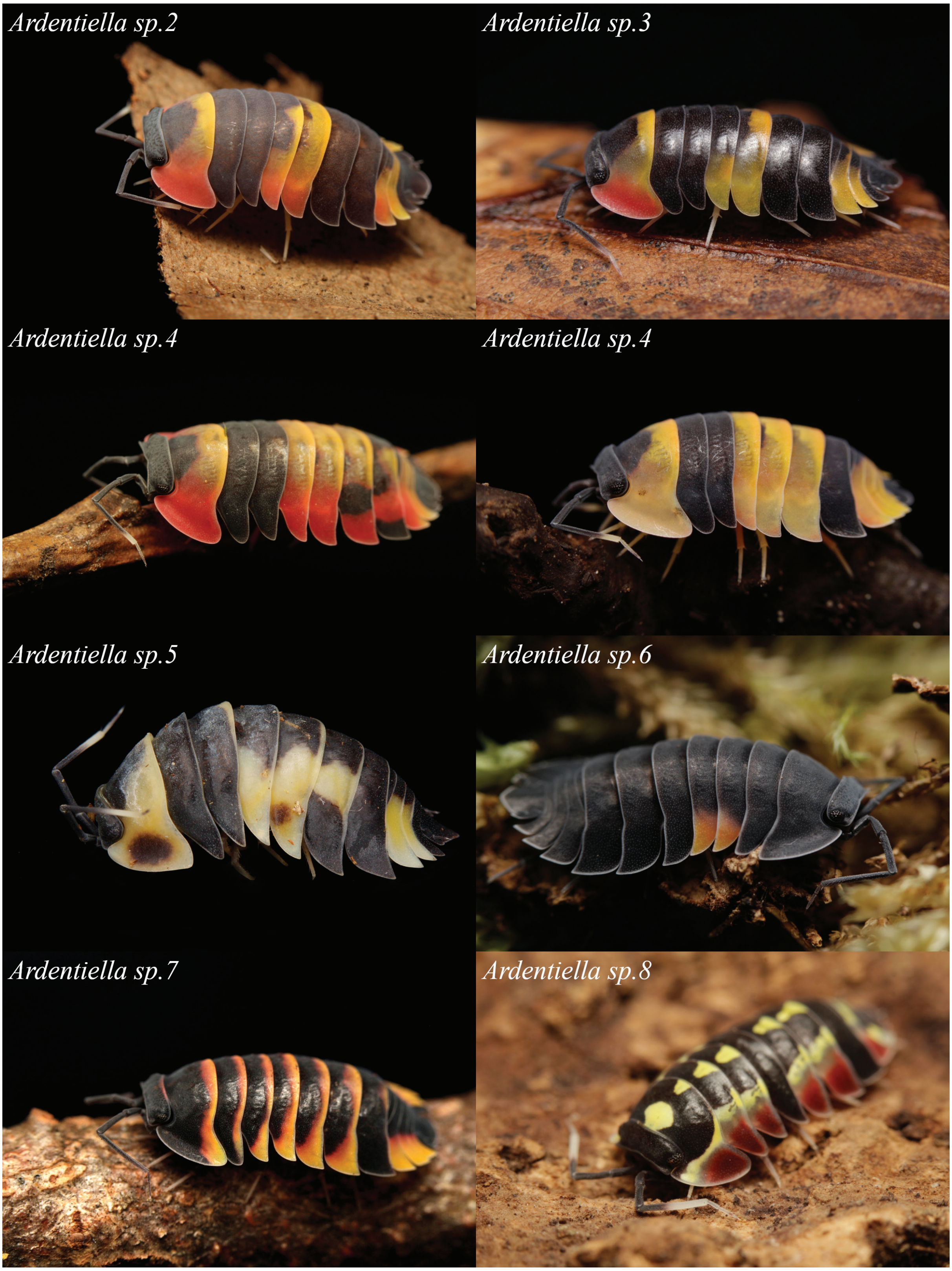

Figure 10. Undescribed species of *Ardentiella* gen. nov. from Vietnam currently circulating in the pet trade (Photos: B. Kästle).

rounded and posterolateral corner weakly projecting posteriorly. Epimera of pleonites 3–5 rectangular. Pleotelson strongly keeled, posterolateral corners strongly rounded, posterior margin convex and terminating in acute posterior tip; pleotelson 1.1 times as wide as long. Uropod fills gap between pleonite 5

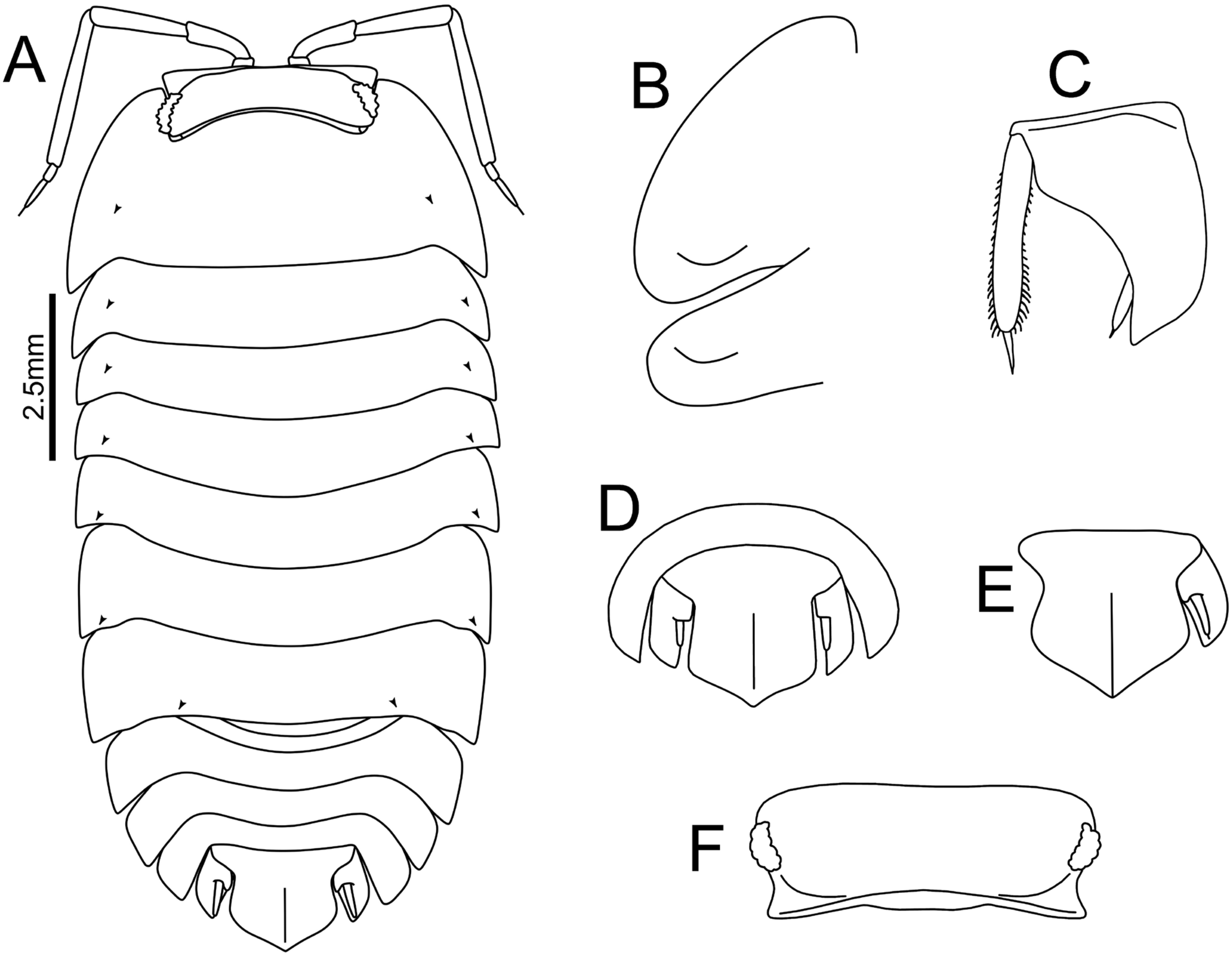

Figure 11. *Ardentiella bicolorata* (Budde-Lund, 1895), gen. et comb. nov. **A** habitus **B** ventral lobes of pereonite 1–2 **C** uropod in ventral view **D** pleotelson and uropods traced from Budde-Lund (1904) **E** pleotelson and uropod **F** cephalon in dorsal view.

and pleotelson. Uropod protopodite elongate, 1.3 times as long as wide, distal portion rectangular; posterolateral corner rounded, posteromedial corner strongly acute. Uropod exopodite almost reaching posteromedial tip of protopodite. Uropod endopodite with long terminal setae, almost reaching posteromedial tip of protopodite.

Remarks. According to the description by Budde-Lund (1904), the species appears to be characterized by *Trachelipus*-style lungs; this, however, requires dissection of specimens to confirm. The type material of *Ardentiella bicolorata* gen. et comb. nov. revealed the inclusion of two apparent morphospecies: a single female specimen was found among the syntypes in Berlin ZMB-CRUST-8615 which is distinct from the other four specimens in having an acuter and stronger keeled pleotelson, uropod exopodites not reaching the posteromedial corner of the protopodite, a more acutely pointed terminal end of the uropod protopodite, a slightly larger ventral lobe on the second pereonite, a stronger rounded lateral margin of pereonite 2, the exact position of the noduli laterales, as well as pereonites 5–7 epimera projecting further posteriorly, and thus featuring a more acute posterolateral corner (Fig. 13). Additional differences might be present but were not possible to be determined without dissection. Budde-Lund's illustration of the pleotelson shows a somewhat inaccurate overall shape but features an acutely pointed, although slightly exaggerated, posterior tip. After thoroughly comparing the specimens with the re-description of the species by Budde-Lund (1904), the description represents the species with only one specimen present, although more specimens might be present in other collections. Because the material was collected at three different localities in the Karen Hills — Bia-Po, Asciuii Cheba and Ghecu — and such a high degree of variation in a single species is highly unlikely, it has to be assumed that Leonardo Fea collected two remarkably similar species. Budde-Lund either did not consider the morphological differences significant enough, did not examine all specimens, or never noticed a difference. In light of the documentation practices in the past, Budde-Lund mentioned three localities for the material, as well as two distinct species being present in the ZMB-Material; material from all three localities was apparently mixed without keeping track of their origin. Therefore, it is unclear at which exact locality in the Karen Hills (Fig. 1B) each specimen was collected. As the single distinct specimen of ZMB-CRUST-8615 conforms best to the re-description by Budde-Lund (1904), the original description by Budde-Lund (1895) being inconclusive and lacking any illustrations, it is designated as the lectotype of *Ardentiella bicolorata* (Fig. 2F) and the remaining four specimens are considered undescribed. Following this, only a single specimen can conclusively be considered representative of *Ardentiella bicolorata*. Further studies, optimally with fresh material, should be conducted to determine conclusive species limits – including the material in the BMNH, ZMH and MSNG. The material deposited in the ZMB is not listed by Jeppesen (2000). Yao et al. (2023) published the first record of "*Merulanella bicolorata*" from Southwestern China. However, the illustrated species does not match *A. bicolorata* and appears to represent another undescribed member of the genus. There is a lot of confusing and contradictory information in the documentation in this regard: while Budde-Lund (1895) mentions that L. Fea collected the specimens from December 1887 to October 1889, the label of the ZMB material is less specific and gives 1885–1889 as the years of collection, whereas the NHM material is catalogued as having been collected in January 1880, 5 years before Leonardo Fea arrived in Burma (Myanmar).

Ardentiella caerula **(Collinge, 1914), gen. et comb. nov.**

Figs 12, 13

Cubaris caeruleus Collinge, 1914: 467–468, pl. XXXII, figs 1–10.
Cubaris caerulea – Schmalfuss, 2003: 89.
nec Armadillo caeruleus – Arcangeli, 1927: 224.

Type material. MYANMAR • "Thingannyinaung to Sukli, Dawna Hills, Tenasserim"; alt. 900–2100ft; 23.–27.11.1911; F. H. Gravely leg.; [not examined]; Indian Museum No.8078/10.

Type locality. Thingannyinaung to Sukli, Dawna Hills; Myanmar.

Diagnosis. Pleotelson convex, not strongly keeled, posterior margin strongly rounded, without terminal tip. Uropod protopodite with acute posterior corner. Uropod exopodite reaching posteromedial corner of protopodite. Noduli laterales on pereonite 6 near posterior margin.

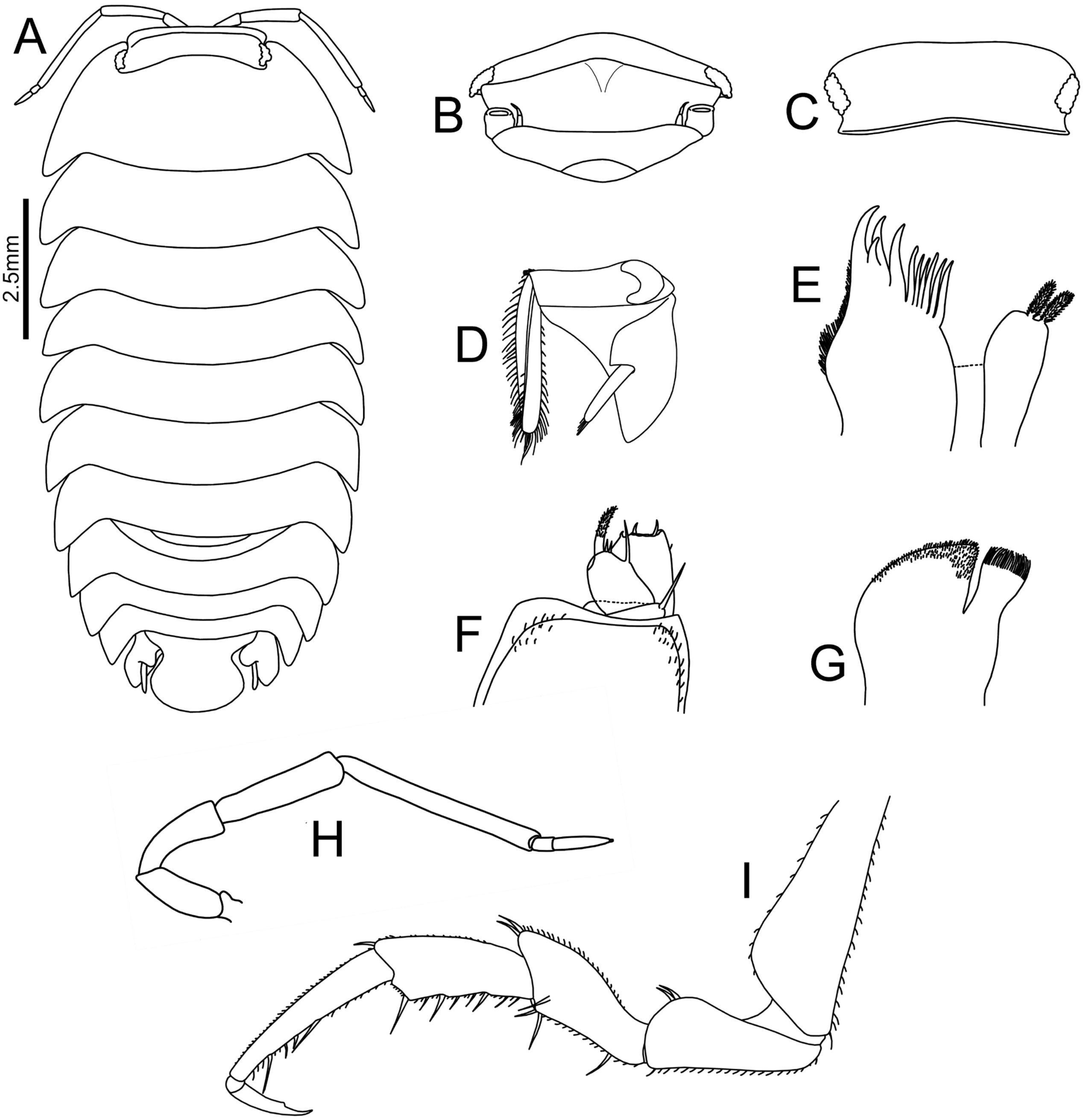

Figure 12. *Ardentiella caerulea* (Collinge, 1914), gen. et comb. nov. **A** habitus **B** in frontal view traced from Collinge (1914) **C** cephalon in dorsal view traced from Collinge (1914) **D** uropod in dorsal view traced from Collinge (1914) **E** maxilliped traced from Collinge (1914) **F** maxillula traced from Collinge (1914) **G** maxilla traced from Collinge (1914) **H** antenna traced from Collinge (1914) **I** pereopod 2 traced from Collinge (1914).

Description. Maximum body length 12 mm. Anterior margin of frontal shield almost straight in dorsal view. Antennae with second article of flagellum 2.5 times the length of first article. Maxilla with outer lobe twice as wide as inner lobe. Maxillula outer endite with 4+6 simple teeth; inner endite with two penicils of equal size. Maxilliped outer margin convexly rounded; maxilliped endite with three terminal setae. Pereonite 1 epimera with anterior corner acutely rounded, posterolateral corner acute. Pereonites 2–7 epimera rectangular, anterolateral corner rounded, posterolateral corner weakly projecting posteriorly. Epimera of pleonites 3–5 rectangular. Pleotelson strongly convex, posterolateral corners strongly rounded, posterior margin strongly convex. Uropod fills gap between pleonite 5 and pleotelson. Uropod protopodite elongate, 1.3 times as long as wide, with rectangular distal portion; posterolateral corner rounded, posteromedial corner strongly acute. Uropod exopodite almost reaching posteromedial tip of protopodite. Uropod endopodite with long terminal setae and almost reaching posteromedial tip of protopodite.

Remarks. The type specimens could not be confirmed to be in the collection of the Zoological Survey of India. However, according to the description and figures given by Collinge (1914), the species is without doubt another member of the genus. Several observations of this species are recorded on the citizen science platform iNaturalist (iNaturalist 2023a). Whether these observed specimens truly represent *Ardentiella caerulea* gen. et comb. nov. is uncertain. As the undescribed species from the original *A. bicolorata* comb. nov. type material is barely distinguishable from what is assumed to be *A. caerulea*, the new record of a very similar-looking, undescribed *Ardentiella* species from China by Yao et al. (2023), as well as the presence of multiple almost identical morphospecies in the pet trade, hints at the presence of a cryptic species complex stretching from the Dawna Hills in Eastern Myanmar and Western Thailand, along the Shan Hills into Yunnan, Southwestern China (Fig. 1B). The specimens identified as *A. caerulea* by Arcangeli (1927) could not be examined. However, due to the stated known distribution, as well as collection efforts in the respective regions not reporting the species (Verhoeff 1928; Kwon and Taiti 1993; GBIF Backbone taxonomy 2023b), the identification by Arcangeli is doubtful to be correct.

***Ardentiella* sp. 1 gen. nov.**

Figs 2G, 13

Material examined. MYANMAR • 4 ♀; in alcohol; “Mte. Carin, Viaggio in Birmania; 1000m”; 1885–1889; L. Feah leg.; ZMB-CRUST-8615. [THAILAND • 5 (sex not determined); in alcohol; Tak Province, Taksin Maharat National Park; 16°46.716'N, 98°51.51'E; 2020; Kühne leg.; ZMB-CRUST-34394].

Remarks. As mentioned above, this species is represented by 4 female specimens previously considered to be syntypes of “*Merulanella bicolorata*”. It can be best differentiated from *Ardentiella caerulea* comb. nov. by the pleotelson featuring a terminal, but broadly rounded tip, as well as slightly longer uropod exopodites. Leonardo Fea collected the specimens in the Karen Hills, but as is the case for *Ardentiella bicolorata* gen. et comb. nov., it was not possible to reconstruct the exact type locality. Additionally, five specimens (ZMB-CRUST-34394) from Tak Province, Thailand, collected in 2020, are deposited in the ZMB. A superficial examination revealed that these specimens appear to correspond to the same species as the four specimens from the Karen Hills. This, however, needs to be investigated in detail in the course of a species description. One of the specimens from Thailand is illustrated in Uebeler et al. (2022, figs 17–19).

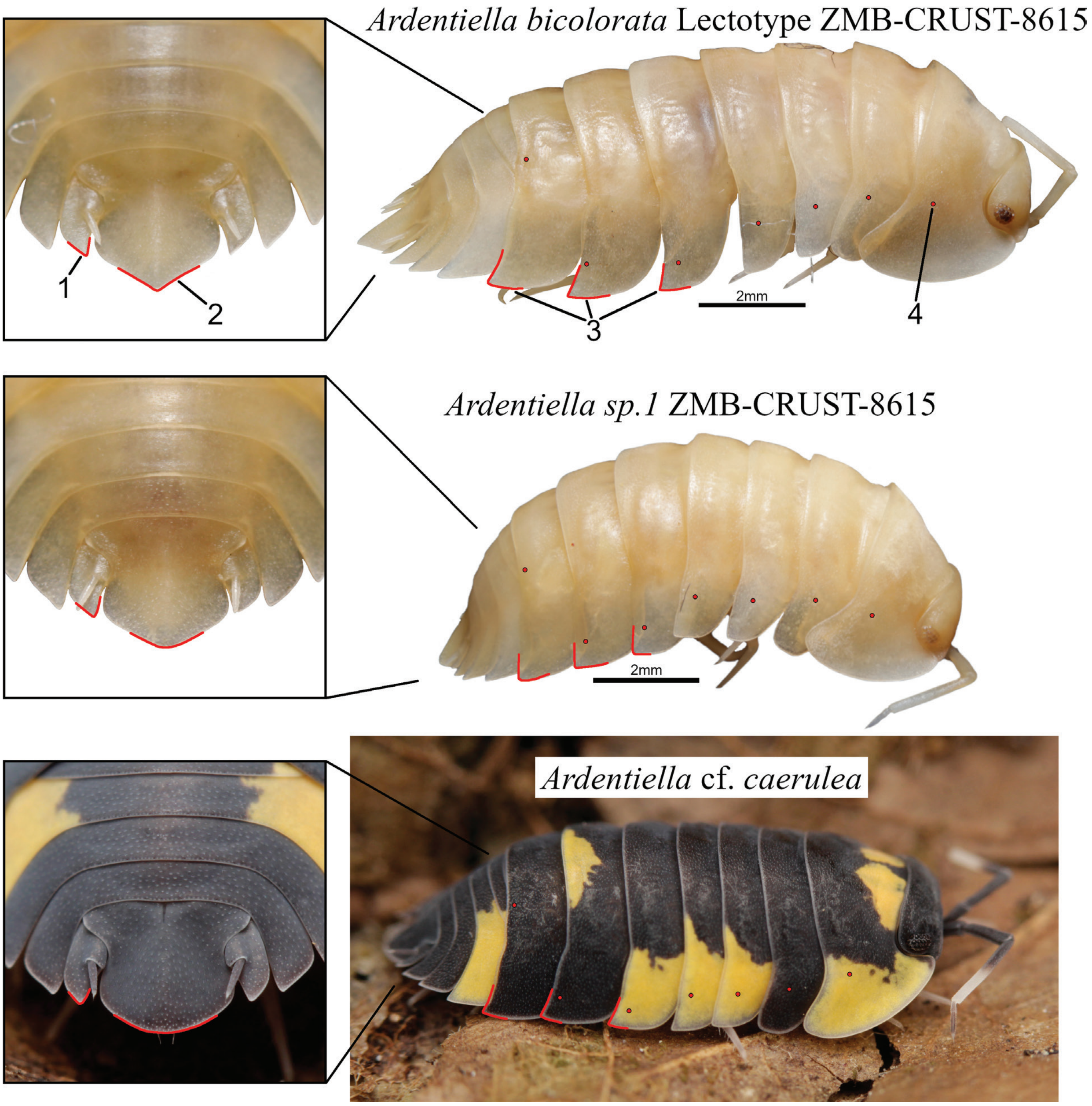

Figure 13. Comparison of *Ardentiella bicolorata* (Budde-Lund, 1895), gen. et comb. nov., *Ardentiella* sp. 1 from Budde-Lunds original material, and *Ardentiella* cf. *caerulea* (Collinge, 1914), comb. nov. from a hobbyist culture, originally from Western Thailand. 1) Posteromedial corner of the uropod protopodite. 2) Posterior margin of the pleotelson. 3) Posterolateral corners of pereonites 5–7 epimera. 4) Noduli laterales.

Discussions

Conservation and the invertebrate pet trade

While no species of *Merulanella*, *Floresiodillo* gen. nov. or *Acutodillo* gen. nov. are currently known to be in the pet trade, there has been an influx of many species of *Ardentiella* gen. nov. into the invertebrate pet trade (Jones et al. 2023). Multiple species originating from Western Thailand are seemingly closely related to *Ardentiella bicolorata* comb. nov. and especially *Ardentiella caerulea* comb. nov. The majority of these species are circulating in commerce under the name “*Merulanella bicolorata*” and show at least four remarkably similar but distinct morphospecies. Examination of several hobbyist cultures revealed that none of these species correspond to *A. bicolorata*. However, some cultures might correspond to *A. caerulea* (Fig. 9), and *Ardentiella* sp.1. Concerns for the genus are regularly expressed among hobbyists due to the frequent collection of a great number of individuals from the wild for the invertebrate pet trade. Especially undescribed species endemic to Vietnam appear to be at risk and are frequently targeted by wildlife collectors. Concerns have also been raised by Yao et al. (2023), and an assessment of the status of wild populations, primarily *Ardentiella*, but also regarding the other three genera, should be conducted.

Morphological dissimilarity within *Merulanella*

The vast morphological differences, as well as the distribution over multiple biogeographic realms (Fig. 1A), necessitate the majority of species in the genus to be removed from *Merulanella* and to be placed within three new genera: *Acutodillo* gen. nov. for "*Merulanella peltata*" from the Seychelles in the Afrotropical realm, *Floresiodillo* gen. nov. for both of Herold's species of the Lesser Sundas deciduous forests bioregion in the Australasian realm, and *Ardentiella* gen. nov. for "*Merulanella bicolorata*" from the Indomalayan realm. "*Cubaris caerulea*" Collinge, 1914 from Myanmar is moved to the genus *Ardentiella* as well. Additionally, a diagnosis for *Merulanella*, now restricted to the New Caledonia Islands bioregion, is provided.

The morphological examination revealed vast differences between *Merulanella*, *Floresiodillo* gen. nov., *Acutodillo* gen. nov., and *Ardentiella* gen. nov. Although all of the species treated here, with the exception of *A. caerulea*, were previously placed in *Merulanella*, they only share a few superficial resemblances. They can be readily distinguished by many morphological characteristics and the large geographic separation (Fig. 1A). While convergence in terrestrial isopods is a common phenomenon, the four genera mentioned in this work are seemingly only distantly related to each other, as the few characters previously considered to be similar are of very different structure. The type material poses several challenges, as the material is either damaged, encompasses very few specimens, is inaccessible, or could not be located either due to inadequate documentation by previous authors or by being lost.

Ideally, acquiring new material from the respective regions would be the best solution. Unfortunately, given the status quo of research on terrestrial isopods (see e.g. Agnarsson and Kuntner 2007; Ebach et al. 2011; Britz et al. 2020), namely the funding for invertebrate collection studies spanning multiple countries and continents not being feasible, the prospects of such surveys taking place in the near future appear very unlikely if not impossible. Especially in the case of *Ardentiella*, the acquisition of fresh material will become uncertain in the foreseeable future due to the ongoing civil war and humanitarian crisis in Myanmar. The type localities of *A. bicolorata*, located in the Karen Hills, which are mostly located in Kayah State, and *A. caerulea*, located in Kayin State, are both inside particular active zones of conflict in the eastern and southern parts of Myanmar where the civilian population faces frequent human rights violations and forced displacement (Simpson 2021; Amnesty International 2022; Dunne et al. 2022; Fortify Rights 2022).

As historical material can usually not be dissected and does not possess the necessary quality to attain viable molecular results, highly detailed morphological and genetic work is greatly hindered. While the here proposed solution is certainly not optimal as it cannot provide conclusive delimitations regarding the alpha taxonomy of the treated species, it achieves more taxonomic stability in the family Armadillidae, supplies a more comprehensive generic diagnosis for *Merulanella*, and offers new insights into the biogeography of the species previously placed under the genus, which in turn makes necessary future research less complicated (Taiti et al. 1998). The morphological results are further reinforced by the great biogeographical separation of the different genera, spanning three biogeographic realms. Additionally, the newly erected genera help with possible future species descriptions, which also provide a necessary basis to assess the conservation status of currently undescribed species. Loss of biodiversity is an ever-increasing threat, and the suborder Oniscidea has received little attention regarding conservation (De Smedt et al. 2025 in review.). To preserve the biodiversity of terrestrial isopods, the need to act is urgent. Taxonomy is fundamental in assessing the conservation status and making efforts to protect threatened species (Mace 2004; Agnarsson and Kuntner 2007). Of the species treated in this work, especially members of *Ardentiella* gen. nov. appear to be threatened, as a majority of the undescribed species seem to have a restricted geographic distribution, implying a great degree of endemism and are likely at risk due to habitat loss, habitat fragmentation, as well as over-collection for the pet trade. In light of a significant portion of oniscidean species being still unknown to science (Sfenthourakis and Taiti 2015) and a great number of previously described species facing taxonomical issues, there is an urgent need for taxonomists to not only describe new species but also remove historically created taxonomical noise to facilitate future research. While striving for meticulousness by employing highly detailed morphological accounts alongside molecular approaches, is certainly favorable; it is, in many cases, not feasible. Especially when confronted with taxa where it is highly unlikely fresh material will be accessible in the near future. Thus, taxonomists have to adapt and improve the knowledge of biodiversity by working within the realms of the given possibilities, as not resolving known taxonomic issues for the foreseeable future in light of a biodiversity crisis characterized by unprecedented loss of taxa and species being lost before they are even formally recognized, cannot be considered a viable option. As demonstrated in this work, highly polyphyletic genera can be readily resolved with historical specimens and non-destructive morphological analysis alone. The results presented here should, of course, be further tested and expanded once new material is available, ideally in the form of complete re-descriptions of the here treated species. While certain genera may lend themselves well to taxonomic cleanup through superficial morphological analysis, others may require additional morphological, molecular, and ecological data to delimit genus and species boundaries, and it is essential that the applicability of the approach taken here to resolve taxonomic issues needs to be evaluated on a case-by-case basis.

Conclusion

Taxonomy needs to be recognized as a scientific endeavor that adds value in its own right. In this case study, we highlighted how the revision of a genus can open more lines of research, such as an overlooked diversity. Scholarly publishers need to be aware of the dimensions and urgency of tackling the taxonomic impediment.

In this case study, many genera in the family Armadillidae Brandt, 1831 are in a sub-optimal taxonomic state, frequently not representing natural groups and based on superficial similarities due to the historical context of the taxonomies where they were conceived. Taxa described before and in the early 20th century are mostly based on the diagnosis method with incomplete descriptions, often lacking the necessary details and figures needed in our current type-specimen-based taxonomies. A complete re-description of the family as a coherent body of published work is unfeasible at this point due to the taxonomic impediment, but the solution proposed in this review reduces taxonomic noise in the family Armadillidae.

Nevertheless, we acknowledge that there are limits to what scholarly publishers can do to accept publications. Thus, we consider that the publication of the following types of revisions could contribute greatly to reducing taxonomic impediments, regardless of their taxonomic rank or disciplinary scope. Although our case study meets all these criteria as an illustrative purpose, any of these priorities should be given space – albeit, this is not by any means an exhaustive list:

Revision of taxonomies based on type-specimens that were collected abroad, either during colonial expansion or after the independence movements, are needed for other countries to come up with policies that will contribute to the development of their taxonomies. In our case, the revision of *Merulanella* has increased our understanding of the diversity of a family in three countries.

Revision of taxonomies that were created before the establishment of key concepts of evolutionary biology could not have considered biogeographic limits. In the case of *Merulanella*, we made the case that the genus does not follow our current understanding of the biogeographic realms, i.e. phylogeography, a field of study consolidated until 1987. However, this is only an arbitrary benchmark: taxonomies completely developed before the 1960s are a snapshot of a time before cladistics, and taxonomies created before the 1970s could not have considered vicariance and plate tectonics.

Revision of taxonomies that were produced before the development and widespread usage of the type-specimen method and where the basis of the species delineation is the genus-differential diagnosis. The confused taxonomy of *Merulanella* stems from the emphasis on differential diagnoses that are prone to contradictions and oversights. Revision of the literature ahead of specimen-based research is useful in itself to identify contradictions or errors carried forward.

Revision of taxonomies that address multi-specific genera or multi-genera families, even if they do not address it in its totality. *Merulanella* sits well within the median of the species richness of genera within the family Armadillidae.

Revision of taxonomies that address specific conservation concerns. This review was motivated by the interest in understanding the pet trade of woodlice, where a widely distributed genus based on an old taxonomy could lead to an over-collection of specimens from endangered species.

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Conflict of interest

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Author contributions

Benedikt Kästle performed the taxonomic revision, illustrations, collection visits and project conception. Omar Rafael Regalado Fernández supervised and revised the project. Both authors wrote, edited and revised the final version.

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Data availability

All of the data that support the findings of this study are available in the main text.

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