Dtsch. Entomol. Z. 71 (1) 2024, 17–47 | DOI 10.3897/dez.71.112278

Forest leaf litter beetles of Taiwan: first DNA barcodes and first insight into the fauna

Fang-Shuo Hu[1], Emmanuel Arriaga-Varela[2], Gabriel Biffi[3], Ladislav Bocák[4], Petr Bulirsch[5], Albert František Damaška[6], Johannes Frisch[7], Jiří Hájek[8], Peter Hlaváč[8], Bin-Hong Ho[1], Yu-Hsiang Ho[9], Yun Hsiao[10], Josef Jelínek[8], Jan Klimaszewski[11], Robin Kundrata[12], Ivan Löbl[13], György Makranczy[14], Keita Matsumoto[15], Guan-Jie Phang[16], Enrico Ruzzier[17,18], Michael Schülke[19], Zdeněk Švec[20], Dmitry Telnov[15,21,22], Wei-Zhe Tseng[23], Lan-Wei Yeh[24], My-Hanh Le[25], Martin Fikáček[1,8]

1 *Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung, Taiwan*
2 *Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland*
3 *Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil*
4 *Czech Advanced Technology and Research Institute (CATRIN), Palacký University, Olomouc,Czech Republic*
5 *Milánská 461, Prague, Czech Republic*
6 *Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic*
7 *Center for Integrated Biodiversity Discovery, Museum für Naturkunde Berlin, Berlin, Germany*
8 *Department of Entomology, National Museum, Prague, Czech Republic*
9 *Department of Entomology, National Chung Hsing University, Taichung, Taiwan*
10 *Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan*
11 *Research Affiliate of the University of Alaska Museum Insect Collection, University of Alaska, Fairbanks, USA*
12 *Department of Zoology, Faculty of Science, Palacký University, Olomouc, Czech Republic*
13 *Muséum d'Histoire Naturelle, Genève, Switzerland*
14 *Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary*
15 *Department of Life Sciences, Natural History Museum, London, UK*
16 *Department of Biomedical Science and Environmental Biology, College of Life Science, Kaohsiung Medical University, Kaohsiung, Taiwan*
17 *Department of Science, Roma Tre University, Rome, Italy*
18 *National Biodiversity Future Center, Palermo, Italy*
19 *Museum für Naturkunde, Berlin, Germany*
20 *Kamenická 4, Prague, Czech Republic*
21 *Institute of Life Sciences and Technology, Daugavpils University, Daugavpils, Latvia*
22 *Institute of Biology, University of Latvia, Rīga, Latvia*
23 *Department of Life Sciences, National Taiwan Normal University, Taipei, Taiwan*
24 *Department of Life Sciences, Tunghai University, Taichung, Taiwan*
25 *Biodiversity Research Center, Academia Sinica, Taipei, Taiwan*

https://zoobank.org/FC195427-80EA-4667-9010-AC9429FC2AB8

Corresponding author: Martin Fikáček (mfikacek@gmail.com)

Academic editor: M. Seidel ♦ **Received** 6 September 2023 ♦ **Accepted** 29 November 2023 ♦ **Published** 8 January 2024

Abstract

We report the publication of 953 DNA barcodes of forest leaf litter beetles from central Taiwan, in total representing 334 species of 36 beetle families. This is the first bulk of data from the Taiwanese Leaf Litter beetles project focused on uncovering the under-explored diversity of leaf litter beetles across Taiwan. Based on these data, we provide the first records of the following taxa for Taiwan: family Sphindidae (genus *Aspidiphorus* Ziegler, 1821); tribes Trichonychini, Ctenistini, and Bythinoplectini (all Staphylinidae: Pselaphinae); genera *Gyrelon* Hinton, 1942, *Thyroderus* Sharp, 1885, *Cautomus* Sharp, 1885 (all Cerylonidae), *Dermatohomoeus* Hlisnikovský, 1963 (Leiodidae), *Paraploderus* Herman, 1970 (Staphylinidae: Oxytelinae), *Thinocharis* Kraatz, 1859 (Staphylinidae: Paederinae), *Cephennodes* Reitter, 1884, *Napoconnus* Franz, 1957 (both Staphylinidae: Scydmaeninae), *Bicava* Belon, 1884 (Latridiidae), *Otibazo* Morimoto, 1961, *Seleuca* Pascoe, 1871 and *Acallinus* Morimoto, 1962 (all Curculionidae); species *Oodes* (*Lachnocrepis*) *japonicus* (Bates, 1873) (Carabidae: Licininae), *Drusilla obliqua* (Bernhauer, 1916) (Staphylinidae: Aleocharinae) and *Coccotrypes advena* Blandford, 1894 (Curculionidae: Scolytinae). The records of *Anapleus* Horn, 1873 (Histeridae) and *Batraxis* Reitter, 1882 (Staphylinidae: Pselaphinae) have been confirmed. The male of *Sivacrypticus taiwanicus* Kaszab, 1964 (Archeocrypticidae) is described for the first time. *Gyrelon jenpani* Hu, Fikáček & Matsumoto, **sp. nov.** (Cerylonidae) is described, illustrated, and compared with related species. DNA barcodes associated larvae of 42 species with adults, we are concisely illustrating some of these: *Oodes japonicus*, *Perigona* cf. *nigriceps* Dejean, 1831 (both Carabidae), *Ptilodactyla* sp. (Ptilodactylidae), *Maltypus ryukyuanus* Wittmer, 1970 (Cantharidae), *Drusilla obliqua*, *Myrmecocephalus brevisulcus* (Pace, 2008), *Diochus* sp., *Mimopinophilus* sp. (all Staphylinidae), *Stelidota multiguttata* Reitter, 1877, *Lasiodites inaequalis* (Grouvelle, 1914) (both Nitidulidae), *Lagria scutellaris* Pic, 1910, and *Anaedus spinicornis* Kaszab, 1973 (both Tenebrionidae). We also report the first cases of *Rickettsia* infections in Scydmaeninae and Pselaphinae. All data (sequences, metadata, and voucher photos) are made public in BOLD database and in a Zenodo Archive.

Key Words

Coleoptera, DNA barcoding, new record, new species, Oxford Nanopore

Introduction

Forest leaf litter, especially in tropical regions, is recognized as a habitat comparable to coral reefs by its ability to support extremely diverse faunas (Giller 1996). Among the diverse leaf litter arthropods, beetles (Coleoptera) are the most common, remarkable and speciose group (Nadkarni and Longino 1990; Olson 1994; Sakchoowong et al. 2008), despite the fact they may be outnumbered by ants, termites and mites in the number of specimens. The immense species diversity of leaf litter beetles corresponds to the fact that leaf litter played a crucial role in the evolution and diversification of several beetle lineages, most notably those of the Staphyliniformia (e.g., McKenna et al. 2015). Consequently, the rove beetles (Staphylinidae) became one of the most species-rich families worldwide (Lü et al. 2020). Yet, our understanding of leaf litter beetle faunas remains very limited. The high number of species and specimens, small body sizes and a high local endemism due to limited dispersal abilities form a 'toxic mix' making the study of leaf litter beetles difficult and extremely time-consuming. Several authors of this paper have spent their whole lives processing leaf litter samples all over the world, yet only a tiny portion of the collected material has been taxonomically treated, and an even smaller part was revised in a way that makes the taxonomic knowledge accessible to non-specialists: ecologists, conservation biologists or the general public. Our knowledge of the immature stages of these beetles is even scarcer: we do not even know what the larvae of most genera look like. This limits our understanding of the biology and ecological role of these beetles, and also obscures our understanding of their evolution, since larval characters are often phylogenetically highly informative.

DNA-based tools, including DNA barcoding, have been advocated to overcome the above problems referred to as 'the taxonomic impediment' (e.g., Tautz et al. 2003; Miller et al. 2016). The identification based on short mitochondrial fragments, DNA barcodes, can indeed speed up the analyses of whole faunas, especially in combination with novel methods of third-generation sequencing (e.g., Srivathsan et al. 2021) and processing of bulk samples without sorting to morphospecies (so-called metabarcoding, e.g. Liu et al. 2020), and were used to analyze species and genetic diversity of whole beetle communities (e.g., Andújar et al. 2015; Arribas et al. 2021). Yet, in most cases, these quick methods require a reference set of DNA barcodes based on specimens identified by experts, so-called DNA barcode libraries. DNA barcode libraries can also help with species identification and discovery, including the identification of pests (e.g., Madden et al. 2019) or species used in forensic entomology (Chimeno et al. 2019), or interception of newly introduced invasive species (e.g., Armstrong and Ball 2005). Importantly, the identification by comparison with expert-identified DNA barcodes may also help to train specialists in countries lacking large comparative collections and those who have limited chances to travel to visit large collections or to study historical types. Moreover, DNA barcodes may also help experts: they bring evidence independent from morphology and may attract attention to overlooked cases of cryptic or polymorphic species requiring detailed studies (e.g., Janzen and Hallwachs 2016). For all these reasons, DNA barcoding libraries have already been completed for some insect groups (e.g., British Culicidae by Hernández-Triana et al. 2019; aquatic biota including insects by Weigand et al. 2019), and a country-wide DNA-barcoding initiative have been launched by countries like Canada (Hebert et al. 2016), Germany (Hendrich et al. 2015), Finland (Pentinsaari et al. 2014) and Costa Rica (Janzen et al. 2017). The goal of our project is to build up such a reference DNA barcoding library for the forest leaf litter beetles in Taiwan.

Taiwan, a small island located in the western Pacific, lies at the intersection of the Oriental and Palaearctic biogeographical regions, which results in a rich diversity of fauna from both areas. Among the diverse insect orders found on the island, beetles (Coleoptera) stand out with an impressive number of recorded species. Taiwan is home to more than 119 families and 7711 species of beetles (Chung and Shao 2022). However, despite this extensive diversity, the taxonomic research on beetles in Taiwan has been somewhat fragmented. While there have been notable contributions such as monographs focusing on canopy phytophagous beetles (Lee and Cheng 2007; Lee et al. 2010, 2016; Ong and Hattori 2019; Ong et al. 2023), the broader study of leaf litter beetles has been largely reliant on the collections made by Aleš Smetana in the 1990s and Stanislav Vít in the 2010s. Studies based on Smetana's and Vít's material revealed a high species diversity of certain beetle groups in the leaf litter, including numerous endemic species (e.g., Smetana 1995; Angelini and De Marzo 1998; Assing 2010, 2014, 2015; Puthz 2010; Cuccodoro 2011; Löbl 2012; Borovec 2014; Cosandey 2023).

In this study, we are announcing the start of the Taiwanese Leaf Litter Beetles Barcoding project that aims at building an expert-identified DNA barcoding library of beetles inhabiting leaf litter in Taiwan. Our goals are (1) to initiate an extensive study of Taiwanese leaf litter beetles across all taxonomic groups, (2) to document the diversity of Taiwanese leaf litter beetles, including endemic and alien species, and (3) to provide a reliable tool for a quick identification facilitating the studies of biology of these beetles. Here, we are publishing the first set of DNA barcodes and the photographs of the sequenced vouchers and present the first taxonomic results: a description of a new species of Cerylonidae, the description of a male of the Taiwan-endemic species of Archeocrypticidae, and several newly recorded taxa. Since DNA barcodes associated many larvae from our samples with adults, we also provide detailed photos of some of them.

Materials and methods

Sampled sites

In this paper, we present the complete data (DNA barcodes, species identification, voucher photographs) of the beetle samples from the Huisun Forest Reserve (Nantou County, central Taiwan) collected from 2019 to 2021 (20 samples in total at 5 different sites at altitudes of 700–1100 m). Further samples are collected continuously from all over Taiwan: from 2021 to July 2023, we accumulated 85 additional samples, of which 27 are in the progress of barcoding (DNA barcodes are already available, but identifications and voucher photos need to be completed) and remaining samples as well as those collected in the future will be gradually processed as well (Fig. 1A). We will keep uploading the data online once the processing of these samples is completed.

Sample collecting and morphospecies sorting

Samples were collected with the help of a sifter with a 5 mm grid. Leaf litter was collected from suitable places where it accumulates and keeps moisture. The final volume of each sample varied between 3 and 6 liters of sifted material. We originally sampled 6 liters of sifted material, but this amount was found to be too large and hence the sampling protocol was subsequently updated to (at least) 3 liters of sifted material per sample; this updated protocol is followed for all samples collected from 2022 on. Beetles were extracted using portable Winkler extractors for 3 days, leaf litter was mixed twice a day to facilitate beetle extractions (Owens and Carlton 2015). Specimens were collected in 95% alcohol. Adults and larvae of each sample were sorted into morphospecies, counted, and 1–2 specimens of each morphospecies were selected for DNA extraction and barcoding. This method allowed us to (1) compare DNA-based and morphology-based species identification and consult inconsistencies with specialists, (2) to separate larvae and adults of the species in case they co-occur, (3) to associate larvae with adults by means of DNA. Additional specimens not used for barcoding were kept in alcohol in the freezer.

DNA extraction and PCR

Most specimens were extracted using the HotSHOT protocol (Truett et al. 2000; Srivathsan et al. 2021), using either the whole specimen in small species or few legs in specimens over 5 mm. A smaller part of the specimens was extracted using standard DNA extraction kits (Qiagen DNeasy Blood and Tissue kit or NautiaZ Tissue DNA Extraction Mini Kit) following the manufacturers' protocols, but with the cell lysis step extended to ca. 8 hours (overnight); these extracts are stored in the Laboratory of Insect Diversity, Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung, Taiwan. Extracts done using HotSHOT protocol were discarded after getting the sequences because their DNA degrades over time (Srivathsan et al. 2021). We amplified the 5' part of mitochondrial cytochrome oxidase I (*cox1*) (Hebert et al. 2003) using the modified LCO1490-HCO2198 primers for 658 bp (Folmer et al. 1994) and MLEPF1-HCO2198 for 407 bp fragment (Hajibabaei et al. 2006). Each primer was tagged with a unique 13 bp tag; the combination of tagged forward and reverse primers unambiguously identifies each sample and allows demultiplexing of reads. We used 96 uniquely tagged reverse (HCO2198) primers to identify the position of the sample in the 96-well plate, and four unique forward primers to identify individual plates. For the list of tagged primers, see Fikáček et al. (2023). For PCR reaction, we mixed 6.25 µl of GoTaqR Green Master Mix (Promega Corporation, USA), 1.75 µl of dH_2O, 2.00 µl of bovine serum albumin (BSA, 1 mg/ml), 1.00 µl of forward primer, 1.00 µl of reverse primer, and 2.00 µl of DNA extract. PCR conditions were: 95 °C:

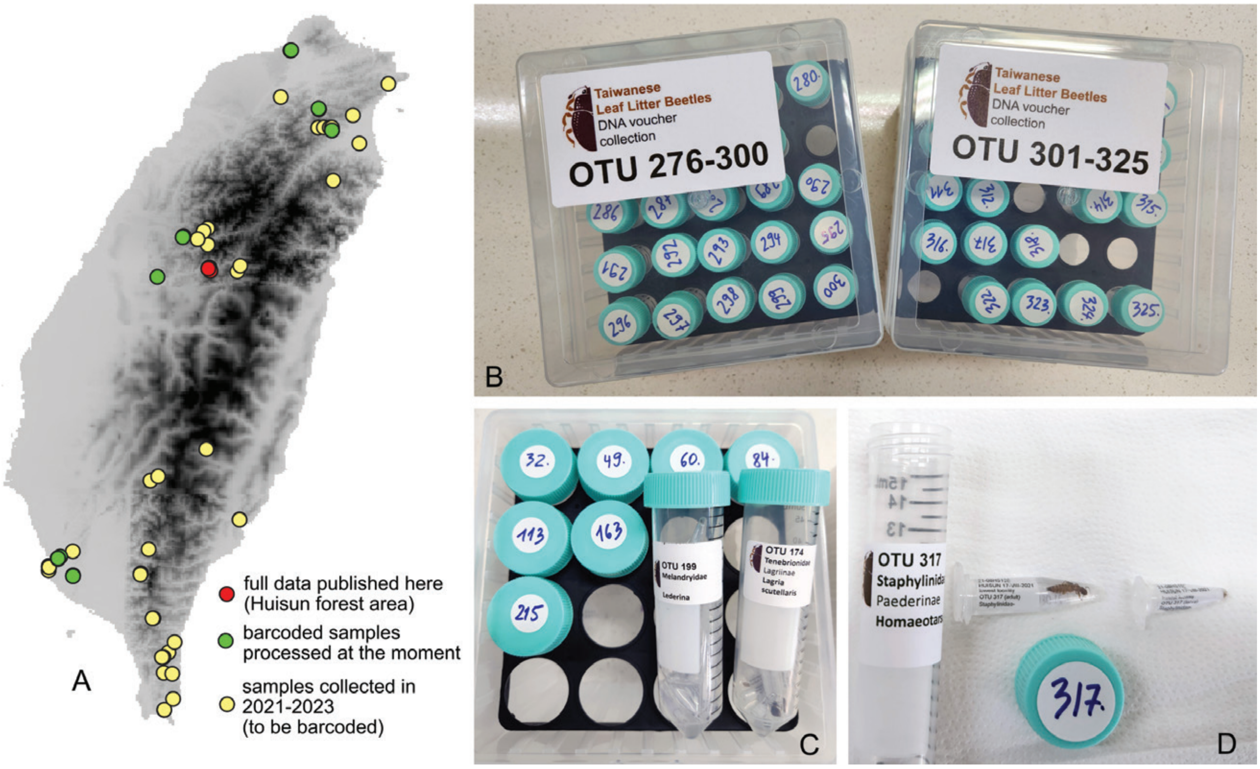

Figure 1. Taiwanese Leaf Litter Beetle Project: summary of the current status. **A.** Map of the samples collected in 2019–2023 (the complete data are published here for the Huisun Forest Reserve); **B–D.** Voucher collection kept in the Insect Diversity Lab, the National Sun Yatsen University, Kaohsiung, Taiwan: all vouchers and duplicates are available for study by specialists.

5 mins – 35 cycles of 94 °C: 30 seconds, 45 °C: 2 mins, 72 °C: 1 min – 72 °C: 5 mins, 12 °C: until removing samples from the machine. After the PCR, 16 samples were randomly selected from the plate and checked using gel electrophoresis to be sure that the complete plate did not fail at amplification. Individual samples were not checked, as we found that we often got sequences from samples without clear electrophoresis bands.

ONT library preparation and sequencing

For sequencing of most samples, we used the Oxford Nanopore R9 Flongle flow cells; the only exception is the samples collected in 2019 that were sequenced using the usual Sanger protocol in Macrogene Europe. For ONT sequencing, we pooled samples from 3–4 plates into each library; 3 µl of each PCR product was used. The pooled mix was cleaned up using AMPure XP magnetic beads (Beckman Coulter, USA), typically using 500 µl of pooled PCR products and 500 µl of beads (1X ratio), using the standard protocol, but with three instead of two washes with 1 ml of 70% ethanol. The amount of DNA in the purified pooled sample was measured by Qubit (Thermo Fisher Scientific, USA). For the final library, we used 200 ng of DNA in total and the ONT Ligation Sequencing Kit SQK-LSK109. NEBNext Ultra II End repair/dA-tailing Module (New England BioLabs, Inc.) was used to repair DNA end and ligate A-tails, AMX adaptors provided in ONT Sequencing Kit were ligated using NEBNext Quick Ligation Module (New England BioLabs, Inc.). Fragment size selection was done using the short fragment buffer (SFB) from the ONT Ligation Kit, combined with AMPure XP magnetic beads. The final 30 µl library consisted of 5 µl of DNA, 15 µl of SQB buffer, and 10 µl of LB buffer (both from the ONT Sequencing Kit). Sequencing was performed using MinKNOW software, for 24 to 48 hours based on the sequencing statistics. The base calling was performed subsequently in Guppy v4.0.11 software (Oxford Nanopore Technologies). For detailed protocols used, see Fikáček et al. (2023).

Demultiplexing and consensus calling

We used ONTbarcoder software (Srivathsan et al. 2021) to sort the reads from each Flongle flow cell run to the individual samples, based on the primer tags. Minimum length and length of the barcode were both set to 658 bp or 407 bp, according to the used primers, the windows for the product and primers were set to 100 bp. Consensus calling was performed using default settings (main consensus calling frequency: 0.3; range of frequencies to assess: 0.2 to 0.5; step size: 0.05) with invertebrate mitochondrial genetic code, using consensus by length (coverage used: 25, 50, 100, 200, 500; maximum deviation of read length: 50), consensus by similarity (coverage used: 100), and consensus by barcode comparison. All final consensus sequences reported in *runsummary* file are included in the final dataset, but those with the higher number of ambiguities were checked carefully in the final tree, and removed when problematic.

Quality control

We implied three steps of the quality control of the resulting consensus sequences. Parts of the contaminations, especially by bacteria (*Wolbachia*, *Rickettsia*, etc.) or phylogenetically distant animal phyla (e.g., nematodes) were easy to recognize as exceptionally long branches not grouping with the rest of the beetles in the maximum likelihood tree constructed in MEGA v10.2.5 (Kumar et al. 2016). All such sequences were removed after their identity was checked using BLAST. This way cannot remove contaminants by other arthropods; hence, in the next step, all remaining sequences were blasted using a BLAST+ app (Camacho et al. 2009). Samples with matches of >90% identity were checked and removed in case none of the five best matches was a beetle. We also checked the match between Sanger-generated and ONT-generated sequences in our samples, as additional quality control of the ONT-generated sequences.

Species delimitation and identification

We grouped sequences into species candidates (OTU, operational taxonomic units) by constructing the maximum likelihood tree in MEGA (Kumar et al. 2016) and searching clusters of similar sequences separated by longer internal branches. All vouchers were checked subsequently, and cases of mismatch (vouchers with different morphology in the same cluster, or identically-looking vouchers divided into separate clusters) were consulted with a specialist for the beetle family. The OTUs delimited in this way were numbered. Larval specimens nested in adult OTUs were considered conspecific with the adults. We consulted the genus and species identifications of the specimens with specialists for each family (in case these are available). All specialists providing help with identifications were offered with co-authorship.

DNA barcodes database

All DNA barcodes which are completely processed at the moment, and the photographs of the vouchers, have been submitted to the Barcode of Life Database (BOLD; Ratnasingham and Hebert 2007; project acronym: TWHUI, 947 sequences). Voucher photos (428 photographs) are provided for at least one adult and one larva of each species. The complete data and all voucher photographs are also available in Zenodo research archive under https://doi.org/10.5281/zenodo.10069183. The BOLD dataset will be continuously updated once new barcodes will get available.

DNA voucher collection

Vouchers of all sequenced specimens are deposited in the Laboratory of Insect Diversity, Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung, Taiwan (Fig. 1B–D). Individual specimens are kept in alcohol in plastic microtubes (0.2 or 0.5 ml, according to the size of the voucher), each specimen is labelled by its extraction number. Microvials with specimens belonging to the same species/OTU are grouped in 15 ml or 50 ml plastic tubes; each tube is labeled by the OTU number on the lid and by OTU number plus its identity at the side of the tube. Tubes are ordered based on the OTU numbers. Although the organization of the collection relies on OTU numbers, it remains flexible at the same moment, based on the progress on the taxonomic work on individual groups. Additional non-sequenced specimens are kept in the same lab in 95% alcohol at -20 °C. All specimens are available for study to taxonomists upon request addressed to M. Fikáček at mfikacek@gmail.com.

Depositories

Specimens examined in detail for taxonomy or morphology are deposited in the following collections:

BHHC coll. Bin-Hong Ho, Taipei, Taiwan;
BMNH Natural History Museum, London, UK (M. Barclay, K. Matsumoto);
FSHC coll. Fang-Shuo Hu, Luodong, Yilan County, Taiwan;
HNHM Hungarian Natural History Museum, Budapest, Hungary (Gy. Makranczy);
IDL Insect Diversity Lab, Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung, Taiwan (M. Fikáček);
NMNS National Museum of Natural Sciences, Taichung, Taiwan (B.-C. Lai, J.-F. Tsai);
NMPC National Museum, Prague, Czech Republic (J. Hájek, L. Sekerka);
ZSPC coll. Zdeněk Švec, Praha, Czech Republic.

Results

The DNA barcode dataset

The currently released dataset is based on a total of 4629 beetle specimens collected at five sites in the Huisun Recreation Forest Area in 2019–2021 (20 samples in total). 903 specimens were larvae (19.5%); the proportion of larvae varied strongly among samples (7–36% of all specimens). In total, we extracted DNA from 1131 specimens, and obtained good-quality non-contaminated DNA barcodes for 947 of them (84%). Based on the current identification, this material represents 328 species candidates (OTUs). In most cases, the DNA-based species delimitation corresponds to that based on morphology. In a few cases, the DNA-based and morphology-based identifications are in conflict (e.g., *Stenasthetus nomurai*, *Lederina* sp., *Coccotrypes papuanus*), with DNA indicating several cryptic species within the morphology-based species.

We do not intend here to solve these cases as they will require a more diverse geographic and gene sampling. Sequenced specimens represent 36 beetle families, of which Staphylinidae are the most diverse (152 species), followed by Curculionidae (30 species), and Tenebrionidae (23 species). Staphylinidae were represented by 14 subfamilies, with Scydmaeninae (36 species), Pselaphinae (29 species) and Aleocharinae (27 species) being the most species-diverse. Larvae were associated with adults for 42 species (12.6%) belonging to 12 families. Sixty-one species (18.2%) belonging to 13 families were collected only in larval stage; they mostly belong to lineages with free-living adults (Cantharidae, Chrysomelidae, Elateridae, Lampyridae, Lycidae, Meloidae, Mordellidae, Phalacridae, Prionoceridae, Ptilodactylidae, Tenebrionidae). Eleven species were collected as accidental catches of groups not living in leaf litter (Cerambycidae, Cleridae, Melandryidae, and Zopheridae). The summary of the material from the Huisun Forest Recreation area sequenced and published here is provided in Table 1. The maximum likelihood tree of all sequences is provided in Suppl. material 1.

Contaminations

In a few cases, we obtained sequences of other organisms than beetles, including bacteria such as *Rickettsia* and *Wolbachia*. Previous studies have reported a few cases of *Rickettsia* infection in beetles (Perlman et al. 2006; Bili et al. 2016). We identified *Rickettsia* sequences from the following taxa: Staphylinidae: Scydmaeninae, *Pseudophanias excavatus* (Staphylinidae: Pselaphinae) and Curculionidae: Scolytinae; these are the first records of *Rickettsia* infection in the Scydmaeninae and Pselaphinae. The presence of *Wolbachia* in beetles has been extensively reviewed in several studies (Kajtoch and Kotásková 2018; Kajtoch 2022). We revealed the presence of *Wolbachia* in the following taxa: Histeridae, Staphylinidae: Tachyporinae and Staphylinidae: Scydmaeninae. Additionally, we revealed several contaminations by nematodes, oomycetes and Amoebozoa in the nitidulid beetles that are possibly related to the preference of these beetles for decaying fruits. In some predatory beetles, we likely got sequences of their prey. Most interestingly, we repeated for sequences of *Burmoniscus* isopods from *Tolmerinus* sp. (both adults and larvae, 3 specimens of 16 sequenced),

Table 1. Summary of the dataset published here, based on 20 samples collected in the Huisun Recreation Forest area in 2019–2021.

Family	Sequences	Species: total	Species: larvae only	Species: larvae+adults	Non-arthropod contaminations
Anthicidae	2	2	–	–	–
Archeocrypticidae	2	1	–	–	–
Bothrideridae	1	1	–	–	–
Cantharidae	13	5	4	1	–
Carabidae	49	12	–	3	–
Cerambycidae	1	1	–	–	–
Cerylonidae	7	4	–	–	–
Chrysomelidae	34	17	11	1	–
Cleridae	1	1	–	–	–
Coccinellidae	2	2	–	–	–
Corylophidae	6	2	–	–	*Rickettsia*
Curculionidae	66	30	1	–	*Rickettsia*
Discolomatidae	12	2	–	1	–
Elateridae	15	9	6	–	–
Endomychidae	7	5	–	1	–
Erotylidae	11	3	–	–	–
Histeridae	4	4	1	–	*Wolbachia*
Hydrophilidae	20	4	–	–	–
Lampyridae	11	6	6	–	–
Latridiidae	8	2	–	–	–
Leiodidae	41	6	–	2	–
Lycidae	35	10	10	1	–
Melandryidae	19	1	–	–	–
Meloidae	1	1	1	–	–
Nitidulidae	16	3	–	2	Amoebozoa, oomycetes, Nematoda
Phalacridae	1	1	1	–	–
Prionoceridae	3	1	1	–	–
Ptiliidae	18	8	–	–	–
Ptilodactylidae	2	1	–	1	–
Ptinidae	2	1	–	–	–
Scarabaeidae	8	3	–	1	–
Scraptiidae	4	1	–	1	–
Sphindidae	2	2	–	–	–
Staphylinidae	449	152	6	24	*Rickettsia*, *Wolbachia*
Tenebrionidae	72	23	13	4	
Zopheridae	2	1	–	–	–

suggesting that isopods may be the preferred food for *Tolmerinus* rove beetles. We also got one case of isopod sequence in *Erichsonius* (Staphylinidae) and one case of collembolan sequence from an unidentified Pselaphinae.

Taxonomic part

Species descriptions or redescriptions

The identification of the species barcoded so far revealed a significant number of species which may be new to science or are improperly characterized in the original descriptions. The taxonomic work on most of these species is in progress by individual specialists, several species have been already described elsewhere (*Scaphobaeocera insinuata*: Löbl 2020; *Scaphisoma hui*: Löbl 2023; *Horniella nantouensis*: Zhang et al. 2021; *Oxyomus alligator*: Ho et al. 2022). Here we provide the complete taxonomic treatment for another two species.

Cerylonidae

Gyrelon jenpani Hu, Fikáček & Matsumoto, sp. nov.

https://zoobank.org/82B176D0-B4A9-4CCA-A4B3-7250E9F498B4

Fig. 2

Type material. ***Holotype*:** male (NMNS): 'Taiwan: Nantou County, Huisun Forest Reserve, track to Xiaochushan Mt., 24.0826139°N, 121.03115869°E, 1050 m, 4.v.2019, Damaška, Fikáček, Hu & Liu lgt., 2019-TW15' (DNA voucher: HS2004). ***Paratypes*:** 1 male (NMNS): Taiwan: Nantou County, Huisun Forest Reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E, 1150 m, 11.x.2020, FS Hu & YJ Chen lgt., old overgrown secondary forest on the slope, sparse understory vegetation: sifting of leaf litter accumulations (DNA voucher: 20-10HS506); 1 male (BMNH): same locality, date and collectors; 1 male (NMNS): same locality data, but 1.iii.2021, Hu, Chen, Fikáček & Peng lgt. (DNA voucher: 21-03HS508); 1 female (NMPC): same locality data, but 24.ii.2020, FS Hu lgt. (DNA voucher: 20-02HS509).

Differential diagnosis. The new species can be easily recognized from *G. rugosus* (Ślipiński, 1982) from southern China by the presence of both coarse and smaller punctures on the pronotum (only small and strongly elongated punctures are present in *G. rugosus*). The new species can be recognized from *G. mila* Hinton, 1942 (Sarawak) and *G. sumatrensis* Dajoz, 1974 (Sumatra) by the following characters: (1) metaventrite with punctures on the anterolateral portion much larger than posterolaterally (in contrast to small widely separated punctures in both latter species), (2) abdominal ventrite 1 with coarse punctures anteriorly and minute ones in the transverse row (with all punctures moderately large and widely spaced in both latter species), (3) transverse rows on abdominal ventrites 2–5 consisting of minute punctures (moderately large punctures in both latter species). The new species differs from *G. compactus* Dajoz, 1979 from Singapore by (1) the presence of 8 elytral series (7 in *G. compactus*), (2) the serially arranged minute seriferous punctures on elytral intervals 1–2 (with irregularly arranged setiferous punctures in *G. compactus*), and (3) the parallel-sided posterolateral margins of the pronotum (posteriorly converging in *G. compactus*). The comparison is based on the examination of the holotype of *G. mila* and two non-type specimens of *G. sumatrensis* in coll. BMNH (from Perak and Fort de Kock). The types of *G. sumatrensis* and *G. compactus* could not be examined as they are lost (A. Mantilleri, pers. comm., March 2023). The types of *G. rugosus* were not examined as the difference is clear from the original description. We also examined unidentified specimens of *Gyrelon* from Sumatra, Borneo, Sulawesi and Thailand in coll. BMNH. All of them are similar to *G. mila* and *G. sumatrensis* in the characters listed above.

Description. ***Body*** widely oval, body length 2.8–3.2 mm (holotype: 3.2 mm), body width 1.7–1.8 mm (holotype: 1.8 mm) (n=5 including holotype). Dorsal and ventral coloration dark reddish brown to black, legs and antennae brown to reddish brown, all body parts bearing yellowish erect setae.

Head relatively small, eyes moderately large, globular; frons with several moderately large punctures, each bearing erect seta, interstices smooth; clypeus weakly concave on anterior margin, dorsal surface bearing many erect setae. Antenna robust, with 11 antennomeres including the 2-segmented club; antennomeres gradually widening from base to apex; antennomere with microsculptures surface, bearing moderately dense erect setae; antennal club covered by dense short setation and moderately dense set of long erect setae; apex of antennal club bluntly pointed. Mentum small, subtriangular, strongly narrowing anteriad. Apical maxillary and labial palpomeres much narrower than the subapical ones.

Thorax. Pronotum subquadratic, nearly parallel-sided in posterior half, strongly narrowing in anterior half; median part of pronotum with elevated longitudinal ridge. Posterior corners nearly rectangular. Pronotal surface with large irregularly circular or oval punctures, each puncture bearing an erect seta; punctures getting smaller in posterolateral direction. Median part of pronotum lacking punctures, surface between punctures micropunctate. Prosternum widely rectangular, smooth, with coarse deep punctures; prosternal process wide, variable in shape, concave to weakly or strongly trifid posteriorly. Procoxal cavities widely separated, antennal grooves moderately wide, hypomeron with coarse punctures similar to those on prosternum. Mesoventrite anteriorly with a series of longitudinal ridges; surface microsculptured. Mesocoxal cavities widely separated by metaventral process. Each elytron with eight slightly irregular longitudinal series of punctures; serial punctures rounded, lacking setae; additional short series of coarse shallow punctures present anteriorly along elytral side; intervals flat dorsally, slightly convex laterally, smooth, each with a series of widely spaced minute punctures,

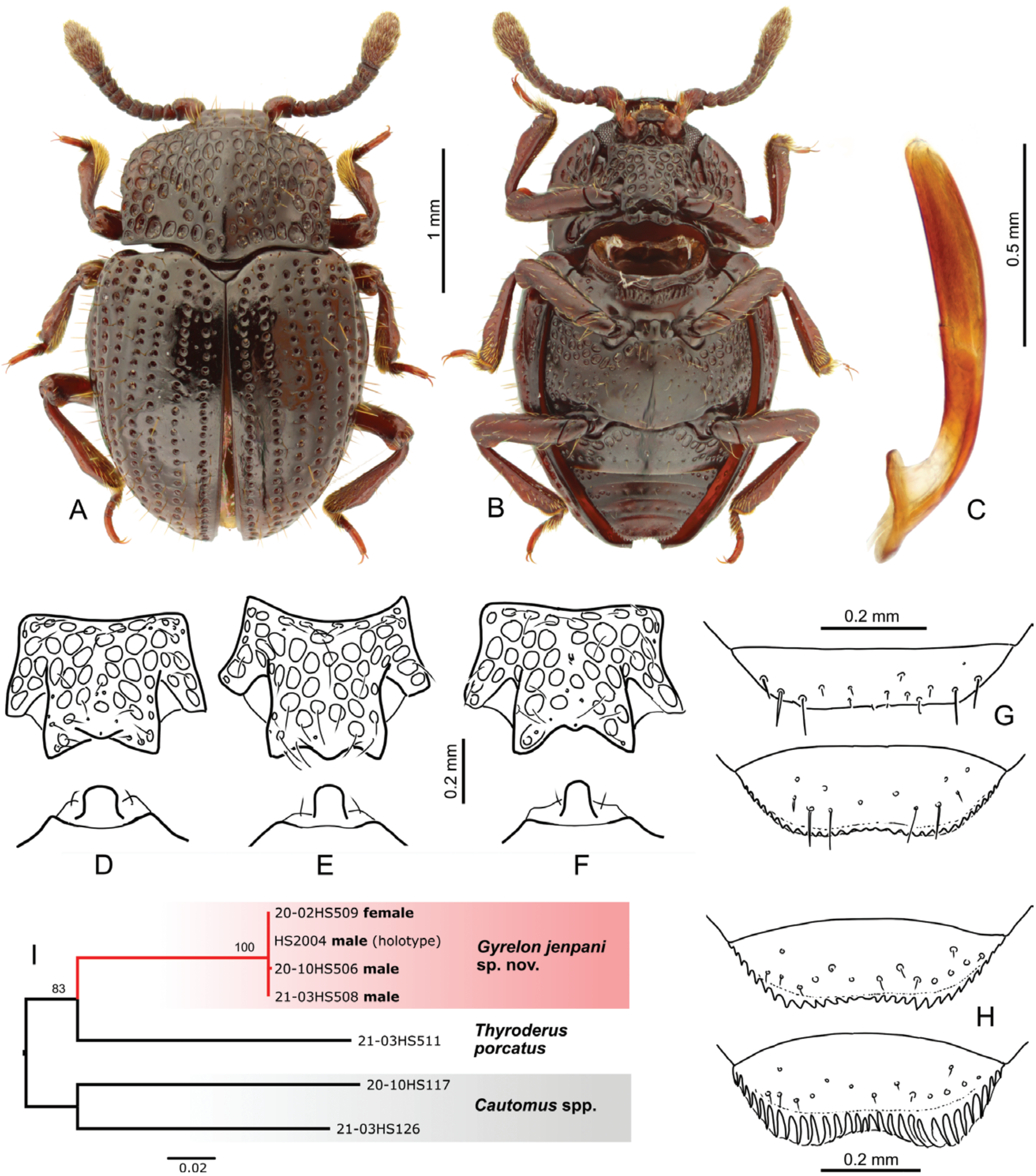

Figure 2. *Gyrelon jenpani* sp. nov. (Cerylonidae). **A, B.** Habitus (**A.** Dorsal view, female; **B.** Ventral view, male); **C.** Tegmen of the aedeagus; **D–F.** Variability of the shape of the prosternal process and metaventral process (**D, E.** Males; **F.** Female). Last abdominal ventrite in ventral and postero-ventral views (**G.** Male; **H.** Female); **I.** Maximum likelihood tree based on *cox1* barcodes of the sequenced Cerylonidae specimens.

each bearing erect seta; epipleuron present throughout elytral length, wide anteriorly, gradually narrowing posteriad. Scutellar shield widely triangular. Metaventral process with a narrow median projection of variable shape. Metaventrite flat mesally, lateral portions with large closely adjacent punctures along posterior margin of mesocoxal cavities, otherwise with relatively small and widely separated punctures, each bearing a decumbent seta; interstices with mesh-like microsculpture. Metathoracic wings absent.

Abdomen with 5 visible ventrites, ventrite 1 with a row of large closely adjacent punctures along anterolateral margin, posterior part with a transverse series of minute punctures, each with a decumbent seta. Ventrites 2–5 each with a transverse series of minute punctures, each bearing a decumbent seta. Interstices of all ventrites with fine mesh-like microsculpture. Ventrite 5 sexually dimorphic, with posterior margin nearly smooth in ventral view in male (finely crenulate in posteroventral view), and strongly crenulate in female (with a longitudinally ridged bar situated below apical part of elytral epipleuron).

Legs long and robust. Coxae and trochanters of all three pairs relatively small, coxa subglobular, trochanter subconical. Femora conical, with sparse erect setation, surface with mesh-like microsculpture. Tibiae flat, widening from base to apex, slightly more expanded in apical third, apical part with moderately dense erect setation; apical part of protibiae with an area of dense yellowish hair-like setae mesally. Tarsi with 4 tarsomeres, tarsomere 1 long and thick with dense long setae, tarsomeres 2–3 short, tarsomere 4 the longest.

Male genitalia. Aedeagus 1 mm long, simple, rod-like, without parameres, slightly widened at mid-length, rounded at apex.

Etymology. The species is dedicated to Dr. Jen-Pan Huang (Biodiversity Center, Academia Sinica, Taipei) as thanks for all his support of this project, including the possibility to work in his lab and for numerous inspiring discussions about evolution, diversity, and beetles.

Distribution. The species is so far only known from the type locality in central Taiwan.

Notes on diagnostic characters. Most previous studies use the form of the dorsal punctation and the shape of the prosternal process as the main diagnostic characters. Despite examining a few specimens only, we found both characters, especially the shape of the prosternal process, individually variable and/or dependent on the precise position of observation. The prosternal processes illustrated in Fig. 2D–F belong to the examined specimens whose conspecific identity was confirmed by the *cox1* barcode (Fig. 2I). A slight variation was also observed in the shape of the median projection of the metaventral process. In contrast, the character of the punctation of the metaventrite and abdominal ventrites seems to be much more distinct among species, and does not vary among the examined specimens of the new species.

Archeocrypticidae

Sivacrypticus taiwanicus Kaszab, 1964

Fig. 3

Type material examined. ***Holotype***: female (HNMB): 'Formosa, Sauter', 'Pilam, 908.II'. We have compared our specimens with the photos of the holotype provided to us by Gy. Makranczy in May 2023 (photos are available in the Zenodo Archive under https://doi.org/10.5281/zenodo.10069183).

New material examined. 1 male (NMNS): Taiwan: Nantou County, Huisun Forest Reserve, beginning of Wading trail, 24.0892139°N, 121.0297836°E, 700 wm, 17.viii.2021, M. Fikáček & WR. Liang, stony disturbed forest on the slope, small leaf accumulations (DNA voucher: 21-08HS169); 1 unsexed specimen (NMPC): same locality data, but 5.v.2019, Damaška, Fikáček, Hu & Liu lgt.; 1 female (NMNS): same locality data, but 28.ii.2021, Hu & Chen lgt. (DNA voucher: 21-03HS119); 1 male, 2 females, 3 unsexed specimens (NMNS, NMPC, BHHC): Taiwan: Taichung, Wufeng, Beikeng Creek trail, 24.0451°N, 120.7827°E, 410 m, 24.v. 2023, lgt. F.S. Hu & Y.J. Chen, lowland tropical forest with large accumulation of leaf litter and sparse understory (TW2023-018, DNA voucher WF1-023 and additional non-sequenced specimens).

Description of male genitalia. Male genitalia 1 mm long. Median lobe thin, strongly bent in the lateral view, with a plate-like expansion on the apex. Tegmen small, freely movable along the median lobe; parameres in lateral view narrowly elongated, pointed at apex and moderately pubescent, in dorsal view plate-like, with a small indentation on lateral margin. Sperm pump present, large, bottle-like, with slightly coiled distal ductus.

Comparison with the holotype. Our specimens correspond to the holotype by all diagnostic characters, including body proportions, the coarse and complete series of punctures on elytra, the double-sized punctation on the pronotum, and the shape of the lateral pronotal margin. On the first view, the specimen in Fig. 3A has much weaker elytral series than the holotype. The additional specimens examined, in which most of the dorsal setation was abraded in the same way as in the holotype, prove that the character of the elytra is in fact identical. In the original description (Kaszab 1964), as well as in subsequent revisions of the genus (Kaszab 1979, 1981), the lateral pronotal ridge of *S. taiwanicus* was mentioned as narrow and not widening anteriad. This stands in contrast to the character state in the holotype as well as in our specimens: the lateral pronotal ridge is, in fact, gradually widening from the base to anterior margin of the pronotum and bends inwards and merges with the anterior margin of the pronotum anteriorly. This fact also corresponds to the illustration of *S. taiwanicus* by Kaszab (1964) in which the anteriorly widening lateral ridge of the pronotum is clearly seen.

Comparison with other species. The previously unknown male of *S. taiwanicus* allows us to compare the male genitalia of the species (type species of *Sivacrypticus*) with those illustrated for other species of the genus. The male genitalia of *S. taiwanicus* are very distinct from the genitalia of most described species by (1) small tegmen, (2) strongly elongated median lobe, and (3) strongly expanded parameres in dorsal view. Its genitalia are, however, very similar to those of *S. philippinus* Merkl, 1988 from Luzon (Manila), but clearly differ from them by the apical expansion of the median lobe in lateral view, and in a less lobate shape of the parameres in dorsal view.

Distribution. The species was described from 'Pilam' (= Beinan township, Taitung County, southern Taiwan). The sequenced specimens examined by us are from lowland to lower montane forest in cenrtal Taiwan (Taichung and Nantou Counties), indicating that the species is likely widespread in lowland and lower montane forests at least in central and southern Taiwan.

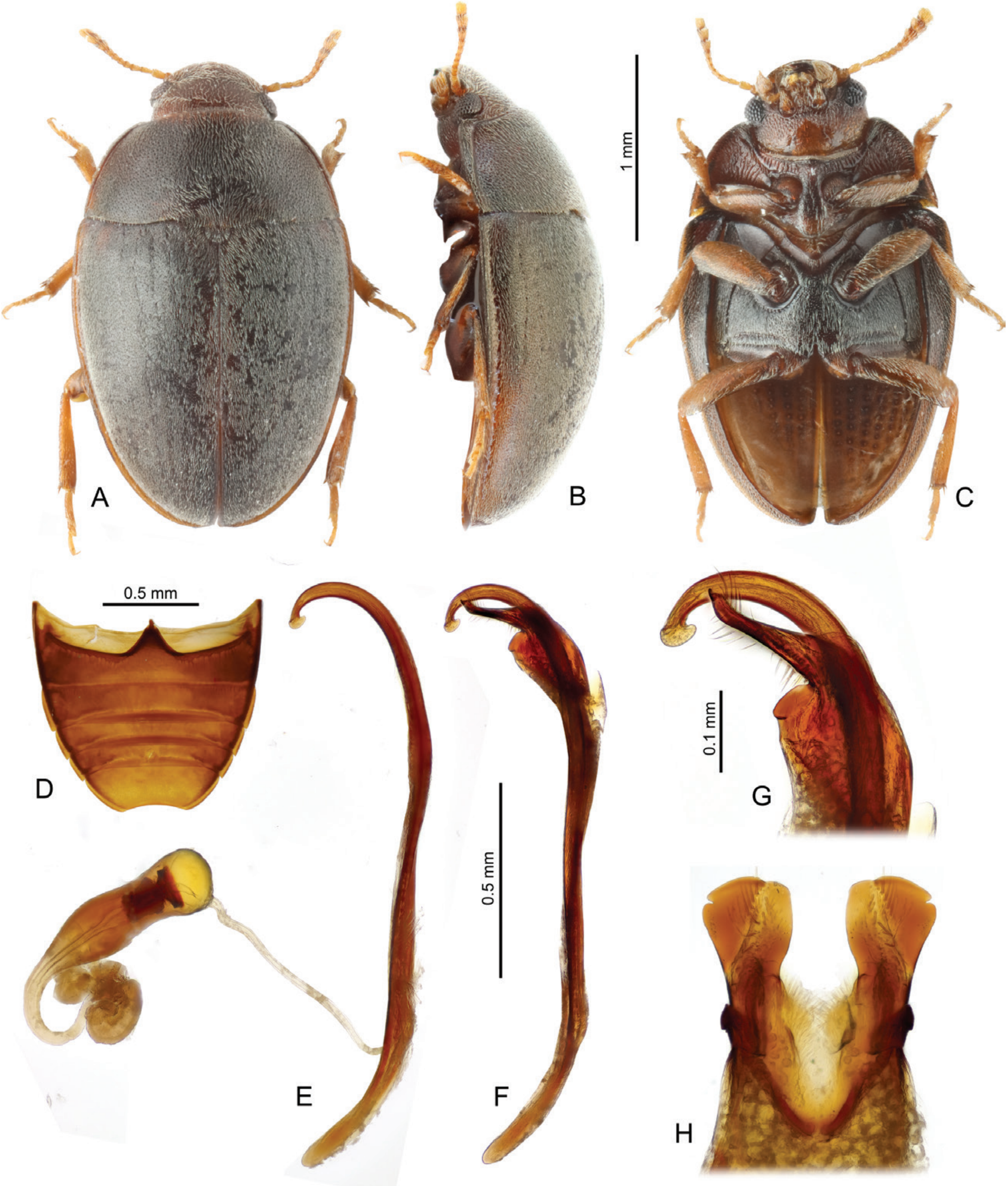

Figure 3. *Sivacrypticus taiwanicus* Kaszab, 1964 (Archeocrypticidae). **A–C.** Habitus (**A.** Dorsal; **B.** Lateral; **C.** Ventral); **D.** Abdominal ventrites, male; **E–H.** Male genitalia (**E.** Median lobe and the sperm pump, lateral view; **F.** Median lobe and parameres, lateral view; **G.** Detail of median lobe and parameres, lateral view; **H.** Detail of parameres, dorsal view).

New records for Taiwan

Since the leaf litter fauna of Taiwan has never been studied in detail, even our small starting dataset from the single area in central Taiwan results in many new records for Taiwan at species, genus or even family levels. Below we concisely report these new records, despite the species-level taxonomic treatment of most of them requiring additional study. The material examined is only listed for taxa identified down to species, for genus-level records, it can be found in the Excel sheet with the complete data (Suppl. material 2). List of all species recorded in this project and identified down to genus or species is available in the Appendix 1.

Carabidae

Oodes (*Lachnocrepis*) *japonicus* (Bates, 1873) (Licininae: Oodini)

Material examined. 1 female (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 20.vi.2020, F.S. Hu lgt., mixed *Cryptomeria* + sparse broadleaf forest on the slope (voucher 20-06HS304); 1 spec. (IDL): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 17.viii.2021, M. Fikáček & W.R. Liang lgt., stony forest on the slope, small leaf accumulations (voucher 21-08HS115). 9 spec. (IDL): Taiwan: Kaohsiung City, Zuoying district (左營區), Banpingshan (半屏山), SW slope, 22.694262 120.305072, 100 m, 22.vii.2021, M. Fikáček lgt. (TW2021-06d), sifting of large to shallow leaf accumulations with some wood and fungi in the forest with *Ficus* in karst area (incl. voucher BP1-001); 17 spec. (IDL): same area and date but 90 m, 22.693469, 120.304979 (TW2021-06f) (incl. DNA voucher BP3-001); 8 spec. (IDL): same area, 90 m, 22.693469, 120.304979, 11.viii. 2022, M. Fikáček lgt. (TW2022-006A) (incl. DNA voucher BP4-010); 2 spec. (IDL): same area and date, 100 m, 22.693469, 120.304979 (TW2022-006B) (incl. DNA voucher BP7-010); 1 spec. (IDL): same area, 22.693469, 120.304979, 90 m, 30.v. 2023, M. Fikáček lgt. (TW2023-015, DNA voucher BP10-002); 1 spec. (IDL): same area, 22.694262, 120.305072, 90 m, 30.v. 2023, M. Fikáček lgt. (TW2023-016, DNA voucher BP9-003).

Comments. Multiple species and genera of the Oodini are reported from Japan or southern China (Guéorguiev 2014; Löbl and Löbl 2017; Guéorguiev and Liang 2020), with only *Oodes desertus* Motschulsky, 1858 reported from Taiwan so far (Guéorguiev and Liang 2020). The species barcoded here belongs to *Oodes* (*Lachnotrepis*) based on the width of elytral interval 7 and 8 and setation of tarsomeres, and corresponds to *O. japonicus* based on all characters in the identification key by Guéorguiev and Liang (2020). The species is widespread from the Russian Far East through China and Japan to Laos and Vietnam (Guéorguiev and Liang 2020). It is recorded from Taiwan for the first time; based on our data it may be widespread in lowland to lower montane forests of central and southern Taiwan. For larval morphology, see below.

Histeridae

Anapleus Horn, 1873 (Dendrophilinae: Anapleini)

Comments. The genus was first recorded from Taiwan by Bickhardt (1913) based on *A. stigmaticus* (Schmidt, 1892). Mazur (2007) mentioned that this record might be based on a misidentification and removed the genus and species from his updated list of the Histeridae of Taiwan. The specimen sequenced here is morphologically different from *A. stigmaticus*; its identification will be done in the future.

Leiodidae

Dermatohomoeus sp.

Material examined. 4 females (ZSPC): Taiwan: Nantou County Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E, 1150 m, 24.ii.2020, F.S. Hu lgt., primary forest on the slope with sparse understory: sifting of small leaf accumulations (incl. DNA voucher 20-02HS511); 17 females (ZSPC): same locality, 20.vi.2020, F.S. Hu lgt. (incl. DNA voucher 20-06HS519); 31 females (ZSPC): same locality, 11.x.2020, F.S. Hu & Y.J. Chen lgt. (incl. DNA voucher 20-10HS521); 19 females (ZSPC): same locality, 16.viii.2021, M. Fikáček & W.R. Liang lgt. (incl. voucher 21-08HS526); 1 female (ZSPC): same locality, 1.iii.2021, M. Fikáček, F.S. Hu & G.J. Peng lgt. (voucher 21-03HS507); 10 females (ZSPC): same locality, 4.v.2019, M. Fikáček, F.S. Hu, A. Damaska & H.C. Liu lgt. (incl. DNA voucher HS1020); 4 females (ZSPC): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 16.viii.2021, mixed *Cryptomeria* + sparse broadleaf forest on the slope, 16.viii.2021, M. Fikáček & W.R. Liang lgt. (incl. DNA voucher 21-08HS339); 1 female (ZSPC): same locality, 20.vi.2020, F.S. Hu lgt. (voucher 20-06HS317); 1 female (ZSPC): same locality, 11.x.2020, F.S. Hu & Y.J.Chen lgt. (voucher 20-10HS310); 8 females (ZSPC): Taiwan: Nantou County, Huisun Forest Reserve, Xiaochushan Mt. track, 0.5 km above hotels 24.0887444°N, 121.0355063°E, 850 m, 4.v.2019; Damaška, Fikáček, Hu & Liu lgt.; large accumulations of leaf litter in a small gorge with lower montane/ lowland broad-leaf forest (incl. voucher HS4031); 2 females (ZSPC): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 28.ii.2020, F.S. Hu & Y.J. Chen lgt., stony forest on the slope, small leaf accumulations (incl. DNA voucher 21-03HS120); 1 female (ZSPC): same locality, 5.v.2019, M. Fikáček, F.S. Hu, A. Damaska & H.C. Liu lgt. (DNA voucher HS5013).

Comments. The genus is newly recorded from Taiwan in the present paper. The previous records of the genus from Taiwan are based on the transfer of *Colenisia miyatakei* (Hisamatsu, 1985) to the *Dermatohomoeus* by Hoshina (1999) that is however not supported by diagnostic characters of *Dermatohomoeus* (Švec 2022). Consequently, *Dermatohomoeus* has not been reported from Taiwan before. All DNA-barcoded specimens from the Huisun Reserve are conspecific, and the examination of additional non-sequenced specimens confirms that all collected specimens are conspecific. Yet, they cannot be identified to species, as all of them are females (in total 99 specimens from 12 collecting events at four different collecting sites). The species of the genus are morphologically uniform, with species-specific characters being the shape of the aedeagus, including the endophallus. Female genitalia and the spermatheca of *Dermatohomoeus* species are of the unique shape within the tribe Pseudoliodini but lack species-specific morphological features. External morphological characters detectable in *Dermatohomoeus* females are hardly sufficient for species identifications. The population of *Dermatohomoeus* consisting exclusively of females found in this study is not the first case of the absence of males. No males have been found so far for *Dermatohomoeus terrenus* (Hisamatsu, 1985), despite altogether several dozen specimens attributed to this species having been examined (Hisamatsu 1985; Hoshina 1999; Park and Ahn 2007; Švec 2022). The species is known from the Japanese islands of Honshu, Shikoku, Kyushu, Izu, Goto, from four Ryukyus islands (Hoshina 1999) and the Awaji Island (Švec 2022). Besides them, the species was recorded also from southern Korea (Park and Ahn 2007). Hoshina (1999) published a hypothesis that *D. terrenus* may be a parthenogenetic species. Perhaps, this type of reproduction is more widespread in *Dermatohomoeus* species or their populations, including those occurring in Taiwan.

Staphylinidae

***Drusilla obliqua* (Bernhauer, 1916) (Aleocharinae: Lomechusini)**

Material examined. 12 spec. (FSHC, IDL): same locality, 20.vi.2020, lgt. F.S. Hu (voucher 20-06HS129, and non-extracted specimens); 1 spec. (IDL): same locality, 17.viii.2021, lgt. M. Fikáček & W.R. Liang (voucher 21-08HS133).

Comments. *Drusilla obliqua* is a widespread species; it has been recorded from India, Nepal, Myanmar, China (Yunnan), Vietnam and Malaysia (Assing 2017, 2019). The species is newly recorded from Taiwan in the present paper.

***Paraploderus* cf. *thailandicus* Makranczy, 2016 (Oxytelinae: Thinobiini)**

Fig. 4

Material examined. 16 spec. (HNHM, IDL): TAIWAN: Nantou County Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E; 1150 m 11.x.2020; Hu & Chen lgt., primary forest on the slope with sparse understory: sifting of small accumulations of leaves (DNA voucher 20-10HS531 and non-extracted specimens). 13 spec. (MHNG): TAIWAN: Taoyuan Co. Twnsh.Fushing S-BaLing km 54, road 7, 22.ii.2010 1140m, decaying wood + forest litter, leg. S. Vit #2; 3 spec. (MHNG): TAIW: Chiayi County Alishan Natural Scenic Area, 11.iv.2009 2350m, leg. S. Vit #18//Road 18, km 02 Old Lulin Tree Track, decaying Wood litter #18.

Comments. The genus is newly recorded from Taiwan in the present paper. György Makranczy examined the specimens of this *Paraploderus* species from Taiwan already earlier, based on the material collected by S. Vít deposited in MHNG (see under Material examined). The male genitalia of these specimens (Fig. 4) show rather slight differences from those of *Paraploderus thailandicus* Makranczy, 2016. Therefore, it requires confirmation whether the Taiwanese populations represent a distinct species or not. This is best done by a comparison of DNA sequences from Taiwan and the mainland, including Thailand from where the species was described.

***Thinocharis* Kraatz, 1859 (Paederinae: Lathrobiini)**

Comments. The genus is newly recorded from Taiwan in the present paper. The species identification will need to be done in the future.

Tribe Trichonychini (Pselaphinae)

Comments. The tribe is newly recorded from Taiwan in the present paper, as well as the supertribe Euplectitae. There are at least two species in our samples. A generic revision of the Trichonychini needs to be done before the confirmation of the generic identifications.

Tribe Ctenistini (Pselaphinae)

Comments. The tribe is here newly recorded from Taiwan. The generic revision of the Ctenistini needs to be done before the confirmation of the generic identifications.

Tribe Bythinoplectini (Pselaphinae)

Comments. The tribe, as well as the supertribe Euplectitae, are newly recorded from Taiwan here. There are at least two species in our samples.

***Batraxis* Reitter, 1882 (Pselaphinae: Brachyglutini)**

Comments. The genus was listed for Taiwan in the Catalogue of Life, based on the occurrence of *B. obesa* Raffray, 1894 (Chung and Shao 2022). However, the source of the record was online only and the link is not available anymore. We formally record the genus from Taiwan for the first time.

***Cephennodes* Reitter, 1884 (Scydmaeninae: Cephenniini)**

Comments. The genus is newly recorded from Taiwan in the present paper. The species identification will be done in the future.

***Napoconnus* Franz, 1957 (Scydmaeninae: Stenichnini)**

Comments. The genus has been newly recorded from Taiwan in the present paper. The species identification will need to be done in the future.

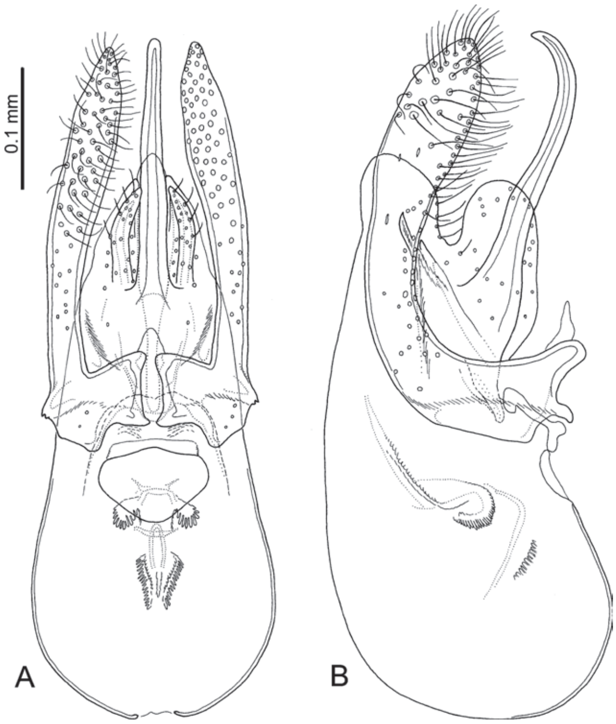

Figure 4. Male genitalia of *Paraploderus* cf. *thailandicus* Makranczy, 2016 from Taiwan. **A.** Frontal view (parameral setation shown on the left); **B.** Lateral view.

Cerylonidae

Thyroderus porcatus **Sharp, 1885 (Ceryloninae)**

Material examined. 2 spec. (FSHC, IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E; 1150 m, 1.iii.2021, M. Fikáček, F.S. Hu & G.J. Peng lgt. (voucher 21-03HS511 and an additional non-sequenced specimen).

Comments. The species was only known from Japan previously (Löbl and Smetana 2007), representing the only species of the genus that occurred in the Palearctic region. The genus and the species are newly recorded from Taiwan.

Cautomus **Sharp, 1885 (Ceryloninae)**

Comments. The genus is newly recorded from Taiwan in this study based on two species from the Huisun Forest Reserve. Both species differ both by the DNA barcode sequences and morphologically. The species identification will be done in the future.

Sphindidae

Aspidiphorus **Ziegler, 1821**

Comments. The family and genus are newly recorded from Taiwan. There are two species in our Huisun samples identified by the DNA barcode sequences; their species identification needs to be done in the future.

Latridiidae

Bicava **Belon, 1884**

Comments. The genus is newly recorded from Taiwan in the present paper. The species identification will be done in the future.

Cartodere **sp.**

Comments. The genus was first recorded from Taiwan by Yao et al. (2011) based on *C.* (s. str.) *constricta* (Gyllenhal, 1827). The specimens sequenced in this study differ from *C.* (s. str.) *constricta* by having three antennomeres clubbed (in contrast to two clubbed antennomeres in *C. constricta*). The species identification will be done in the future.

Curculionidae

Otibazo **Morimoto, 1961**

Comments. The genus is newly recorded from Taiwan in the present paper. An extensive taxonomic study on this genus in Taiwan is in preparation and will be published in the near future (Wei-Zhe Tseng, in prep.).

Seleuca **Pascoe, 1871**

Comments. The genus is newly recorded from Taiwan in the present paper. The species identification needs to be completed in the future.

Acallinus **Morimoto, 1962**

Comments. The genus is newly recorded from Taiwan in the present paper. Based on the DNA barcodes, the samples reported here (Taiwan: Nantou County, Huisun Forest Reserve) contain two or three species. The species identification needs to be done in the future.

Coccotrypes advena **Blandford, 1894**

Material examined. 1 female (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0826139°N, 121.0315869°E; 1050 m, 4.v.2019, Damaška, Fikáček, Hu & Liu lgt., sparse secondary forest with dense understory incl. tree ferns on the margin of a tree plantation (voucher HS2015); 1 female (IDL): Taiwan: Nantou County, Huisun Forest res., Xiaochushan Mt. track, 0.5 km above hotels 24.0887444°N, 121.0355063°E, 850 m, 4.v.2019; Damaška, Fikáček, Hu & Liu lgt., large accumulations of leaf litter in a small gorge with lower montane/lowland broad-leaf forest (voucher HS4007); 4 females (IDL): Taiwan: Nantou County, Huisun Forest reserve, Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 11.x.2020, F.S.Hu & Y.J.Chen lgt. (incl. voucher 20-10HS114); 2 females (IDL): same locality, 17.viii.2021, M. Fikáček & W.R. Liang lgt. (incl.

voucher 21-08HS170); 1 female (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 11.x.2020, F.S.Hu & Y.J.Chen lgt. (voucher 20-10HS308); 1 female (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E, 1150 m, 16.viii.2021, M. Fikáček & W.R.Liang lgt. (voucher 21-08HS559).

Comments. This is a generalist seed-boring scolytine species widespread in SE Asia, Australia and Oceania, America from Florida through the Caribbean to Suriname (Wood and Bright 1992; Bright 2021) and also recorded from Africa (Uganda: Jordal et al. 2002). In Asia, it has been recorded from India, Sri Lanka, Thailand, Vietnam, Indonesia, Malaysia, the Philippines, and Japan; here we are recording it from Taiwan for the first time. Jordal et al. (2002) report a high intraspecific variation of *cox1* sequences, possibly indicating that it represents a complex of species. The *cox1* sequences of our specimens cluster with those of the Japanese specimen sequenced by Jordal et al. (2002) (uncorrected *p*-distance to the Japanese specimen: 0.7–1.6%).

Examples of larvae associated with adults

Carabidae

Oodes (*Lachnocrepis*) *japonicus* (Bates, 1873) (Licininae: Oodini)

Fig. 5

Material examined. Larvae: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 20.vi.2020, F.S. Hu lgt., stony forest on the slope, small leaf accumulations (voucher 20-06HS179); 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 16.viii.2021, M. Fikáček & W.R. Liang lgt., mixed *Cryptomeria* + sparse broadleaf forest on the slope (voucher 21-08HS350). Adults: see above under New records for Taiwan.

Comments. The knowledge on larval morphology of the Oodini is quite limited so far, with larvae of several species of *Oodes* Bonelli, 1810 described and illustrated (van Emden 1942; Lindroth 1942; Chu 1945; Thomson 1979); the larva of an unidentified North American *Oodes* illustrated by Chu (1945) differs from others in very narrow mandibles, transverse head, multidentate nasale and frontale reaching posterior margin of the head, and may actually represent a different taxon than *Oodes* or Oodini. The larva of *Oodes* (*Lachnocrepis*) *japonicus* corresponds to *Oodes* s.str. larvae illustrated by van Emden (1942) and Lindroth (1942) by general morphology, but differs from them in the shape of the nasale (*O. japonicus* with 4 sharp teeth, compared to 3 or 5 low rounded teeth in *O. helopioides* and *O. gracilis*, respectively), more slender mandibles, shorter and more robust antennomeres, and wider and more robust labial palpomere 2.

Perigona cf. *nigriceps* Dejean, 1831 (Lebiinae: Perigonini)

Fig. 6

Material examined. Larvae: 2 larvae (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 20.vi.2020, F.S. Hu lgt., mixed *Cryptomeria* + sparse broadleaf forest on the slope (voucher 20-06HS344 and one additional specimen). Adults: 1 spec. (IDL): same locality, date and collector (voucher 20-06HS305); 1 spec. (IDL): same locality but 16.viii.2021, M. Fikáček & W.R. Liang lgt. (voucher 21-08HS313).

Comments. *Perigona* Laporte, 1835 is a species-rich world-wide genus (e.g., Baehr 2014) with larva only illustrated for *P.* (*Xenogona*) *termitis* Jeannel, 1941 (Jeannel 1941, 1942). Sequenced and examined adult specimens from Huisun belong to the subgenus *Trechicus* LeConte, 1853 based on the triangular arrangement of the subapical elytral punctures. Genetically it stands close (uncorrected *p*-distance 6.4–6.6%) but does not cluster with available sequences of the world-wide invasive *P. nigriceps* Dejean, 1831 for which DNA barcodes are available from Europe, Africa, South America, the Caribbean and New Zealand in the BOLD database (these moreover form two separate clusters). The larva examined and illustrated here corresponds to that of *P. termitis* in all characters including the multidentate slightly projecting nasale; it slightly differs from the larva of *P. termitis* by more robust labial palpomere 1.

Ptilodactylidae: Ptilodactylinae

Ptilodactyla sp.

Fig. 7

Material examined. Larvae: 3 larvae (IDL): Taiwan: Nantou County, Huisun Forest reserve, Wading trail, 24.0892139°N, 121.0297836°E, 700m, 24.ii.2020, F.S. Hu lgt., stony disturbed forest on the slope, small leaf accumulations (incl. sequenced voucher 20-02HS155). Adults: 3 adults (NMPC): same locality, 5.v.2019, Damaška, Fikáček, Hu & Liu lgt. (2019-TW18) (incl. sequenced voucher HS5011).

Comments. Larvae of *Ptilodactyla* Illiger, 1807 have been mentioned and illustrated by numerous authors (e.g., Costa et al. 1988), including that of *P. exotica* Chapin, 1927 which is introduced with tropical plants in the USA and Europe (e.g., Aberlenc and Allemand 1997; Mann 2006; Viñolas et al. 2020). Here we are concisely illustrating the sequenced larva of *Ptilodactyla* from subtropical lowland forest in central Taiwan. The examined specimen has clearly visible proventriculus armored with numerous spines (Fig. 7A), a structure not yet documented for larval Ptilodactylidae; we suppose this may be an adaptation for processing the food, indicating that *Ptilodactyla* larvae likely feed also on decaying wood and detritus, not only on plant roots as stated by some authors (e.g., Lawrence 2005).

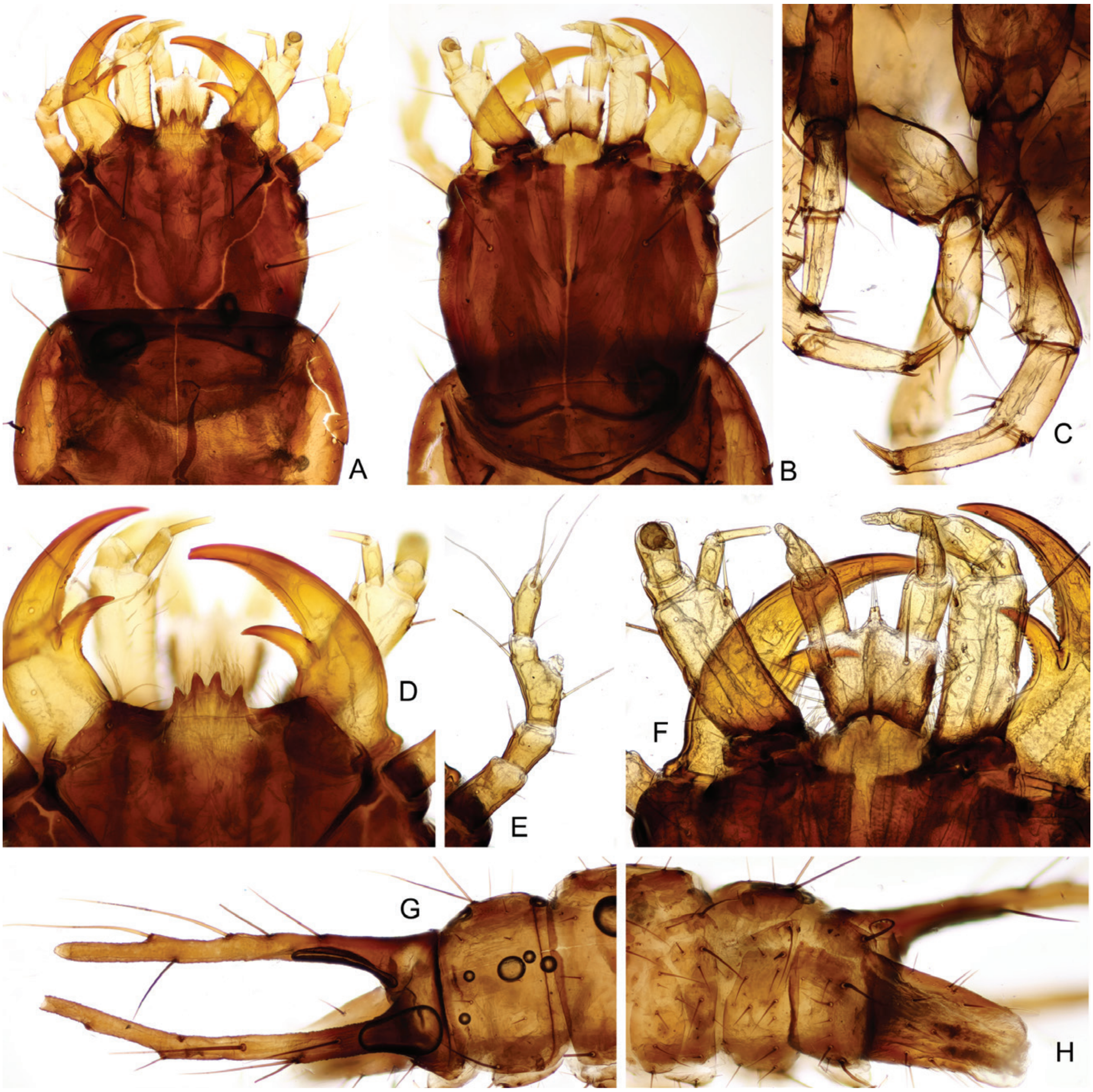

Figure 5. Carabidae: Oodini: larva of *Oodes* (*Lachnocrepis*) *japonicus* (Bates, 1873) (OTU159, voucher 20-08HS350) associated with adults by DNA. **A, B.** Head (**A.** Dorsal view; **B.** Ventral view); **C.** Middle and hind legs; **D.** Nasale and mandibles, dorsal view; **E.** Antenna, dorsal view; **F.** Mouthparts, ventral view; **G, H.** Abdominal apex (**G.** Dorsal view; **H.** Ventral view).

Cantharidae: Malthininae

***Maltypus ryukyuanus* Wittmer, 1970 (Malthodini)**
Fig. 8

Material examined. Larva: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0826139°N, 121.0315869°E; 1050 m, 4.v.2019; Damaška, Fikáček, Hu & Liu lgt., sparse secondary forest with dense understory incl. tree ferns on the margin of a tree plantation: sifting (2019-TW15) (sequenced voucher HS4055L). Adult: 1 specimen (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 20.vi.2020, F.S. Hu lgt., mixed conifer/broadleaf forest + sparse broadleaf forest on the slope (sequenced voucher 20-06HS319).

Comments. In Malthininae, larvae are only known for two genera, *Malthinus* Latreille, 1806 (Malthinini) and *Malthodes* Kiesenwetter, 1852 (Malthodini), with the data about their morphology are scattered. Klausnitzer (1997) assembled all the data and proposed a key to species. Fitton (1976) presented the similarities and differences between both genera. The examined larva of *Maltypus* Motschulsky, 1860 is similar to that of *Malthodes* sp. illustrated by Fitton (1976) in the shape of the median tooth of nasale and the absence of setae on the median tooth, but resembles the larva of *Malthinus* in the inner tooth of the mandible situated more basally. The larva of *Maltypus* is illustrated for the first time here.

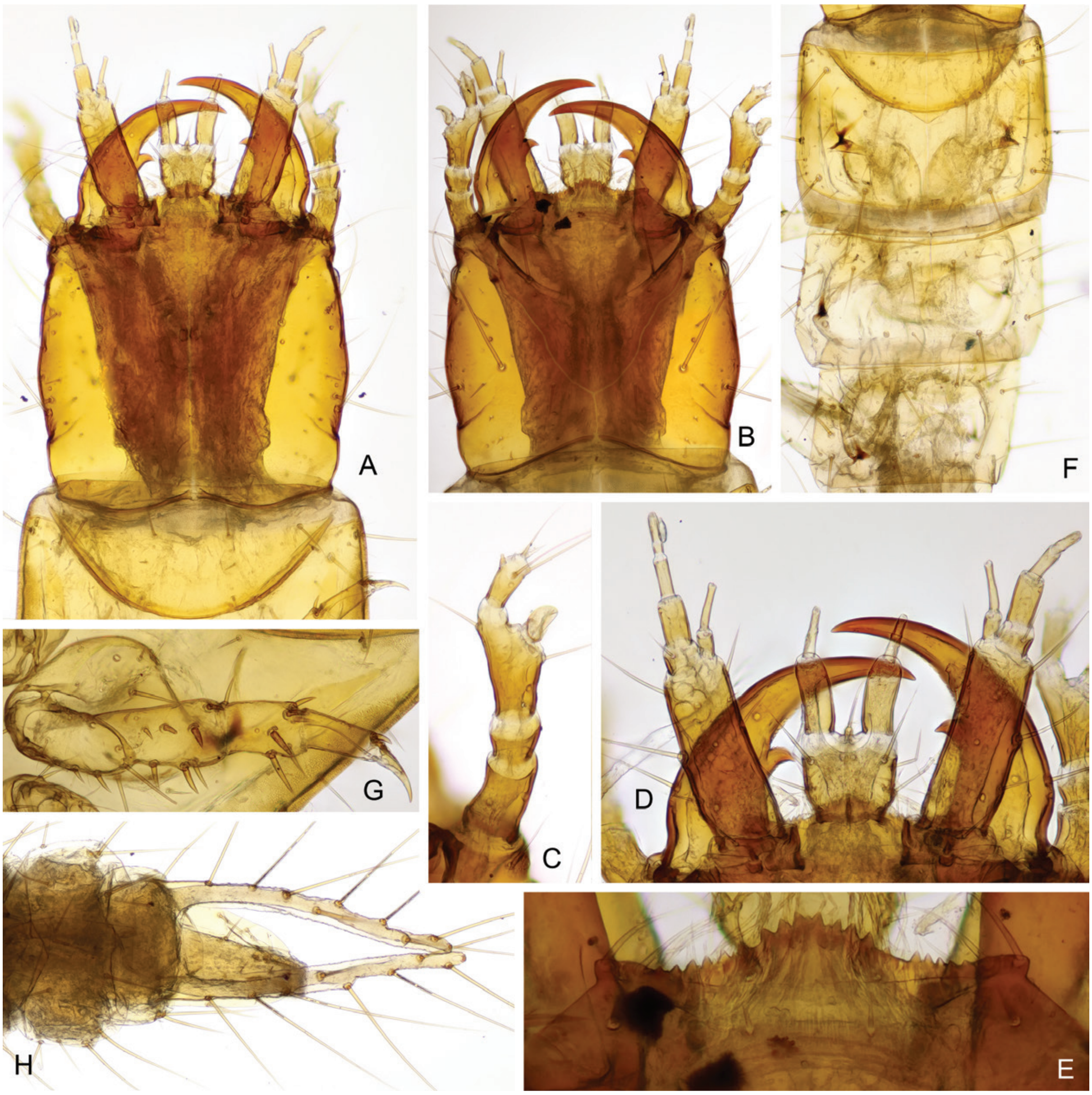

Figure 6. Carabidae: Perigonini: larva of *Perigona* cf. *nigriceps* Dejean, 1831 (OTU158, voucher 20-06HS344) associated with adults by DNA. **A, B.** Head (**A.** Ventral view; **B.** Dorsal view); **C.** Antenna; **D.** Mouthparts, ventral view; **E.** Nasale; **F.** Thorax, dorsal view; **G.** Middle leg; **H.** Abdominal apex.

Staphylinidae
Aleocharinae

***Drusilla obliqua* (Bernhauer, 1916) (Lomechusini)**
Fig. 9

Material examined. Larvae: 2 larvae (IDL): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 30.vi.2020, F.S. Hu lgt., stony forest on the slope, small leaf accumulations (vouchers 20-06HS176 and 20-06HS187); 2 larvae (IDL): same locality but 17.viii.2021, M. Fikáček & W.R. Liang lgt. (vouchers 21-08HS152 and 21-08HS153). Adults: 1 spec. (IDL): same locality, 20.vi.2020, lgt. F.S. Hu (voucher 20-06HS129); 1 spec. (IDL): same locality, 17.viii.2021, lgt. M. Fikáček & W.R. Liang (voucher 21-08HS133).

Comments. Larvae of two species of *Drusilla* Leach, 1819 have been described: *Drusilla canaliculata* (Fabricius, 1787) (Paulian 1941; Topp 1978; Schminke 1982) and *D. italica* (Bernhauer, 1903) (De Marzo 2007). Larvae of all species of *Drusilla* are very similar and further comparisons are needed to distinguish them.

***Myrmecocephalus brevisulcus* (Pace, 2008) (Falagriini)**
Fig. 10

Material examined. Larvae: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 20.ii.2020, F.S. Hu lgt., stony forest on the slope, small leaf accumulations (voucher 20-02HS154); 2 larvae (IDL): same locality but 11.x.2020, F.S. Hu & Y.J. Chen lgt. (vouchers 20-10HS163–164); 1 larva

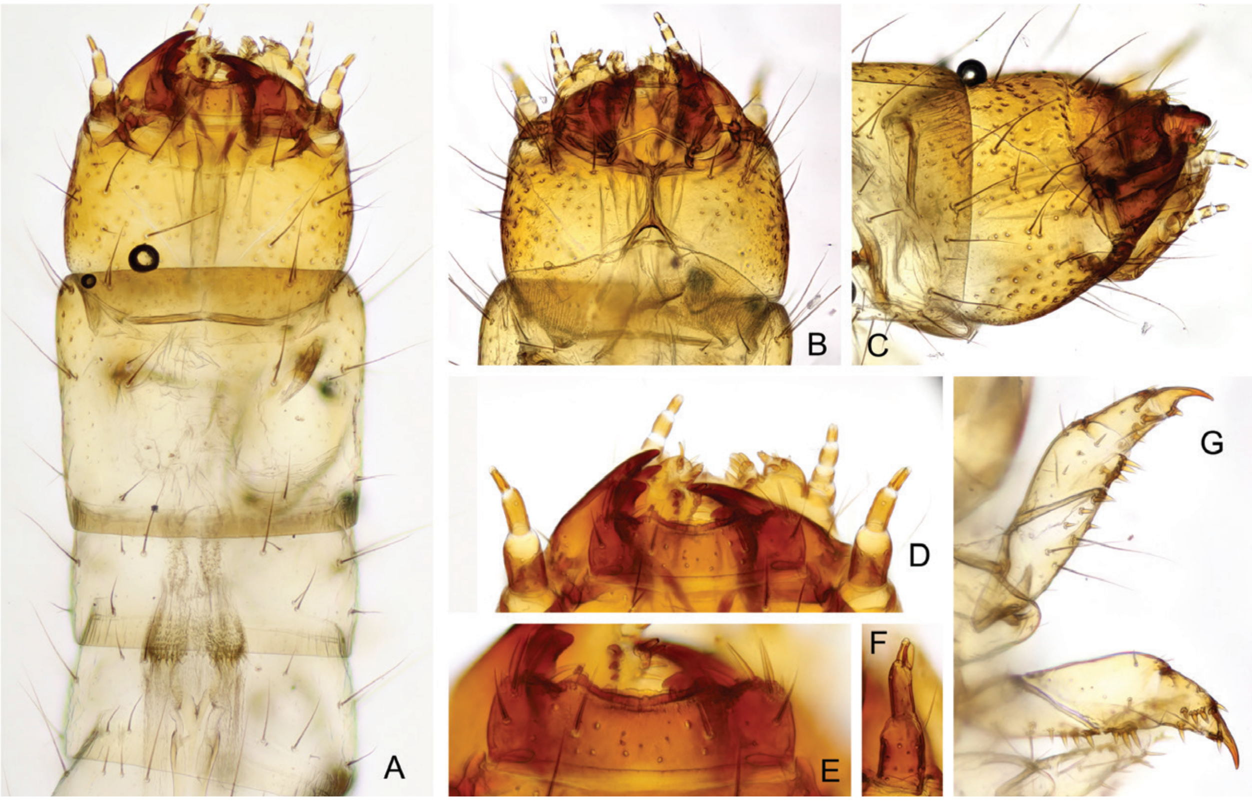

Figure 7. Ptilodactylidae: larva of *Ptilodactyla* sp. (OTU83, voucher 20-02HS155) associated with adults by DNA. **A.** Head and thorax in dorsal view; **B.** Head, ventral view; **C.** Head, lateral view; **D.** Anterior part of the head, dorsal view; **E.** Detail of labrum; **F.** Antenna in lateral view; **G.** Front and middle leg.

(IDL): same locality but 28.ii.2021, F.S. Hu & Y.J. Chen lgt. (voucher 21-03HS157); 1 larva (IDL): same locality but 5.v.2019, Fikáček, Hu, Damaška & Liu lgt. (voucher HS5071L); 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 4.v.2019; Damaška, Fikáček, Hu & Liu lgt., mixed conifer/broadleaf forest + sparse broadleaf forest on the slope (2019-TW16) (voucher HS3067L); 1 larva (IDL): same locality but 20.vi.2020, F.S. Hu lgt. (voucher 20-06HS348); 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E, 1150 m, 20.vi.2020, F.S. Hu lgt., oldgrown secondary forest on the slope with sparse understory (voucher 20-06HS573); 1 larva (IDL): same locality but 11.x.2020, F.S. Hu & Y.J. Chen lgt. (voucher 20-10HS563). Adults: 1 adult (FSHC): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 20.ii.2020, F.S. Hu lgt., stony forest on the slope, small leaf accumulations (voucher 20-02HS132); 1 adult (FSHC): same locality but 20.vi.2020 (voucher 20-06HS130); 1 adult (FSHC): same locality but 11.x.2020, F.S. Hu & Y.J. Chen lgt. (voucher 20-10HS135); 1 adult (IDL): same locality but 28.ii.2021, F.S. Hu & Y.J. Chen lgt. (voucher 21-03HS139); 1 adult (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E, 1150 m, 20.vi.2020, F.S. Hu lgt., oldgrown secondary forest on the slope with sparse understory (voucher 20-06HS533); 1 adult (IDL): same locality but 11.x.2020, F.S. Hu & Y.J. Chen lgt. (voucher 20-10HS529); 1 adult (IDL): same locality but 16.viii.2021, M. Fikáček & W.R. Liang lgt.

Comments. Larvae of several genera of Falagriini have been described or illustrated, including *Cordalia* Jacobs, 1925, *Falagria* Leach, 1819 and *Myrmecopora* Saulcy, 1864 (Topp 1978; De Marzo 2000, 2002, 2008, 2009). The larva of *Myrmecocephalus brevisulcus* is similar to that of *Myrmecopora* by the posterior part of the head becoming remarkably narrower. *Myrmecocephalus* can be distinguished from the *Myrmecopora* by the longer and stouter first antennal segment. The larva of *Myrmecocephalus* is illustrated for the first time here.

Staphylininae

Diochus sp. (Diochini)

Fig. 11

Material examined. Larva: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 20.vi.2020, F.S. Hu lgt., stony forest on the slope, small leaf accumulations (voucher 20-06HS182). Adults: 1 adult (coll. J. Janák, Prague): same locality but 11.x.2020, F.S. Hu & Y.J. Chen lgt. (voucher 20-10HS136); 1 adult (coll. J. Janák, Prague): same locality but 17.viii.2021, M. Fikáček & W.R. Liang lgt. (voucher 21-08HS124); 1 adult (IDL): Taiwan:

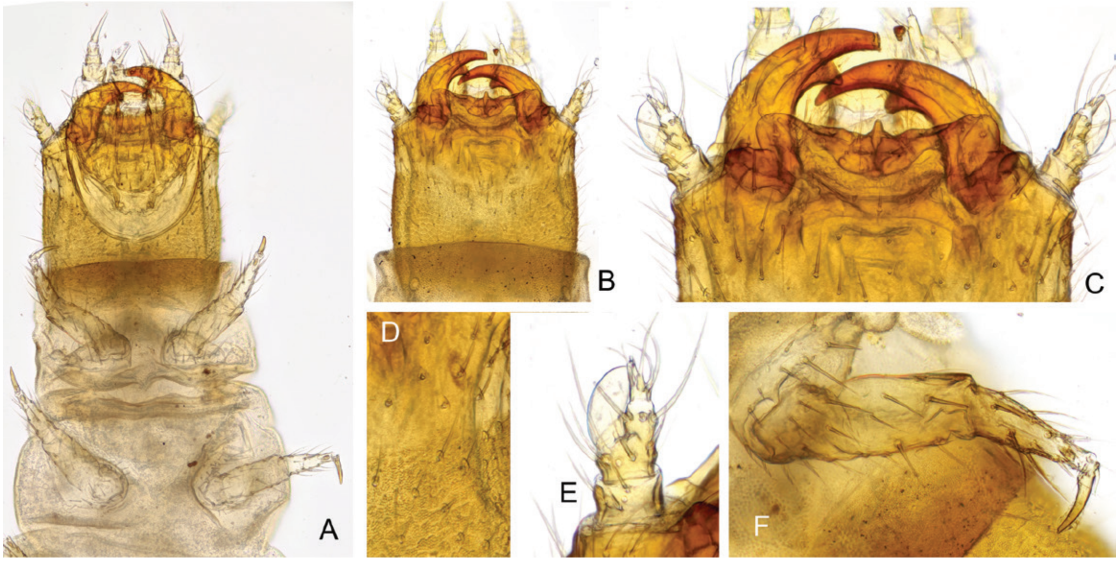

Figure 8. Cantharidae: larva of *Maltypus ryukyuanus* (OTU66, voucher HS4055L) associated with adults by DNA. **A.** Head and pro- and mesothorax, ventral view; **B.** Head, dorsal view; **C.** Detail of anterior part of the head, dorsal view; **D.** Detail of the head surface, with smooth anterior and sculptured posterior part; **E.** Antenna; **F.** Front leg.

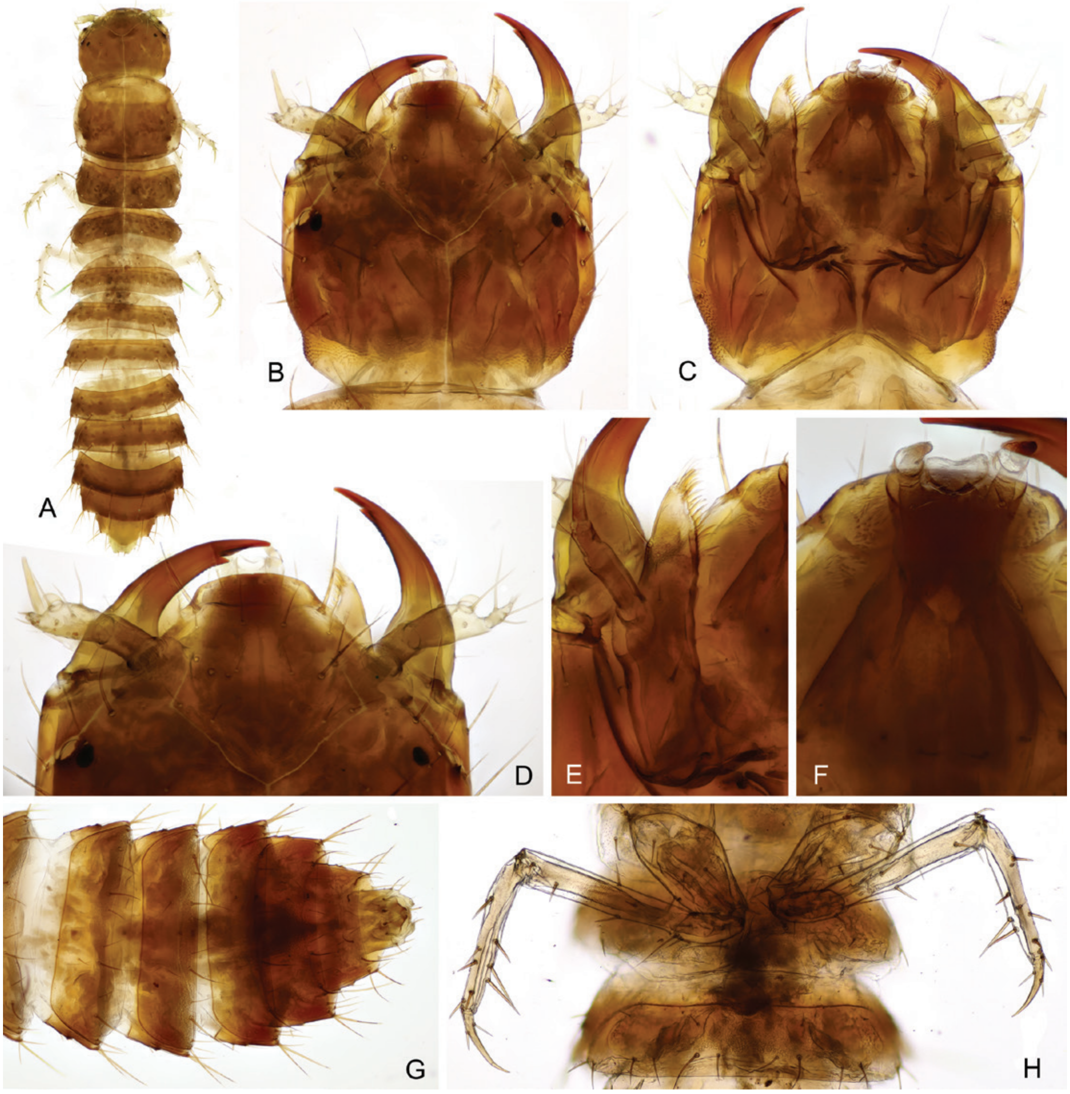

Figure 9. Staphylinidae: Aleocharinae: Lomechusini: larva of *Drusilla obliqua*. (OTU216, voucher 21-08HS152) associated with adults by DNA. **A.** Dorsal habitus; **B–F.** Head: **B.** Dorsal view; **C.** Ventral view; **D.** Details of anterior part in dorsal view; **E.** Maxilla; **F.** Labium; **G.** Abdominal apex in ventral view; **H.** Hind legs.

Kaohsiung City, Zuoying district (左營區), Banpingshan (半屏山), SW slope, 22.694296°N, 120.305797°E, 100 m, 22.vii. 2021, M. Fikáček lgt., sifting of shallow leaf accumulations with some wood and fungi and fallen figs in the forest with *Ficus* in karst area (TW2021-06e) (voucher BP2-012).

Comments. The tribe Diochini contains two genera: *Antarctothius* Coiffait & Sáiz, 1969 and *Diochus* Erichson, 1839; the larva of *Antarctothius* is unknown. The larva of the American *Diochus schaumii* Kraatz, 1860 is currently the only known larva in the tribe; it has been mentioned in the phylogenetic study by Solodovnikov and Newton (2005) and listed in the material examined by Irmler (2017), but neither of these works provides a detailed description of the larva. Newton (1990) illustrated an unidentified larva of *Diochus* from Mexico, which is very similar to the *Diochus* sp. from Taiwan. Here we document the larva of *Diochus* sp. which seems to be widespread in lowland forests of Taiwan because this species was found in central (Huisun) and southern Taiwan (Banpingshan) in this study. The adult of this species is similar to one of *D. japonicus* Cameron, 1930 based on the shorter second antennal segment, but the morphology of aedeagus is completely different. The species identification needs to be done by further comparisons.

Paederinae

Mimopinophilus sp. (Pinophilini)

Fig. 12

Material examined. Larvae: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E, 1150 m, 16.viii.2021, M. Fikáček & W.R. Liang lgt., old-grown secondary forest on the slope with sparse understory (voucher 21-08HS568); 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 16.viii.2021, M. Fikáček & W.R. Liang lgt., mixed conifer/broadleaf forest + sparse broadleaf forest on the slope (voucher 21-08HS346). Adults: 1 spec. (IDL): same locality, but 24.ii.2020, F.S. Hu lgt. (voucher 20-02HS316); 1 spec. (IDL): same locality, 20.vi.2020, lgt. F.S. Hu (voucher 20-06HS321); 1 spec. (IDL): same locality, 11.x.2020, lgt. F.S. Hu & Y.J. Chen (voucher 20-10HS313).

Comments. The larvae of Pinophilini are poorly understood (Staniec et al. 2022). Paulian (1941) described and illustrated a larva of Pinophilini from Brazil; however, the genus to which the larva belongs was not determined. Grebennikov and Newton (2009) coded the larval character states of Paederinae from Australia for the phylogenetic work, which is putative as a larva of *Pinophilus* Gravenhorst 1802. Assing (2022) subdivided the former *Pinophilus* into several separate genera; the species examined here (as well as all other Taiwanese species) correspond to the recently established *Mimopinophilus* Assing, 2022.

Nitidulidae

Stelidota multiguttata Reitter, 1877

Fig. 13A–H

Material examined. Larvae: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 20.vi.2020, F.S. Hu lgt., stony forest on the slope, small leaf accumulations (voucher 20-06HS169); 1 larva (IDL): same locality, 17.viii.2021, M. Fikáček & W.R. Liang lgt. (voucher 21-08HS158). Adults: 1 spec. (IDL): same locality, 24.ii.2020, lgt. F.S. Hu (voucher 20-02HS116); 1 spec. (IDL): same locality, 11.x.2020, lgt. F.S. Hu & Y.J. Chen (voucher 20-10HS111); 1 spec. (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 24.ii.2020, F.S. Hu lgt., mixed *Cryptomeria* + sparse broadleaf forest on the slope (voucher 20-02HS302); 1 spec. (IDL): same locality, 11.x.2020, F.S. Hu & Y.J. Chen lgt. (voucher 20-10HS302); 1 spec. (IDL): same locality, 1.iii.2021, lgt. M. Fikáček, F.S. Hu & G.J. Peng; 1 spec. (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E; 1150 m, 11.x.2020, lgt. F.S. Hu & Y.J. Chen (voucher 20-10HS501).

Comments. The larvae of Nearctic species, *Stelidota geminata* (Say, 1825), *S. ferruginea* Reitter, 1873 and *S. octomaculata* (Say, 1825), have been described (Peng et al. 1990). The larva of *S. multiguttata* is very similar to *S. geminata*; both species possess longer second antennomere. Further comparision between *Stelidota multiguttata* and other species is needed to distinguish these similar species.

Lasiodites inaequalis (Grouvelle, 1914)

Fig. 13I–N

Material examined. Larva: 1 spec. (IDL): Taiwan: Nantou County, Huisun Forest res., Wading trail, 24.0892139°N, 121.0297836°E, 700 m, 20.vi.2020, F.S. Hu lgt., stony forest on the slope, small leaf accumulations (voucher 20-06HS172). Adults: 1 spec. (IDL): same locality, 17.viii.2021, lgt. M. Fikáček & W.R. Liang (voucher 21-08HS107); 1 spec. (IDL): same locality, 11.x.2020, lgt. F.S. Hu & Y.J. Chen (voucher 20-10HS110); 1 spec. (NMPC): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 4.v.2019; Damaška, Fikáček, Hu & Liu lgt., mixed conifer/broadleaf forest + sparse broadleaf forest on the slope: sifting (2019-TW16).

Comments. Although the larvae of the invasive *Lasiodites picta* are sometimes reported in literature (e.g., Serri et al. 2023), the larva of the genus has never been illustrated. Here, we are illustrating an early instar larva of *L. inaequalis*. It differs from the examined larvae of *Stelidota* Erichson, 1843 by the form of the urogomphi and

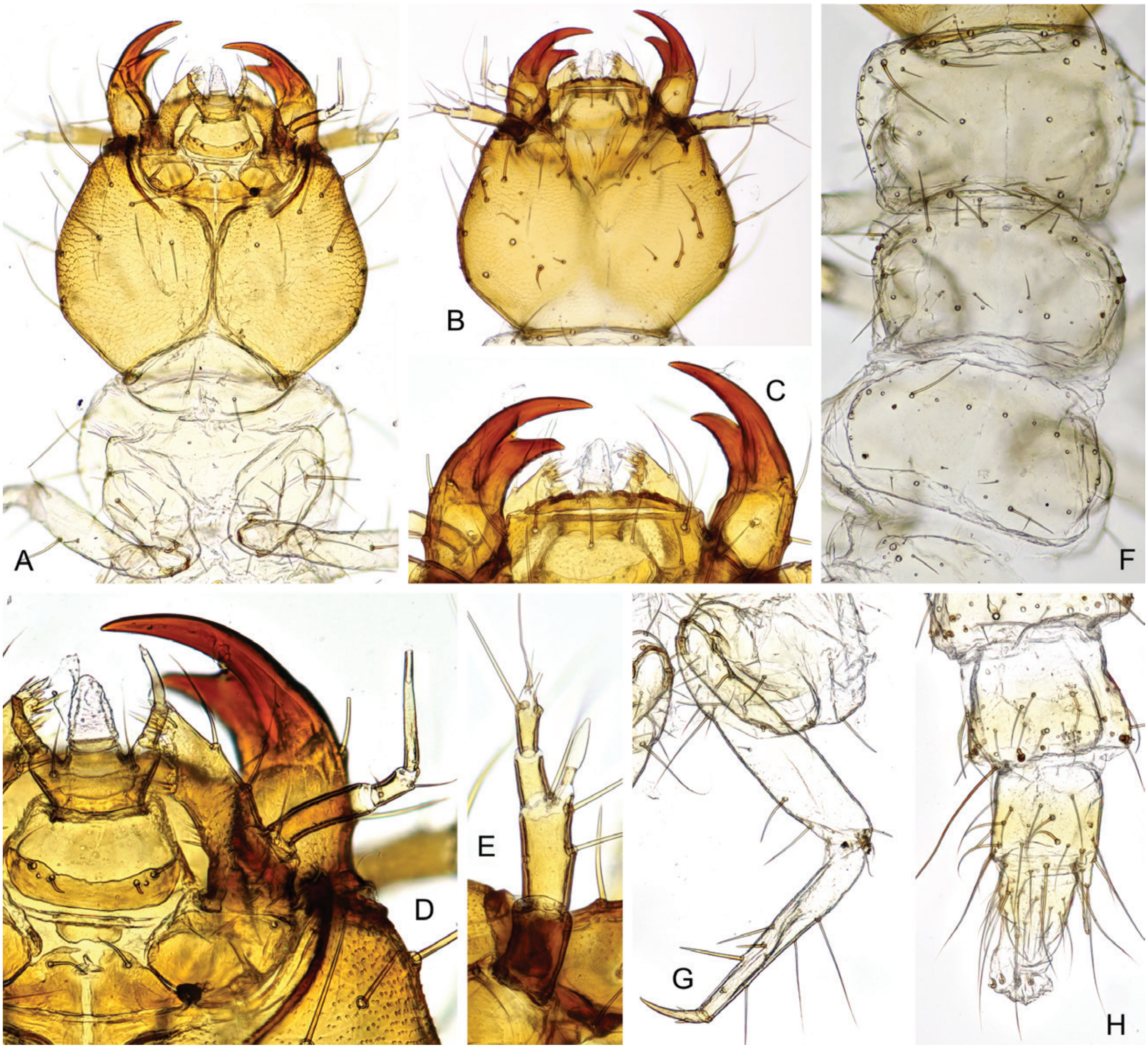

Figure 10. Staphylinidae: Aleocharinae: Falagriini: larva of *Myrmecocephalus brevisulcus* (OTU84, voucher 20-06HS573) associated with adults by DNA. **A.** Head and prothorax in ventral view; **B.** Head in dorsal view; **C.** Clypeus, labrum and mandibles in dorsal view; **D.** Mouthparts in ventral view; **E.** Antenna; **F.** Thorax in dorsal view; **G.** Hind leg; **H.** Abdominal apex.

by the multidentate mandibles. The species is sometimes placed in *Phenolia* Erichson, 1943 which comprises similar-looking yet unrelated American species (see Jelínek 1999; Lawrence 2019).

Tenebrionidae: Lagriinae

Lagria scutellaris Pic, 1910 (Lagriini)

Fig. 14

Material examined. Larvae: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E; 1150 m, 24.ii.2020, lgt. F.S. Hu, old-grown forest on the slope with sparse understory (voucher 20-02HS537); 1 larva (IDL): same locality, 11.x.2020, lgt. F.S. Hu & Y.J. Chen (voucher 20-10HS556); 1 larva (IDL): Taiwan: Nantou County,

Huisun Forest reserve, Wading trail, 24.0892139°N, 121.0297836°E, 700m, 5.v.2019, Damaška, Fikáček, Hu & Liu lgt., stony forest on the slope, small leaf accumulations (2019-TW18) (voucher HS5060L); 1 larva (IDL): same locality, 24.ii.2020, lgt. F.S. Hu (voucher 20-02HS159); 1 larva (IDL): same locality, 20.vi.2020, lgt. F.S. Hu (voucher 20-06HS167); 1 larva (IDL): same locality, 11.x.2020, lgt. F.S. Hu & Y.J. Chen (voucher 20-10HS159); 1 larva (IDL): same locality, 28.ii.2021, lgt. F.S. Hu & Y.J. Chen (voucher 21-03HS102); 1 larva (IDL): same locality, 17.viii.2021, M. Fikáček & W.R. Liang lgt. (voucher 21-08HS163). Adults: 1 spec. (IDL): same locality, 28.ii.2021, leg. F.S. Hu & Y.J. Chen (voucher 21-03HS102).

Comments. Although some species of *Lagria* Fabricius, 1775 are recognized as pests and are also used as model organisms and their life cycle is hence well known and studied (e.g., Zhou 1996, 2001; Janke et al. 2022), the larval morphology is rarely illustrated in detail, and are mostly available for European species *L. hirta* (Linnaeus, 1758) and the invasive African *L. villosa* Fabricius,

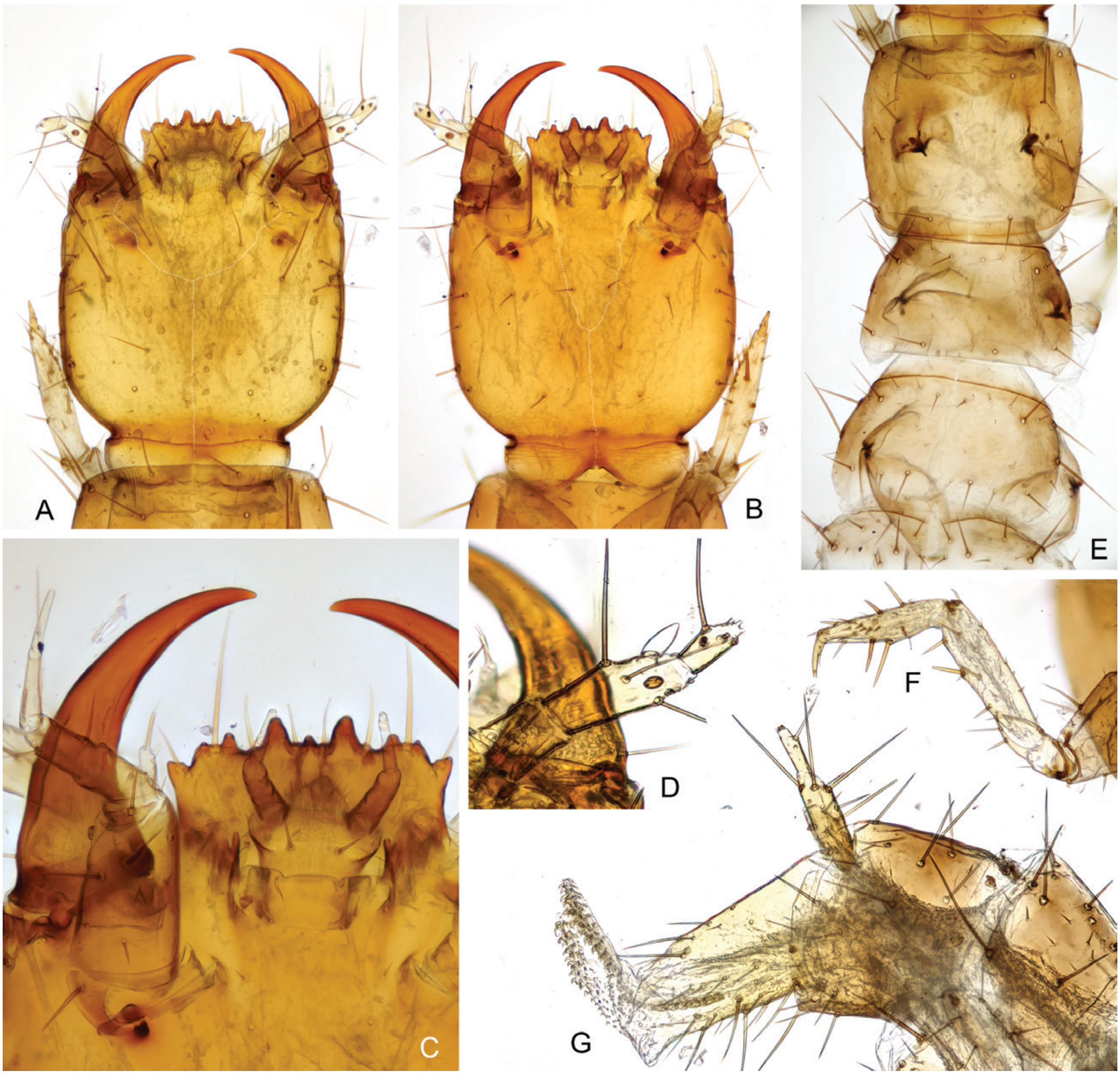

Figure 11. Staphylinidae: Staphylininae: Diochini: larva of *Diochus* sp. (OTU206, voucher 20-08HS182) associated with adults by DNA. **A–D.** Head: **A.** Dorsal view; **B.** Ventral view; **C.** Details of anterior part in ventral view; **D.** Antenna; **E.** Thorax in dorsal view; **F.** Fore leg; **G.** Apex of abdomen in lateral view.

1781 (see Spilman 1978 and online resources). We illustrate the larva of the Taiwan-endemic *L. scuttelaris* as it is often a dominant larval morphotype in forest leaf litter samples in Taiwan. It resembles the larva of *L. hirta* by dorsal color patterns (in contrast to uniformly black larva of *L. villosa*), but differs from it by larger and more widely separated urogomphi (very small and closely situated in *L. hirta*).

Anaedus spinicornis **Kaszab, 1973 (Goniaderini)**
Fig. 15

Material examined. Larvae: 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0847025°N, 121.0274161°E, 1000 m, 20.vi.2020, F.S. Hu lgt., mixed conifer/broadleaf forest + sparse broadleaf forest on the slope (voucher 20-06HS334); 1 larva (IDL): same locality, 4.v.2019, Damaška, Fikáček, Hu & Liu lgt. (2019-TW16) (voucher HS3055L); 1 larva (IDL): Taiwan: Nantou County, Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602°N, 121.0366337°E; 1150 m, 20.vi.2020, lgt. F.S. Hu, old-grown forest on the slope with sparse understory (voucher 20-06HS557); 1 larva (IDL): same locality, 4.v.2019, Fikáček, Hu, Damaška, Liu lgt. (voucher HS1062L). Adults: 1 spec. (IDL): same locality, 24.ii.2020, F.S. Hu lgt. (voucher 20-02HS502); 1 spec. (IDL): same locality, 20.vi.2020, lgt. F.S. Hu (voucher 20-06HS501).

Comments. The larva of American *Anaedus brunneus* (Ziegler, 1844) has been illustrated without a detailed description (Böving and Craighead 1930). Arndt (1993) described the African species *Anaedus camerunus* Gebien, 1920. The larvae of *A. spinicornis* can be distinguished from the two known species by a rel-

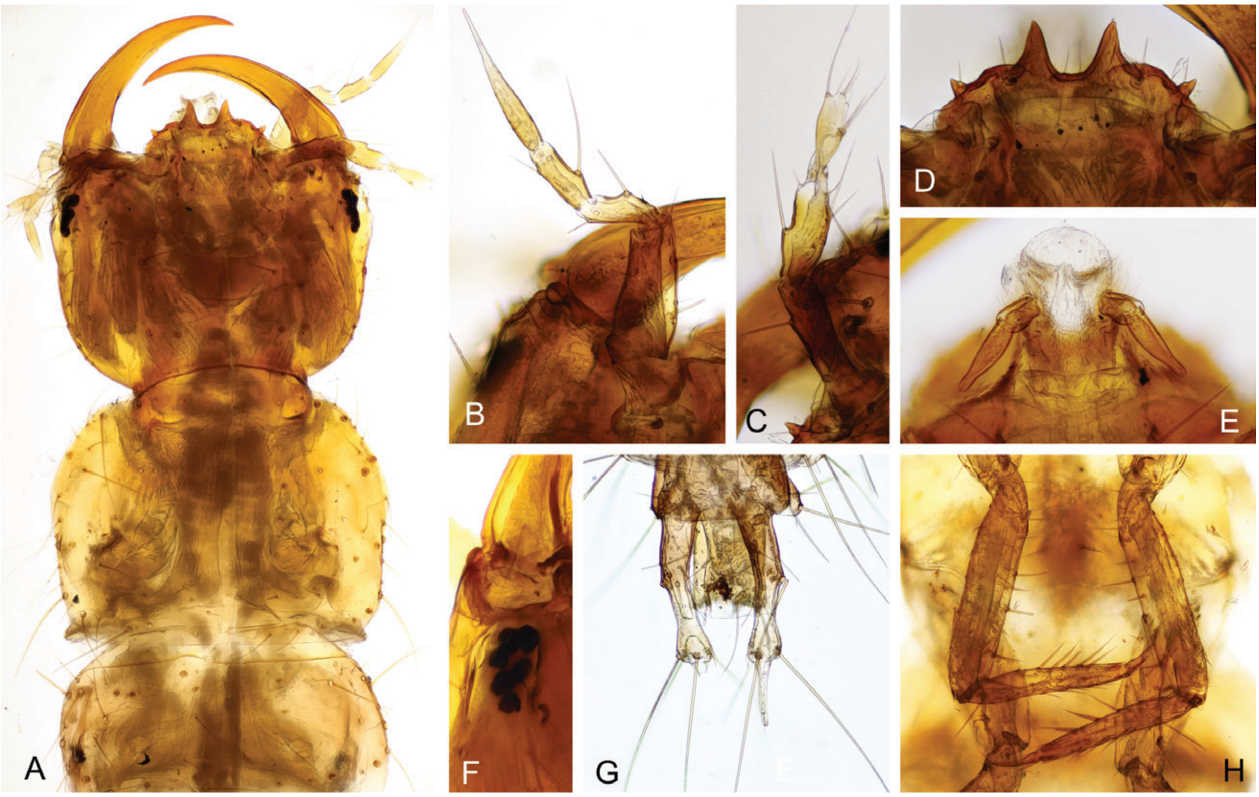

Figure 12. Staphylinidae: Paederinae: Pinophilini: larva of *Mimopinophilus* sp. (OTU271, vouchers 21-08HS346 and 21-08HS568) associated with adults by DNA. **A.** Head and anterior part of thorax, dorsal view; **B.** Maxilla; **C.** Antenna; **D.** Nasale; **E.** Eye in lateral view; **F.** Labium; **G.** End of the abdomen with urogomphi, dorsal view; **H.** Front legs.

atively shorter and broader head. It can also be distinguished from *A. camerunus* by the coloration without a pair of spots on the anterior portion of the pronotum and with longer stripes on the lateral portion of the meso- and metanota.

Discussion

The dataset published here is based on 20 samples collected in 2019–2021 in a single forest reserve in central Taiwan, and is hence limited geographically. Still, it illustrates challenges of studies on subtropical and tropical leaf litter beetle faunas: we sorted 4629 specimens that represent 334 species of 36 beetle families. It also demonstrates that the integrative approach combining DNA barcodes and morphology makes the study of largely unknown but species-diverse fauna more efficient. DNA barcodes allowed us to sort the material to species candidates for all groups, including taxonomically difficult ones or those for which taxonomic experts are not available at the moment. We were also able to sort larval specimens into species and associate part of them with co-occurring adults. This task would be impossible using morphology (see Fikáček et al. (2023)). In several widespread species, we were also able to compare DNA barcodes from Taiwan with those published from other areas: some were found nearly identical (e.g., in *Hypomedon debilicornis* (Wollaston, 1857)), others indicate that the East Asian specimens form an isolated lineage (e.g., in *Perigona* cf. *nigriceps* and *Coccotrypes advena*) and urge for a more detailed taxonomic study.

The contribution of experts on taxonomy of particular groups is crucial for our project, providing the bridge between the DNA-based 'species candidates' (called OTU or MOTU in general, and BIN in the BOLD database) and taxonomic species with associated knowledge about morphology, lifestyle and evolutionary history. Although ecological studies may be based purely on numbers of unnamed species estimated by hand-sorting (e.g., Hopp et al. 2010) or DNA barcoding (e.g., Arribas et al. 2021), even these studies may benefit from accurate species identifications, especially when using functional and phylogenetic diversity measures (e.g., Basset et al. 2023). Expert-identified DNA barcodes, including those published here, make the taxonomic knowledge easily available for such studies, as well as for those focused on conservation, biogeography, physiology, etc. Moreover, DNA can help non-experts identify common species accurately. Experts can then focus on rare or newly discovered species, those with detailed lifestyle data, or species requiring further study due to differences between DNA and morphological traits.

We explicitly declare that our aim is not to support the DNA-only systematics proposed recently in some insect studies (e.g., Meierotto et al. 2019; Sharkey et al. 2021, 2023) despite the critique of such an approach (e.g.,

Figure 13. Nitidulidae. **A–G.** Late instar larva of *Stelidota multiguttata* (OTU119, voucher 21-08H158); **H–M.** Early instar larva of *Lasiodites inaequalis* (OTU180, voucher 20-08HS172). **A, I.** Habitus in dorsal view; **B.** Abdominal apex in lateral view; **C.** Head in dorsal view; **D, K.** Antenna; **E. L.** Mouthparts in ventral view; **F.** Head and thorax in ventral view; **G, M.** Detail of leg; **H, N.** End of abdomen in dorsal view; **K.** Detail of antenna and mandible in dorsal view.

Zamani et al. 2022; Meier et al. 2022). Taiwanese beetle fauna, despite island-based and highly endemic, overlaps with that of southern Japan, southern China, and northern Philippines, where many beetle groups have been previously studied using traditional taxonomic methods. Taiwanese beetles have also been studied for more than

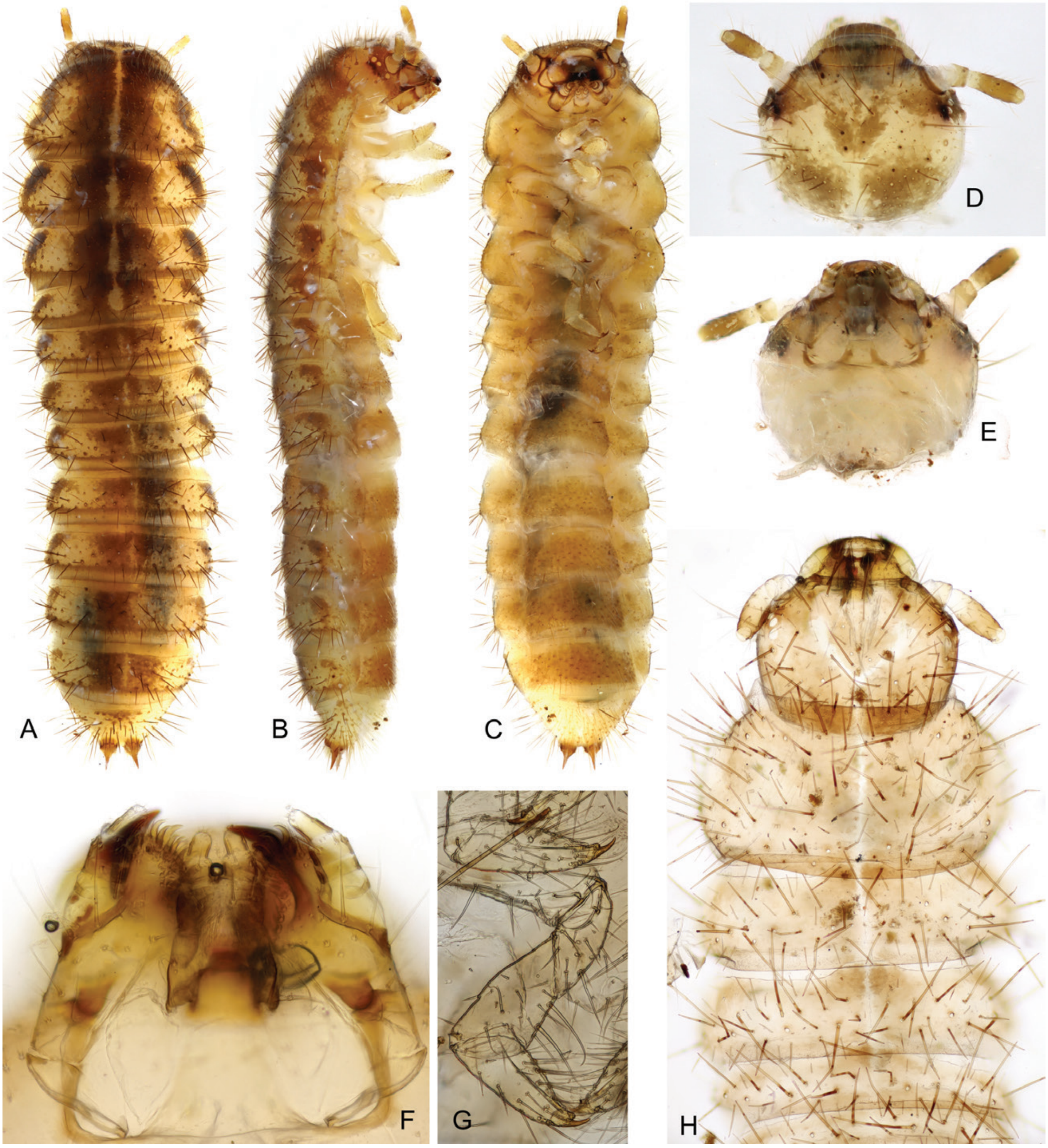

Figure 14. Tenebrionidae: Lagriinae: Lagriini: larvae of *Lagria scutellaris* (OTU174) associated with adults by DNA. **A–C.** Habitus of late instar larva (voucher 20-10HS556; **A.** Dorsal; **B.** Lateral; **C.** Ventral); **D, E.** Head of the late instar larva (voucher 21-08HS163; **D.** Dorsal; **E.** Ventral); **F–H.** Early instar larva (voucher HS5060L): **F.** Mouthparts, ventral view; **G.** Hind leg; **H.** Head and thorax in dorsal view.

a century as well. Taiwanese leaf litter beetles must be hence studied in geographic and taxonomic context, with DNA barcodes providing a tool for a more efficient work, not a replacement of the previous effort.

The DNA barcodes, new faunistic records and the first taxonomic conclusions reported here are the first results of the Taiwanese Leaf Litter Beetles project. Voucher specimens for all DNA sequences published here, as well as the non-sequenced conspecific specimens from the same samples, are available for further studies by experts, e.g. those focused on particular genera and their larvae (e.g., Löbl 2020, 2023; Zhang et al. 2021; Ho et al. 2022). We will update the identifications of the DNA barcodes submitted to the BOLD database based on the subsequent research, to keep the DNA barcode dataset published here as an up-to-date resource facilitating

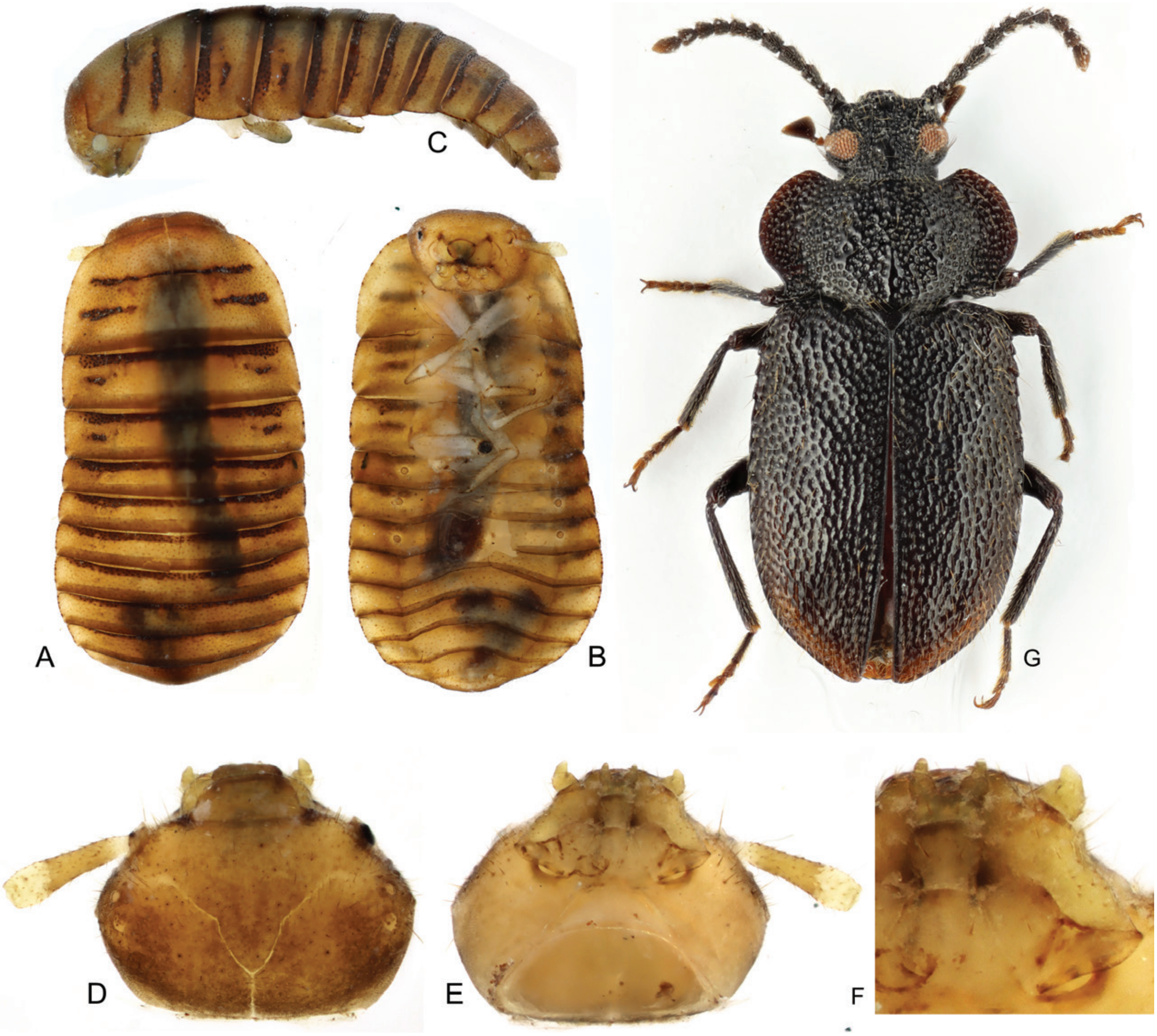

Figure 15. Tenebrionidae: Lagriinae: Goniaderini: larva of *Anaedus spinicornis* (OTU49, voucher HS1062L) associated with adults by DNA. **A–C.** Habitus (**A.** Dorsal; **B.** Ventral; **C.** Lateral); **D–F.** Head (**D.** Dorsal; **E.** Ventral; **F.** Ventral, close-up).

future studies. As the next step, we continue sampling across Taiwan, to cover the Taiwanese leaf litter beetle fauna more completely in all regions, altitudinal zones, and various types of forest. Based on results from the Huisun Forest Reserve, we decided to sample a smaller volume of leaf litter per sample (3 litres) which allows quicker collecting, sorting, and processing per sample, and consequently, taking multiple samples. Our data indicate that the multi-sample sampling design can detect a larger proportion of the local species diversity during a single visit: samples collected at five nearby sites on the same day in May 2019 covered ca. 40% of the estimated species richness living in the area, whereas a single 6-litre sample only covered ca. 10% of the local fauna (see also Fikáček et al. (2023)). We also continue sorting and DNA barcoding all larval morphotypes. New findings will be published continuously, either as summaries similar to this one, or as studies led by taxonomic experts and focused on particular taxa.

Acknowledgements

We are grateful to Wei-Ren Liang (The Kyushu University Museum, Japan), Hsing-Che Liu (Taichung, Taiwan), and Yu-Jing Chen (Taichung, Taiwan) for their company and assistance with sample collecting. We are deeply indebted to Jen-Pan Huang (Biodiversity Research Centre, Academia Sinica, Taiwan) for providing his lab and massive support and encouragement for this project, and to Yi-Hsiu Kuan, Ming-Hsu Chou and Zong-Yu Shen from the same lab for lab support and discussions. Volker Assing (deceased), Ching-Shan Lin (Taichung, Taiwan), Paweł Jałoszyński (University of Wroclaw, Poland), Hiroshi Sugaya (Nantou, Taiwan), Mateusz Sapieja (University of Wroclaw, Poland), Shih-Pi Kao (Taichung, Taiwan), Wei-Ren Liang (Kyushu University, Japan), Adam Ślipiński (Australian National Insect Collection, Canberra), Chi-Feng Lee (Taiwan Agriculture Research Institute, Taichung), Jan Růžička (Czech University of Life Sciences Prague, Czech Republic), and

Manfred Uhlig (Museum für Naturkunde, Berlin, Germany), and Hume Douglas (Agriculture and Agri-Food Canada, Ottawa, Canada) helped with the identifications of part of the DNA-barcoded specimens. The data presented in this study were generated under the support by the Taiwanese National Science and Technology Council projects MOST 110-2621-B-110-001 and MOST 111-2621-B-110-003. The initial step of the project and the visit of Fang-Shuo Hu to Prague in 2019 was possible thanks to European Commission's SYNTHESYS project CZ-TAF-2524. The work in the National Museum, Prague was supported by the Ministry of Culture of the Czech Republic (DKRVO 2019–2023/5.I.e, National Museum, 00023272). The work of Gabriel Biffi was supported by Vale Institute of Technology and Fundação Guamá (Pará, Brazil). The project was partly funded by the SVV 260686/2023 grant to AFD.

References

Aberlenc HP, Allemand R (1997) Acclimatation en France de *Ptilodactyla exotica*, à maeurs anthropophiles (Coleoptera, Ptilodactylidae). Bulletin de la Société Entomologique de France 102(2): 93–102. https://doi.org/10.3406/bsef.1997.17314

Andújar C, Arribas P, Ruzicka F, Crampton-Platt A, Timmermans MJTN, Vogler AP (2015) Phylogenetic community ecology of soil biodiversity using mitochondrial metagenomics. Molecular Ecology 24(14): 3603–3617. https://doi.org/10.1111/mec.13195

Angelini F, De Marzo L (1998) Supplement to the knowledge of the Agathidiini of Taiwan (Coleoptera, Leiodidae). Revue Suisse de Zoologie 105(1): 125–138. https://doi.org/10.5962/bhl.part.80034

Armstrong KF, Ball SL (2005) DNA barcodes for biosecurity: Invasive species identification. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 360(1462): 1813–1823. https://doi.org/10.1098/rstb.2005.1713

Arndt E (1993) Description of the larva of *Anaedus camerunus* Gebien (Coleoptera: Tenebrionidae, Lupropini). Koleopterologische Rundschau 63: 273–277.

Arribas P, Andújar C, Salces-Castellano A, Emerson BC, Vogler AP (2021) The limited spatial scale of dispersal in soil arthropods revealed with whole-community haplotype-level metabarcoding. Molecular Ecology 31(1): 48–61. https://doi.org/10.1111/mec.15591

Assing V (2010) On the Lathrobiina of Taiwan (Coleoptera: Staphylinidae: Paederinae). Beiträge zur Entomologie 60(2): 301–361. https://doi.org/10.21248/contrib.entomol.60.2.301-361

Assing V (2014) Three new species and a new species group of *Medon* from China and Taiwan (Coleoptera: Staphylinidae: Paederinae). Linzer Biologische Beitrage 46: 515–523.

Assing V (2015) A revision of the *Megalopaederus* species of Taiwan (Coleoptera: Staphylinidae: Paederinae). Stuttgarter Beiträge zur Naturkunde A, Neue Serie 8: 53–94.

Assing V (2017) On the Lomechusini fauna of the East Palaearctic and Oriental regions, with a focus on the genera *Orphnebius* and *Amaurodera* (Coleoptera: Staphylinidae: Aleocharinae). Beiträge zur Entomologie 67(1): 63–106. https://doi.org/10.21248/contrib.entomol.67.1.63-106

Assing V (2019) On the Lomechusini fauna of the Palaearctic and Oriental regions. XXVI. New species, a new synonymy, and additional records (Coleoptera: Staphylinidae: Aleocharinae). Beiträge zur Entomologie 69(1): 33–70. https://doi.org/10.21248/contrib.entomol.69.1.033-070

Assing V (2022) Monograph of Palaearctic, Oriental, and New Guinean Pinophilina (Coleoptera: Staphylinidae: Paederinae). Acta Musei Moraviae. Scientiae Biologicae 107(Supplement): 1–419.

Baehr M (2014) The species of the genus *Perigona* Castelnau from New Guinea, Sulawesi, Halmahera and Australia, and of the *parvicollis-pygmaea*-lineage (Coleoptera, Carabidae, Perigonini). Entomologische Blätter und Coleoptera 109: 1–132.

Basset Y, Blažek P, Souto-Vilarós D, Vargas G, Ramírez Silva JA, Barrios H, Perez F, Bobadilla R, Lopez Y, Ctvrtecka R, Šípek P, Solís A, Segar ST, Lamarre GPA (2023) Towards a functional classification of poorly known tropical insects: The case of rhinoceros beetles (Coleoptera, Dynastinae) in Panama. Insect Conservation and Diversity 16(1): 147–163. https://doi.org/10.1111/icad.12613

Bickhardt H (1913) H. Sauter's Formosa Ausbeute. Histeridae II. (Col.) (16. Beitrag zur Kenntniss der Histeriden). Entomologische Mitteilungen 2: 166–177. https://doi.org/10.5962/bhl.part.14989

Bili M, Cortesero AM, Mougel C, Gauthier JP, Ermel G, Simon JC, Outreman Y, Terrat S, Mahéo F, Poinsot D (2016) Bacterial community diversity harboured by interacting species. PLoS ONE 11(6): e0155392. https://doi.org/10.1371/journal.pone.0155392

Borovec R (2014) Study on Trachyphloeini of the Oriental Region (Coleoptera: Curculionidae: Entiminae). Studies and Reports. Taxonomical Series 10(1): 1–39.

Böving AG, Craighead FC (1930) An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana. A Journal of Entomology, New Series, XI(1): 1–351. https://doi.org/10.5962/bhl.title.6818

Bright DEA (2021) Catalog of Scolytidae (Coleoptera): Supplement 4 (2011–2019) with an Annotated Checklist of the World Fauna (Coleoptera: Curculionidae: Scolytidae). Contributions of the C. P. Gillette Museum of Arthropod Diversity, Department of Agricultural Biology, Colorado State University, 654 pp.

Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K, Madden TL (2009) BLAST+: Architecture and applications. BMC Bioinformatics 10(1): 1–9. https://doi.org/10.1186/1471-2105-10-421

Chimeno C, Morinière J, Podhorna J, Hardulak L, Hausmann A, Reckel F, Grunwald JE, Penning R, Haszprunar G (2019) DNA Barcoding in Forensic Entomology - Establishing a DNA reference library of potentially forensic relevant arthropod species. Journal of Forensic Sciences 64(2): 593–601. https://doi.org/10.1111/1556-4029.13869

Chu H-F (1945) The larvae of the Harpalinae unisetosae (Coleoptera: Carabidae). Entomologica Americana 25(1): 1–71.

Chung K-F, Shao K-T (2022) Catalogue of life in Taiwan. Web electronic publication. Version 2022. http://taibnet.sinica.edu.tw

Cosandey V (2023) Description of six new species of *Lederina* Nikitsky & Belov, 1982 (Coleoptera: Melandryidae: Melandryinae) from Taiwan. Revue Suisse de Zoologie 130(1): 11–23. https://doi.org/10.35929/RSZ.0085

Costa C, Vanin SA, Casari-Chen SA (1988) *Larvas de Coleoptera do Brasil*. Museu de Zoologia, Universidade de São Paulo, São Paulo, 282 pp. [+ 165 pls] https://doi.org/10.5962/bhl.title.100233

Cuccodoro G (2011) *Megarthrus* of Taiwan, with notes on phylogenetic relationship within the genus (Coleoptera: Staphylinidae: Proteininae). Studies and Reports. Taxonomical Series 7(1–2): 25–92.

Dajoz R (1974) Description de Coléoptères nouveaux de la famille des Cerylonidae. Bulletin du Muséum National d'Histoire Naturelle 238(162): 1059–1067.

Dajoz R (1979) Coléoptères Cerylonidae nouveaux ou peu connus. Bulletin Mensuel de la Societe Linneenne de Lyon 48(7): 441–452. https://doi.org/10.3406/linly.1979.10380

De Marzo L (2000) Coleotterofauna dei depositi di *Posidonia*: Morfologia larvale in alcune specie caratteristiche (Sphaeridiidae, Histeridae, Ptiliidae, Staphylinidae). Annali del Museo Civico di Storia Naturale. Giacomo Doria 93: 461–471.

De Marzo L (2002) Larve di coleotteri in detriti vegetali di origine agricola: lineamenti morfologici e presenza stagionale (Polyphaga: 20 famiglie). Entomologica (Bari) 34: 65–131.

De Marzo L (2007) Note sullo sviluppo preimmaginale in *Drusilla italica* (Bernhauer) (Coleoptera Staphylinidae Aleocharinae). Entomologica (Bari) 39: 211–220.

De Marzo L (2008) Allestimento della cella pupale e del bozzolo nei Coleotteri: qualche dettaglio etologico (Polyphaga: 7 famiglie). Entomologica (Bari) 40: 91–100.

De Marzo L (2009) Verifica del numero di età larvali in alcuni stafilinidi (Coleoptera, Staphylinidae). Annali del Museo Civico di Storia Naturale. Giacomo Doria 100: 649–670.

Fikáček M, Hu F-S, Le M-H, Huang J-P (2023) Can immature stages be ignored in studies of forest leaf litter arthropod diversity? A test using Oxford Nanopore DNA barcoding. Insect Conservation and Diversity. https://doi.org/10.1111/icad.12702

Fitton MG (1976) The larvae of the British genera of Cantharidae (Coleoptera). Journal of Entomology Series B, Taxonomy 44(3): 243–254. https://doi.org/10.1111/j.1365-3113.1976.tb00015.x

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Giller PS (1996) The diversity of soil communities, the ‘poor man's tropical rainforest’. Biodiversity and Conservation 5(2): 135–168. https://doi.org/10.1007/BF00055827

Grebennikov VV, Newton AF (2009) Good-bye Scydmaenidae, or why the ant-like stone beetles should become megadiverse Staphylinidae sensu latissimo (Coleoptera). European Journal of Entomology 106(2): 275–301. https://doi.org/10.14411/eje.2009.035

Guéorguiev B (2014) Two new related oodine genera in the Oriental Region, with remarks on the systematic position of the genera *Hololeius* and *Holosoma* (Coleoptera, Carabidae). Deutsche Entomologische Zeitschrift 61(2): 87–104. https://doi.org/10.3897/dez.61.7754

Guéorguiev B, Liang H (2020) Revision of the Palaearctic and Oriental representatives of *Lachnocrepis* LeConte and *Oodes* Bonelli (Coleoptera: Carabidae), with special account on Chinese species. Zootaxa 4850(1): 1–89. https://doi.org/10.11646/zootaxa.4850.1.1

Hajibabaei M, Janzen DH, Burns JM, Hallwachs W, Hebert PDN (2006) DNA barcodes distinguish species of tropical Lepidoptera. Proceedings of the National Academy of Sciences of the United States of America 103(4): 968–971. https://doi.org/10.1073/pnas.0510466103

Hebert PDN, Ratnasingham S, DeWaard JR (2003) Barcoding animal life: Cytochrome c oxidase subunit 1 divergences among closely related species. Proceedings. Biological Sciences 270(suppl_1): S96–S99. https://doi.org/10.1098/rsbl.2003.0025

Hebert PDN, Ratnasingham S, Zakharov EV, Telfer AC, Levesque-Beaudin V, Milton MA, Pedersen S, Jannetta P, deWaard JR (2016) Counting animal species with DNA barcodes: Canadian insects. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 371(1702): 20150333. https://doi.org/10.1098/rstb.2015.0333

Hendrich L, Morinière J, Haszprunar G, Hebert PDN, Hausmann A, Köhler F, Balke M (2015) A comprehensive DNA barcode database for Central European beetles with a focus on Germany: Adding more than 3500 identified species to BOLD. Molecular Ecology Resources 15(4): 795–818. https://doi.org/10.1111/1755-0998.12354

Hernández-Triana LM, Brugman VA, Nikolova NI, Ruiz-Arrondo I, Barrero E, Thorne L, de Marco MF, Krüger A, Lumley S, Johnson N, Fooks AR (2019) DNA barcoding of British mosquitoes (Diptera, Culicidae) to support species identification, discovery of cryptic genetic diversity and monitoring invasive species. ZooKeys 832: 57–76. https://doi.org/10.3897/zookeys.832.32257

Hinton HE (1942) A revision of the Cerylonini of Borneo (Coleoptera, Colydiidæ). Annals & Magazine of Natural History 9(51): 141–173. https://doi.org/10.1080/03745481.1942.9755474

Hisamatsu S (1985) Notes on some Japanese Coleoptera, 1. Transactions of the Shikoku Entomological Society 17: 5–13.

Ho B-H, Hu F-S, Fikáček M (2022) The dung beetle *Oxyomus* of Taiwan (Coleoptera: Scarabaeidae): Review of the fauna, a new species and its larva associated by DNA barcoding. Zoological Studies (Taipei, Taiwan) 61: e80. https://doi.org/10.6620/ZS.2022.61-80

Hopp PW, Ottermanns R, Caron E, Meyer S, Roß-Nickoll M (2010) Recovery of litter inhabiting beetle assemblages during forest regeneration in the Atlantic forest of Southern Brazil. Insect Conservation and Diversity 3(2): 103–113. https://doi.org/10.1111/j.1752-4598.2010.00078.x

Hoshina H (1999) A taxonomic study on the genera *Dermatohomoeus* and *Colenis* (Coleoptera, Leiodidae) from Japan. Entomological Science 2(3): 413–423.

Irmler U (2017) A review of the Neotropical genus *Diochus* Erichson, 1840 (Coleoptera: Staphylinidae: Staphylininae). Contribution to Entomology 67(1): 1–62. https://doi.org/10.21248/contrib.entomol.67.1.1-62

Janke RS, Moog S, Weiss B, Kaltenpoth M, Flórez LV (2022) Morphological adaptation for ectosymbiont maintenance and transmission during metamorphosis in *Lagria* beetles. Frontiers in Physiology 13(979200): 1–15. https://doi.org/10.3389/fphys.2022.979200

Janzen DH, Hallwachs W (2016) DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservacion Guanacaste, northwestern Costa Rica. Genome 59(9): 641–660. https://doi.org/10.1139/gen-2016-0005

Janzen DH, Burns JM, Cong Q, Hallwachs W, Dapkey T, Manjunath R, Hajibabaei M, Hebert PDN, Grishin NV (2017) Nuclear genomes distinguish cryptic species suggested by their DNA barcodes and ecology. Proceedings of the National Academy of Sciences of the United States of America 114(31): 8313–8318. https://doi.org/10.1073/pnas.1621504114

Jeannel R (1941) Un carabique termitophile nouveau de l’Afrique Tropicale. Revue Française d’Entomologie 8(3): 135–146.

Jeannel R (1942) Faune de France. 40. Coléoptères Carabiques. Deuxieme partie. Paul Lechevalier, Paris, 1172 pp.

Jelínek J (1999) Contribution to taxonomy of the beetle subfamily Nitidulinae (Coleoptera: Nitidulidae). Folia Heyrovskyana 7(5): 251–281.

Jordal BH, Normark BB, Farrell BD, Kirkendalld LR (2002) Extraordinary haplotype diversity in haplodiploid inbreeders: Phylogenetics and evolution of the bark beetle genus *Coccotrypes*. Molecular Phylogenetics and Evolution 23(2): 171–188. https://doi.org/10.1016/S1055-7903(02)00013-1

Kajtoch Ł (2022) Evolutionary and ecological signals in *Wolbachia*-beetle relationships: A review. European Journal of Entomology 119: 215–226. https://doi.org/10.14411/eje.2022.023

Kajtoch Ł, Kotásková N (2018) Current state of knowledge on *Wolbachia* infection among Coleoptera: A systematic review. PeerJ 6: e4471. https://doi.org/10.7717/peerj.4471

Kaszab Z (1964) The zoological results of Gy. Topál's collectings in South Argentina. 13. Coleoptera – Tenebrionidae. Annales Historico-Naturales Musei Nationalis Hungarici, pars. Zoologica 56: 353–387.

Kaszab Z (1979) Die Arten der Gattung *Sivacrypticus* Kaszab, 1964 (Coleoptera, Tenebrionidae). Annales Historico-Naturales Musei Nationalis Hungarici 71: 185–204.

Kaszab Z (1981) Die Gattungen und Arten der Tribus Archeocrypticini (Coleoptera: Tenebrionidae). Folia Entomologica Hungarica 52(34): 95–115.

Klausnitzer B (1997) 51. Familie: Cantharidae. In: Klausnitzer B (Ed.) Die Larven der Käfer Mitteleuropas. 4. Band. Polyphaga Teil 3 sowie Ergänzungen zum 1. bis 3. Band. Goecke & Evers, Krefeld im Gustav Fischer Verlag Jena, Stuttgart, Lübeck, Ulm, Germany, 124–140.

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Lawrence JF (2005) 18.9. Ptilodactylidae. In: Beutel RG, Leschen RAB (Eds) Handbook of Zoology. Volume IV Arthropoda: Insecta. Part 38 Coleoptera, beetles Vol. 1: Morphology and systematice (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter, Berlin-New York, 536–542. [567 pp]

Lawrence JF (2019) Australian Nitidulinae: general review with descriptions of new genera and species (Coleoptera: Nitidulidae). Zootaxa 4657(2): 261–290. https://doi.org/10.11646/zootaxa.4657.2.3

Lee C-F, Cheng H-T (2007) The Chrysomelidae of Taiwan I. Sishou-Hills Insect Observation Network Press, Taipei, Taiwan, 199 pp.

Lee C-F, Cheng H-T, Yu S-F, Tsou M-H, Chen H-J, Lee H (2010) The Chrysomelidae of Taiwan II. Sishou-Hills Insect Observation Network Press, Taipei, Taiwan, 191 pp.

Lee C-F, Tsou M-H, Cheng H-T, Yu S-F, Chen H-J, Lee H, Chen J-C (2016) The Chrysomelidae of Taiwan III. Sishou-Hills Insect Observation Network Press, Taipei, Taiwan, 199 pp.

Lindroth CH (1942) *Oodes gracilis* Villa. Eine thermophile Carabide Schwedens. Notulae Entomologicae 22: 109–157.

Liu M, Clarke LJ, Baker SC, Jordan GJ, Burridge CP (2020) A practical guide to DNA metabarcoding for entomological ecologists. Ecological Entomology 45(3): 373–385. https://doi.org/10.1111/een.12831

Löbl I (2012) On Taiwanese species of *Baeocera* Erichson (Coleoptera: Staphylinidae: Scaphidiinae). Zoological Studies (Taipei, Taiwan) 51(1): 118–130.

Löbl I (2020) Four new Taiwanese species of *Scaphobaeocera* CSIKI (Coleoptera, Staphylinidae, Scaphidiinae). Linzer Biologische Beiträge 52(1): 327–335.

Löbl I (2023) New species and records of Scaphidiinae (Coleoptera: Staphylinidae) from mainland China and Taiwan. Vernate 42: 135–142.

Löbl I, Löbl D (2017) Catalogue of Palaearctic Coleoptera. Archostemata-Myxophaga-Adephaga. Vol. 1. Revised and updated edition. Brill, Leiden, Boston, 1443 pp. https://doi.org/10.1163/9789004330290_002

Löbl I, Smetana A (2007) Catalogue of Palaearctic Coleoptera Volume 4 Elateroidea - Derodontoidea - Bostrichoidea - Lymexyloidea - Cleroidea - Cucujoidea. Apollo Books, Stenstrup, Denmark, 935 pp. https://doi.org/10.1163/9789004260894

Lü L, Cai C-Y, Zhang X, Newton AF, Thayer MK, Zhou H-Z (2020) Linking evolutionary mode to palaeoclimate change reveals rapid radiations of staphylinoid beetles in low-energy conditions. Current Zoology 66(4): 435–444. https://doi.org/10.1093/cz/zoz053

Madden MJL, Young RG, Brown JW, Miller SE, Frewin AJ, Hanner RH (2019) Using DNA barcoding to improve invasive pest identification at U.S. ports-of-entry. PLoS ONE 14(9): e0222291. https://doi.org/10.1371/journal.pone.0222291

Mann DJ (2006) *Ptilodactyla exotica* Chapin, 1927 (Coleoptera: Ptilodactylidae: Ptilodactylinae) established breeding under glass in Britain, with a brief discussion on the family Ptilodactylidae. Entomologist's Monthly Magazine 142: 67–79.

Mazur S (2007) On new and little known Histerids (Coleoptera: Histeridae) from Taiwan with additional notes on the species composition and zoogeography. Formosan Entomologist 27: 67–81.

McKenna DD, Farrell BD, Caterino MS, Farnum CW, Hawks DC, Maddison DR, Seago AE, Short AEZ, Newton AF, Thayer MK (2015) Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: Forest litter as a stepping stone for diversification of nonphytophagous beetles. Systematic Entomology 40(1): 35–60. https://doi.org/10.1111/syen.12093

Meier R, Blaimer BB, Buenaventura E, Hartop E, von Rintelen T, Srivathsan A, Yeo D (2022) A re-analysis of the data in Sharkey et al.'s (2021) minimalist revision reveals that BINs do not deserve names, but BOLD Systems needs a stronger commitment to open science. Cladistics 38(2): 264–275. https://doi.org/10.1111/cla.12489

Meierotto S, Sharkey MJ, Janzen DH, Hallwachs W, Hebert PD, Chapman EG, Smith MA (2019) A revolutionary protocol to describe understudied hyperdiverse taxa and overcome the taxonomic impediment. Deutsche Entomologische Zeitschrift 66(2): 119–145. https://doi.org/10.3897/dez.66.34683

Merkl O (1988) Novelties of *Sivacrypticus* Kaszab, 1864 and *Enneboeus* Waterhouse, 1878 (Coleoptera, Archeocrypticidae). Annales Historico-Naturales Musei Nationalis Hungarici 80: 71–78.

Miller SE, Hausmann A, Hallwachs W, Janzen DH (2016) Advancing taxonomy and bioinventories with DNA barcodes. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 371(1702): 20150339. https://doi.org/10.1098/rstb.2015.0339

Nadkarni NM, Longino JT (1990) Invertebrates in Canopy and Ground Organic Matter in a Neotropical Montane Forest, Costa Rica. Biotropica 22(3): 286. https://doi.org/10.2307/2388539

Newton AF (1990) Insecta: Coleoptera: Staphylinidae adults and larvae. In: Dindal DL (Ed.). Soil biology guide. John Wiley & Sons, New York, 1137–1174. [xviii + 1349 pp]

Olson DM (1994) The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. Journal of Tropical Ecology 10(2): 129–150. https://doi.org/10.1017/S0266467400007793

Ong U, Hattori T (2019) Jewel Beetles of Taiwan Vol.1. Ministry of Beetles, Tainan, Taiwan, 235 pp.

Ong U, Curletti G, Hattori T (2023) Jewel Beetles of Taiwan Vol. 2. Ministry of Beetles, Tainan, Taiwan, 219 pp.

Owens BE, Carlton CE (2015) "Berlese vs. Winkler": Comparison of two forest litter coleoptera extraction methods and the Ecoli (Extraction of Coleoptera in Litter) protocol. Coleopterists Bulletin 69(4): 645–661. https://doi.org/10.1649/0010-065X-69.4.645

Park SJ, Ahn KJ (2007) Two Pseudoliodinae genera *Dermatohomoeus* Hlisnikowský and *Pseudcolenis* Reitter (Coleoptera: Leiodidae: Leiodinae) in Korea with the description of *Pseudcolenis hoshinai* new species. Zootaxa 1427(1): 49–56. https://doi.org/10.11646/zootaxa.1427.1.3

Paulian R (1941) Les premiers états des Staphylinoidea (Coleoptera). Étude de morphologie comparée. Mémoires du Muséum national d'Histoire naturelle 15: 1–361.

Peng C, Williams RN, Galford JR (1990) Descriptions and key for identification of larvae of *Stelidota* Erichson (Coleoptera: Nitidulidae) found in America North of Mexico. Journal of the Kansas Entomological Society 63(4): 626–633.

Pentinsaari M, Hebert PDN, Mutanen M (2014) Barcoding beetles: A regional survey of 1872 species reveals high identification success and unusually deep interspecific divergences. PLoS ONE 9(9): e108651. https://doi.org/10.1371/journal.pone.0108651

Perlman SJ, Hunter MS, Zchori-Fein E (2006) The emerging diversity of *Rickettsia*. Proceedings of the Royal Society B, Biological Sciences 273(1598): 2097–2106. https://doi.org/10.1098/rspb.2006.3541

Puthz V (2010) *Edaphus* aus Taiwan (Coleoptera: Staphylinidae) 101. Beitrag zur Kenntnis der Euaesthetinen. Revue Suisse de Zoologie 116(2): 265–336. https://doi.org/10.5962/bhl.part.117785

Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System: Barcoding. Molecular Ecology Notes 7(3): 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Sakchoowong W, Jaitrong W, Ogata K, Nomura S, Chanpaisaeng J (2008) Diversity of soil-litter insects: comparison of the pselaphine beetles (Coleoptera: Staphylinidae: Pselaphinae) and the ground ants (Hymenoptera: Formicidae). Thai Journal of Agricultural Science 41: 11–18. https://doi.org/10.1111/j.1479-8298.2008.00281.x

Schminke G (1982) Larven und Fortpflanzungsverhalten von *Drusilla canaliculata*, *Zyras humeralis*, *Geostiba circellaris* und *Othius myrmecophilus* (Coleoptera: Staphylinidae). Drosera 82(1): 91–100.

Serri S, Moradi M, Audisio P (2023) First report of an exotic sap beetle, *Phenolia* (*Lasiodites*) *picta* (Macleay, 1825) (Coleoptera, Nitidulidae) from Iran with notes on its distribution range and damage on different hosts. Journal of Insect Biodiversity and Systematics 9(1): 33–38. https://doi.org/10.52547/jibs.9.1.33

Sharkey MJ, Janzen DH, Hallwachs W, Chapman EG, Smith MA, Dapkey T, Brown A, Ratnasingham S, Naik S, Manjunath R, Perez K, Milton M, Hebert P, Shaw SR, Kittel RN, Solis MA, Metz MA, Goldstein PZ, Brown JW, Quicke DLJ, van Achterberg C, Brown BV, Burns JM (2021) Minimalist revision and description of 403 new species in 11 subfamilies of Costa Rican braconid parasitoid wasps, including host records for 219 species. ZooKeys 1013: 1–665. https://doi.org/10.3897/zookeys.1013.55600

Sharkey MJ, Baker A, McCluskey K, Smith A, Naik S, Ratnasingham S, Manjunath R, Perez K, Sones J, D'Souza M, Jacques BS (2023) Minimalist revision of *Mesochorus* Gravenhorst, 1829 (Hymenoptera: Ichneumonidae: Mesochorinae) from Área de Conservación Guanacaste, Costa Rica, with 158 new species and host records for 129 species. Revista de Biología Tropical 71(supplement 2): 1–174. https://doi.org/10.15517/rev.biol.trop..v71iS2.56316

Ślipiński SA (1982) New and little known species of the Cerylonidae (Coleoptera). Polskie Pismo Entomologiczne 52: 31–58.

Smetana A (1995) Revision of the tribes Quediini and Tanygnathinini. Part III. Taiwan. (Coleoptera: Staphylinidae). Special Publication 6. National Museum of Natural Science, Taichung.

Solodovnikov AY, Newton AF (2005) Phylogenetic placement of Arrowinini trib.n. within the subfamily Staphylininae (Coleoptera: Staphylinidae), with revision of the relict South African genus *Arrowinus* and description of its larva. Systematic Entomology 30(3): 398–441. https://doi.org/10.1111/j.1365-3113.2004.00283.x

Spilman TJ (1978) *Lagria villosa* in Brazil, with new descriptions and illustrations of the larva and pupa (Coleoptera, Lagriidae). Ciéncia e Cultura (São Paulo) 30(3): 342–347.

Srivathsan A, Lee L, Katoh K, Hartop E, Kutty SN, Wong J, Yeo D, Meier R (2021) ONTbarcoder and MinION barcodes aid biodiversity discovery and identification by everyone, for everyone. BMC Biology 19(1): 1–21. https://doi.org/10.1186/s12915-021-01141-x

Staniec B, Pietrykowska-Tudruj E, Wagner GK, Mazur A, Kowalczyk M (2022) Synthesis of current knowledge of the morphology of the larval stages of Paederinae (Coleoptera; Staphylinidae), with a first insight into the mature larva of *Pseudomedon* Mulsant & Rey, 1878, in the light of a new systematic division. Insects 13(11): 982. https://doi.org/10.3390/insects13110982

Švec Z (2022) Eight new species of Pseudoliodini (Coleoptera: Leiodidae: Leiodinae) from the East and the Southeast Asia with new morphological, distributional and bionomical data. Studies and Reports. Taxonomical Series 18(2): 437–468.

Tautz D, Arctander P, Minelli A, Thomas RH, Vogler AP (2003) A plea for DNA taxonomy. Trends in Ecology & Evolution 18(2): 70–74. https://doi.org/10.1016/S0169-5347(02)00041-1

Thomson RG (1979) 2.26. Larvae of North American Carabidae with a key to tribes. In: Erwin TL, Ball GE, Whitehead DR, Halpern AL (Eds) Carabid Beetles. Their Evolution, Natural History, and Classification. Dr. W. Junk, the Hague, 209–291. https://doi.org/10.1007/978-94-009-9628-1_11

Topp W (1978) Bestimmungstabelle für die Larven der Staphylinidae. In: Klausnitzer B (Ed.). Ordnung Coleoptera (Larven). Dr. W. Juml, The Hague, 304–334.

Truett GE, Heeger P, Mynatt RL, Truett AA, Walker JA, Warman ML (2000) Preparation of PCR-quality mouse genomic dna with hot sodium hydroxide and tris (HotSHOT). BioTechniques 29(1): 52–54. https://doi.org/10.2144/00291bm09

van Emden FI (1942) A key to the genera of larval Carabidae (Col.). Transactions of the Royal Entomological Society of London 92(1): 2–99. https://doi.org/10.1111/j.1365-2311.1942.tb03318.x

Viñolas A, Miralles-Nuñez A, Necoechea A (2020) Primeros datos sobre la presencia de *Ptilodactyla exotica* Chapin, 1927 en la Península Ibérica (Coleoptera, Ptilodactylidae). Revista Gaditana de Entomología 11: 93–98.

Weigand H, Beermann AJ, Čiampor F, Costa FO, Csabai Z, Duarte S, Geiger MF, Grabowski M, Rimet F, Rulik B, Strand M, Szucsich N, Weigand AM, Willassen E, Wyler SA, Bouchez A, Borja A, Čiamporová-Zaťovičová Z, Ferreira S, Dijkstra KDB, Eisendle U, Freyhof J, Gadawski P, Graf W, Haegerbaeumer A, van der Hoorn BB, Japoshvili B, Keresztes L, Keskin E, Leese F, Macher JN, Mamos T, Paz G, Pešić V, Pfannkuchen DM, Pfannkuchen MA, Price BW, Rinkevich B, Teixeira MAL, Várbíró G, Ekrem T (2019) DNA barcode reference libraries for the monitoring of aquatic biota in Europe: Gap-analysis and recommendations for future work. The Science of the Total Environment 678: 499–524. https://doi.org/10.1016/j.scitotenv.2019.04.247

Wood SL, Bright DE (1992) A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2. Taxonomic Index. Great Basin Naturalist Memoirs 13: 1–1553.

Yao M-C, Lee C-Y, Chiu H-W, Yang E-C, Lu K-H (2011) Application of light traps to monitor population fluctuation of stored-product pests in imported brown rice storehouses. Formosan Entomologist. 31: 351–366.

Zamani A, Fric ZF, Gante HF, Hopkins T, Orfinger AB, Scherz MD, Bartoňová AS, Pos DD (2022) DNA barcodes on their own are not enough to describe a species. Systematic Entomology 47(3): 385–389. https://doi.org/10.1111/syen.12538

Zhang W-X, Hu F-S, Yin Z-W (2021) Six new species of *Horniella* Raffray from the Oriental region (Coleoptera, Staphylinidae, Pselaphinae). ZooKeys 1042: 1–22. https://doi.org/10.3897/zookeys.1042.66576

Zhou H (1996) Population seasonality and larval development of *Lagria hirta* L. (Coleoptera: Lagriidae). Insect Science 3(4): 329–337. https://doi.org/10.1111/j.1744-7917.1996.tb00282.x

Zhou H (2001) Reproduction of *Lagria hirta* (Coleoptera: Lagriidae) and its life-history trait correlation. Environmental Entomology 30(4): 686–691. https://doi.org/10.1603/0046-225X-30.4.686

Appendix 1. List of identified taxa recorded from Huisun Forest Reserve

Below, we are listing all taxa recorded in the dataset published in this study which are currently identified to genus or species levels. For details about the number of OTUs in the genera listed, the collecting details of all taxa, and their DNA barcodes, please refer to the Suppl. material 2.

Anthicidae: *Sapintus plectilis*, *Macrotomoderus* sp. **Archeocrypticidae:** *Sivacrypticus taiwanicus*. **Bothrideridae:** *Antibothrus* sp. **Cantharidae:** *Maltypus ryukyuanus*. **Carabidae:** *Trichotichnus* sp., *Lebia* sp., *Pentagonica subcordicollis*, *Perigona* cf. *nigriceps*, *Oodes japonicus*, *Rhyzodiastes rimoganensis*, *Trilophus* cf. *alternans*. **Cerambycidae:** *Pterolophia laterialba*. **Cerylonidae:** *Cautomus* sp., *Gyrelon jenpani*, *Thyroderus porcatus*. **Chrysomelidae:** *Ivalia* sp., *Aphtona* sp., *Clavicornaltica* sp., *Trachytetra takizawai*, *Smaragdina nigripennis*, *Xanthonia taiwana*, *Morphosphaera* sp., *Paleosepharia* sp. **Cleridae:** *Omadius zebratus*. **Curculionidae:** *Trachyphloeosoma* sp., *Phaeopholus ornatus*, *Otibazo* sp., *Acallinus* sp., *Seleuca* sp., *Coccotrypes advena*, *Coccotrypes papuanus*, *Coccotrypes longior*, *Orthotomicus* sp., *Microperus* sp., *Hypothenemus eruditus*, *Xyleborinus saxesenii*. **Discolomatidae:** *Aphanocephalus* sp. **Elateridae:** *Adelocera* cf. *shirozui*, *Cardiotarsus* sp., *Ryukyucardiophorus babai*, *Csikia dimatoides*, *Neopsephus* sp. **Endomychidae:** *Mycetina* sp., *Chondria nigropunctata*, *Ectomychus tappanus*. **Erotylidae:** *Cryptophilus* sp., *Neosternus* sp. **Histeridae:** *Anapleus* sp., *Margarinotus curvicollis*, *Tribalus* sp. **Hydrophilidae:** *Anacaena* sp., *Armostus* sp., *Psalitrus* sp. **Lampyridae:** *Luciola kagiana*. **Latrididae:** *Bicava* sp., *Cartodere* sp. **Leiodidae:** *Ptomaphaginus* sp., *Agathidium amictum*, *Agathidium pictum*, *Dermatohomoeus* sp. **Lycidae:** *Macrolycus* sp. **Melandryidae:** *Lederina* sp. **Meloidae:** *Epicauta* sp. **Nitidulidae:** *Lasiodites inaequalis*, *Lasiodites pictus*, *Stelidota multiguttata*. **Phalacridae:** gen. sp. **Prionoceridae:** *Idgia* sp. **Ptiliidae:** genn. spp. **Ptilodactylidae:** *Ptilodactyla* sp. **Ptinidae:** *Myrmecoptinus* sp. **Scarabaeidae:** *Oxyomus alligator*, *Rhyparus azumai*, *Onthophagus yangi*. **Scraptiidae:** gen. sp. **Sphindidae:** *Aspidiphorus* sp. **Staphylinidae: Aleocharinae:** *Aleochara* sp., *Myrmecocephalus brevisulcus*, *Gyrophaena* sp., *Drusilla obliqua*, *Orphnebius* sp., *Zyras formosae*. **Euasthethinae:** *Edaphus* cf. *taiwanensis*, *Stenaesthetus nomurai*. **Mycetoporinae:** *Ischnosoma duplicatum*, *Ischnosoma quadriguttatum*, *Lordithon* sp. **Osoriinae:** *Thoracochirus* sp., *Arpagonus* sp., *Osorius* cf. *huangi*, *Nacaeus* sp. **Oxytelinae:** *Anotylus* cf. *amicus*, *Anotylus* cf. *cimicoides*, *Paraploderus* cf. *thailandicus*. **Paederinae:** *Homaeotarsus* sp., *Astenus* sp., *Hypomedon debilicornis*, *Rugilus japonicus*, *Thinocharis* sp., *Mimopinophilus* sp., *Palaminus* sp. **Proteininae:** *Megarthrus* sp. **Pselaphinae:** *Harmophorus* sp., *Cratna* sp., *Physomerinus* sp., *Sathytes rufus*, *Batraxis* sp., *Reichenbachia* sp., *Plagiophorus amygdalinus*, *Morana* sp., *Pseudophanias excavatus*, *Pseudophanias yaimensis*, *Centrophthalmus* sp., *Horniella nantouensis*, *Horniella taiwanensis*, *Labomimus* sp. **Scaphidiinae:** *Baeocera caliginosa*, *Baeocera cooteri*, *Scaphisoma hui*, *Scaphobaeocera* sp., *Scaphoxium* cf. *taiwanum*. **Scydmaeninae:** *Cephennodes taurus* species group, *Cephennomicrus* sp., *Euconnus* sp., *Himaloconnus* sp., *Scydmaenus* sp., *Napoconnus* sp. **Staphylininae:** *Diochus* sp., *Erichsonius* sp., *Hesperopalpus venustus*, *Indoquedius* sp., *Philonthus* sp., *Tolmerinus* sp. **Steninae:** *Stenus* sp. **Tachyporinae:** *Coproporus* cf. *brunnicollis*. **Xantholininae:** gen. sp. **Tenebrionidae:** *Ades* sp., *Derispia* cf. *nanshanchiensis*, *Anaedus spinicornis*, *Lagria scutellaris*, *Stenochinus* sp., *Amarygmus* cf. *taiwanus*. **Zopheridae:** *Pseudotarphius lewisi*.

Supplementary material 1

Maximum likelhihood tree

Authors: Fang-Shuo Hu, Martin Fikáček, My-Hanh Le

Data type: pdf

Explanation note: The maximum likelhihood tree based on all DNA barcode sequences of the leaf litter beetles from the Huisun Forest Reserve, Taiwan.

Link: https://doi.org/10.3897/dez.71.112278.suppl1

Supplementary material 2

The DNA barcodes of the leaf litter beetles from Huisun Forest Reserve and the associated metadata

Authors: Fang-Shuo Hu, Emmanuel Arriaga-Varela, Gabriel Biffi, Ladislav Bocák, Petr Bulirsch, Albert František Damaška, Johannes Frisch, Jiří Hájek, Peter Hlaváč, Bin-Hong Ho, Yu-Hsiang Ho, Yun Hsiao, Josef Jelínek, Jan Klimaszewski, Robin Kundrata, Ivan Löbl, György Makranczy, Keita Matsumoto, Guan-Jie Phang, Enrico Ruzzier, Michael Schülke, Zdeněk Švec, Dmitry Telnov, Wei-Zhe Tseng, Lan-Wei Yeh, My-Hanh Le, Martin Fikáček

Data type: xlsx

Explanation note: The voucher photos of these specimens are available in the BOLD database and in the Zenodo research archive under under https://doi.org/10.5281/zenodo.10069183.

Link: https://doi.org/10.3897/dez.71.112278.suppl2